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A Laboratory Study of Predation on the Trinidadian Guppy, *Poecilia reticulata*, by Two Natural Piscine Predators: Effects of Predator Size, Prey Size, and Habitat Complexity

Hayden Thomas Mattingly
Old Dominion University

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A LABORATORY STUDY OF PREDATION ON THE TRINIDADIAN GUPPY, POECILIA RETICULATA, BY TWO NATURAL PISCINE PREDATORS: EFFECTS OF PREDATOR SIZE, PREY SIZE, AND HABITAT COMPLEXITY

by

Hayden Thomas Mattingly
B. S., Biology, May 1988, Western Kentucky University

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Approved by:

M. J. Butler, IV (Director)

R. S. Birdsong

R. W. Alden, III

ABSTRACT

A LABORATORY STUDY OF PREDATION ON THE TRINIDADIAN GUPPY, POECILIA RETICULATA, BY TWO NATURAL PISCINE PREDATORS: EFFECTS OF PREDATOR SIZE, PREY SIZE, AND HABITAT COMPLEXITY

Hayden Thomas Mattingly
Old Dominion University, 1991
Director: Dr. Mark J. Butler, IV

Test populations of different-sized guppies, *Poecilia reticulata*, were exposed to individuals of two natural predatory species, the pike cichlid *Crenicichla alta* and the killifish *Rivulus harti*, under conditions of varying prey (guppy) density and habitat complexity in the laboratory. *Rivulus* fed most frequently on newborn and juvenile guppies < 14 mm. *Crenicichla* consumed more and larger guppies than did *Rivulus*. The mean guppy size eaten by *Crenicichla* was dependent on the length of the individual predator, but as a group, the 15 *Crenicichla* tested were non-selective with respect to guppy size and gender. The prey gender preference of *Rivulus* could not be determined because they primarily ate immature guppies. High habitat complexity and a shallow water refuge reduced *Crenicichla* predation rates from 9.88 to 2.92 guppies/day, but did not change prey-size selectivity. *Rivulus* predation rates never exceeded 1.0 guppies/day, regardless of habitat complexity. Under test conditions which mimicked typical field conditions of habitat complexity and prey density, *Crenicichla* was a much more dangerous guppy predator than *Rivulus*. However, *Rivulus* could be an important predator of immature guppies in situations where guppy densities are high and *Rivulus* are abundant.

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Introduction

The relationships between predators and their prey have long attracted the interest of ecologists. In the past 25 years, extensive research efforts have focused on many facets of predator-prey interactions in aquatic communities. The classic works of Brooks and Dodson (1965), Paine (1966), Pulliam (1974), Werner and Hall (1974), and Lubchenco (1978) are examples of such efforts.

Predation has been shown to be an important force in shaping prey characteristics (see reviews by Zaret 1980; Sih et al. 1985; Havel 1987) such as morphology and physiology (Hoogland et al. 1957; Keenleyside 1979; Dodson 1984; see papers in Sih 1987 and in Crowl and Covich 1990), behavior (Peckarsky 1980; Pitcher 1986; Power 1987), and life-history traits (Reznick 1982a; Reznick and Endler 1982; Crowl and Covich 1990). Recently, the indirect effects of predation on aquatic communities, along with direct (lethal) effects, were more clearly defined and discussed in Kerfoot and Sih (1987).

Aquatic predators often select certain sizes of prey (Brooks and Dodson 1965; Werner and Hall 1974; among others). Size-selective predation functions as one of the mechanisms by which significant changes in prey populations and community compositions evolve (Galbraith 1967; Zaret 1980; O'Brien 1987). Habitat can mediate a predator's impact on prey (Werner et al. 1983; Anderson 1984; Schramm and Zale 1985; Mittelbach 1984, 1986; Gilliam and Fraser 1987; Power 1987; Schlosser 1988), and may influence the size-dependent mortality risks of prey (Mittelbach 1981). For example, the presence of predators often restricts prey to refuges that are inaccessible to predators due to water depth or habitat complexity; however, these refugia are often of reduced foraging value (e.g., Werner et al. 1983). Many researchers have shown that susceptibility to predation increases as environmental complexity decreases (e.g., Stein and Magnuson 1976; Stein 1977, 1979; Crowder and Cooper 1982; Savino and Stein 1982).

Shifts in the life-history traits of aquatic prey populations due to direct and indirect predation effects have been studied recently by Reznick and Endler (1982), and Crowl and Covich (1990), among others. Stearns (1976) listed four life-history traits he considered key to survival: brood size, size of young at birth, age distribution of reproductive effort, and the interaction of reproductive effort with adult mortality. Theoretically, size-selective predation could have a profound effect on the evolution of life histories of prey populations. For example, life-history theory (Gadgil and Bossert 1970; Law 1979; Michod 1979; Charlesworth 1980) predicts that high mortality rates for juvenile prey will result in populations that have small numbers of large offspring which reach sexual maturity at an advanced size and age. Conversely, those populations in which large adults suffer high mortality rates will tend to have greater numbers of smaller offspring that reach sexual maturity at a smaller size and age. These life-history shifts can reflect a large degree of phenotypic plasticity for certain characters (Crowl and Covich 1990), or can have a strong heritable component (Reznick and Endler 1982).

Perhaps the most compelling evidence for predator-driven evolution of prey life-history traits is based on studies of guppies (*Poecilia reticulata*) and their predators in the Northern Range Mountain streams of Trinidad, West Indies (Liley and Seghers 1975; Reznick and Endler 1982; Reznick, et al 1990).

Guppies are small livebearing fish, rarely exceeding 35 mm in standard length (SL), native to the streams of Venezuela, Guiana, Margarita, Trinidad and Tobago (Seghers 1973; Yamamoto 1975; Endler 1980). They are sexually dimorphic in color and size. Male guppies have highly polymorphic color patterns, controlled by many X- and Y-linked genes, and grow little after attaining sexual maturity at about 15 mm SL. Females are drab tan in color and grow larger than males, sometimes approaching 30 mm SL. Guppies mature in 1 to 4 months and females produce broods of two to 30 offspring every 25 to 30 days during their one- to four-year lifespan (Haskins et al. 1961; Yamamoto 1975; Reznick 1983).

In the streams draining the southern slopes of the Northern Range Mountains of Trinidad, guppy populations within the same stream are often isolated or semi-isolated by physical barriers such as waterfalls and rapids. Separated populations exhibit differences in sex ratio (Haskins et al. 1961; Seghers 1973), color pattern (Endler 1978, 1980, 1983), behavior (Seghers 1974; Farr 1975; Liley and Seghers 1975; Luyten and Liley 1985; Houde 1987, 1988a,b), and life-history traits (Reznick 1982 a,b, 1983, 1989; Reznick and Endler 1982; Reznick and Bryga 1987; Reznick et al. 1990). These patterns are generally attributed to differences in the intensity and size specificity of predation by fishes on guppies.

Assemblages of predatory fishes change along the stream gradients. Thus, guppy populations are exposed to different types and intensities of predation. In some headwater streams, the only documented piscine guppy predator is the killifish, *Rivulus* *harti* (Cyprinodontidae). Adult killifish are approximately 4-8 cm SL and an analysis of their stomach contents indicated that they feed predominantly on aquatic and terrestrial invertebrates and, less frequently, on small sizes of guppies (Seghers 1973; Liley and Seghers 1975). At downstream sites, guppies are exposed to an array of potential predators, including the following fishes: blue acaras (*Aequidens pulcher*; Cichlidae), pike cichlids (*Crenicichla alta*; Cichlidae), characins (*Astyanax bimaculatus* and *Hemibrycon dentatum*) and wolffish (*Hoplias malabaricus*; Haskins et al. 1961; Seghers 1973; Liley and Seghers 1975). These authors and others (Endler 1978; Reznick and Endler 1982) believe that the most important guppy predator at downstream sites is the pike cichlid, *Crenicichla alta*. Adult pike cichlids, typically 12-16 cm SL, are thought to prey heavily on large, sexually mature guppy size classes, but little evidence exists to support this hypothesis.

Hoplias, although generally less abundant than *Crenicichla*, has the potential to consume a considerable number of guppies. Even though no guppies were recovered from the stomachs of seven field-collected wolffish (Seghers 1973), Gilliam (pers. comm.; Zoology Dept., N.C. State Univ., Raleigh) has found that small adult *Hoplias* consume guppies in the Guanapo River. The food habits of large adult wolffish are poorly known, but they probably consume fish much larger than the guppy. Six out of the seven wolffish examined by Seghers (1973) had empty stomachs; *Crenicichla* was present in the seventh. In April 1991, I observed a wolffish in the El Cedro River that had partially swallowed a smaller conspecific. *Astyanax* and *Aequidens* most likely feed on arthropods (Zaret and Rand 1971) and, along with *Hemibrycon dentatum*, are probably occasional predators of small guppies (Liley and Seghers 1975).

Several researchers have reported traits and behavior patterns that differ between upstream and downstream guppy populations. Haskins et al. (1961) noticed that guppy populations that coexist at upstream locales with *Rivulus* have more colorful males than downstream populations. In addition, Haskins et al. (1961) and Seghers (1973) reported that most guppy populations are female-dominated (0.61 - 0.74 males per female) and that upstream populations tend to have even larger percentages of females than downstream populations. Using wild-caught stock, Haskins et al. (1961) and Seghers (1973) determined that the uneven field ratios do not persist under laboratory conditions; the first generations assumed a Mendelian-predicted 1:1 balance. Although his laboratory tests of prey-gender selection by *Rivulus* were inconsistent, Seghers (1973) states that size-selective predation by *Rivulus* could place male guppies, which have a determinate growth pattern, at a disadvantage in headstream locations. Seghers' (1973) and Liley and Seghers' (1975) diet study of *Rivulus* (n=259, collected from three streams) revealed that no guppies greater than 17 mm SL were consumed by *Rivulus*. Furthermore, his laboratory tests showed that males were less adept at avoiding capture than similar-sized females. Both of these observations could help explain the uneven field sex ratios.

