NONLETHAL IMPACTS OF PREDATOR INVASION: FACULTATIVE SUPPRESSION OF GROWTH AND REPRODUCTION[1]

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Abstract. We asked whether invasions by a predator in a patchy environment altered only the death rate of the prey, or whether there were also nonlethal effects, i.e., alterations in three other vital rates: net emigration, reproduction, and individual growth rates. Field studies documented the patch use of the guppy *Poecilia reticulata* and the killifish *Rivulus hartii* in pools of a second-order forest stream in Trinidad, before and after invasion by the piscivorous fish *Hoplias malabaricus.* Experiments revealed that the predator altered the within-pool use of space by *Poecilia* and *Rivulus,* and caused significant emigration of the prey from pools in which it was present. Further, intimidation by the predator in an experimental stream suppressed total egg production in *Rivulus* by ≈50%, and created spatial patchiness (more eggs laid in safer pools) and temporal patchiness (pulses of eggs) in egg production. The presence of the predator also induced shifts to shallow riffle areas and significantly reduced the growth rate of adult but not juvenile *Rivulus.*

In contrast to the familiar paradigm that increased predation rates result in compensatory increases in per capita reproductive rates and/or growth rates as the population is thinned, we found that the threat of predation suppressed rates of reproduction and growth in predator-occupied patches.

Key words: artificial stream; growth; habitat use; Hoplias; *patches; patchy habitat;* Poecilia; *predation; reproduction;* Rivulus; *tropical stream.*

INTRODUCTION

Changes in the number of individuals in any population are determined by three rates: births, deaths, and net emigration (emigration minus immigration). When a population is subdivided into discrete patches these rates apply to the local population in each patch, and the rates occurring in each patch collectively determine properties of "metapopulations" summed across patches (e.g., Fahrig and Merriam 1985, Pulliam 1988, Taylor 1990). Changes in age and size structure of the population reflect these same rates, together with a fourth rate, individual growth rate, acting on an age- or size-specific basis. Predators might, in principle, affect local prey population dynamics by acting through any of these four processes.

When a predator enters a patch, perhaps the most obvious effect on prey is the lethal one: the predator may kill prey, increasing the prey's death rate. A large body of empirical and theoretical work on prey dynamics has assessed the impact of predators on prey populations by focusing on the lethal effect (Taylor 1990). The predator may also have nonlethal effects on the prey, i.e., behavioral responses by the prey, such

as alterations in microhabitat use, feeding behavior, or courtship (reviewed by Lima and Dill 1990). It is clear that such behavioral responses by prey can alter the second vital rate, net emigration from a patch (e.g., Sih 1982, Fraser et al. 1987, Gilliam and Fraser 1987, Schlosser 1987). However, it has often been less clear whether behavioral responses by the prey translate to changes in the other two vital rates (birth rate and individual growth rate), although some workers have found that chemical or visual cues can alter the morphology of prey (e.g., Yoshioka 1982, Lively 1986) or delay reproduction by prey (Crowl and Covich 1990, Magnhagen 1990). In addition, Werner et al. (1983) and Skelly and Werner (1990) found that prey grew slower when predators induced a shift from one habitat to another, or induced alterations in the use of space. If behavioral responses to predators commonly lower reproduction and/or growth by the prey, these effects over behavioral time scales would be opposite to the familiar paradigm that increased predation pressure will increase per capita birth and/or growth rates over longer time scales as the population is thinned.

In Trinidad, forest streams of the Northern Range Mountains have alternating pools and riffles, and thus are patchy to the resident fish community. While no detailed surveys have been published, Seghers (1973),

Liley and Seghers (1975), and Endler (1978) noted a general distributional pattern for the guppy, *Poecilia reticulata* and the jumping guabine, *Rivulus hartii*, in such streams; *Poecilia* densities are relatively high in almost all accessible aquatic habitats, while *Rivulus* densities appear substantially higher in those habitats that are inaccessible to piscivorous fish, e.g., headwater streams above waterfalls. These observations suggested that the local population dynamics of *Rivulus*, and perhaps *Poecilia*, in patchy environments may be especially sensitive to the invasion of predators, making these species good candidates for investigating the nonlethal effects of predation threat in a patchy environment.

In this study we investigated the invasion of forest stream pools in Trinidad by a predatory fish. We asked whether the predator would restructure habitat use by *Rivulus* and *Poecilia*, and if its presence could alter the four vital rates: death, net emigration, reproductive output, and individual growth. We made three field censuses of pools in the study stream during a period in which some pools had been invaded by the piscivorous fish *Hoplias malabaricus*, and conducted two series of field experiments. The first experimental series addressed how *Rivulus* and *Poecilia* shift habitats within a pool upon invasion by a predator, while the second series asked whether death and net emigration rates differed in relative magnitude. Because of the sensitivity of *Rivulus* to predation threat, we focused on *Rivulus* in two additional experiments to test whether the presence of an invading predator can suppress growth and reproductive rates of *Rivulus*.

MATERIAL AND METHODS

Study stream and species

Ramdeen Stream is a second-order tributary of the Arima River in Trinidad (10°41'32" N, 61°17'36" W), averaging 0.5–1.0 m wide, with alternating pools and riffles. The study area comprises 23 pool–riffle sections in the middle third of the 1.4 km long stream. The 23rd pool is immediately downstream of a series of waterfalls above which *Rivulus* is present but *Poecilia* is absent. All subsequent references to Ramdeen Stream will be to the study area below the waterfalls. The stream flows through an abandoned cocoa plantation in which cocoa, *Theobroma cacao*, is the predominant understory tree. The fish community is numerically dominated by *Poecilia* and *Rivulus*. *Poecilia* are live-bearers whose social behavior has been extensively studied (e.g., Baerends et al. 1955, Breden and Stoner 1987, Houde and Endler 1990), while *Rivulus* are continuously reproducing egg-layers. *Rivulus* males aggressively court females, which spawn by a twisting motion that brings the cloaca of the female into contact with the substrate where a single, sticky egg is attached (D. F. Fraser and J. F. Gilliam, *personal observations*). The body of the male is in contact with the female

during this sequence. Nothing is known about oviposition in nature, but these fish readily deposit eggs in floating vegetation in aquaria.

