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RAIN FOREST CANOPY COVER, RESOURCE AVAILABILITY, AND LIFE HISTORY EVOLUTION IN GUPPIES

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Abstract. Life history traits in guppies (*Poecilia reticulata*) vary geographically along a predator assemblage gradient, and field experiments have indicated that the association may be causal; guppies introduced from high predation sites to low predation sites have evolved the phenotype associated with low predation in as few as seven generations. It has long been recognized, however, that low predation sites tend to have greater forest canopy cover than high predation sites. Stream differences in canopy cover could translate into stream differences in resource availability, another theoretically potent agent of selection on life history traits. Moreover, new computer simulations indicate that the high predation phenotype would outcompete the low predation phenotype under both mortality regimes. Thus, predation alone may not be sufficient to explain the observed life history patterns.

Here we show that food availability for guppies decreases as forest canopy cover increases, among six low predation streams in the Northern Range of Trinidad. Streams with less canopy cover received more photosynthetically active light and contained a larger standing crop of algae (the primary food of guppies), as measured by algal pigments (chlorophylls and carotenoids) on both natural cobble and artificial tile substrates, but did not contain a greater biomass of guppies (per square meter of streambed). Consequently, algae availability for guppies (in micrograms of algal pigments per milligram of guppy) increased with decreasing canopy cover. The biomass of guppies and algae both decreased after a series of floods, with no net effect on algae availability. Field mark–recapture studies revealed that female and juvenile guppies grew faster, and that the asymptotic size of mature males was larger, in streams with less canopy cover. Canopy cover explained 84% of the variation among streams in algae availability which, in turn, explained 93% of the variation in guppy growth rates. Laboratory “common garden” experiments indicated that the stream differences in growth and adult male size in the field were largely environmental (non-genetic). These results strongly suggest that stream differences in canopy cover result in consistent stream differences in food availability, independent of predation.

Our preliminary data indicate that some life history traits (offspring size and litter size) vary genetically along the canopy cover gradient, among low predation streams, in the same direction as along the predation gradient. Another recent study shows that food availability is higher at high predation sites than at low predation sites, partly as an indirect effect of predators reducing guppy densities. Further research is required to disentangle the direct effects of predation from those of resource availability in the evolution of life histories.

Key words: canopy cover; density-dependent selection; environmental gradient; growth rate; life history evolution; periphyton; *Poecilia reticulata*; predation; primary productivity; resource availability; tropical stream; Trinidad, West Indies.

INTRODUCTION

Species distributed along replicated environmental gradients have provided some of the most compelling evidence for evolution by natural selection. Guppies (*Poecilia reticulata*) are perhaps the premier example. In the dendritic watersheds of Trinidad, predation on

guppies tends to decrease as one moves upstream, from the lowland rivers to the headwater streams, in step with waterfalls that truncate the distributions of predatory fish (Haskins et al. 1961, Seghers 1973, 1974, Endler 1978, 1983, Gilliam et al. 1993, Reznick et al. 1996a). At “high predation” sites below the barrier waterfalls, guppies typically co-occur with several species of strongly piscivorous fish, such as *Crenicichla alta* and *Hoplias malabaricus*. At “low predation” sites above the barrier falls, the main predator of gup-

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pies is the killifish *Rivulus hartii*, which primarily consumes invertebrates (Liley and Seghers 1975, Gilliam et al. 1993). Multiple suites of traits in guppies have been shown to vary genetically along this predator assemblage gradient, including coloration, behavior, and life history (reviewed in Endler 1995, Reznick et al. 1996a, b). In the case of life history, guppies from low predation sites mature later, grow to a larger size before maturing, and produce smaller litters of larger offspring than guppies from high predation sites (Reznick 1982, Reznick and Endler 1982, Reznick et al. 1996a, b). These differences persist when the descendants of guppies from high and low predation sites are raised in a common environment in the laboratory, and therefore are partly genetic.

When guppies from high predation sites have been introduced to low predation sites that previously lacked guppies, the transplanted populations evolved rapidly toward the phenotype associated with low predation sites (Endler 1980, Reznick et al. 1990, 1996b, Magurran et al. 1992). This has been especially well documented for life history traits, which have been inferred to evolve to the low predation equilibrium in as few as four years (about seven generations; Reznick et al. 1997).

The above introduction experiments provide compelling evidence for evolution by natural selection but fall short of identifying the specific ecological mechanisms of selection. Since predation was not manipulated independently of other habitat characteristics associated with upstream and downstream fish communities, it remains possible that predation is not the primary selective factor, or that predation interacts with other environmental factors in selecting for the evolution of life history traits. New computer simulations based on field survivorship data indicate that the high predation life history phenotype would out-reproduce the low predation phenotype under both mortality regimes (Reznick et al. *in press*). If so, why does the low predation phenotype evolve?

One theoretically plausible scenario is that the low predation life history phenotype evolves through density-dependent selection driven by low resource availability (Stearns 1992, Charlesworth 1994, Abrams and Rowe 1996). There are two reasons to think food availability for individual guppies may be lower at low predation sites than at high predation sites. First, predators may keep guppy populations farther below carrying capacity at high predation sites (Reznick et al. 1996a, 2001). Second, independent of predation, food availability may tend to be higher at downstream sites than at upstream sites because forest canopy cover decreases, and thus light for photosynthesis increases, as banks widen and make larger gaps in the forest (Reznick and Endler 1982). On the other hand, if the densities of guppies or other consumers closely track variation in primary productivity, canopy cover and food availability might be uncorrelated (Feminella and Hawkins 1995).

Under the exploitation ecosystem hypothesis, increases in primary productivity result in increases in the biomass of consumers at the top of the food chain and at alternating trophic levels below (reviewed in Paine 1980, Wootton and Power 1993, Estes 1995, Power 1995, Polis and Strong 1996). It is not clear, however, how many functional (strongly interacting) trophic levels are present in Trinidadian streams or that such a classification is even possible. Like most animals, guppies are omnivores (their diet includes both unicellular algae and benthic invertebrates; Dussault and Kramer 1981, Gilliam et al. 1993) and therefore occupy an intermediate trophic position. Although *Rivulus* is thought to be the main predator of guppies in low predation streams (Liley and Seghers 1975, Reznick et al. 1990), guppies appear to have a net negative effect on *Rivulus* densities (Gilliam et al. 1993). This may be because guppies out-compete *Rivulus* for benthic invertebrates, reduce benthic invertebrate productivity by consuming algae, or prey upon newly hatched *Rivulus* (Gilliam et al. 1993). Such complexities, which are common in natural food webs, may preclude general predictions about how changes in one component of a food web will affect another (reviewed in Strong 1992, Polis and Strong 1996). In short, ecological theory does not offer a clear prediction about how forest canopy cover should affect food availability for omnivorous fish.

To examine the effects of forest canopy cover on food availability for guppies, independent of predation, we made paired within-drainage comparisons between streams differing significantly in canopy cover but containing the same predator community. This was possible because some relatively large streams flow over impressive waterfalls that guppies and *Rivulus*, but not larger fish, have managed to breach. For brevity, we refer to the streams with relatively less canopy cover in their respective drainages as "high light" streams and to the others as "low light" streams. The purpose of pairing streams within drainages was to control, as much as possible, for biotic factors (e.g., parasites) and physical factors (e.g., water chemistry) that may vary on a broader biogeographic or geological scale. We selected undisturbed streams in intact rainforest (primary or old secondary growth), to eliminate potentially confounding anthropogenic effects (e.g., pollution) and because, ultimately, we are interested in the long term, evolutionary consequences of variation in forest canopy cover.