By varying "background" gravel color and size in experimental tanks, accompanied with different types and intensities of predation, Endler (1978, 1980) demonstrated that male color patterns in large laboratory populations shifted fairly rapidly (in six to eight generations) to achieve a balance between predator avoidance and successful courtship display. Endler found that when predation intensity was low (*Rivulus* present), or nonexistent (no predator present), males with color patterns that optimized their contrast to the background predominated. When predation pressures were high (*Crenicichla* present), however, males were more cryptically colored and had fewer spots. Houde (1987, 1988a,b) found that females choose males on the basis of coloration, orange patterns being the most favored. Orange colors are common in males from the headwaters of the Paria River (a *Rivulus* locality), where there is presumably little predation pressure on adult guppies.

Differences in shoaling (schooling) behavior in guppies have been reported by Seghers (1973, 1974) and Liley and Seghers (1975). In downstream locations, where potential piscine guppy predators are large and numerous, guppies tend to shoal along the perimeter of stream pools, whereas upstream populations of guppies exhibit little shoaling behavior. Farr (1975) stated that guppies from upstream localities, where *Rivulus* densities were high, lack "cohesiveness" (i.e., tendency to shoal). However, Farr (1975) also concluded that guppy cohesiveness in Trinidadian streams is not necessarily a response to large predators because he observed shoaling behavior in locations where no predatory fish were present.

Luyten and Liley (1985) observed that male guppies from upstream sites, under field and laboratory conditions, exhibited more frequent sigmoid courtship displays of longer duration than males from more turbid downstream localities. These workers proposed that the upstream conditions of less-intense predation and better water clarity facilitate frequent courtship display. In contrast, Farr (1975) reported that downstream populations display more frequently than upstream guppies. Farr agreed with Seghers' (1973) conclusions that (1) *Rivulus*'s feeding strategy (e.g., hiding behind leaves and darting out to capture prey) could deter male courtship display upstream and (2) the shoaling behavior of downstream guppies provides protection from predators, permitting more frequent displays. Farr's downstream study sites all had clear water, however, suggesting that both water clarity and predation intensity may play a role in male courtship behavior.

Reznick and Endler (1982) have documented naturally occurring life-history differences between upstream and downstream guppy populations which persisted in subsequent laboratory generations. They proposed that size-selective predation, *Rivulus* on juvenile guppies and *Crenicichla* on adult guppies, is the major selective force driving the evolution of the different traits. They suggested that if *Crenicichla* preys primarily on large, sexually mature guppies, then life-history theory predicts that guppies in downstream populations should evolve to produce large, frequent broods with small offspring that reach maturity at a small size and early age. Conversely, if *Rivulus* consumes only small, immature guppies, then the upstream populations should possess life-history traits opposite those of the downstream guppies. Predation on primarily immature size classes would also have little effect on male color, which is only expressed in adults, clearing the way for sexual selection for highly-colored adult males. The life-history traits of the different guppy populations reported by Reznick and Endler (1982) and color patterns reported by Endler (1978, 1980) are consistent with these predictions from life-history theory.

It is likely that additional predators, such as other fishes or crustaceans, may contribute to guppy mortality (Seghers 1973). For example, Seghers (1973) reported that the freshwater eel *(Synbranchus marmoratus)*, which occurs at upstream and downstream sites (J. Endler, unpubl. ms.), attacked guppies in aquaria. Large invertebrates such as prawns (*Macrobrachium crenulatum*), freshwater crabs (*Pseudothelfusia garmani*), and various insect larvae (e.g., Odonata and Hemiptera) are present throughout the streams (Endler unpubl. ms.; M. Butler, pers. comm., Dept. Biological Sciences, Old Dominion Univ., Norfolk, VA) and are potential guppy predators. Snakes such as *Liemodiphis regini* (J. Endler, pers. comm., Dept. Biological Sciences, Univ. of California, Santa Barbara), amphibians, birds (e.g., kingfishers; *Chloroceryle* spp.) and fish-eating bats (*Noctilio leporinus*) may also consume guppies (Seghers 1973). The importance of these potential predators remains largely unknown.

It is also possible that some of the observed differences between populations are the result of differences in habitat or environmental gradients (e.g., water temperature and productivity) between upstream and downstream sites (Seghers 1973). Complex interactions, including predator-influenced habitat use by guppies, habitat-specific productivity, density-dependent guppy growth, and indirect interactions among piscine and invertebrate predators, could also contribute to the observed guppy life-history patterns, and are the subject of a recently completed field study by Reznick and Butler (unpubl. data). Yet, the experiments conducted by Reznick and Endler (1982), Reznick and Bryga (1987), Reznick et al. (1990), and a multivariate analysis of field data by Strauss (1990), strongly suggest that environmental effects are less important than the direct and indirect effects of predation.

Few researchers have studied, explicitly, the predator-prey relationships between *Crenicichla*, *Rivulus*, and guppies, particularly under controlled test conditions. Haskins et al. (1961) recorded mortality rates and selection for guppy gender, and Endler (1978, 1980) studied selection for color patterns. Only Seghers (1973) investigated selection for gender and size in the field and laboratory, while Seghers (1973) and Liley and Seghers

(1975) examined the stomach contents of field-caught *Rivulus* and *Crenicichla*.

Seghers (1973, 1978) and Liley and Seghers (1975) found, from examining fish stomach contents, that 10.2% of the *Rivulus* collected from three streams in Trinidad fed on small, immature guppy size classes at those locations. A positive curvilinear relationship existed between *Rivulus* size and maximum prey size consumed (Liley and Seghers 1975). Although ants were the most frequent prey item in *Rivulus* stomachs (present in 42.1% of the killifish), the frequency of occurrence of a given prey item does not necessarily reflect its overall energetic importance to the predator (Bowen 1983; see also Lagler 1956, Carlander 1977).

Seghers' (1973) results for *Crenicichla* were less conclusive and based on relatively few predators. In laboratory tests, four large (17-21 cm TL) *Crenicichla* only slightly reduced the mean guppy length of populations of various-sized test guppies. Liley and Seghers (1975) concluded that *Crenicichla* generally were not size-selective in the laboratory trials. *Crenicichla* appeared to be less efficient at handling (i.e., attempting to eat) the smaller guppy sizes, although both small and large sizes were easily seen and attacked. *Crenicichla*, in contrast to *Rivulus*, consumed both sexes with equal ease and frequency.

In the gut analysis survey (Seghers 1973), identifiable guppies were present in the stomachs of only two out of 14 *Crenicichla* individuals examined; however, unidentifiable fish occurred in six of the 14. *Crenicichla* was found not to be a strict piscivore, as originally implied in Haskins et al. (1961); snails and both larval and adult insects were often consumed by pike cichlids. Caddisfly larvae are eaten in substantial quantities by *Crenicichla* in certain localities (J. Endler, pers. comm., Dept. Biological

Sciences, Univ. of California, Santa Barbara, CA).

Introduction experiments (Reznick and Bryga 1987; Reznick et al. 1990) are currently underway in which downstream guppy populations were introduced into upstream pools above barrier waterfalls where only *Rivulus* was present. This presumably released the transplanted guppies from an environment of heavy predation to an area of less-intense predation pressure. After 11 years, or 30-60 generations, many of the life-history traits (some of which are heritable) of these transplanted populations have shifted to those characteristic of an upstream population (Reznick et al. 1990). In a separate set of predator introductions and, eventually, as a continuation of the introduction experiments, *Crenicichla* are being introduced to upstream pools to determine if the life-history traits and behavior patterns of the upstream, *Rivulus*-locality guppy populations will shift to those of a downstream population. If the shifts do occur, then this would be further evidence confirming the evolutionary importance of predation in shaping the life-history characteristics of a prey population. However, these experiments cannot distinguish between (1) size-selective predation or (2) predation intensity as mechanisms driving these population-level shifts.

Size-specific guppy mortality in Trinidadian streams is being evaluated by a series of mark-recapture field experiments (Reznick and Butler, unpubl. data). These tests, however, cannot distinguish between the potential sources of guppy mortality (i.e., among predatory species). They are also conservatively biased estimates of size-specific mortality and of the potential for selection, given the uneven size distributions of the natural guppy populations.

The goal of this thesis was to conduct a series of controlled laboratory experiments to compare the intensity and size-selectivity of predation by *Crenicichla* and *Rivulus* on guppies, and to evaluate the role of habitat complexity in mediating those effects. I offered individuals of these two predatory species different-sized Trinidadian guppies under various conditions of prey density and habitat complexity. My specific objectives were to determine: (1) if *Crenicichla* and *Rivulus* select certain sizes of guppies, (2) if the size of the predator influences which prey sizes are consumed, (3) if habitat complexity (i.e., bottom structure and depth) alters predation intensity and prey-size selectivity, (4) if *Crenicichla* and *Rivulus* display a preference for male or female guppies, and (5) if *Crenicichla* consumes more guppies than *Rivulus* under similar conditions.