The piscivorous, characiform fish *Hoplias malabaricus* was not found in three surveys conducted between 1984 and 1986, but we found one in our survey of the stream conducted in August 1988. Since that time *Hoplias* has occurred in one or two of the study pools, and we noted qualitatively that, relative to fish in other pools, fish in *Hoplias*-occupied pools appeared to show microhabitat shifts and reduced numbers. We have never found juvenile *Hoplias*, <80 mm total length, in Ramdeen Stream, suggesting that *Hoplias* is a transient, rather than a breeding resident. However, *Hoplias* is common in the adjoining Arima River. *Hoplias* is a large piscivore that hunts moving prey by either ambushing or slow stalking (Costa 1987, Prejs 1987, Winemiller 1990). Since Seghers (1978) found small *Poecilia* in the stomachs of *Rivulus* taken from three streams in the Northern Range, in pilot experiments we assayed for behavioral shifts by *Poecilia* while alone vs. in the presence of *Rivulus* and/or *Hoplias*, but found no indication of *Rivulus* effects, while *Hoplias* produced conspicuous effects. In view of this, we analyzed the stomach contents of 72 *Rivulus* from Ramdeen Stream and none contained *Poecilia*, their diets consisting mainly of terrestrial and aquatic insects. Thus, while not ruling out predator–prey interactions between *Rivulus* and *Poecilia*, we chose to focus on the apparently stronger effects of *Hoplias*. Two additional species, the catfish *Rhamdia sebae*, and the eel *Synbranchus marmoratus*, occur at low densities. Our survey data failed to suggest any negative impact of these species on the pool densities of *Rivulus*, and they are not considered in this study.

Stream surveys

To document the pool distributions and densities of the predator, *Hoplias*, and its potential prey, *Poecilia* and *Rivulus*, we censused the 23 study pools at the beginning of the wet season in August 1988, at the end of the wet season in January 1989, and during the dry season in March 1990. We sampled the 23 pools, in succession, beginning with the lowermost pools, using 3-mm mesh seines. We isolated the pool with blocking nets, temporarily removed large objects and then seined the pool repetitively until no more fish were caught on two consecutive seinings. We followed each seining by visually searching roots, rock crevices, and other possible refugia, catching any missed fish with a dip net. To further insure that we did not miss fish, we left the blocking nets in place and returned after dark with lights and made visual searches of the pool. We usually found one or two missed fish. The latter procedure was abandoned in the March census when the postseining use of an electroshocker (Coffelt BP-4) enabled us to catch missed fish. In the March survey, we made a preliminary night census of pools by counting *Rivulus*

that were visible in the water column. All fish were released back into their respective pools after being identified, sexed, and measured. The total length (TL) of *Poecilia* ranged from 7.0 to 50.0 mm ($\bar{X} \pm 1$ SE = 22.4 ± 0.24 mm); *Rivulus* ranged from 8.0 to 102.0 mm (37.9 ± 0.45 mm). The maximum length and width of pools were measured and surface area calculated as an ellipse ($A = (\pi/4) \times$ length $\times$ width).

Within-pool experiments

A prey may choose not to leave a patch when a predator is near, e.g., if energy costs or mortality risks may be greater elsewhere (Gilliam and Fraser 1987, Holbrook and Schmitt 1988). Under such circumstances the prey might still alter its use of space within a patch in response to predation risk. To evaluate the within-pool use patterns of *Poecilia* and *Rivulus* under predation threat, we conducted an experiment in which we observed the use patterns of the two prey species in the presence and absence of the predator. We made observations during the day, 0900–1600, when *Hoplias* is relatively inactive, and of presumably low threat to the prey, and also during the crepuscular period, 1710–1840, when predation threat typically increases as ambient light declines (Helfman 1979, Cerri 1983).

We selected three pools, averaging 2.6 m² in surface area and 23 cm maximal depth, and screened at the up- and downstream ends. After removing all resident fish, we stocked eight large ($\bar{X} \pm 1$ SE = 27.8 ± 0.88 mm TL) and eight small ($\bar{X} \pm 1$ SE = 17.8 ± 0.95 mm TL) female *Poecilia* into each pool and recorded the use of space by all fish in each of four treatments: the presence and absence of *Rivulus* (three large: $\bar{X} \pm 1$ SE = 59.0 ± 2.0 mm TL, and three small: 40.0 ± 8.1 mm TL), cross-classified with the presence and absence of *Hoplias* (160 mm TL). The small *Poecilia* were sexually immature. *Rivulus* in Ramdeen Stream mature at ≈35 mm TL. We recorded the number in each of the four prey types (small and large *Poecilia*, small and large *Rivulus*) located in three, approximately concentric zones: the pool center (17.6–23.0 cm in depth), an intermediate zone (6.1–17.5 cm in depth), and the shallow edge (0–6 cm in depth), at 10-min intervals during the above two observation periods. At each reading we recorded the light level 0.5 m above one pool as micromoles of photons per square metre per second, using a LI-COR LI-185B quantum radiometer (see Endler 1987 for discussion of procedure and instrument). At this location molar photon flux and lux were approximately convertible as 1 $\mu m \cdot m^{-2} \cdot s^{-1}$ = 14.9 millilux over the range of 0–20 lux.

Each of the three test pools received each treatment in random order. Prey and the predator, *Hoplias*, were restocked at the end of the daily observation period (1900) from a holding tank. We began observations on the following day. Initially, we attempted to make observations from a blind, but later found that the subjects appeared to behave normally, e.g., they searched

for food, fed, and courted, within minutes after the observer sat quietly by the side of the pool.

To ask whether *Poecilia* and *Rivulus* altered their use of the pool in daytime, we calculated the mean depth for each prey type by taking the proportion of fish in each depth zone, multiplied by the average depth in that zone. We analyzed the three replicates of pool depth of *Poecilia* in the presence and absence of *Hoplias* and *Rivulus* by a two-way ANOVA. The distribution of *Rivulus* in the presence and absence of *Hoplias* was compared with a *t* test (three replicates in the presence of *Hoplias*, two replicates in the absence of *Hoplias*, because in the initial replicate, four extra *Rivulus* appeared in the pool due to inadequate screening). In addition, for crepuscular observations, we plotted the mean depths for each prey type as a function of time in the presence and absence of the *Hoplias*. In either case, "depth" refers to the depth of water in the three zones (edges, intermediate, center) where the fish was located, so shallower depths indicate fish closer to the pool edge.