Floods can have dramatic effects on stream communities (Power 1995, Peterson 1996). Stream differences in food availability for guppies could be altered or even reversed by floods, depending on how the effects of floods on algal standing crops and guppy densities interact with stream size and geomorphology. We therefore timed our study to coincide with Trinidad's wet season and took our algal standing crop and guppy biomass measurements both before and after the floods

that normally occur during this time of year (July–December).

METHODS

Study streams

We selected pairs of low predation streams in intact forest representing the available extremes in canopy cover in each of three river drainages in the Northern Range of Trinidad (Table 1). Two of the drainages (Marianne and Paria) run down the north slope of the Northern Range into the Caribbean Sea; the third drainage (Quare) runs down the south slope into the Atlantic Ocean. All six study streams were separated from each other by multiple barriers to guppy dispersal, including two or more waterfalls. We use the term study stream instead of study site or locality to emphasize that multiple sites (pools) were sampled along each stream (see below). Preliminary canopy cover measurements were taken and streams were chosen in April 1996 (dry season); the main field study was completed between 15 August and 15 December 1996 (wet season).

Study pools

Within streams, pools are the scale at which guppy populations are subdivided and are also an appropriate sampling unit for comparing streams (Reznick et al. 1996a, see also Peckarsky et al. [1997] on the general issue of scale in stream studies). Guppies forage in pools, as opposed to riffles, and rarely disperse between pools. In mark–recapture studies, <5% of guppies moved between pools in a 12-d period (Reznick et al. 1996a). Females typically spend their entire lives within a single pool; most of the movement is by adult males (M. Bryant, *unpublished data*). Since guppies primarily feed on attached algae and benthic invertebrates (Dussault and Kramer 1981, Gilliam et al. 1993), food availability for guppies in downstream pools is unlikely to be affected by guppies foraging in upstream pools, or vice versa.

We selected 18–21 pools containing guppies in each stream, distributed as evenly as possible along the study streams, but otherwise at random. In the four narrowest streams, pools were separated from each other by riffles or cascades and spanned the width of the stream. In the two widest streams, most pools occurred downstream of boulders or snags and did not span the width of the stream. We estimated the surface area of each pool by measuring the distance to the pool margin at 22.5° intervals from a point near the center and integrating with a smoothing function. The area covered by emergent objects, such as boulders, was measured and subtracted from the total surface area. Depth measurements were taken at the center point and at the midpoint of each “spoke” and combined with surface measurements to estimate pool volume. The proportion of the bottom covered by different substrates was estimated visually (see Table 1 for substrate categories).

We classified large emergent rocks as boulders, submerged rocks greater than about 6 cm in length as cobbles, and submerged rocks less than about 6 cm in length as gravel. All measurements were made once for each pool by the same pair of observers in August or September 1996, prior to the wet season floods.

Canopy openness and light

The most accurate way to measure photosynthetically active light at a given location is to record continuously with a quantum radiometer. This would have required placing a sensor and datalogger at each pool for the duration of our study, which unfortunately was not feasible. Instead, we measured the forest canopy above each pool from hemispherical photographs (Chan et al. 1986, Becker et al. 1989, Rich 1990, ter Steege 1996) and also with a concave spherical densiometer (Lemmon 1957). We also took instantaneous readings of photosynthetically active radiation (PAR) with a quantum radiometer (Licor LI-189, LI-COR, Lincoln, Nebraska, USA).

The hemispherical photographs were taken under cloudy skies or low sun angles (to avoid scattering of light) with a tripod-mounted 35 mm camera through a 180° equiangular fish eye lens (Nikon 7.5 mm, Nikon Corporation, Tokyo, Japan) pointing directly up from the center of the pool with a small light positioned on the edge of the lens' field of view to indicate north (see ter Steege 1996). The film (Kodak Gold 200, Eastman Kodak Company, Rochester, New York) was professionally developed in a single batch. The resulting color prints (100 × 150 mm) were digitized in 256 level gray scale with a blue-pass filter between the photograph and the scanner; the blue-pass filter removed green reflections from leaves. Broadband (white) reflections were removed by reference to the original photographs, and contrast was adjusted to make open sky pure white and solid objects pure black, using Adobe Photoshop 4.0. The processed images were analyzed with WinPhot (ter Steege 1996) to obtain estimates of canopy openness (percentage) and photosynthetically active photon flux density (PPFD, moles per square meter per day). Winphot takes into account the shape and orientation of canopy gaps in relation to sun tracks for estimating PPFD (see ter Steege 1996). We integrated PPFD over a full 12-mo solar cycle assuming a constant cloud cover of 40%.

To standardize the instantaneous PAR readings, we took measurements at midday (1100–1300) and only if the sun was not blocked by clouds. Multiple PAR readings were taken from just above the water surface at each pool and, when possible, also in nearby light gaps with an unobstructed view of the sun. Mean PAR for each pool was calculated in quantum units (micromoles per square meter per second), and also as a percentage of gap PAR.

Algal standing crops

Attached unicellular algae (periphyton) are the only significant primary producers in the study streams (G.

TABLE 1. Study stream characteristics.

Characteristic	Drainage basin					
	Marianne		Paria		Quare	
	High	Low	High	Low	High	Low
Stream order	fourth	third	fourth	second	second	first
GPS reference†	858 895	842 894	911 920	895 907	970 806	969 809
No. pools sampled in dry season	18	30	20	20	22	10
No. pools sampled in wet season	20	20	20	20	21	18
Physical characteristics						
Length of study reach (m)	788	616	894	563	949	208
Typical stream width (m)	7	2	10	1.5	2	1
Pool surface area (m ²)	7.9 ± 1.4	13.3 ± 1.5	8.8 ± 1.7	13.1 ± 1.6	3.5 ± 0.6	2.4 ± 0.4
Maximum pool depth (cm)	32.7 ± 4.2	32.3 ± 2.3	34.6 ± 3.0	33.5 ± 3.5	20.8 ± 1.6	20.5 ± 2.3
Pool volume (L)	2133 ± 608	2535 ± 387	2222 ± 506	2661 ± 427	529 ± 145	322 ± 58
Pool bottom cover (%)						
Bedrock	8.2 ± 0.6	10.8 ± 3.0	8.7 ± 4.9	5.9 ± 2.3	3.8 ± 2.1	7.9 ± 4.6
Boulder	0.6 ± 0.5	2.6 ± 1.2	2.8 ± 1.4	0.5 ± 0.3	1.7 ± 0.8	2.4 ± 0.9
Cobble	24.1 ± 5.9	23.4 ± 4.5	19.3 ± 5.8	9.8 ± 2.5	25.4 ± 4.7	31.4 ± 5.7
Gravel	33.1 ± 4.5	48.1 ± 5.0	28.4 ± 5.4	61.0 ± 4.0	53.3 ± 4.6	37.0 ± 5.5
Sand	24.7 ± 5.6	6.4 ± 1.3	28.9 ± 6.7	5.0 ± 1.7	9.8 ± 3.2	7.5 ± 2.7
Leaves	4.7 ± 1.4	4.8 ± 1.3	7.2 ± 1.5	13.5 ± 2.6	5.6 ± 1.3	5.0 ± 2.1
Wood and roots	3.8 ± 1.1	3.2 ± 1.1	4.6 ± 1.6	3.8 ± 0.9	0.4 ± 0.2	7.6 ± 4.6
Silt	0.7 ± 0.3	0.7 ± 0.4	0.0	0.5 ± 0.2	0.0	1.2 ± 0.6
Canopy openness (%)						
Dry season (photograph method)	8.0 ± 0.4	5.9 ± 0.2	8.9 ± 0.2	6.8 ± 0.3	5.7 ± 0.3	3.6 ± 0.3
Wet season (photograph method)	7.8 ± 0.3	5.9 ± 0.4	8.5 ± 0.3	5.1 ± 0.2	7.1 ± 0.4	5.5 ± 0.5
Wet season (densiometer method)	13.9 ± 0.9	7.7 ± 0.7	17.8 ± 1.2	7.4 ± 0.6	12.6 ± 1.2	7.4 ± 0.5
Photosynthetically active light						
PPFD (mol/m ² /d)‡	8.1 ± 0.5	5.7 ± 0.5	9.0 ± 0.4	4.4 ± 0.3	7.6 ± 0.4	5.2 ± 0.6
PAR (log[μmol/m ² /s])	2.2 ± 0.2	1.4 ± 0.1	1.8 ± 0.1	0.9 ± 0.1	2.0 ± 0.1	1.5 ± 0.2
Percentage of gap PAR (log[x + 1])§	0.89 ± 0.15	0.18 ± 0.13	0.53 ± 0.09	-0.40 ± 0.07	0.70 ± 0.13	0.16 ± 0.17
Afternoon temperature (°C, mean)	24.5	24.4	24.4	24.4	24.4	24.4
pH	7.2	7.2	7.2	7.2	7.3	7.2
Ca and Mg hardness (μL/L)	115	65	100	50	95	65
Total dissolved solids (μL/L)	160	100	130	60	110	130