A major advantage of this laboratory study was my control of prey sizes and genders and their availability to predators, which permitted specific tests of prey-size and prey-gender selectivity. Mark-recapture studies and other field experiments are limited by the unequal size distributions and sex ratios existing in nature (i.e., "the ghosts of predation past"), and by their inability to identify specific sources of guppy mortality.

Materials and Methods

I. Laboratory Conditions and Description of Experimental Fish. Most of the fish studied in this investigation were collected (by M. Butler) in Trinidad in March 1990, and then transported to Old Dominion University, Norfolk, Virginia by airplane. Additional fish were obtained (by H. Mattingly) during a subsequent trip in April 1991. All experiments were conducted in an indoor laboratory at Old Dominion University under a photoperiod of approximately 12 h light (0830 to 2030) and 12 h dark. Dawn and dusk were simulated with a series of sequentially timed lights. The minimum and maximum water temperatures in the laboratory were 19.5 and 25.5 C, but temperatures typically ranged from 22 to 24 C.

Prey species - *Poecilia reticulata*. The *Crenicichla*-site guppies were collected in the Oropuche River and the *Rivulus*-site guppies were collected from the Aripo Tributary in March 1990. Additional guppies from the Arima River, the Quare River (*Rivulus* sites), and the Mausica River (*Crenicichla* site) were also used in small numbers. These additional guppies, collected in 1989, were previously maintained in a laboratory at York University, Ontario, Canada. Hand-held nets were used to collect guppies from the streams. In the laboratory, the guppies were maintained in 38 L aquaria with sponge filters, a layer of calcium carbonate gravel, and various aquatic plants. Guppies from different streams were kept in separate aquaria whenever possible. The guppies were fed staple flake food each day and an occasional ration of brine shrimp

(*Artemia salina*) nauplii.

Predatory species - *Crenicichla alta* and *Rivulus harti*. Twelve adult *Crenicichla*, 118 to 162 mm SL, were collected from the Oropuche River, seven in March 1990 and five in April 1991. These 12 *Crenicichla* were obtained by hook-and-line methods using artificial and natural (small *Rivulus*, guppies, prawns, earthworms) lures. Three juvenile *Crenicichla* were collected with hand nets from the Mausica River in March 1990 and were held at the University of California, Riverside until June 1990. The 15 *Crenicichla* individuals were kept in separate aquaria that contained gravel and filters, and ranged in volume from 38 to 209 L. Twenty-one *Rivulus*, 41 to 92 mm SL, were collected with hand-held nets in the Aripo Tributary and the Mausica River in March 1990. The *Rivulus* were maintained in separate 8.8 L aquaria with gravel, filters, and plants. Thus, each individual fish of both predatory species was housed in its own aquarium. The *Rivulus* were fed flake food each day and were occasionally offered various sizes of domestic "feeder" guppies (also *Poecilia reticulata*); *Crenicichla* were maintained on a diet of domestic guppies. The frequency and quantity of guppies fed to the *Crenicichla* varied with the size and hunger level of each individual; however, the average pike cichlid received four domestic guppies per day.

II. Experimental Design and Protocol. I established five different guppy size classes, representing different ontogenetic stages, for the predation tests. The 6-10 mm size class represents newborn guppies, 10-14 mm represents juveniles, 14-18 mm represents young adults, 18-22 mm represents large adult males and medium-sized adult females, and >22 mm represents large adult females. Adult males rarely exceed 22 mm in the wild.

To initiate each predation experiment, the test guppies were (1) anesthetized in water containing approximately 230 mg/L tricaine methanesulfonate (MS-222), (2) measured with calipers and sorted into appropriate size classes, (3) placed into a post-anesthesia recovery tank for 1 h, and (4) introduced into the test environment which contained a single predatory fish. The time at which the guppies were added to the test tank was recorded as the beginning of the test. Preliminary observations of post-anesthesia guppy behavior suggested that 1 h provided ample recovery time to ensure a return to normal pre-anesthesia activities, such as male courtship displays and gonopodal thrusting. At the end of the testing period, the surviving guppies were remeasured to determine, by their absence, the sizes of the individuals consumed by the predator. The predator was measured soon after the completion of a test; the same concentration of MS-222 was also used to anesthetize the predators. Unless noted otherwise, all fish lengths throughout this investigation were recorded as standard lengths (in mm), which is the distance from the tip of the snout to the posterior margin of the caudal peduncle.

Small-tank Tests (Experiment 1). In Experiment 1, I examined prey-size selection by predators in their "home tanks". Eight *Crenicichla* and 18 *Rivulus* were tested twice using three size classes (6-10 mm, 10-14 mm, 14-18 mm) of domestic guppies in their home tanks (i.e., the relatively small aquaria in which they were normally maintained). The *Crenicichla* and *Rivulus* ranged in length from 101 to 155 mm (mean=127.4 mm) and from 41 to 75 mm (mean=57.4 mm), respectively. The predators were starved for approximately three days before each test.

For the *Crenicichla* tests, 15 guppies, five from each size class, were placed into each *Crenicichla* home tank at approximately 0900 h. Due to variation in the size of the home tanks, test densities ranged from approximately 0.07 to 0.39 guppies/L. After 24 h, the surviving guppies were removed and remeasured; observations were recorded as the number of guppies eaten in each size class.

For the *Rivulus* tests, six guppies, two from each size class, were placed into each *Rivulus* home tank at approximately 0900 h. This procedure yielded a density of 0.68 guppies/L in each tank. Again, the surviving guppies were removed and remeasured after 24 h and the number of guppies eaten by *Rivulus* in each size class was recorded.

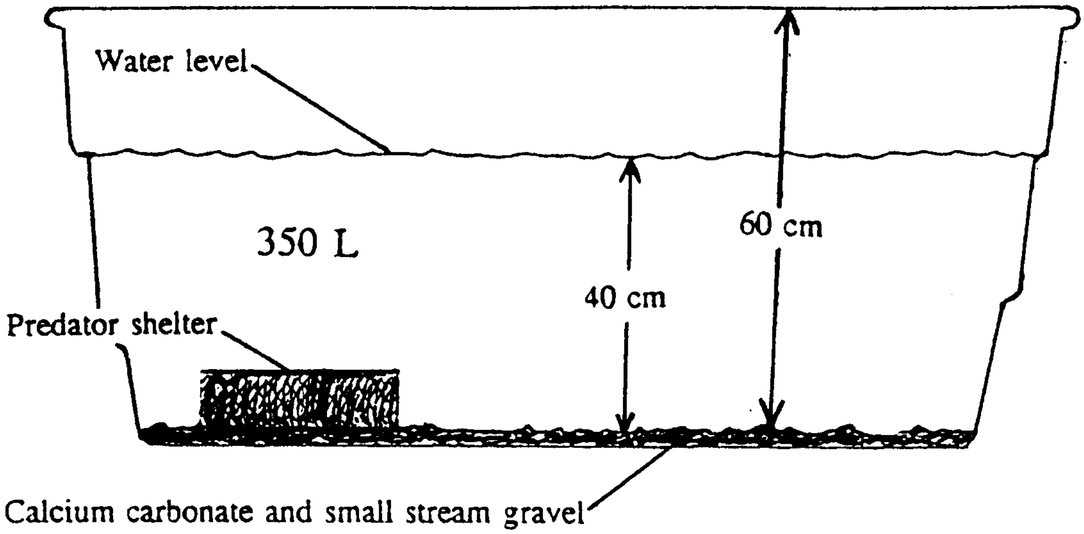
The data from Experiment 1 were analyzed using two techniques. Chi-square tests of independence, as used in a similar situation by Morin (1983), were conducted to determine if predatory species and prey-size selection were independent (i.e., that the predators consumed equal numbers of guppies from each of the three size classes, and therefore showed no size selectivity). If more than one analysis was conducted per experiment (e.g., separate trials within an experiment), the experiment-wise error rates were adjusted accordingly. A one-factor repeated measures MANOVA was employed to determine whether the number of guppies eaten in each size class differed between the two predatory species. The independent variable was the predatory species (*Rivulus* or *Crenicichla*) and the dependent variables were measured as mortalities in the three size classes of guppies. The analysis was a "repeated measures" design because two trials were conducted using the same individual predators in each trial for both species.

Large-tank Tests (Experiment 2). The prey-size selectivity of *Crenicichla* and *Rivulus* was further investigated using 570-L gray plastic cattle troughs set up to resemble small, first-order stream pools. Side-mounted filter pumps created a slight circulating current (approximately 2 cm/s) in each of the three "stream pool" tanks, which were filled to a volume of approximately 350 L. In May 1990, all three tanks had a bottom layer of calcium carbonate gravel and small stream gravel (<50 mm in diameter), which provided the test conditions for the unstructured stream pool predation tests (Fig. 1a). To satisfy the structured-habitat aspect of the experimental design, shallow (2-10 cm deep) "stream edge" refugia with sand, gravel, and cobbles were established in two of the three tanks in February 1991 (Fig. 1b). The third tank was kept in the unstructured condition for the duration of Experiment 2. White PVC plastic pipe (diameter=7.6 cm, approx. length=25 cm for *Crenicichla*; diameter=2.5 cm, approx. length=10 cm for *Rivulus*) and two or three flat stream rocks were used as predator shelters in the structured and unstructured tanks. To prevent *Rivulus* from jumping out of the test tanks, lids were constructed with plastic mesh window screen stretched across wooden frames. Lids were not needed during tests with *Crenicichla*. The light levels in the *Rivulus* tanks may have been slightly reduced by the presence of the mesh screening, but this difference was not detectable with a hand-held GE light meter.