Between-pool experiments

The invasion of a predator may have immediate effect on patch dynamics if the prey are killed or emigrate. Thus, in this experiment we tested for differences in the relative magnitude of death and emigration by *Poecilia* and *Rivulus*, and for differences between the subject species with respect to these rates, when a *Hoplias* was present in a pool. We did short-term experiments, using two adjacent pools: one upstream and one downstream. We introduced the predator, *Hoplias*, into one pool and allowed the prey to choose between the threatened and the adjacent predator-free pool over a 24-h period. The pools averaged 2.2 m² in surface area, 10.4 cm in depth, and were screened at the up- and downstream ends. The pools were separated by a 30 cm long riffle that was screened midway with 12.5 mm² hardware cloth that permitted *Poecilia* and *Rivulus* to pass between pools, but not *Hoplias*. The prey were taken from holding tanks and either eight small ($\bar{X} \pm 1$ SE = 19.4 ± 0.46 mm TL) and eight large (26.8 ± 1.5 mm TL) *Poecilia*, or eight small (38.6 ± 3.4 mm TL) and four large (55 ± 6.2 mm TL) *Rivulus* were stocked into each pool. The two species were tested in separate trials.

Two *Hoplias* (115 mm TL, 170 mm TL) were introduced into one of the two pools. After 24 h all of the prey were caught by dip netting them between the hours of 1900 and 2230, and their pool locations noted. The predators were also recovered at this time. Since two predator-free preliminary trials showed no missing fish, we assumed missing fish in the presence of *Hoplias* to represent predatory deaths (the 115 mm *Hoplias* spontaneously regurgitated a 58-mm *Rivulus* after one of the trials). Any excess of fish in the predator-free pool, above the number stocked, represented net emigration (any leaving minus any entering) from the pool

with the *Hoplias*. All prey subjects were returned to the holding tanks, allowed to mix, and then a new sample drawn and restocked as before, except that the predators were stocked into the previously predator-free pool; the sequence of predator-free pools along the stream being up, down, up, down, giving four replicates for the small and large *Poecilia* and small *Rivulus*. Adult *Rivulus* were tested in two replicates. Alternating the location of the *Hoplias* in this manner controlled for any up- or downstream bias in direction of movement by the prey.

We used a 2 × 4 ANOVA to test whether the number of fish appearing in each of two categories, death vs. net emigration, differed among the four categories of prey fish (small and large *Poecilia* and *Rivulus*). We did four planned orthogonal contrasts, testing for differences between death and net emigration rates for each of the four categories of prey fish. The number of prey killed and the number emigrating cannot be assumed to be independent variables, because if a fish is killed, it cannot emigrate and vice versa. These rates appeared to be independent in our experiment (correlation analysis of percent killed vs. percent emigrating, $N = 16$, $r = -0.32$, $P > .05$), so we proceeded with the analysis.

Reproductive suppression experiments

Our previous observations suggested that the predator might disrupt reproduction by *Rivulus*, by making the fish less willing to risk exposure by courting and laying eggs. We investigated the possibility of reproductive suppression in *Rivulus* by conducting a controlled experiment in a New York experimental field stream facility. We chose *Rivulus* because we could assay reproductive output on a daily basis by counting eggs laid on artificial substrates in the presence and absence of the predator. The New York stream facility is fully described in Fraser and Cerri (1982). We used two independent, parallel streams (Streams A and B), modified from Fraser and Cerri (1982) to consist of three pools (0.3 m wide × 3.0 m long × 0.1 m deep), separated by stony riffle sections (0.2 m long × 0.05 m deep).

We asked if the presence of the predator would alter the number of eggs deposited in the stream. Each of the three pools, described above and referred to here as upstream, middle, and downstream, contained a synthetic "grass" doormat, 0.14 × 0.25 m, located 0.5 m upstream of the three riffles. *Rivulus* readily deposited eggs in the grass of the mat, and the eggs were easily counted by flexing the mat under a light.

Natural silty sediments formed the benthic substrate. One male and two female adult *Rivulus* ($\bar{X} \pm 1$ SE = 71.0 ± 0.93 mm TL) were added to each pool in the two streams. These fish had been collected from Ramdeen Stream 5 mo previously and were maintained in the laboratory where the females produced eggs daily on the grass doormats. *Rivulus* assumed normal behavior and began laying eggs within 24 h. Over the next 2 d they laid eggs on all of the mats in both streams, with a total of 28 eggs in Stream A and 26 in Stream B. In the absence of predators, the fish resided in the pools, and were rarely found in the riffles of either stream.

We compared reproductive output in the presence and absence of an invading predator by introducing *Hoplias* into one stream while holding the other predator free, and later reversing the treatments. Hence, one stream (Stream A) was selected randomly for the addition of one *Hoplias* (150 mm TL), which, like the *Rivulus*, could move freely among the pools. By using the single predator and three pools, we did not unnaturally force *Rivulus* to be in constant visual presence of the predator, but rather mimicked the patchy distribution in Ramdeen Stream. The *Hoplias* was left in Stream A for a 12-d period, and then switched to Stream B following an intervening predator-free period of 14 d. Nightly, throughout the experiment, the location of each *Rivulus* and the predator were recorded, and the number of eggs on each mat was counted by removing the mat and replacing it with a new one. At the end of each replicate we searched possible alternative oviposition sites as well. Riffle areas were searched by removing and inspecting every stone with a fine-mesh, downstream blocking net in place. Pool sediments were also sieved at this time. No eggs occurred in these sites. A few eggs (<10) were occasionally found on the wooden sides of the experimental stream, usually adjacent to the egg mats. These eggs were not included in the final analysis, because we did not search for them on a daily basis, and thus could not always be sure of the day of deposition, since the eggs take 10–21 d to hatch. However, we added them in trial counts to be certain that their inclusion could not make a difference in the outcome.

While the mouth morphology and hunting behavior of *Hoplias* made it highly unlikely that it would consume *Rivulus* eggs deposited in the mats, we nonetheless confirmed this directly. Subsequent to the above experiment, the *Hoplias* used in the experiment was confined with egg-containing mats (17 eggs). Daily counts revealed that no eggs were consumed prior to hatching; newborn *Rivulus* hiding in the mats also appeared to be safe, but were consumed immediately if exposed in the water column by removal of the mats.

We compared egg production between the predator-free and the predator-occupied stream using a paired *t* test. We examined spatial and temporal pattern of egg deposition (patchiness) using an index of patchiness, the variance/mean ratio. We tested variance/mean ratios by the method of David and Moore (Pielou 1977).

Growth reduction experiment

Predation threat may reduce a prey's foraging rate if altered habitat use disrupts feeding patterns or forces the prey into less profitable microhabitats. Whatever

the mechanism, a nonlethal effect of predation threat may be reduced growth. We used *Rivulus* to investigate this effect, because relative to *Poecilia, Rivulus* grows through a larger size range (≥ 80 mm from hatchling to maximum size), providing an opportunity to test for size-specific growth reduction as the foraging characteristics of the fish change with ontogeny.