Notes: Marianne, Paria, and Quare are the river drainages. High and low refer to within-drainage light level categories of the streams. Pools are the sampling unit within streams, except for pH, hardness, and total dissolved solids, which were measured once per stream. All characteristics refer to the wet season unless otherwise noted. Means are presented ± 1 SE, except for afternoon temperature, which was nearly invariant.

† Universal Transverse Mercator Grid, zone 20.

‡ Photosynthetically active photon flux density.

§ Photosynthetically active radiation.

F. Grether, *personal observation*) and the main food source of guppies (Dussault and Kramer 1981). To estimate algal biomass (standing crop) in each of the study streams, we quantified algal pigments (chlorophylls and carotenoids) on natural cobbles and unglazed terra-cotta tiles (8.8 × 19.1 cm). We placed four tiles in each pool and harvested one tile per pool at 46

d and any remaining tiles at 92 d. We also collected one cobble from half the pools at the first tile harvest, and from all pools at the second tile harvest. We selected cobbles that appeared average in algal growth compared with other cobbles in the same pool and that were relatively flat (to facilitate surface area measurements; mean ± 1 SE cobble surface area, 21.4 ± 0.9

cm²; range, 4.3–115.9 cm²). The surface area of cobbles and broken tiles was estimated by tracing them on paper and digitizing the tracings.

Multiple floods occurred in every stream between the two harvests. Immediately after the floods or on the following day, we searched for displaced tiles and returned them to their original pools (tiles were marked on the lower surface with a unique number). One or more tiles were collected at the second harvest from 112 of the original 119 pools. All tiles were lost from three pools in the high light Marianne and Paria streams, and from one pool in the low light Paria stream, as a result of the floods.

Because we did not sample algal standing crops immediately after the floods, but instead at the 92-d mark, some algal recolonization occurred before the second harvest. Within drainages, the recolonization periods were similar. Both Quare streams had 10 d to recolonize, the Paria high and low light streams had 13 and 14 d, respectively, and the Marianne high and low light streams had 21 and 22 d, respectively.

For the algal pigment analyses, periphyton was scraped from the upper surface of harvested tiles and cobbles with a wire brush, collected and vacuum dried on Whatman GF-C filters, promptly frozen in liquid nitrogen, and stored in darkness until analysis at less than or equal to -80°C . Frozen filters were placed in 100% acetone, sonicated, and allowed to stand in darkness for at least 12 h at -20°C . Filtered extracts (75–150 μL) were injected directly into a Hewlett-Packard model 1090 HPLC (Hewlett-Packard, Palo Alto, California) equipped with one Hewlett Packard ODS-Hypersil C18 column (200 \times 4.6 mm, 4 μm), two Vydac 201TP C18 columns (250 \times 4.6 mm, 5 μm ; Hesperia, California) in series, and a diode array detector set at 436 nm. The mobile phases and solvent flow rates followed that described by Pinckney et al. (1996) and the column temperature was 38°C . Pigments were identified and quantified using authentic standards for chlorophylls (Sigma Chemical Company, St. Louis, Missouri) and carotenoids (U.S. Environmental Protection Agency, Cincinnati, Ohio).

Algal composition

The nutritional quality of periphyton may be affected by the types of algae present and their proportions. In particular, diatoms appear to be a poorer quality food source for fish than unicellular green algae (Lamberti 1996). The carotenoid profile of a periphyton sample can provide information on algal composition, because different algal phylogenetic groups contain different carotenoid pigments (see Tester et al. 1995). We used fucoxanthin, lutein, and zeaxanthin as indicators of diatoms, green algae, and blue-green algae, respectively. Multiple regression of the indicator carotenoids on chlorophyll *a* was used to estimate the proportion of chlorophyll *a* contributed by the different algal groups (see Tester et al. 1995).

Field growth rates and adult male size

Growth rates of guppies are closely linked to food availability in the laboratory (Reznick 1983). To check our algae-based estimates of food availability, we measured growth rates of guppies in the field by catching all of the guppies in a pool, marking them by size class, and remeasuring them 2 wk later. This method yields estimates of asymptotic growth that are consistent with estimates based on much longer mark–recapture intervals (up to 7 mo; D. N. Reznick, *personal observation*). Before the wet season floods, we measured growth rates in eight pools per stream, except for the high light Paria stream where time limited us to seven. It was not logistically feasible for us to measure growth rates again after the floods. The procedure involves catching fish with butterfly nets and transporting them to a field laboratory in water treated with antibiotics (Fungus Guard, Jungle Products, Jungle Laboratories Corporation, Cibolo, Texas), stress reducers (Novaqua, Kordon, a division of Novalek Incorporated, Hayward, California), and a NH_3 detoxifier (Amquel, Kordon). Fish ≥ 12 -mm standard length were sedated with ethyl 3-aminobenzoate methane sulfonic acid salt (MS-222), measured with calipers (0.01-mm readout) under a microscope, and marked in the caudal peduncle with an injection of acrylic latex paint diluted with sterilized Teleost Ringers (for further details on this method, see Reznick et al. 1996a). The color (red or black) and location of the mark identified the initial size class in 1-mm increments. Eight fish died after being marked but the remaining 1662 recovered; another 853 were < 12 mm long and not marked (2523 total). The fish were released in their original pool after being held for 48 h in the treated water. Two weeks from the date of initial capture, the process was repeated, except that the original size class of each fish was recorded and no new marks were applied (892 marked fish were recaptured, along with 610 unmarked fish ≥ 12 mm and 1022 fish < 12 mm; 2524 total).

Sexually mature males (as judged from gonopodium development) were not included in the growth rate estimates because males stop growing at sexual maturity (Reznick 1990). Since the size of adult males is largely a function of their rate of growth up to maturity (Reznick 1990), the mean length of adult males provided an independent, long-term measure of stream differences in growth rates.