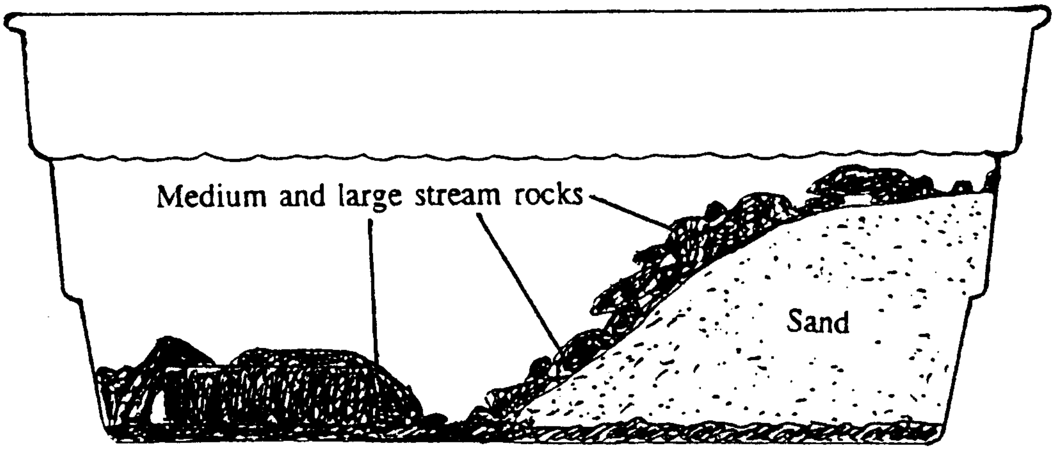
To standardize predator hunger levels in Experiment 2, an acclimation procedure was used before each test. First, the predator and 15 to 20 domestic guppies were placed into the test tank. As soon as the predator began feeding, it was given an additional 24 h to feed before all remaining domestic guppies were removed and the predator began a 24-h fast. The actual test began when the guppy test population was added to the tank following the 24-h predator fast. This acclimation procedure worked well for *Crenicichla*, but many times *Rivulus* did not consume any of the "acclimation" guppies, even after two to three weeks of acclimation. When this happened, the tests were conducted as if the *Rivulus* had eaten during the acclimation period (i.e., the guppy test

Figure 1. Diagram of the two tank treatments, (a) unstructured tank and (b) structured tank, used to evaluate the effects of habitat differences on guppy mortality when exposed to two species of predator in Experiment 2. Test tanks were: 60 cm total depth; 40 cm water depth; 90 cm wide; and 140 cm long. The 570 L (150 gallon) tanks were filled to a volume of approximately 350 L during the tests.

(a) Unstructured Tank



(b) Structured tank



population was introduced to the test tank 24 h after the removal of the acclimation guppies). Only a few *Rivulus* consumed guppies during Experiment 2.

Crenicichla alta tests - All 15 *Crenicichla* were tested in the unstructured stream pool treatment and eight of those 15 were also tested in the structured treatment. The order of treatment was haphazard and second treatments followed the first treatments as soon as possible. In addition, three *Crenicichla* were tested twice in the unstructured treatment to determine if predation rates and size selectivity changed with age. In summary, 18 unstructured and eight structured tests were carried out with the 15 *Crenicichla* available.

Each test population consisted of 48 native *Crenicichla*-site guppies, 12 in each of four size classes (10-14 mm, 14-18 mm, 18-22 mm, and >22 mm), which yielded a prey density of approximately 0.14 guppies/L. In most tests, a proportion of each test population, especially in the smaller size classes, was laboratory-bred from native stock. The 6-10 mm guppy size class was incompatible with the >22 mm class because large female guppies tended to cannibalize newborn guppies, that is, I could not be certain of the source of mortality (predator or large female guppy?) in the 6-10 mm class if large female guppies were present. Therefore, *Crenicichla* tests excluded 6-10 mm guppies and *Rivulus* tests excluded >22 mm guppies (which exceeded *Rivulus*' gape) due the incompatibility of these two size classes. The tests proceeded until either (1) the guppy test population had suffered approximately 15% mortality or (2) four days had elapsed, at which point the test was terminated regardless of prey mortality.

Rivulus harti tests - Nine *Rivulus* which fed well on guppies in Experiment 1 were tested in the unstructured tanks and eight of these nine were also tested in the structured tanks. Thus, each habitat-effects treatment had eight replicates. Two of the eight *Rivulus* were tested twice in the unstructured treatment to assess individual variability; a random number chart was used to determine which test, for each of the two retested *Rivulus*, would be included in the habitat-effects analysis. In addition, an unstructured test with four *Rivulus* in the same test tank was conducted to determine how the presence of more than one predator would affect predation intensity and size selectivity.

Most guppy test populations consisted of 40 Trinidadian *Rivulus*-site guppies, ten in each of four size classes (6-10 mm, 10-14 mm, 14-18 mm, and 18-22 mm), which yielded a prey density of approximately 0.11 guppies/L. For four tests (Appendix 2b), however, domestic guppies were used in place of Trinidadian guppies when the laboratory stocks of *Rivulus*-site guppies were deficient in a needed size class. All *Rivulus* tests were allowed to proceed until at least 96 h had passed; the longest test ran for six days. Prey mortality level was not a criterion for ending a test because no single *Rivulus* ate more than three guppies during any of the tests in Experiment 2.

Control tests - A total of three control tests, two with Aripo Tributary (*Rivulus* site) guppies and one with Oropuche River (*Crenicichla* site) guppies, were conducted during September 1990 in the unstructured tanks. The control populations consisted of 48 guppies, 12 in each of four size classes (10-14 mm, 14-18 mm, 18-22 mm, and >22 mm); no predators were present in the tanks. The control tests were each run for 96 h to determine if guppy test populations could potentially suffer mortalities not due to predation.

In the *Crenicichla*, *Rivulus*, and control tests of Experiment 2, the guppy test populations were counted by non-intrusive visual censuses every 24 h and fed a small amount of finely-crumbled staple flake food. It is possible that *Rivulus* was able to consume some portion of the daily flake-food ration during the tests.

The data from Experiment 2 were analyzed in three ways. As in Experiment 1, Chi-square tests of independence were used to determine if prey-size selection had occurred within a given predatory species. One-factor MANOVAs evaluated the effects of the habitat treatments (structured versus unstructured tanks) on the size selectivity of each predatory species, using habitat type as the independent variable and the four size classes as dependent variables. Finally, two-sample and paired t-tests were employed in a number of situations, for example, to analyze for differences in predation intensity within and between predatory species.

Results

Size selectivity. In the small-tank tests of Experiment 1, where 6-10 mm, 10-14 mm, and 14-18 mm guppies were added to the predators' home tanks, *Crenicichla* exhibited significant size selectivity in the first trial ($X^2=9.51$, df=2, $P<0.025$), but not in the second trial ($X^2=0.63$, df=2, $P>0.025$; Table 1). *Rivulus* displayed significant selectivity in both the first ($X^2=7.54$, df=2, $P<0.025$) and the second trial ($X^2=10.39$, df=2, $P<0.025$). Seven out of eight *Crenicichla* consumed guppies in the largest size class, 14-18 mm, whereas only one-third (six out of 18) of the *Rivulus* ate mature guppies. Although *Crenicichla* and *Rivulus* tended to prey upon larger- and smaller-sized guppies, respectively (Fig. 2), there was no overall difference between the size selectivities of the two species in Experiment 1 (Wilks' lambda=0.387; df=3,5; F=2.64; P=0.16). Table 1 summarizes the Chi-square tests of independence and the raw data are presented in Appendix 1.

In the large-tank tests of Experiment 2, where four size classes of guppies were exposed to solitary predators in artificial stream pools, *Crenicichla* showed no significant selectivity among guppy size classes in unstructured tanks ($X^2=0.16$, df=3, $P>0.05$; Table 1). Small guppies 10-14 mm were eaten just as frequently as large guppies >22 mm (Table 2). The presence of structure in the test environment did not change *Crenicichla*'s lack of prey-size selection ($X^2=2.49$, df=3, $P>0.05$).

Rivulus consumed relatively few guppies in the large tanks; nonetheless, significant

Table 1. Chi-square tests of independence to determine significant prey-category selection in Experiments 1 and 2. The deviations from equal selection of available size and gender classes are shown along with appropriate X^2 statistics. $P<.01$ is indicated by **, $P<.05$ is indicated by *, and NS indicates no significant deviation from equal selection ($P>.05$). When multiple analyses were conducted on the same experiment, the experiment-wise ereor rates were adjusted accordingly. (i) Differential selection of guppy size classes by *Crenicichla alta* and *Rivulus harti* in small (Experiment 1) and large (Experiment 2) tanks. The letters A, B, C, D, and E represent size classes of 6-10 mm, 10-14 mm, 14-18 mm, 18-22 mm, and >22 mm, respectively. (ii) Differential selection of guppy gender in Experiment 2 by *Crenicichla* based on the numbers of males and females eaten in the 14-22 mm (C & D) size range.