We used a tropical stream facility, built alongside Ramdeen Stream. The Trinidad experimental stream is a replica of the New York stream with respect to size and arrangement of pools and riffles. Water is piped by gravity flow a short distance (50 m) from a collecting tank located on a nearby, first-order tributary of Ramdeen Stream. We constructed pools and riffles in the bed of the experimental stream by translocating sections of the natural stream bed. The benthic substrate of pools and riffles consisted of sand and gravel (stone size <2.5 cm), except in the riffles where some stones were between 2.5 and 10.0 cm, overlaid by a characteristic layer of silt. A benthic fauna and flora established between 18 November 1989 and 29 January 1990 when we started the growth reduction experiments.

We screened the downstream end of each of the three riffles, providing three pool–riffle habitats in each stream. We used a table of random numbers to randomly assign three pool-riffle habitats to receive one *Hoplias* each (*Hoplias* TL = 135–170 mm, $\bar{X} \pm 1$ SE = 152.3 $\pm$ 4.6 mm), the remaining three pool-riffle habitats serving as predator-free controls.

Subjects were caught in nearby first- and second-order streams and maintained in laboratory aquaria prior to testing. At the start of each trial subjects were starved for 24 h, anesthetized in tricaine methanesulfonate (MS222), total length measured to the nearest 0.5 mm (juveniles measured under a dissecting scope), blotted once on each side to remove excess moisture, and weighed on an electronic balance.

We conducted three trials ($N = 9$ replicates) for juvenile *Rivulus* and two trials ($N = 6$ replicates) for adult *Rivulus*. For each replicate we stocked eight juvenile (starting TL = 19.0 − 27.0 mm, $\bar{X} \pm 1$ SE = 21.98 $\pm$ 0.68 mm) and three adult (starting TL = 52.0–68.5 mm, $\bar{X} \pm 1$ SE = 59.4 $\pm$ 2.8 mm) *Rivulus*. To control for possible size-related mortality and possible biasing of our results, we marked individual adult *Rivulus* by injecting them with an acrylic paint at the caudal peduncle, enabling us to calculate a growth rate for each fish. Juveniles could not be practically marked, so we used a narrow range of initial ranges in each replicate. For the first six replicates, all fish were within 3 mm of the median. For the final three replicates, all fish were of identical length at our scale of measurement, i.e., all fish were 21.0 mm in Replicate 7, 22.0 mm in Replicate 8, 23.0 mm in Replicate 9, with measurements to the nearest 0.5 mm. The last three replicates gave the same result as the first six, i.e., no predator effect on juvenile growth (see *Results*), so the nine replicates were combined for final analysis and presentation.

The juveniles and adults were tested separately. The time course of the trials varied from 7 to 16 d, so we analyzed final length and mass on a per day basis. The predators were added 48 h after stocking the prey. We monitored the prey nightly with lights. At night, nonthreatened *Rivulus* are almost always found out of cover, either in the water column or resting on the bottom. Threatened *Rivulus* were usually hiding, but we could locate them by probing leaves or gently tipping up small stones with the end of a pencil. We recorded the location of these fish as being in the pool or the riffle.

At the end of a trial we removed all subjects and repeated the weighing and measuring procedure used at the start of the trial. The total time course of the growth reduction experiment was 76 d. The entire experiment was run within the dry season. Since benthic resources might be depleted during each trial, at the end of each trial a portion of the sediments from each pool and riffle was replaced with "fresh" sediments from Ramdeen Stream. Control subjects were returned to the holding tanks where they could be drawn again, but subjects used in the predator treatments were never reused in subsequent trials.

In preliminary trials we found that the predation rate of *Hoplias* on *Rivulus* was unacceptably high. Because we felt that it was essential to retain the movement and chase stimuli that would appropriately mimic a predator invading a pool in Ramdeen Stream, alternatives such as confining the *Hoplias* in a glass cage were not acceptable. However, the effectiveness of *Hoplias* predation was reduced by anesthetizing the *Hoplias* in MS222, and threading a piece of monofilament fishing line, dorsoventrally, through the membrane between the premaxilla and maxillary bones (as far anterior as possible) and through the lower lip, distal to the dentary. A small bead was passed down each free end and locked in place by heating the end of the line. Because only one side was clamped, the *Hoplias* retained mobility on the other side, enabling it to capture *Rivulus*, but the predation rates were reduced by about two-thirds ($\bar{X} \pm 1$ SE = 2.1 $\pm$ 0.5%/d for juveniles in the full experiment, vs. 5.9 $\pm$ 2.2%/d in the preliminary trials; adult mortality rates were 2.6 $\pm$ 0.7%/d in the full experiment). We were able to control for changes in prey density due to predation by replacing lost fish with marked replacements. The replacements were not used in the growth analysis. At the end of a trial we sacrificed each *Hoplias*. As expected, we found fish in their guts (0–2 per *Hoplias*), but we never found invertebrate remains, which satisfied us that any growth reduction in the prey could not be caused by competing *Hoplias*.

We analyzed for behavioral shifts in habitat use by calculating the percent of the prey fish present in the riffle portion of the habitat, as opposed to the pools, once during each replicate ($N = 9$ for juveniles, $N = 6$

for adults), and then analyzed the arcsine-transformed percentages in a 2 × 2 design by an analysis of variance (age × predator). Growth rates in the presence and absence of the predator were compared with t tests (two-tailed).

RESULTS

Stream surveys

Overall densities of *Rivulus* and *Poecilia* varied greatly among pools and years. Fish were almost 6 times as abundant in Ramdeen Stream at the beginning of the wet season in August 1988 as they were at the end of the wet season in January 1989 (*Rivulus*: $N = 560$ vs. 100; *Poecilia*: $N = 602$ vs. 107). Pool fish densities were not correlated between years; a pool with few fish in 1988 may have had many in 1989 ($N = 16$ pools, $r = -0.042$, $P > .05$). In any year the densities of *Rivulus* and *Poecilia* also varied greatly between pools (*Rivulus*: 0–11.8 fish/m^2; *Poecilia*: 0–12.0 fish/m^2). The two species co-occurred in pools, and the total number of fish in a pool was independent of pool size in all but the largest pools (pools $> 5.50 m^2$). However, regardless of pool size, *Rivulus* densities were lowest when the predator *Hoplias* was present (Fig. 1).

We found no consistent suggestion of elevated or depressed *Rivulus* densities in pools adjacent to predator locations, but we did find a correlation between the nighttime number of *Rivulus* (> 20 mm TL) active in the water column (visual count expressed as percent of total netted on the following day) and the distance (expressed as number of pools) from the nearest *Hoplias* pool ($N = 10$, $r = 0.79$, $P < .01$). In contrast, those in the most distant pools remained in the water column when approached, seeking cover only when directly disturbed.