Laboratory growth rates and adult male size

Variation among streams in growth rates and adult male size may in part be genetic, which could complicate the interpretation of the field data. Stream differences in growth rate were most extreme in the Marianne drainage (see *Results*), so we chose this drainage for a study of growth rates under “common garden” conditions. We placed second laboratory generation (G2) virgin females with unrelated males from their

own stream for ≥ 24 h, and then isolated the females in 6-L aquaria to give birth. To prevent maternal cannibalism, nylon mesh tank dividers (3.4×3.4 mm) and aquatic plants (*Fontinalis*) provided refuge for neonates. Females were fed live *Artemia* nauplii in the morning and Tetraamin flakes (Tetra Incorporated, Blacksburg, Virginia) in the afternoon and checked daily for newborn young. The standard length of mothers and their first brood of young was measured ~ 24 h after parturition. To measure growth rates, up to three young from each brood were housed together in 38-L tanks maintained on a 12-h light–dark cycle with undergravel filtration and *Fontinalis*. Water was treated with 2-chloro-4, 6-bis-(ethylamino)-s-triazine (Algae Destroyer, Aquarium Pharmaceuticals Incorporated, Chalfont, Pennsylvania) to retard algal growth (no algae were visible in the tanks) and kept at $\sim 24 \pm 1^\circ\text{C}$. Offspring were fed measured amounts of frozen *Artemia* nauplii in the morning and Tetra Growth flakes (~ 0.01 g; Tetra Incorporated, Blacksburg, Virginia) in the afternoon. Food was measured by filling a small well in a Plexiglas spatula. Broods of one ($n = 1$) and two young ($n = 2$) were given one-third and two-thirds as much food as broods of three young ($n = 16$), respectively. The amount of food provided was doubled when the fish reached 14 d of age. Each fish was re-measured with calipers at 7, 14, and 21 d of age. In total, we obtained growth data for 19 broods (12 high light, 7 low light) and birth size data alone for another five (4 high light, 1 low light). Brood means were used in the analysis because the fish were not individually marked.

To measure genetic variation among streams in adult male size, we raised G2 males from all six streams in aquaria under common garden conditions and measured them after sexual maturity. The males used in this study were born to outbred G1 females that had mated with unrelated wild or G1 males from the same stream. Each brood of G2 offspring was raised on a flake food diet (50% white fish meal, 48% wheat flour, 1% soybean oil, 1% vitamin mix). The water was treated with Algae Destroyer (no algae were visible) and kept at $\sim 24 \pm 1^\circ\text{C}$. Offspring were sexed prior to the development of male coloration and functional gonopodia. The males from a given brood were split into three groups of 1–4 individuals per group (broods containing < 3 males were not used in this study), housed in 6-L tanks, and provided with flake food twice daily. Tanks containing fish from the six streams were spatially interspersed in a temperature-regulated greenhouse (22 – 26°C) and treated identically. For logistical reasons, the amount of food was not measured precisely, but tanks were provisioned roughly in proportion to the number of males in the tank. Males were measured with calipers between 154 and 256 d of age (mean ± 1 SE, 200.6 ± 2.9 d) well after the development of mature coloration and gonopodia (396 males; 54–85 males per stream;

12 broods for each Marianne and Paria stream; 14 broods for both Quare streams).

Guppy biomass

The field growth rate study provided data on pre-flood pool densities and size distributions of guppies for 7–8 pools of the 20 study pools in each stream. To obtain post-flood data on the rest of the study pools, we again captured all the fish but measured and released them without delay. Three pools were not sampled: two in the high light Paria stream were destroyed by floods, one in the low light Paria stream was accidentally missed. Standard length measurements were taken quickly (to 1 mm) by placing fish in a transparent petri dish and aligning them with a ruler held against the bottom.

To estimate the biomass (standing crop) of guppies in each pool from the length data, we used sex-specific allometric equations based on a sample of wild-caught guppies (from the same six streams) for which we also obtained live masses (165 females, 321 males). Mass was predicted from the relationship $a \times \text{length}^b$, where for females $a = 0.0219$ and $b = 3.0576$, and for males $a = 0.0204$, $b = 3.0652$ (R^2 for the allometric equations was 0.97 and 0.93 for females and males, respectively). We divided the sum of predicted masses for all fish in a pool by the surface area of the pool, to obtain a rough estimate of guppy biomass per unit of algal substrate (grams per square meter). Dividing algal biomass by guppy biomass yielded a measure of algae availability (in units of micrograms chlorophyll *a* per milligram guppy). A total of 5006 fish contributed to the biomass estimates.

Statistical procedures and sampling units

The study was designed to permit three replicate within-drainage comparisons of dependent variables between high and low light streams. An alternative approach would be to construct a single model with drainage and light level as fixed effects. However, treating light level as a fixed effect would imply that “low” and “high” correspond to the same absolute light levels in all three drainages, which was not the case for our study.

We treated pools as sampling units, by reducing the data to pool means before analysis or by including a pool(stream) term in the model, as opposed to using individual fish or periphyton samples as sampling units, to avoid pseudoreplication (Hurlbert 1984). Repeated-measures ANOVAs with random effects pool(stream) terms were used when the dependent variable had been measured for the same pools before and after the floods. The field growth data were reduced to stream size class means before analysis. In the laboratory studies, broods were treated as sampling units by reducing the data to brood means before analysis (offspring size and growth rate) or by including a random effects brood(stream) term in the model (mature male length). Some variables

required a $x^{1/2}$, $\log(x)$, or $\log(x + 1)$ transformation to meet parametric assumptions. Statistics were computed with JMP 3.2.2 or StatView 5.0 (SAS Institute 1995, 1998). The P -values we report are two-tailed.

RESULTS

Canopy openness and light

Light levels and canopy openness differed between streams within drainages as planned (Table 1). In each drainage, the high light stream received more photosynthetically active light than the low light stream (one-way ANOVA planned comparisons for PPFD, $\log_{10}(\text{PAR})$, and $\log_{10}(\text{percentage of gap PAR})$: Marianne $P \leq 0.0002$, Paria $P < 0.0001$, Quare $P \leq 0.01$).

The direction of the within-drainage stream differences in canopy openness were the same in the wet season as in the preceding dry season (Table 1). In a two-way ANOVA with canopy openness as the dependent variable, stream and stream \times season interaction effects were significant (two-way ANOVA: stream $F_{5,227} = 34.95$, $P < 0.0001$, interaction $F_{5,227} = 6.46$, $P < 0.0001$), but there was no significant season effect ($F_{1,227} = 0.64$, $P = 0.4$). The significant interaction term indicates that some streams increased in canopy openness between seasons while others decreased. Nevertheless, all three within-drainage stream comparisons of canopy openness were highly significant ($P < 0.0001$). Canopy openness was measured on different sets of pools in the wet and dry season, so no pool(stream) term was used in this analysis.

Algal standing crops

Algal standing crops were greater in the high light stream than in the low light stream in all three drainages at both the pre- and post-flood harvests and on both cobble and tile substrates (see Fig. 1 for statistics). The results were qualitatively the same whether algal biomass was measured as chlorophyll a or all algal pigments combined; for brevity, only the chlorophyll a results are presented. Across drainages, mean canopy openness explained 78–88% of the variation in mean algal standing crop ($n = 6$; cobbles, pre-flood $r^2 = 0.86$, $P = 0.008$, post-flood $r^2 = 0.88$, $P = 0.006$; tiles, pre-flood $r^2 = 0.88$, $P = 0.005$, post-flood $r^2 = 0.78$, $P = 0.02$). These results indicate that primary productivity is limited by light in these streams.