Test Situation	Prey Size/Gender Classes	No. Prey Eaten Per Class	n	X^2	df	P
(i) Prey-Size Selection						
Exp. 1; *Crenicichla*; Trial 1	A:B:C	7:21:24	8	9.51	2	*
Exp. 1; *Crenicichla*; Trial 2	A:B:C	12:13:16	8	0.63	2	NS
Exp. 1; *Crenicichla*; Sum of Trials 1 and 2	A:B:C	19:34:40	8	7.55	2	*
Exp. 1; *Rivulus*; Trial 1	A:B:C	20:13:6	18	7.54	2	*
Exp. 1; *Rivulus*; Trial 2	A:B:C	25:15:7	18	10.39	2	*
Exp. 1; *Rivulus*; Sum of Trials 1 and 2	A:B:C	45:28:13	18	17.88	2	**
Exp. 2; *Crenicichla*; No Structure	B:C:D:E	32:34:35:33	15	0.16	3	NS
Exp. 2; *Crenicichla*; No Structure; tests conducted Jul-Sep 1990	B:C:D:E	16:15:15:22	10	2.13	3	NS
Exp. 2; *Crenicichla*; No Structure; tests conducted May 1991	B:C:D:E	16:19:20:11	5	2.97	3	NS
Exp. 2; *Crenicichla*; Structure	B:C:D:E	9:10:16:13	8	2.49	3	NS
Exp. 2; *Rivulus*; No Structure	A:B:C:D	7:0:0:0	8	21.00	3	**
Exp. 2; *Rivulus*; Structure	A:B:C:D	1:0:0:0	8	2.96	3	NS
(ii) Prey-Gender Selection						
Exp. 2; *Crenicichla*; No Structure	M:F(C&D)	33:36	15	0.13	1	NS
Exp. 2; *Crenicichla*; Structure	M:F(C&D)	13:13	8	0.00	1	NS

Figure 2. The size selectivities of *Crenicichla alta* and *Rivulus harti* in small-tank tests averaged over two trials in Experiment 1. The histograms represent the mean percentage of guppies consumed by the predators in each size class; error bars are ± one standard error of the mean. For *Rivulus*, 18 individuals were each offered a total of six guppies, two in each of the size classes 6-10 mm, 10-14 mm, and 14-18 mm. For *Crenicichla*, eight individuals were each offered 15 guppies, five in each of the size classes 6-10 mm, 10-14 mm, and 14-18 mm.

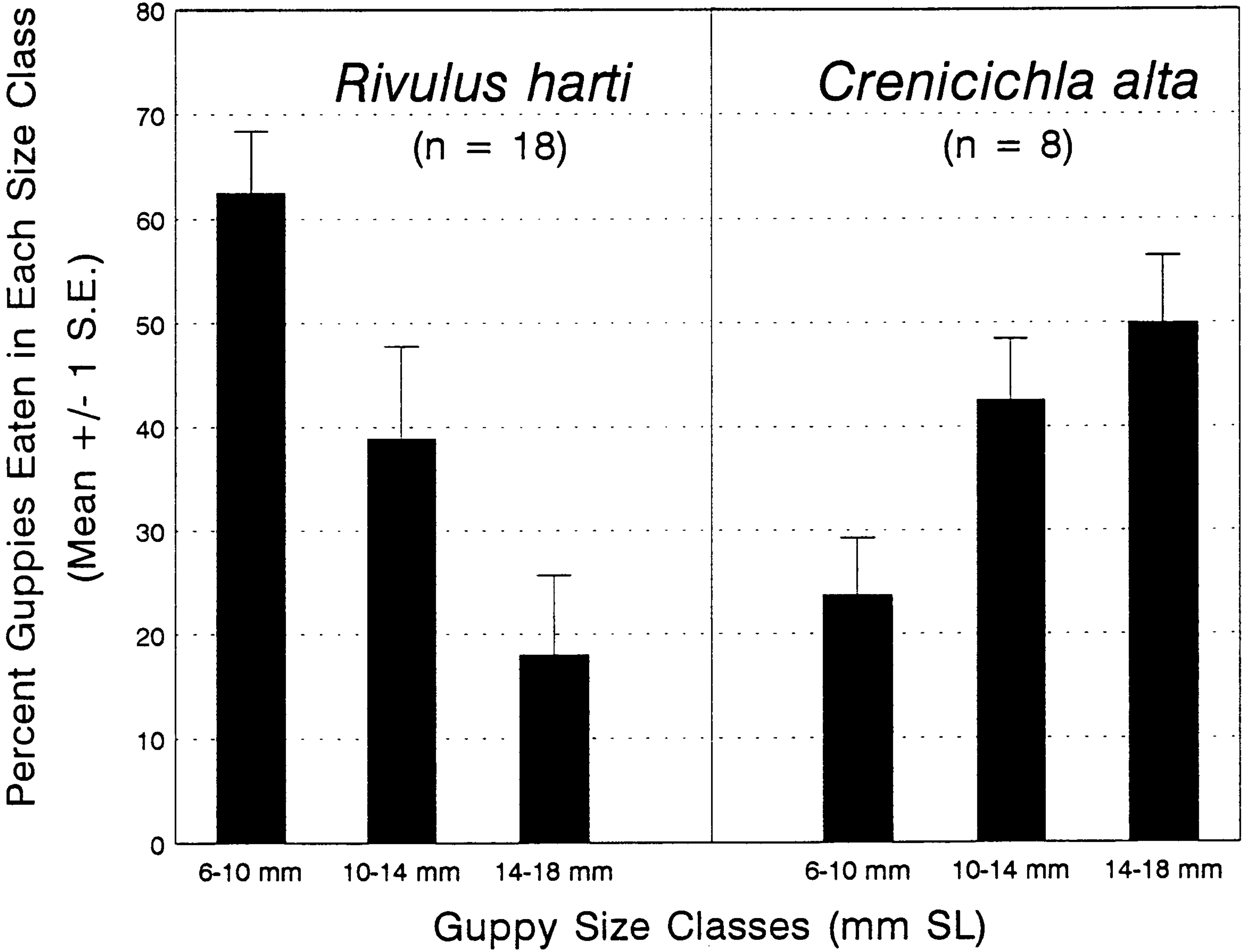

Rivulus harti
(n = 18)
Crenicichla alta
(n = 8)
Percent Guppies Eaten in Each Size Class
(Mean +/- 1 S.E.)
80
70
60
50
40
30
20
10
0
6-10 mm
10-14 mm
14-18 mm
6-10 mm
10-14 mm
14-18 mm
Guppy Size Classes (mm SL)

Table 2. Experiment 2: Prey (guppy) selection by *Crenicichla alta* and *Rivulus harti* in large-tank (350 L) tests with two levels of habitat complexity (structure and no structure). Values are means ± one standard error.

Test Habitat	n	Predator length (range mm)	Test Duration (h)	Number of Guppies Eaten	Number of Guppies Eaten/24 h	Prey Size (mm) Consumed	Number of Guppies Eaten in Each Size (mm) Class				
							6-10	10-14	14-18	18-22	> 22
Crenicichla alta											
Structured	8	118-162	77.9 ± 12.1	6.0 ± 1.6	2.9 ± 1.2	20.4 ± 0.9	N/A	1.1 ± 0.7	1.3 ± 0.5	2.0 ± 0.4	1.6 ± 0.5
Unstructured	8	118-162	41.9 ± 9.2	11.9 ± 1.5	9.9 ± 2.6	18.9 ± 0.8	N/A	2.9 ± 0.7	3.3 ± 0.8	3.6 ± 0.7	2.1 ± 0.6
Rivulus harti											
Structured	8	53-92	116.1 ± 3.0	0.1 ± 0.1	< 0.1	1.2 ± 1.2	0.1 ± 0.1	0	0	0	N/A
Unstructured	8	53-92	122.6 ± 3.2	0.9 ± 0.5	0.2 ± 0.1	3.3 ± 1.6	0.9 ± 0.5	0	0	0	N/A

size selection was demonstrated by the killifish in the unstructured tanks (X^2=21.00, df=3, P<0.01). Just as in Experiment 1, newborn guppies (6-10 mm) were consumed in the greatest numbers. In fact, the largest guppy eaten by *Rivulus* in the large-tank tests was a 12.1 mm juvenile consumed by a 92 mm female killifish. *Rivulus* predation rates were also low in the structured tanks, where only one guppy was consumed. Therefore, no prey-size selection was observed for *Rivulus* in the structured tests of Experiment 2 (X^2=2.96, df=3, P>0.05).

In addition, the data from Experiments 1 and 2 were regrouped into two classes of prey, immature (<14 mm) versus mature (>14 mm) guppies, and Chi-square tests of independence were conducted to further evaluate prey-size selection by *Crenicichla* and *Rivulus* (Appendix 2). The results of these analyses were similar to those conducted with the guppies grouped in the original "ontogenetic" classes (i.e., 6-10 mm, 10-14 mm, 14-18 mm, 18-22 mm, and >22 mm). *Crenicichla* showed a tendency to consume more adult than immature guppies in the small tanks (Experiment 1), but was not selective in any of the large tank tests (Experiment 2). *Rivulus* consistently consumed more immature than mature guppies in both experimental situations.