Within-pool experiments

The daytime pool use patterns of both prey species were altered by the presence of *Hoplias* (Fig. 2). *Hoplias* was usually concealed in silt or under leaves in the deepest part of the pool; large *Poecilia* tended to avoid that part of the pool when *Hoplias* was present, spending more time in the intermediate areas between the edge and center, but showed no significant shift attributable to the presence of *Rivulus* (ANOVA: *Hoplias* main effect, $F_{1,8} = 14.9$, $P = .005$; *Rivulus* main effect, $F_{1,8} = 3.8$, $P = .088$; interaction, $F_{1,8} = 0.6$, $P = .46$). However, small *Poecilia*, which tended to use the shallow portions of the pool, even in the absence of the predator, showed no shift in location when the predator was present (ANOVA: *Hoplias* main effect, $F_{1,8} = 3.9$, $P = .08$; *Rivulus* main effect, $F_{1,8} = 0.1$, $P = .77$; interaction, $F_{1,8} = 1.4$, $P = .27$). Small *Rivulus* also shifted in the presence of *Hoplias* ($t = 3.15$, df = 3, $P = .05$), while large *Rivulus* did not ($t = 0.51$, df = 3, $P = .65$). *Poecilia* appeared to be wary of the *Hoplias* in that they avoided the immediate vicinity of the predator, but
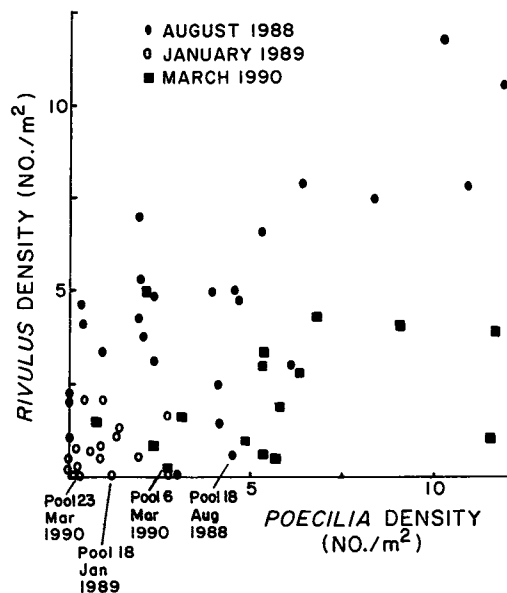

FIG. 1. The density of *Rivulus* vs. the density of *Poecilia* in pools of Ramdeen Stream in surveys conducted in 1988, 1989, and 1990. Pools containing the predatory fish *Hoplias* are marked on the figure. Pools 18 and 23 each contained a single *Hoplias* on the dates shown, while Pool 6 contained two. On each date, pools containing *Hoplias* yielded the lowest densities of *Rivulus* for that date.

otherwise foraged actively in all areas of the pools. However, we noted qualitatively that *Rivulus* remained inactive and often hidden during the day when *Hoplias* was present.

The pattern of small *Poecilia* shallow, large *Poecilia* deep continued into the crepuscular period. However, as ambient light decreased after 1700 (Fig. 2), large *Poecilia* and *Rivulus* began to move into the shallow edges, overlapping in their use of the shallow zone with the small size class of *Poecilia*. The presence of the *Hoplias* had the effect of making this convergence more pronounced, especially with respect to large *Poecilia* (Fig. 2). *Hoplias* emerged from its daytime retreat between 1759 and 1822 ($\bar{X}$ time = 1809), when light levels ranged from 0 to 0.165 μmol·m^{-2}·s^{-1}, and assumed its typical ambush posture close to the bottom.

Between-pool experiments

Following the appearance of a *Hoplias* in a pool, over the next 24 h about one-half of the fish remained in the pool (Table 1), with the remainder being killed or emigrating. Emigration tended to be a stronger influence on the local population dynamics, with emigration exceeding death rate for both species and size classes considered together ($F_{1,20} = 8.29$, $P < .01$). Comparing each species and size class individually, emigration rate exceeded death rate for large *Poecilia* (orthogonal contrast, $F_{1,20} = 13.43$, $P < .01$), while death and emigration rates did not differ significantly for small *Poecilia* and both size classes of *Rivulus* (or-
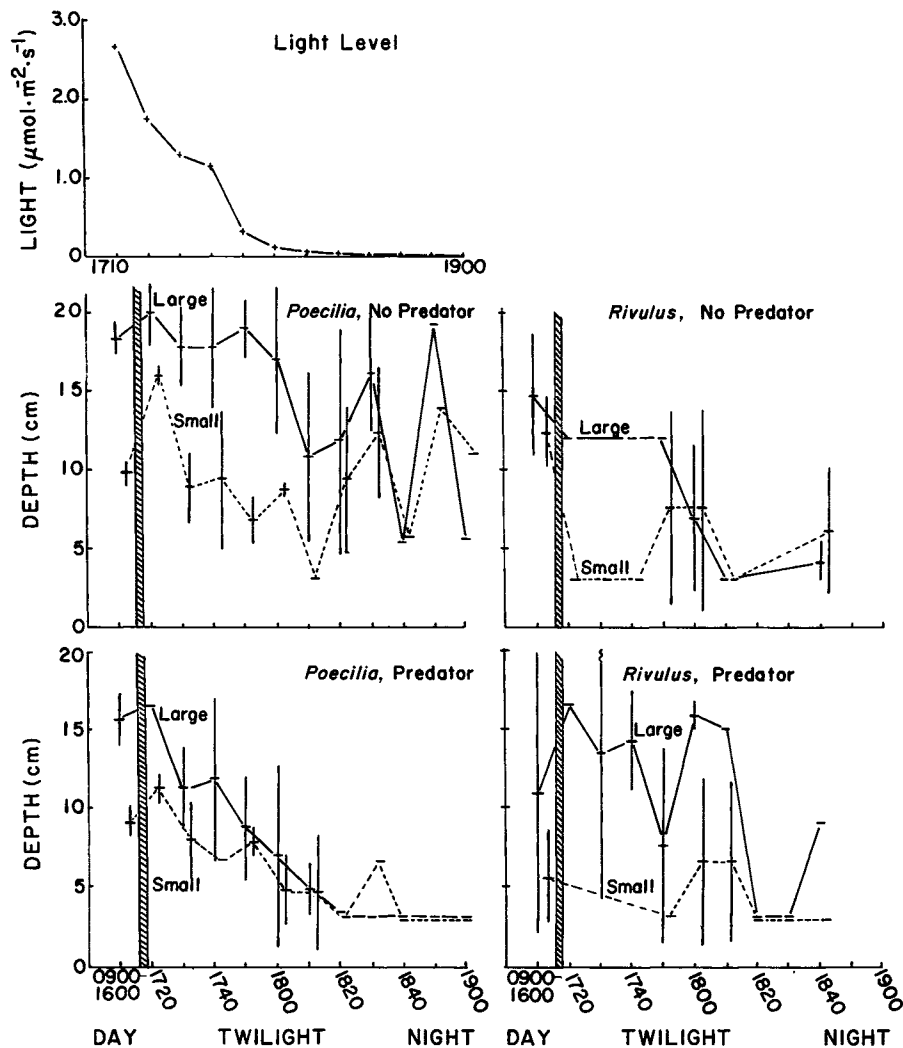
FIG. 2. Depth of pool use in Ramdeen Stream by two size classes of *Poecilia* and *Rivulus* in the presence and absence of the predatory fish *Hoplias* (means ± 1 SE). Shallower depths indicate the use of pool edges. The averages of daytime observations, taken between 0900 and 1600, are given to the left of the hatched bar; observations made at 10-min intervals through the crepuscular period are given to the right. In daytime, the presence of the predator resulted in a shift towards the shallower (edge) areas of the pool by large *Poecilia* and small *Rivulus*. With decreasing light, *Hoplias* induced a systematic shift to shallow edge areas by large and small *Poecilia*.