The amount of algae on cobbles decreased after the floods (Fig. 1a), except in the low light Marianne stream, which had the longest recolonization period (22 d between the last flood and the second harvest). For cobbles, most of the variation in algal standing crops was explained by a two-way repeated-measures ANOVA with stream and harvest as factors ($R^2 = 0.93$, stream $F_{5,145.5} = 36.39$, $P < 0.0001$; harvest $F_{1,56} = 4.30$, $P = 0.04$; stream \times harvest $F_{5,56} = 4.20$, $P = 0.003$; pool(stream) $F_{112,56} = 2.44$, $P = 0.0002$). The significant stream \times harvest interaction indicates that

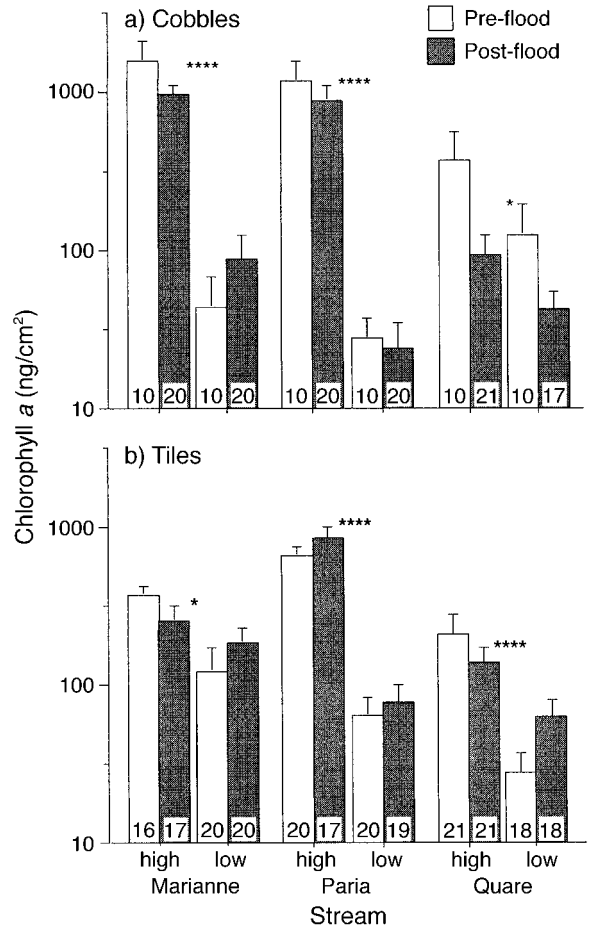


FIG. 1. Algal standing crops (note log scale) in relation to stream light level category (high vs. low) and harvest (pre-flood vs. post-flood) for (a) cobbles and (b) tiles. Columns and error bars represent means + 1 SE. The number of pools sampled is shown at the base of each column. P values are for within-drainage stream contrasts from the repeated-measures ANOVA model described in the *Methods: Statistical procedures*. * $P < 0.05$; **** $P < 0.0001$.

the degree to which algal standing crops decreased after the floods varied among streams. For tiles, slightly less of the variation in algal standing crops was explained and there was no significant post-flood decrease in algal standing crops ($R^2 = 0.87$, stream $F_{5,113.2} = 22.88$, $P < 0.0001$; harvest $F_{1,104} = 2.21$, $P = 0.14$; stream \times harvest $F_{5,104} = 3.51$, $P = 0.006$; pool(stream) $F_{111,104} = 2.92$, $P < 0.0001$). A possible explanation for the different results for cobbles and tiles is that tiles had not reached a stable standing crop in all streams by the time of the first harvest (see Cattaneo and Amireault 1992). Consistent with this explanation, the standing crop of algae on cobbles exceeded that on tiles at the first harvest ($F_{1,56} = 7.43$, $P = 0.008$) but not at the second ($F_{1,105} = 3.01$, $P = 0.08$).

Algal composition

The carotenoid pigments observed in the periphyton (fucoxanthin, beta carotene, lutein, didinoxanthin,

TABLE 2. Estimated algal composition of periphyton samples.

Algal group	Harvest	Substrate	Marianne		Paria		Quare	
			High	Low	High	Low	High	Low
Bacillariophyta (diatoms)	pre-flood	cobble†‡	49.8	97.6†‡	74.9	100.0†‡	90.4	80.9
		tile†	72.8	96.4†‡	73.7	97.5†‡	90.3	86.7
	post-flood	cobble†	90.1	95.7	79.4	84.4	97.7	80.5
		tile†	77.5	92.3	59.1	91.4†‡	75.6	84.5†‡
Chlorophyta (green)	pre-flood	cobble†	23.1	1.1†‡	19.3	0.0†‡	4.6	7.0
		tile†	11.7	3.5†‡	24.1	0.0†‡	3.4	5.0
	post-flood	cobble	7.6	2.5	9.9	15.6	2.3	18.2
		tile†	16.8	5.4	25.2	6.1†‡	7.3	1.8†‡
Cyanophyta (blue-green)	pre-flood	cobble†	27.1	1.3†‡	5.8	0.0	5.0	12.1
		tile†	15.5	0.2†‡	2.2	2.5	6.4	8.3
	post-flood	cobble†	2.4	1.7	10.7	0.0†‡	0.0	1.3
		tile†	2.7	2.3	15.7	2.5†‡	17.1	10.9†‡

Note: The values shown are the mean percentage representation of algal groups within harvest × substrate categories.

† Significant Kruskal-Wallis test for stream effects ($P < 0.01$).

‡ Significant Mann-Whitney test for within-drainage stream contrasts ($P < 0.05$).

neoxanthin, violaxanthin, zeaxanthin, siphonein, and diatoxanthin) indicate the presence of three algal phylogenetic groups: Bacillariophyta (diatoms), Chlorophyta (green algae), and Cyanophyta (blue-green algae). Fucoxanthin was dominant in all streams at both harvests, which implicates diatoms as the dominant algal group (see Goodwin 1980). Together, the indicator pigments fucoxanthin, lutein, and zeaxanthin explained 84% of the variation in chlorophyll *a* when all algal samples were pooled (chlorophyll *a* = 20.11 + 3.83 fuco + 13.34 lutein + 14.45 zea; $R^2 = 0.84$, $F_{3,528} = 893.86$, $P < 0.0001$). Stream-specific regressions yielded higher R^2 values (0.90–0.97) than the pooled regression, but the results of the algal composition analyses were qualitatively the same. Diatoms appeared to be the only algal group present in 238 of the 532 algal samples, resulting in highly non-normal distributions for the algal composition variables. Parametric ANOVAs were not appropriate for these data, so we used Kruskal-Wallis tests to detect overall stream effects and Mann-Whitney tests for pairwise comparisons. Although the results for different algal groups are not independent, algal composition clearly varied among streams at both harvests and for both substrates (Table 2). Of the 36 within-drainage stream contrasts, 17 contrasts were significant at $P < 0.05$ (11 contrasts at $P < 0.001$) and all significant contrasts were in the same direction: the high light streams had a higher proportion of green and blue-green algae and a lower proportion of diatoms than the low light streams (Table 2).