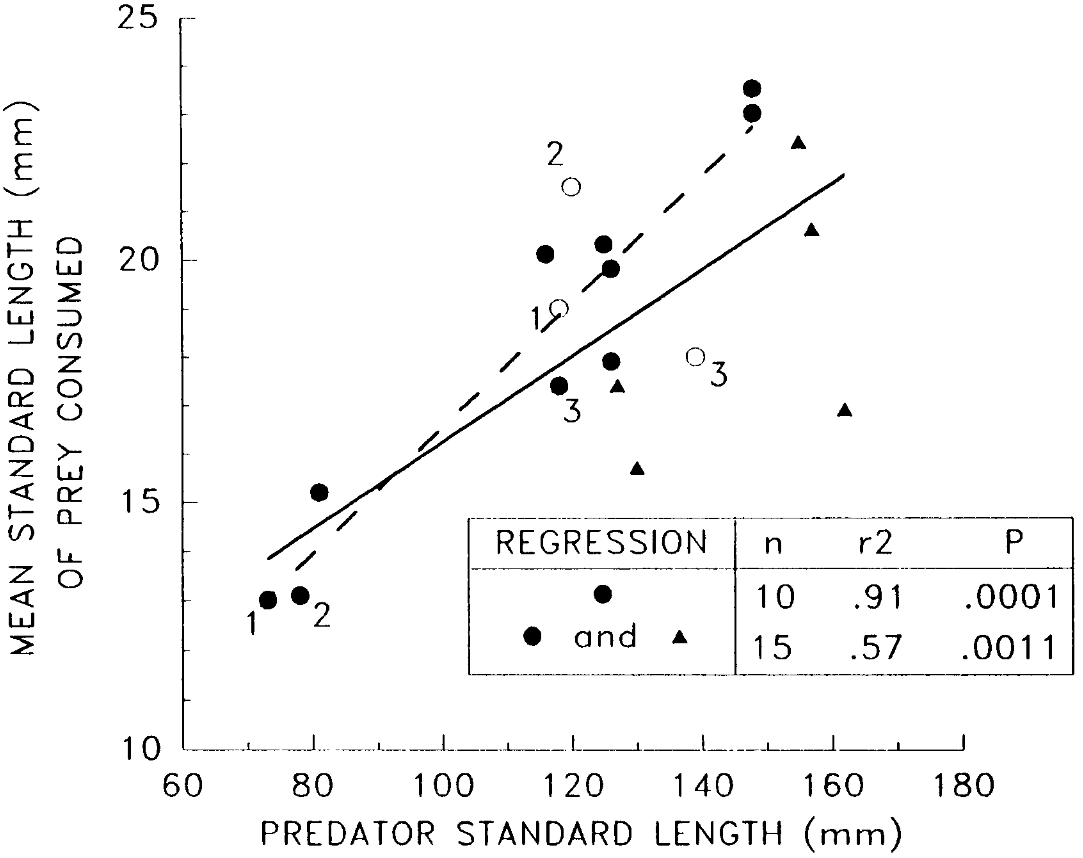
There was a high guppy survival rate (99.3%) in the three Experiment 2 control tests (no predator in the test tank); only one guppy, in the 10-14 mm size class, out of 144 did not survive. Therefore, it is unlikely that more than 1% of the mortalities recorded in Experiment 2 tests with *Crenicichla* were attributable to causes other than predation.

Predation intensity and effects of habitat complexity. The presence of structure in the large tanks (Experiment 2) did not significantly alter the prey-size selectivity for either *Crenicichla* (Wilks' lambda=0.524; df=4,11; F=2.49; P=0.10) or *Rivulus* (Wilks' lambda=0.859; df=1,14; F=2.29; P=0.15). For *Crenicichla*, the mean prey size consumed in the unstructured tanks, 18.9 mm, was not significantly different from the mean eaten in the structured tanks, 20.4 mm (t=1.49; df=7; P>.05).

However, the difference between the predation intensities of *Crenicichla*, expressed as the number of guppies eaten per 24 h, in the structured versus unstructured treatments was significant (t=3.31, df=7, P<0.05); guppies were more vulnerable to predation in the absence of structure. In the unstructured tanks, *Crenicichla* consumed a mean of 9.88 guppies/day compared to a mean of 2.92 guppies/day in the structured tanks (Table 2). The difference in predation intensity between the structured versus unstructured treatments was not significant for *Rivulus* (t=1.39, df=7, P>0.05; Table 2). The predation intensity of *Rivulus* never exceeded 1.0 guppies/day. In the single unstructured test with four *Rivulus* in the same tank, the killifish consumed four small guppies in five test days for a predation intensity of 0.81 guppies/day. Appendix 3 contains summaries of the large-tank predation tests (Experiment 2) for each individual *Crenicichla* (3a) and *Rivulus* (3b).

Predator length effects. For *Crenicichla*, the length of the individual predator had a significant effect on which prey sizes were consumed, yet this effect was somewhat confounded by the predatory behavior of the five *Crenicichla* collected in April 1991 and tested predominantly during May 1991. A significant regression (r^2=0.91; P= 0.0001) exists for the ten *Crenicichla* collected in March 1990 and tested in the unstructured large tanks during July-September 1990 (Fig. 3); however, when the five *Crenicichla* tested in May 1991 were added to the analysis, the r^2 dropped to 0.57 (P=0.0011). The three

Figure 3. Regression analyses for *Crenicichla alta* in unstructured tanks (Experiment 2) relating *Crenicichla* length to the mean length of prey consumed. The solid circles represent the ten *Crenicichla* collected in March 1990 and tested during July-September 1990. The regression equation for the solid circles (dashed line) is: $y = 0.13x + 3.36$. The three open circles represent three *Crenicichla* that were retested at a later date; they are numbered by individual (1,2, and 3). The open circles were not included in the regression analyses. The second regression includes the ten fish initially tested (solid circles), plus an additional five *Crenicichla* (solid triangles) that were collected in April 1991 and tested in May 1991. The solid line represents this second regression: $y = 0.09x + 7.38$.



MEAN STANDARD LENGTH (mm)
OF PREY CONSUMED
PREDATOR STANDARD LENGTH (mm)
10
15
20
25
60
80
100
120
140
160
180
1
2
1
2
3
3
REGRESSION
n
r2
P
●
10
.91
.0001
● and ▲
15
.57
.0011

Crenicichla that were retested in the unstructured tanks showed predictable changes in their prey-size selectivities. The three *Crenicichla* were initially 73, 78, and 118 mm in length and consumed mean prey sizes of 13.0, 13.1, and 17.4 mm SL, respectively. Their prey-size preferences shifted to guppies with mean sizes of 19.0, 21.5, and 18.0 mm SL when the predators had grown to respective lengths of 118, 120, and 139 mm (Fig. 3). The results of the regression analyses, along with the retests of the same individuals, confirm that prey-size selection by *Crenicichla* is significantly dependent on the length of the individual predator.

It was difficult to draw conclusions regarding the relationship between *Rivulus* length and mean prey size consumed because (1) only four of the killifish ate guppies in the large-tank tests of Experiment 2, and (2) none of the guppies eaten exceeded 12.1 mm. In Experiment 1, however, six of the ten largest *Rivulus* consumed mature guppies in the 14-18 mm size class. The smallest *Rivulus* that ate mature guppies was 58 mm (Appendix 1); the mean (n=18) killifish length for Experiment 1 was 57.4 mm. Therefore, only large killifish consumed adult guppies, and this was only possible in the small tanks (prey density = 0.68 guppies/L; Experiment 1). The same *Rivulus* that ate adult guppies in the small tanks did not do so in the large tanks (Experiment 2).

Selection for guppy gender. There was no evidence that either predatory species selectively fed on male or female guppies. In Experiment 2, where sex ratios were equal in two (14-18 and 18-22 mm) of the four size classes, *Crenicichla* consumed equal numbers of males and females in both the structured (X^2=0.00, df=1, P>0.05) and the unstructured tanks (X^2= 0.13, df=1, P>0.05; Appendix 4). Because *Rivulus* did not consume sexually mature guppies (i.e., greater than 14 mm) in Experiment 2, the prey-gender preference of the killifish could not be determined.

Discussion

Prey-Size Selection and Predation Intensity.

The results of this investigation indicate that *Rivulus* consistently select small, immature guppies when feeding, whereas *Crenicichla* appear non-selective with respect to guppy size or gender. These findings are consistent with the results of previous studies for *Rivulus* (Seghers 1973, Liley and Seghers 1975), but do not support the assumption made in other studies, for example Reznick and Endler (1982), that *Crenicichla* preys predominantly on large mature guppies. The impact of these two predators on guppy populations in the wild should be re-examined, particularly with respect to predation by *Crenicichla*.

Prey-size selectivity by *Crenicichla* in this investigation was more variable than that for *Rivulus* and was dependent on several factors. Although *Crenicichla* displayed significant size selection in one of the two small-tank trials, consuming fewer 6-10 mm than 10-18 mm guppies (Table 1; Appendix 1), *Crenicichla*, in general, displayed no significant selection for guppies of a particular size. However, the length of the pike cichlid had a significant influence on which prey sizes were consumed (Fig. 3). Small, juvenile pike cichlids consumed small guppies. Although adult *Crenicichla* often ate larger guppies, the selectivity of adults was variable (Fig. 3). Wootton (1990) summarizes studies which have described ontogenetic shifts in the diets of fishes and states that most ontogenetic changes are associated with morphological developments such as increased mouth size and increased locomotory ability. Therefore, any evaluation of the impact of *Crenicichla* predation on natural guppy populations requires information including the numbers and lengths of pike cichlids present in the streams.

Two of the most important factors that are likely to affect size-selective predation by *Rivulus* on guppies are their locomotory ability and gape size. Although I did not quantify locomotory differences between the two predatory species, my laboratory and field observations suggest that *Rivulus* cannot move at the same velocity as *Crenicichla* for distances greater than about 10 cm. *Rivulus* capture prey by hiding motionless, often under rocks or leaves, and then dart out to attack over a short distance. This scenario is sometimes followed by a slower, continuous pursuit. *Crenicichla* can dash at a rapid velocity, sometimes several meters, to attack prey.