TABLE 1. Between-pool experiment to test for differences in emigration and death rates when a *Hoplias* invades the pool. Means (± SE) refer to the pool containing the predatory *Hoplias*.

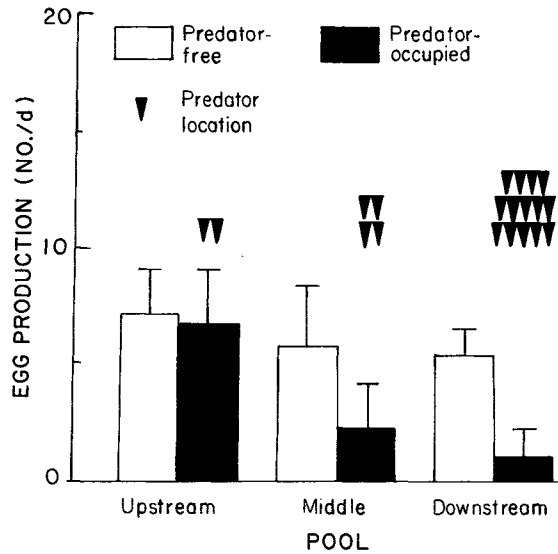|	Death rate (percent)	Net emigration (percent)	Net staying (percent)	Background mortality (control)
Poecilia				
Large	3.1 ± 3.1	46.9 ± 06.0	50.0 ± 08.8	0
Small	12.5 ± 5.1	18.8 ± 10.8	68.8 ± 12.0	0
Rivulus				
Large	12.5 ± 12.5	25.0 ± 25.0	62.5 ± 12.5	0
Small	15.6 ± 11.8	28.1 ± 10.7	56.3 ± 08.1	0

FIG. 3. Egg production in each pool by *Rivulus hartii* in the absence and presence of the predator *Hoplias* (means and 1 SE). Intimidation by the predator reduced total reproductive output by about one-half, and induced a spatial gradient in egg production.

thogonal contrasts, all $P > .05$). In no case was there any suggestion that death rate exceeded emigration rate.

Reproductive suppression experiments

With the introduction of the predator into a stream line, we observed clear, immediate (<24 h) behavioral changes in the prey. As expected from our field observations, the introduction of the *Hoplias* resulted in decided shifts to shallow riffle areas, with 57% of the *Rivulus* in the riffles in the predator-occupied treatments vs. 12% in the predator-free treatments. We also noted qualitatively other behavioral differences between treatments. In predator-free treatments, *Rivulus* were often in the water column and reacted quickly to overhead movement by seeking cover, but those in predator-occupied treatments were usually close to the bottom and remained motionless when subjected to overhead movement. We also observed that *Rivulus* in the presence of *Hoplias* were noticeably darker than those in predator-free treatments. These changes occurred despite the absence of any successful predation on *Rivulus* by *Hoplias,* as all fish survived the experiment.

Patterns of egg production were substantially altered in the presence of *Hoplias*. First, the predator suppressed total egg production. Summed across pools, the total rate of egg production in the predator-occupied stream was about one-half of that in the paired predator-free stream (Fig. 3). The difference in egg production between the predator-free stream and the predator-occupied stream was 9.33 eggs/d in the original introduction (Replicate 1) and 8.20 eggs/d in the reversal (Replicate 2), a significant reduction (paired t

test; $N = 2, t = 16.3, P = .02$). Thus, while the reduction was most evident in the downstream pool, where the predator was most often found, the predation threat did not simply redistribute eggs among pools, but rather reduced the total laid over the course of the experiment. The suppression occurred even though the predator did not deplete the prey population and could have occupied only one of the three pools at any given instant.

Second, the presence of the predator resulted in a more patchy pattern of number of eggs produced (Fig. 4). As judged by the criterion of the variance/mean ratio, both distributions of Fig. 4 are clumped (var/mean >1), but eggs in the predator-occupied stream are significantly more clumped (var/mean = 6.3, predator-free vs. 24.6, predator-occupied, pooled across both replicates; David and Moore $w = 0.74, P < .05$). Each replicate considered separately showed the same pattern (Replicate 1, 6.0, predator-free vs. 26.5, predator-occupied; Replicate 2, 5.7 vs. 13.9). This is because pools in the predator-occupied stream tended not to have eggs on most days, interspersed with pulses of eggs. The highest egg count in the experiment was recorded in a predator-occupied treatment, in which a large pulse of eggs (58 eggs) was deposited in the upstream pool after several days of zero-egg counts.