Algal composition changed after the floods but not in a consistent direction (Table 2). With data from all streams combined, the dominance of diatoms increased after the floods on cobbles (Mann-Whitney, $z = 2.42$, $P = 0.016$) but decreased on tiles ($z = 2.43$, $P = 0.015$). In separate analyses by stream, cobble diatoms were significantly elevated after the floods only in the high light Marianne ($z = 3.76$, $P = 0.0002$) and Quare streams ($z = 2.03$, $P = 0.04$). Tile diatoms were sig-

nificantly reduced after the floods in both Paria streams (high light $z = 2.09$, $P = 0.04$, low light $z = 2.53$, $P = 0.01$) and the high light Quare stream ($z = 3.08$, $P = 0.002$).

Field growth rates and adult male size

Females and juveniles in the high light streams grew faster than those in the low light streams (Fig. 2a). We tested for growth rate differences between pairs of streams within drainages using ANCOVAs with initial size class as the covariate and size-specific growth (mean change in size for each size class) as the dependent variable. We used only the first eight 1-mm size classes (12–20 mm) because the number of fish in size classes >20 mm was too small for reliable growth estimates. The ANCOVA models explained 78–97% of the variation in growth (Marianne $R^2 = 0.96$, $F_{3,15} = 84.1$, $P < 0.0001$; Paria $R^2 = 0.97$, $F_{3,15} = 185.4$, $P < 0.0001$; Quare $R^2 = 0.78$, $F_{3,15} = 14.8$, $P = 0.0002$). None of the covariate by stream interactions were significant (Marianne $F_{1,12} = 0.40$, $P = 0.54$; Paria $F_{1,12} = 0.04$, $P = 0.85$; Quare $F_{1,12} = 4.43$, $P = 0.06$). With the interaction terms removed, growth was significantly greater in the high light stream in all three drainages (Fig. 2a; Marianne $F_{1,12} = 197.12$, $P < 0.0001$; Paria $F_{1,12} = 237.44$, $P < 0.0001$; Quare $F_{1,12} = 12.87$, $P = 0.003$).

Adult males in the high light streams were significantly larger than those in the low light streams (Fig. 2b; one-way ANOVA of pool means, $R^2 = 0.69$, overall $F_{5,87} = 38.34$, $P < 0.0001$; within-drainage stream comparisons: Marianne $P = 0.01$, Paria $P < 0.0001$, Quare $P < 0.0001$).

Laboratory growth rates and adult male size

Laboratory reared (G2) females from the high light Marianne stream gave birth to smaller young than those from the low light Marianne stream (Fig. 3; $t = 4.41$, $df = 22$, $P = 0.0002$). This was not a maternal size effect; offspring size did not correlate with dam size

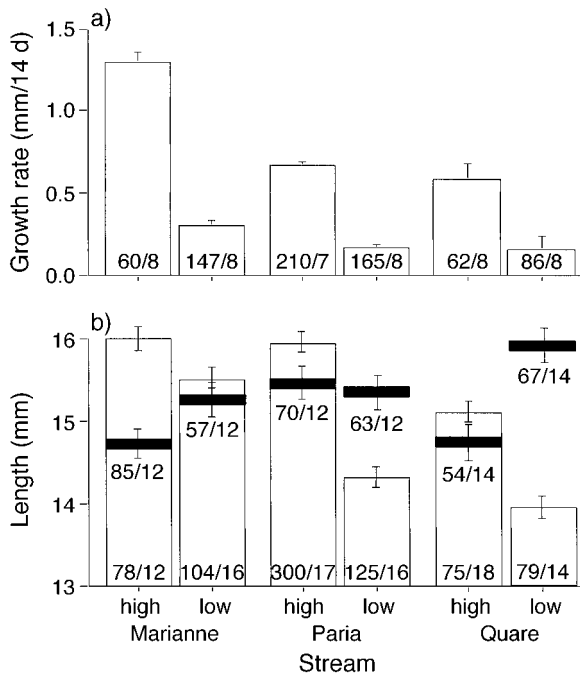


FIG. 2. (a) Growth rates of females and immature males in the field and (b) standard lengths of mature males in the field (columns) and under common garden conditions in the laboratory (black cross bars). All plotted values are least squares means ± 1 SE from the statistical models described in the *Methods: Statistical procedures*. The number of individual fish sampled is shown above the slashes, and the number of pools (field data) or broods (laboratory data) is shown below the slashes. The number of pools represented in (b) differs from the total number of pools in the study because not all pools contained mature males.

within streams (high light $r = -0.11$, $P = 0.69$, $n = 16$; low light $r = 0.49$, $P = 0.24$, $n = 8$). Males only provide sperm to females so there is no possibility of nongenetic paternal effects. Offspring grew linearly over their first 21 d (Fig. 3). There was no significant difference between streams in growth rate, as measured by the mean change in size between day 0 and day 21 ($t = 1.44$, $df = 17$, $P = 0.17$). Growth of fish from the high light stream exceeded that of fish from the low light stream by 10% in the laboratory vs. 319% in the field. Hence, at least for the Marianne drainage, the large stream differences in growth rate in the field were probably environmental, not genetic.

The mean length of mature G2 males reared in the laboratory under common garden conditions varied both within and among streams (Fig. 2b; nested ANOVA, with Satterthwaite df approximation, $R^2 = 0.63$, stream, $F_{5,72.5} = 5.50$, $P = 0.0002$; brood within stream $F_{70,320} = 5.45$, $P < 0.0001$), which suggests that some of the variation in adult male size is genetic. Nonetheless, the direction of the within-drainage stream differences in mean adult male length was the reverse of that seen in wild caught fish in the Marianne ($P = 0.05$) and Quare ($P = 0.0001$) drainages. In the Paria drain-

age, the trend was the same as in the field but not significant ($P = 0.7$). Moreover, the difference between field and laboratory mean adult male lengths was significantly greater in the high light stream than in the low light stream in all three drainages (one-way ANOVA on pool means, $R^2 = 0.80$, overall $F_{5,87} = 70.8$, $P < 0.0001$; all within-drainage stream comparisons $P < 0.0001$). These results were not confounded by laboratory tank density effects. There was a weak negative correlation between the number of the males in a tank (tank density) and mean adult male length when all six streams were pooled ($R^2 = 0.02$, $P = 0.03$, $N = 227$ tanks) but not within any single stream (high light Marianne stream $R^2 = 0.05$, $P = 0.10$, $N = 36$ tanks; all others $R^2 \leq 0.02$, $P > 0.5$; $N = 36$ –42 tanks). When tank density was included as a covariate in the model to estimate stream differences, the tank density and tank density by stream terms were nonsignificant (density $F_{1,314} = 2.78$, $P = 0.10$, interaction $F_{5,314} = 1.23$, $P = 0.29$). With the interaction term removed from the model, the tank density term was still nonsignificant ($F_{1,319} = 1.91$, $P = 0.17$) and the stream comparison results were qualitatively the same as described above. Measurement age also was not a confounding factor because it did not correlate significantly with mean adult male length when all six streams were pooled ($R^2 = 0.00007$, $P = 0.94$, $N = 76$ broods) or within any single stream (high light Marianne stream $R^2 = 0.21$, $P = 0.07$, $N = 12$ broods; all others $R^2 \leq 0.07$, $P > 0.3$; $N = 12$ –14 broods). These results strongly imply that the direction of the stream differences in mean adult male length in the field (i.e., high light > low light) was an environmental effect.