Large *Rivulus* (>58 mm SL) can consume small (14-20 mm) adult guppies, given the results of Experiment 1 and the findings of Seghers' (1978) stomach content analysis, but large female guppies >20 mm SL probably exceed the gape limits of most *Rivulus*, and are therefore unlikely prey at upstream sites. I measured the gape and body dimensions of one *Rivulus* and several guppies to cursorily examine the gape limits of the killifish. The maximum vertical and horizontal mouth gape dimensions of a single, large *Rivulus* (67 mm SL) were 8.1 mm and 6.7 mm, respectively. However, the body depth and width measurements of a large female guppy (30 mm SL) were 8.4 mm and 6.6 mm, respectively. It would be physically impossible for this killifish to consume the 30 mm guppy. Yet, a 16-mm male guppy (body depth of 4.3 mm and width of 2.5 mm), and a 18-mm female guppy (body depth of 5.0 mm and width of 3.6 mm) could be easily by eaten by a killifish >60 mm SL. Thus, gape limitation presumably constrains *Rivulus* predation to smaller guppy size classes, although uncommonly large *Rivulus* may be capable of consuming larger guppies. If a predictable relationship exists between *Rivulus* length and maximum consumable prey size, then field censuses of *Rivulus* lengths and densities at specific locales could be used to help evaluate the potential impact of *Rivulus* predation on their coexisting guppy populations.

An important result of this study (Experiment 2), and one confirmed by Reznick and Butler (unpubl. data), is that guppies exposed to *Crenicichla* predation suffered much higher mortality rates than those exposed to *Rivulus*. Reznick and Butler (unpubl. data) determined, in a mark-recapture study of size-specific patterns of guppy mortality in several Trinidadian streams, that significant selection for size is not occurring at *Crenicichla* localities. They also found that mortality rates for juvenile guppies < 12 mm at *Crenicichla* sites are higher than those for juveniles at upstream *Rivulus* sites. Furthermore, at downstream sites, newborn, juvenile, and adult guppies all experience higher mortality, presumably due to predation, than do upstream guppies. Their findings are consistent with the results of this laboratory study.

Therefore, according to life-history theory, size-selective predation could be at least partially responsible for shaping the characteristics of the upstream (*Rivulus* localities) guppy populations, because the mortality rates of juvenile guppies exceed those of adults at these sites. But size-selective predation cannot adequately explain the life-history traits of the downstream (*Crenicichla* localities) guppy populations, because adult predation mortality rates there do not exceed those of juveniles. It is possible that the distinct differences in overall guppy mortality rates between the upstream and downstream environments, in addition to differences in mortality risk for adults, could be more important than prey-size selection in shaping guppy life histories and behavior. Further development of life-history theory is needed regarding the predictable effects of high predation intensity, without commensurate changes in size-specific mortality, on the life-history traits of prey populations.

The difference in predation rates by *Rivulus* in the small- versus large-tank experiments of this study is presumably related to prey density and encounter rates. In the small tanks of Experiment 1 with prey densities of 0.68 guppies/L, *Rivulus* consumed many guppies, including guppies in size classes larger than 6-10 mm (Fig. 2; also Appendix 1). One-third of the killifish were able to eat adult (14-18 mm) guppies under those conditions. Yet, when prey densities were 0.11 guppies/L in the large tanks in Experiment 2, *Rivulus* was simply not an effective guppy predator. Predation rates under these conditions were low, never exceeding 1.0 guppies/day. Thus, *Rivulus* is probably not a serious predator of adult guppies in many situations in the wild, unless *Rivulus* and guppy densities are unusually high, as in the situation studied by Seghers (1978) in the Petite Curucaye River.

Seghers (1973, 1978) and Liley and Seghers (1975) found that 10.2% of the killifish they collected (n=259) from the Petite Curucaye River, Blue Basin, and a tributary of the Tompire River had guppies in their stomachs. Although most of the guppies eaten by *Rivulus* in their study were small, a positive relationship between *Rivulus* length and the lengths of guppies eaten was evident; large *Rivulus* consumed larger guppies (up to 16.8 mm SL) than their smaller conspecifics (Liley and Seghers 1975). Using guppy densities per m^2 and maximum pool depths reported by Seghers (1978), I calculated the mean guppy density in Seghers' study area of the Petite Curucaye

River to be 1.82 guppies/L. This is substantially higher than the mean densities measured in the upstream pools of Reznick and Butler's (unpubl. data) study (i.e., 0.19 - 0.15 guppies/L), and also higher than those densities employed in my laboratory study (0.68 guppies/L and 0.11 guppies/L in Experiments 1 and 2, respectively).

In the field, *Rivulus* densities can be as high as 16 fish/m^2 (approximately 0.8 *Rivulus*/L; Seghers 1978). The effectiveness of *Rivulus* as a guppy predator could be strongly dependent on predator densities, as well as prey densities. Previous predation experiments with *Rivulus* were conducted with more than one killifish per test tank (Haskins et al. 1961; Seghers 1973; Endler 1980). These authors justified the use of multiple *Rivulus* by noting that field densities of *Rivulus* are usually higher than *Crenicichla* densities. I did conduct one test with four killifish in a large tank (Appendix 3) and observed a higher predation intensity (0.81 guppies consumed/d) than in tests with only a single killifish (mean=0.17 guppies consumed/d). Seghers (1973) observed several guppy pursuits in the wild involving multiple *Rivulus*, and suggested that some killifish may forage in groups. If so, my laboratory trials in the large tanks may have underestimated the effect of *Rivulus* predation rates. Thus, predation rates by *Rivulus* in the field may depend on prey density (both guppies and alternative prey) and *Rivulus* density. More comprehensive field estimates of these densities are needed to evaluate the impact of *Rivulus* predation on guppies in nature.

Predation-Habitat Relationships.

The indirect effects of predation could be as important as direct predation effects in determining the patterns of guppy habitat use and, therefore, growth, mortality, and ultimately life history. For example, Power's (1987) work with tropical stream fishes, and similar studies in temperate systems (e.g., Gilliam and Fraser 1987; Schlosser 1988), indicate that prey distributions in stream pools are often determined by predation risk. Werner and Gilliam (1984) predict that prey will locate in areas where the ratio of mortality/growth is minimized. Thus, when dangerous predators are common, prey fishes should utilize stream habitats that offer protection, even though resource availability may be lower there. In this way, risk of predation can indirectly influence prey growth, fecundity, and mortality, and over time may potentially alter prey life-history characteristics.

Based on estimates of periphyton (a major food resource for guppies) productivity and determinations of site-(*Rivulus* versus *Crenicichla*) and habitat-specific (stream edge versus middle) predation risk, a conceptual model can be built and predictions made (Table 3) regarding the habitat use of guppies in streams. In Trinidad, periphyton productivity and guppy growth are lower in upstream locations than at downstream locations; however, productivity (and presumably growth) do not differ between edge and midstream pool habitats at either location (Reznick and Butler unpubl. data). The risk of predation for guppies is higher downstream (*Crenicichla* locales) and lower upstream (*Rivulus* locales; Reznick and Butler unpubl. data; this study); furthermore, my laboratory data suggest that predation rates at *Crenicichla* localities should be lower in the shallow stream edge habitat (Table 3). Thus, one can rank each locality with respect to the potential for guppy growth and mortality and, using the "minimize mortality/growth" criterion developed by Werner and Gilliam (1984), derive predictions describing guppy habitat-use patterns in the field (Table 3). At upstream *Rivulus* localities, guppies should be equally distributed between the edge and midstream habitats.

Table 3. Conceptual model and predictions of guppy habitat-use patterns at upstream (*Rivulus* localities) and downstream (*Crenicichla* localities) sites. Mortality and periphyton productivity (i.e., potential for guppy growth) are ranked (low to high; from 1 to n) across habitats and locales. The mortality/growth (M/G) ratios (*sensu* Werner and Gilliam 1984) for each habitat yield the habitat-use predictions; preferred habitats have lower M/G ratios.

	Habitat			
	Upstream		**Downstream**	
Variables	**Edge**	**Midstream**	**Edge**	**Midstream**
Mortality (M)	1	1	2	3
Productivity (Potential Growth; G)	1	1	2	2
M/G	1	1	1	1.5
Predicted Habitat Use:	Edge = Midstream		Edge > Midstream	

At downstream *Crenicichla* localities, guppies should utilize the stream edge more often than the midstream to minimize mortality.

The distribution of guppies among habitats in the field is consistent with these predictions. Several researchers (Farr 1975, Butler and Reznick, unpubl. data) have noted that guppies in upstream *Rivulus* locations utilize nearly all areas of their stream pools, yet downstream (*Crenicichla* localities) guppies tend to avoid the deep sections where predation risks are presumably higher. Seghers (1973, 1974) also noted that guppies from downstream populations tend to form shoals along the shallow edges of pools, whereas guppies from upstream populations show no shoaling behavior. Butler and Reznick (unpubl. data) have quantified this difference in habitat utilization, and found that the mean guppy density along the edge of a typical downstream pool was 0.49 guppies/L, seven times the mean density in deeper, midstream habitats (0.07 guppies/L). At *Rivulus* upstream localities, the mean guppy densities along the edge and in the middle of a typical pool were nearly identical at 0.19 and 0.15 guppies/L, respectively.