Growth reduction experiment

In the absence of the predator, few juvenile and adult *Rivulus* were in the riffle portion of each pool–riffle experimental unit, but when *Hoplias* was present in the pool (we never found *Hoplias* in the riffles), most of the juvenile *Rivulus* and all of the adults were found in the riffles (Table 2). The differences in riffle usage between the predator and control treatments were highly significant for both age classes of prey fish. Qualitatively we observed that fish in the predator treatment appeared frightened; as in the reproductive suppression experiment above, they were usually hiding beneath
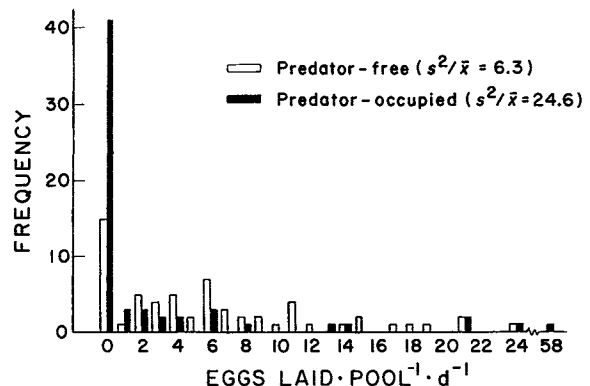

FIG. 4. Distributions of daily egg production in the presence and absence of the predator. In the presence of the predator, egg production was more pulsed, with more zero-egg events.
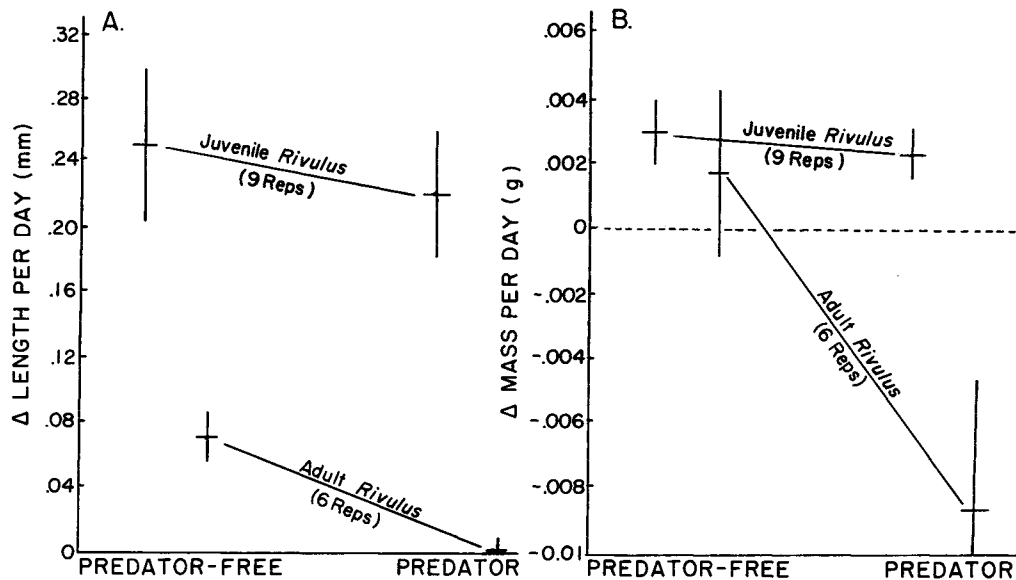
FIG. 5. Change in total length per day (A) and mass per day (B) by *Rivulus hartii* in the absence and presence of the predator *Hoplias* (means ± 1 SE). In the presence of the predator, adult *Rivulus* changed from a positive to a negative energy budget, while juvenile *Rivulus* remained positive.

stones or leaves in the riffles, and often remained motionless when subjected to overhead movement.

The presence of *Hoplias* induced a strong change in growth rate of adult *Rivulus* (Fig. 5), whether measured by length ($t = 5.92$, df = 10, $P < .001$) or mass ($t = 3.02$, df = 10, $P < .02$). Juveniles exhibited no statistically significant differences in growth in the presence and absence of *Hoplias* ($t = 0.71$, df = 16, $P > .45$ for length; $t = 0.71$, df = 16, $P > .45$ for mass).

DISCUSSION

The findings of this study support the hypothesis that nonlethal predator effects can be important in patch dynamics. In addition to restructuring microhabitat use patterns of both prey species (*Poecilia* and *Rivulus*) within pools, the predator *Hoplias* altered all four vital rates of the prey: death, net emigration, individual growth, and fecundity. The first three findings (altered microhabitat use, death rate, and emigration) were not surprising given related work in temperate stream systems. Previous work on minnows (family Cyprinidae) in similarly patchy temperate streams has shown some similar effects: invasions of a pool by a predator can

TABLE 2. Percent of *Rivulus* in riffle section of pool-riffle experimental unit in the growth reduction experiment (means ± 1 SE).

Rivulus age class	No predator	Predator	Orthogonal contrasts	
			F	P
Juvenile	24.5 ± 5.9	90.0 ± 4.7	76.1	<.001
Adult	0 ± 0	100 ± 0	157.2	<.001

restructure the prey's use of space within the pool, and induce some fish to shift between pools (Fraser and Sise 1980, Fraser and Cerri 1982, Power et al. 1985, Fraser et al. 1987, Power 1987, Schlosser 1987, 1988, Harvey et al. 1988). In addition, predation threat may have been the cause of a reduction in feeding rate of several species of prey fish that were trapped in pools with predatory fish, among them *Hoplias malabaricus* and *Crenicichla alta* (Prejs 1987). However, the consequences of the threat of predation on growth and reproductive patterns, if any, have been in doubt. Perhaps the most striking findings of this study are that the microhabitat shifts can be accompanied by real demographic consequences for growth rate, and that the threat of predation alone, acting on behavioral rather than evolutionary time scales, can substantially alter reproductive output.

The depression of growth in the tropical stream system to some extent corroborates the work of Werner et al. (1983) in a temperate pond, who found that a shift by small fish to littoral areas was accompanied by decreased growth, Skelly and Werner (1990) who found that tadpoles grew more slowly and metamorphosed at smaller sizes in the presence of predation threat, and Semlitsch (1987) who found that salamander larvae threatened by fish in experimental containers stayed among the leaf litter and grew more slowly, although he noted that exploitative competition with the fish may have also occurred. While each of these studies differ from one another and the present study in various ways, all four emphasize the breadth of the nonlethal effects of predation threat. Of particular interest in this study was the unexpected finding that

adult *Rivulus* showed growth reduction, while juvenile *Rivulus* showed no statistically detectable response, and at most a small response relative to adults, even though both sizes made strong behavioral shifts to shallow riffles when the predator was in the pool.