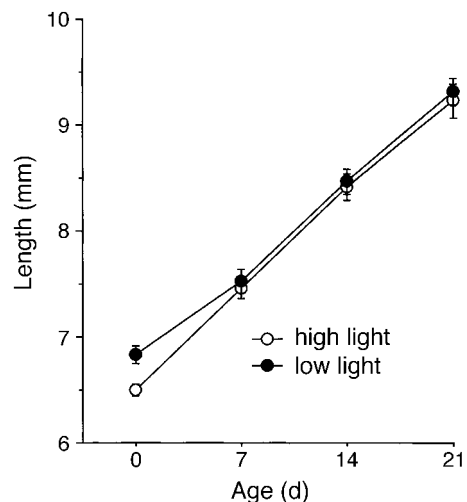


FIG. 3. Growth of immature G3 guppies from the high and low light Marianne streams, raised under standardized conditions in the laboratory, from birth to 21 d of age. Each symbol represents the mean ± 1 SE of brood means at the indicated age.

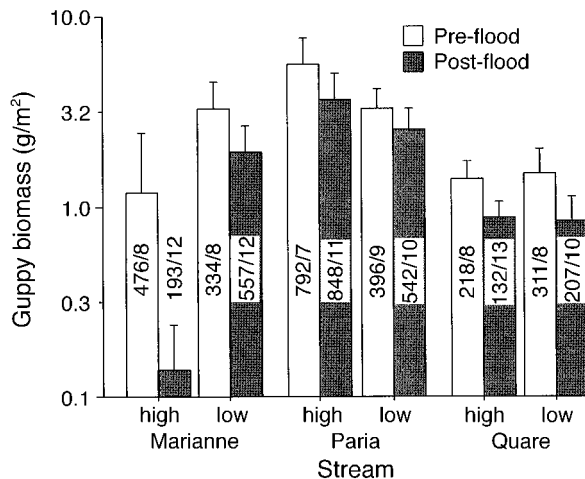


FIG. 4. Guppy biomass (\log_{10} scale) in relation to light levels and flooding (mean \pm 1 SE). The number of individual fish contributing to the biomass estimates is shown above the slashes, and the number of pools is shown below the slashes.

Guppy biomass

Guppy biomass (in grams per square meter) was lower after the floods in all six streams (Fig. 4; pre- vs. post-flood $F_{1,104} = 12.44$, $P = 0.0006$), although the magnitude of the reduction varied among streams, as reflected by a significant stream \times flood interaction ($F_{5,104} = 2.36$, $P = 0.04$). Post-flood reductions in biomass ranged from 22% in the low light Paria stream to 92% in the high light Marianne stream.

Guppy biomass varied significantly among streams ($F_{5,104} = 6.46$, $P < 0.0001$), but there was no consistent relationship between guppy biomass and canopy cover. In the Paria drainage, guppy biomass was greater in the high light stream than in the low light stream ($P = 0.01$), but the reverse trend was seen in the other two drainages (Marianne $P = 0.01$, Quare $P = 0.32$). Across drainages, there was no significant correlation between canopy openness and guppy biomass before or after the floods (pre-flood $r^2 = 0.18$, $P = 0.4$, $n = 6$; post-flood $r^2 = 0.02$, $P = 0.8$).

Algae availability

The analyses above show that the biomass of guppies and their algal food base varied among streams and were lower after the floods. We now combine these data to examine variation in algae availability (in units of micrograms chlorophyll *a* per milligram guppy). Analyses using all algal pigments in place of chlorophyll *a* yielded similar results; only chlorophyll *a* results are presented. Three pools in the high light Marianne stream were excluded from this analysis because they contained no guppies after the floods.

Both before and after the floods, and on both cobble and tile substrates, algae availability was higher in the high light streams than in the low light streams (cobble, stream $F_{5,78} = 8.13$, $P < 0.0001$, tiles, stream $F_{5,96}$

$= 8.12$, $P < 0.0001$; all within-drainage stream contrasts: $P < 0.01$). The post-flood reduction in algal standing crops roughly compensated for the reduction in guppy biomass, such that neither flood nor flood by stream interaction terms were significant (cobble, flood $F_{1,78} = 0.02$, $P = 0.88$; interaction $F_{5,78} = 1.30$, $P = 0.27$; tiles, flood $F_{1,96} = 2.95$, $P = 0.09$; interaction $F_{1,96} = 0.76$, $P = 0.58$).

As shown in Fig. 5, canopy openness explained 84% of the variation among streams in pre-flood algae availability ($r^2 = 0.84$, $F_{1,5} = 21.06$, $P = 0.01$) and algae availability, in turn, explained 93% of the variation in field growth rates ($r^2 = 0.93$, $F_{1,5} = 50.71$, $P = 0.002$).

DISCUSSION

To summarize our main results, algal standing crops were larger (Fig. 1), female and juvenile guppies grew faster, and male guppies matured at larger sizes in the streams with less forest canopy cover in each of three river drainages (Fig. 2). Across drainages, canopy cover explained 84% of the variation among streams in algae availability, which in turn explained 93% of the variation in guppy growth rates (Fig. 5). Laboratory "common garden" experiments showed that the stream differences in growth rates and adult male size in the field were not confounded by genetic divergence between streams (Figs. 2 and 3). The wet season floods reduced the standing crop of both algae and guppies (Figs. 1 and 4), resulting in no net change in algae availability for guppies. Since our pre-flood growth rate and algae availability estimates were taken several months after the previous wet season's floods, the correlation between canopy cover and algae availability probably persists year-round. We infer that relatively small differences between streams in forest canopy cover have substantial and consistent effects on food availability for guppies, independent of the predator assemblage.

In addition to containing larger standing crops of algae, the high light streams contained a higher proportion of green and blue-green algae and a lower proportion of diatoms than the low light streams. This may have important implications for guppies, since not all types of algae are of equal nutritional value for fish (Allan 1995, Mustafa and Nakagawa 1995, Reitan et al. 1997). If diatoms are a poorer quality food than unicellular green algae, as nutritional data indicate (Lamberti 1996; M. Lamon, *personal communication* 2000), then the differences in food availability between high and low light streams are probably greater than our results based on chlorophyll *a* suggest. Algal composition, hence food quality, changed between the pre- and post-flood periods, but not in a consistent direction.

Because we did not manipulate canopy cover experimentally, it remains possible that some other factor besides canopy cover accounts for the differences between high and low light streams in algae availability and guppy growth rates. However, the criteria we used

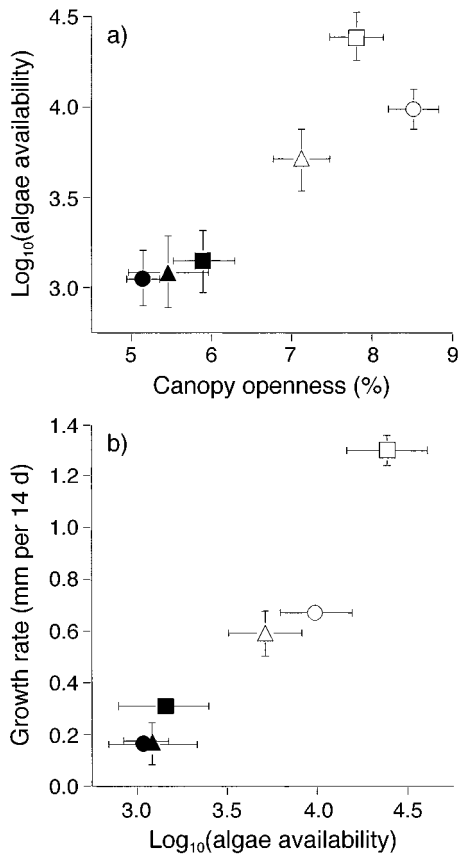


FIG. 5. Cross-drainage relationships between (a) canopy openness and algae availability (measured in $\mu\text{g}/\text{mg}$) and (b) algae availability (measured in $\mu\text{g}/\text{mg}$) and guppy growth rates. Squares, circles, and triangles represent the Marianne, Paria, and Quare drainages, respectively, with filled symbols for low light streams and open symbols for high light streams (± 1 SE).

for selecting study streams were designed to eliminate all known potentially confounding factors. Specifically, we have no evidence or reason to suspect that parasites or competitors of guppies are more prevalent in the low light streams (also see Reznick et al. 2001).