The lack of a decided growth response by small *Rivulus* agrees with Morin (1986), in that habitat shifts while avoiding predators do not necessarily incur measurable growth costs. The reasons for the contrast between large and small *Rivulus* are not known, but we believe that one or more of four related factors are likely candidates. First, in studies with marked fish (D. F. Fraser and J. F. Gilliam, *unpublished data*) adult *Rivulus* appeared to maintain feeding and courtship territories, while smaller *Rivulus* occupied subordinate roles. In this respect, the presence of the *Hoplias* might be more disruptive to adult *Rivulus* than to juveniles. Second, stomach analyses of *Rivulus* (Seghers 1978; J. F. Gilliam and D. F. Fraser, *unpublished data*) reveal a preponderance of terrestrial insects in the diet. In the presence of the predators, the shift to the riffles places *Rivulus* between stones in water barely covering the fish's body, and the shift to the riffles may decrease the effective feeding area of adults more than juveniles. Third, the shift to riffles was starkly complete for adults (Table 2), while juvenile *Rivulus* spent some time (10% of sightings) in the pools in the presence of the predator. The difference between juveniles and adults might reflect a difference in the value that each places on obtaining food vs. avoiding predators. Finally, juveniles simply require less food to maintain a positive growth trajectory. Whatever the reasons for negative growth by adults in the presence of the predator, the finding may explain, in part, the distributional pattern of *Rivulus* in drainages in Trinidad, i.e., its reduction or near absence in rivers in which large piscivores can be common.

Several studies have indicated that courtship and reproduction carry a cost of increased likelihood of being killed by predators (reviewed by Lima and Dill 1990). However, there is little evidence that mature animals facultatively alter reproductive behavior when the threat of predation is changed. Some studies have found that males shift mating behavior so as to become less conspicuous when predators are near or active (Tuttle and Ryan 1981, Endler 1987, Sih 1988). However, if females can find willing males when ready to mate, such changes in male behavior, while interesting from a behavioral point of view, may have no net consequence for the reproductive output of a population. Closer to our results, Resetarits and Wilbur (1989) found that female frogs tend to oviposit in pools without certain potential predators, concluding that predators cause a redistribution of eggs among pools, but with no indication that total output was altered. The suppression of reproductive output that we found had not been reported previous to this study, but reproductive suppression by predation threat may exist in

a variety systems. Crowl and Covich (1990) reported that predators delayed maturation in a freshwater snail, and Magnhagen (1990) found that a species of marine fish delays nesting if predators are visually detectable in large aquaria.

The present study has addressed facultative alterations in habitat use and vital rates of the prey over behavioral time scales of a few hours or days following a predator invasion of a given pool, with the main results being movement away from the pool, and suppression of growth and reproduction of *Rivulus* that stay in or near the pool. However, over longer time scales, the effect of predator presence on vital rates might be different, if the invertebrate populations exploited by *Poecilia* and *Rivulus* increase following declines in the densities of those fish species in the pool (cf. Gilliam et al. 1989, Schlosser and Ebel 1989, Cooper et al. 1990 for temperate streams), and if higher resource levels then translate to higher growth and/or reproduction by fish using the pool. However, it appears that *Poecilia,* rather than *Rivulus,* is most likely to exhibit any benefits of increased resource levels in a predator-occupied pool. In Ramdeen Stream *Hoplias*-occupied pools tend to have more *Poecilia* than *Rivulus* (Fig. 1); *Hoplias* acts as a factor separating the two species spatially. Such segregation of species across hazardous and safer sites is to be expected when animals choose to feed in hazardous sites when resources in the hazardous site exceed some critical threshold (Gilliam and Fraser 1987), but with those resource thresholds differing between species due to different vulnerabilities to predation (Gilliam and Fraser 1988). We would also expect such segregation if the species differ in the extent to which the predator disrupts reproduction. Sperm storage by female *Poecilia,* and nearly continuous courtship by males make it unlikely that reproductive output by *Poecilia* would be as disrupted as we found for *Rivulus.* Expected patterns of segregation between species will also depend upon how often the predator *Hoplias* moves between pools, and hence whether resource gradients are allowed to develop. Since decisions by *Hoplias* to move should depend on the behavior of the prey (e.g., the rate at which *Poecilia* and *Rivulus* immigrate into a *Hoplias*-containing pool), and vice versa, a fuller understanding of population processes in this system will require knowledge of the co-behavior of predator and prey (e.g., Iwasa 1982, Sih 1984).

While we found that invasion of pools by the predator *Hoplias* decreased reproduction by *Rivulus* on behavioral time scales, over evolutionary time scales the impact of the invasion of a predator into a previously predator-free stream might instead be selection for higher reproductive output. If we consider heightened predation threat as a stress, the impact should depend on whether the stress is sudden and short term, or long term and continuous (Underwood 1989). If the stress is short term, as in our experiments and in Ramdeen

Stream, we would expect to find spatial and temporal patchiness in reproduction, with suppression during times when the predator is near or active. Alternatively, long-term threat, such as from the permanent and ubiquitous invasion of an abundant new predator, could select for altered life history patterns (Reznick et al. 1990), with higher or lower reproductive output depending on whether increased mortality is associated with reproductive activities or nonreproductive activities (Ricklefs 1977), and might ultimately lead to stress tolerance (Calow 1989), in which reproduction is no longer facultatively suppressed by the frequent appearance of a predator. Continued phenotypic plasticity in reproductive output might be most expected in sites such as Ramdeen Stream, if a rare but effective predator is a permanent feature of the environment.

The effect of predators on growth and reproduction can reflect facultative responses to the current predatory environment, "predators now," the present study, as well as the past evolutionary effects of selection by predators, "predators past," e.g., Reznick et al. (1990). Ecologists have been concerned mainly with the influence of "predators now," usually without explicit comparison of populations with different evolutionary histories, while a standard evolutionary approach is to identify genetic differences between populations by raising individuals from both populations in a predator-free environment (Reznick et al. 1990). A problem with generalizing about the effect of predators on reproductive output from either of these types of studies is the possibility that the findings would be reversed by cross-classifying evolutionary history and current predator threat. For example, our finding of decreased reproductive output in the presence of a predator could, in principle, be reversed in studying a population with a different history of predation, e.g., if the animals facultatively increased reproductive effort upon increased likelihood of imminent death. Indeed, in a previous study of feeding behavior of Poecilia and Rivulus (Fraser and Gilliam 1987), Poecilia from high-predation sites fed faster than Poecilia from low-predation sites, when a predator stimulus was present, but the ordering was reversed or indistinguishable in the absence of a predator stimulus. Given the suggestion of an interaction between the "predator past" and the "predator present," it may be useful to consider effects of predators in the context of a reaction norm (Stearns 1989), in which current predatory threat is treated as a current environmental factor, on a par with such factors as food level or temperature, and to consider natural selection as shaping reaction norms (here, rules of behavior) rather than acting on demographic traits such as reproduction or growth rate, per se.

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