Ecological mechanisms

The relative importance of bottom-up vs. top-down processes in natural ecosystems is a topic of ongoing debate in ecology. The basic issues can be evoked by a deceptively simple question: how would a change in primary productivity affect the abundance of a particular consumer species? The answer may depend on numerous factors, including species-specific behavioral responses, the exact position of the focal species in the food web, the number of trophic levels in the food web, the strength of the interactions between species, and the frequency, nature, and severity of the abiotic disturbance regime (Hart 1992, Strong 1992, Power 1995, Polis and Strong 1996, Wootton et al. 1996, Peckarsky et al. 1997).

Experiments in which specific components of an ecosystem are manipulated independently are the preferred method of testing theory. For example, by manipulating the abundance of caddisfly larvae and juvenile steelhead in mesocosms, Wootton et al. (1996) were able to confirm several predictions of a multitrophic dynamic model. Unfortunately, it is difficult to conduct experiments on a spatial scale large enough to permit natural patterns of dispersal or on a temporal scale long enough for demographic processes to occur (Peckarsky et al. 1997). Most models are based on demographic (birth–mortality) equations, but experiments are often done on time scales too short for reproduction to occur. Models incorporating short-term behavioral responses may do a better job of describing what actually occurs during short-term experiments, but their relevance to longer time scales is questionable (Peckarsky et al. 1997), especially given that behavior, and ecological interactions in general, can evolve (Loehle and Pechmann 1988, Holt 1995).

A complementary approach is to study the long-term outcome of natural experiments, in the form of replicated environmental gradients. Fraser and Gilliam (1992, Gilliam et al. 1993, Fraser et al. 1995) used this approach, in combination with small-scale experiments, to study the role of species interactions in structuring the fish community of Trinidadian watersheds. They found that *Rivulus hartii* was most abundant in the smallest headwater streams where it occurs with no other species of fish, least abundant in large rivers inhabited by predators such as *Hoplias*, and at intermediate abundance in streams where guppies were the only other species of fish present. These and other observations suggest that *Rivulus* populations are limited by interspecific interactions (predation and competition), except in the smallest headwater streams where they may be limited by food availability or abiotic factors (e.g., floods).

Our comparison of *Rivulus*–guppy streams with different levels of forest canopy cover suggests that some guppy populations are limited by floods. We found no consistent relationship between canopy cover and guppy population biomass, before or after the floods, despite the faster somatic growth of guppies in high light streams, which suggests that factors other than or in addition to algae production limit guppy populations. Our results are consistent with the predictions of a three-level food chain model, in which the abundance of predators and producers, but not herbivores, is expected to increase with primary productivity (Paine 1980). However, *Rivulus* appears to be the most serious predator of guppies in these streams (Liley and Seghers 1975, Reznick et al. 1990). Top-down control of guppies by *Rivulus* seems very unlikely, given the negative effect of guppies on *Rivulus* densities (Gilliam et al. 1993). Instead, we suspect that floods keep guppy populations below carrying capacity, to different degrees in different streams, and mask bottom-up effects.

Although we did not follow the fate of individual guppies after the floods, the population reductions were probably caused by a combination of mortality and forced dispersal. Backwaters and large immobile obstacles, such as boulders and snags, may shield periphyton during floods (Peterson 1996) and serve as refugia for guppies (which may otherwise be washed downstream or crushed by tumbling cobbles). We did not find guppies trapped in desiccating pools after the floods, as has been reported for other tropical fish, including *Poecilia gillii* (Chapman and Kramer 1991). The availability of refuges, and the overall stability of the streambed substrata, may be major determinants of how flooding affects populations of guppies and other fishes. The floods we observed in the high light Paria and Marianne streams appeared similar hydrologically, but the reductions in guppy and algal biomass were much greater in the Marianne stream where the streambed was more heavily disrupted (G. F. Grether, *personal observation*). The 92% reduction of guppies observed in the latter stream (Fig. 4) hints that floods may occasionally drive guppy populations in the upper reaches of a drainage extinct or through genetic bottlenecks.

Life history evolution

One shortcoming of our study is that we did not measure food availability in high predation streams. It could be argued that some counterbalancing factor prevents food availability for guppies from continuing to increase as canopy cover decreases downstream. For example, behavioral responses of guppies to predators in high predation streams, such as congregating along stream margins (Seghers 1973), could potentially reduce per capita food availability to or below the levels found in low predation streams. However Reznick et al. (2001) report that predators indirectly increase food availability for guppies. While we compared streams with similar (low) predation levels that differ in size (hence canopy cover), they compared streams of similar size that differ in predation levels. Their results indicate that predators increase per capita food availability for guppies by reducing guppy densities (despite the fact that guppies tended to forage nearer the margins of the high predation streams). Thus, across the full spectrum of low and high predation streams, both stream size and predation appear to have positive effects on food availability for guppies.

Resource availability is thought to be a potent agent of selection on life history traits, although different theoretical approaches have led to different conclusions regarding the direction of selection on particular traits (Stearns 1992, Charlesworth 1994, Kozłowski and Janczur 1994, Mylius and Diekmann 1995, Abrams and Rowe 1996). Classical *r*- and *K*-selection logic (MacArthur and Wilson 1967, Pianka 1970, Brockelman 1975, Stearns 1976, 1977) suggests that density-dependent selection would be stronger in habitats with lower food availability, favoring the production of

smaller broods of larger, more competitive offspring. We found a genetic offspring size difference in this direction in the Marianne drainage (Fig. 3) and preliminary data indicate that brood size differs genetically in the expected direction in all three drainages (G. F. Grether, *unpublished data*). However, *r*- and *K*-selection theory has largely been discarded, primarily because it fails to take population age structure into account (reviewed in Stearns 1992, Charlesworth 1994). Currently accepted theory does not provide general predictions about how specific life history traits should evolve in response to changes in food availability (Kozłowski and Janczur 1994, Mylius and Diekmann 1995, Abrams and Rowe 1996). In part this is because organisms are affected by and can adapt to changes in food availability in multiple ways.

Nevertheless, our preliminary data suggest that some life history traits in guppies have evolved in response to differential food availability, independent of predation. The trend that we detected (larger broods of smaller young at downstream sites) is the same as that previously reported (Reznick 1982, Reznick and Endler 1982, Reznick et al. 1990, 1997), except that, in the current study, the downstream sites contained the same weak guppy predators as the upstream sites; in past studies, the downstream sites also contained stronger predators (e.g., *Crenicichla alta*). Thus, the rapid genetic divergence of life history traits between high and low predation sites (Reznick et al. 1997) might result, in part, from differential food availability. Further theoretical and empirical work is needed to disentangle the effects of resource availability from predation in the evolution of life histories.

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product and imply no approval of a product to the exclusion of others that may be suitable.

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