Although the distribution of guppies among habitats in the field match the model predictions, the model and results are general and do not include important detail like size-specific prey habitat use and potential density-dependent predator and prey effects. In laboratory experiments, increased habitat complexity and a shallow water refuge resulted in no significant change in size-specific mortality for guppies exposed to *Crenicichla* or *Rivulus*. I expected *Crenicichla* to eat fewer juvenile (10-14 mm) guppies in the structured tanks, given (1) the availability of a shallow water refuge where prey capture rates are presumably lower, and (2) field observations (M. Butler, pers. comm.) that small guppies utilize shallow habitats more often than large guppies. All eight

Crenicichla in the unstructured tanks ate 10-14 mm guppies, whereas only three out of those eight consumed 10-14 mm guppies in the structured tanks (Appendix 3). Overall predation rates on 10-14 mm guppies did not differ significantly between habitat treatments, although the result borders on significance ($P=0.10$) and the power of this test is probably low. Data on (1) habitat- and size-specific prey distributions, (2) predator and prey field densities, and (3) habitat-specific interactions between productivity, guppy density, and guppy growth are needed to develop more detailed predictive models. In summary, the interplay between environmental complexity, productivity, and predator-guppy behavior may play a major role in mediating the impact of predators on guppy populations and the evolution of guppy behavior and life-history characters.

Variation in Predator Behavior in the Laboratory.

The behavioral patterns of *Crenicichla* changed with their length of residence in the laboratory. Two groups of pike cichlids were brought into the laboratory, one in March 1990 and the other in April 1991. In the first week following their arrival, the pike cichlids in both groups were somewhat secretive and tended to remain in their shelters. After one or two weeks, however, most of the *Crenicichla* began to anticipate feeding, that is, they would remain outside of their shelters, near the surface of the water, waiting for their ration of guppies. After three to six months, and disturbances associated with their use in experimental trials, many resumed their secretive behavior. The latter observation was much more variable with respect to time and individual; in fact, two *Crenicichla* retained the anticipative pattern for more than six months. These behavioral fluctuations were less pronounced for *Rivulus*. Given these temporal shifts in *Crenicichla* behavior in the laboratory, the large-tank test comparisons of the effect of habitat complexity (Experiment 2) were made with as little time between trials as possible (see Appendix 3 for test dates).

In the regression analyses, relating *Crenicichla* length to mean guppy size consumed (Fig. 3), I separated the two groups of pike cichlids because the first ten *Crenicichla* (solid circles in Fig. 3) had been in the laboratory for more than four months prior to testing, whereas the latter five *Crenicichla* (triangles in Fig. 3) were only in the laboratory for two to four weeks before their tests began. Although all 15 *Crenicichla* were treated to the same pre-test maintenance feeding and acclimation protocol, those collected in April 1991 displayed less prey-size selectivity and consumed greater quantities of guppies than their comparably sized counterparts collected in March 1990. Although all pike cichlids consistently consumed more guppies in the unstructured tanks than in the structured tanks, the variation in the prey-size selectivities of the five laboratory-naive *Crenicichla* (i.e., those collected in April 1991 and tested within 2 - 4 weeks) was high. The three *Crenicichla* that had been held in the laboratory for at least four months prior to testing consistently ate fewer and larger guppies in the structured tanks than they did in the unstructured tanks.

Although time spent in captivity is one explanation for the behavioral differences described above, it is also possible that the observed differences are simply an artifact of small sample size and inadequate sampling across *Crenicichla* sizes. The five *Crenicichla* collected in April 1991 were all larger than 120 mm SL (i.e., there were no small fish in this group). Therefore, the lack of prey-size selectivity and higher consumption rates observed for this group of fish, as compared to the group collected in

March 1990 (size range: 73 - 148 mm SL), may also be attributed to differences in the size ranges of fish in these two groups. That is, large *Crenicichla* eat more guppies from a variety of size classes.

Other Predatory Fishes.

Newborn and juvenile *Crenicichla* and *Hoplias*, if present in sufficient numbers, along with other fishes such as *Astyanax* and *Hemibrycon*, could potentially consume large numbers of guppies at downstream sites. Little is known, however, about their impact on guppy populations. I conducted laboratory tests of prey-size selectivity with a juvenile *Hoplias* from the El Cedro River, (southern slope), and also with a predatory eleotrid (*Gobiomorus dormitor*) from the Damier River, a stream on the north slope of the Northern Range Mountains. Endler (unpubl. ms.) suggests that predatory eleotrids, such as *Eleotris pisonis*, *Gobiomorus dormitor*, and *Dormitator* sp., could be the ecological equivalents of *Crenicichla* for northern slope streams, where *Crenicichla* do not occur. The *Gobiomorus* that I tested showed a strong preference for large (>22 mm) guppies. A summary of these predation tests appears in Appendix 5.

Conclusions.

In summary, this laboratory study demonstrated that *Rivulus* fed selectively on immature guppies, probably due to gape-limitation. *Rivulus* predation rates may be dependent on prey densities and were much lower than those for *Crenicichla*, which consumed large numbers of guppies of all sizes. In addition, greater habitat complexity reduced *Crenicichla* predation rates, which (along with low *Rivulus* predation rates regardless of habitat complexity) could explain the differences in habitat use between guppies in upstream versus downstream locations. Although *Crenicichla* prey-size selection was dependent on the length of the individual predator, size-selective predation by *Crenicichla* on large guppies does not seem to be a plausible mechanism for driving the evolution of downstream guppy life histories.

A broader baseline of information on Trinidadian stream biota is needed to further our understanding of the impact of predation on guppy populations by *Rivulus*, *Crenicichla*, and other predators. With the exception of the field mark-recapture studies of Reznick and Butler (unpubl. data) and two laboratory prey-selection experiments (Seghers 1973, and this study), most of our knowledge of the predator-prey interactions in this system is based on stomach content analyses and anecdotal reports of predation events.

Future work should include stream surveys to obtain better field estimates of species distributions, densities, growth, and mortality in a variety of habitats. The behavioral and dietary changes associated with predator ontogeny should also be examined in detail. Mathematical life-history theory should be amended to include predictions based on differences in predation intensity. Finally, the conservation and appreciation of these unique ecosystems could only be enhanced by greater interaction with local researchers (University of West Indies, among others), who potentially have valuable, lifelong experience and knowledge of Trinidadian mountain streams.

Literature Cited

Anderson, O. 1984. Optimal foraging by largemouth bass in structured environments. Ecology 65: 851-861.

Bowen, S. H. 1983. Quantitative description of the diet. pp. 325-336 In: Fisheries Techniques, L. A. Nielsen and D. L. Johnson (eds.), American Fisheries Society, Bethesda, Maryland.

Brooks, J. L. and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35.

Carlander, K. D. 1977. Handbook of Freshwater Fishery Biology. Vol. 2. Iowa State Univ. Press, Ames. pp. 73-124.

Charlesworth, B. 1980. Evolution in Age-structured Populations. Cambridge University Press, New York. 300 pp.

Crowder, L. B. and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802-1813.

Crowl, T. A. and A. P. Covich. 1990. Predator-induced life-history shifts in a freshwater snail. Science 247: 949-951.

Dodson, S. I. 1984. Predation of *Heterocope septentrionalis* on two species of *Daphnia*: morphological defenses and their cost. Ecology 65: 1249-1257.

Endler, J. A. 1978. A predator's view of animal color patterns. Evol. Biol. 11: 319-364.

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

___________. 1983. Natural and sexual selection on color patterns in poeciliid fishes. Environ. Biol. Fish. 9: 173-190.

___________. A preliminary report on the distribution and abundance of fishes and crustaceans of the Northern Range Mountains, Trinidad. Unpublished manuscript.

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

Gadgil, M. and P. W. Bossert. 1970. Life historical consequences of natural selection. Amer. Natur. 104: 1-24.

Galbraith, M. G. 1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. Trans. Am. Fish. Soc. 96: 1-10.

Gilliam, J. F. and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68: 1856-1862.

Haskins, C. P., E. F. Haskins, J. J. A. McLaughlin, and R. E. Hewitt. 1961. Polymorphism and population structure in *Lebistes reticulata*, an ecological study. pp. 320-395 In: Vertebrate Speciation, W. F. Blair (ed.). Univ. of Texas Press, Austin.

Havel, J. E. 1987. Predator-induced defenses: a review. pp. 263-278 In: Predation: Direct and indirect impacts on aquatic communities, W. C. Kerfoot and A. Sih (eds.), University Press of New England, Hanover, New Hampshire.

Hoogland, R. D., D. Morris, and N. Tinbergen. 1957. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as a means of defense against predators (*Perca* and *Esox*). Behaviour 10: 205-237.

Houde, A. E. 1987. Mate choice based upon naturally occurring color-pattern variation in a guppy population. Evolution 41: 1-10.

__________. 1988a. Genetic difference in female choice between two guppy populations. Anim. Behav. 36: 510-516.

__________. 1988b. The effects of female choice and male-male competition on the mating success of male guppies. Anim. Behav. 36: 888-896.

Keenleyside, M. H. A. 1979. Diversity and adaptation in fish behaviour. Springer-Verlag, Berlin. 208 pp.

Kerfoot, W. C. and A. Sih. 1987. Predation: Direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire. 386 pp.

Lagler, K. F. 1956. Freshwater Fishery Biology. William C. Brown Publ. Co., Dubuque, Iowa. pp. 123-124.

Law, R. 1979. Optimal life histories under age-specific predation. Amer. Natur. 114: 399-417.

Liley, N. R. and B. H. Seghers. 1975. Factors affecting the morphology and behavior of guppies in Trinidad. pp. 92-118 In: Function and Evolution in Behavior, G. P. Baerends, C. Beer, and A. Manning (eds.). Oxford Univ. Press, Oxford.

Lubchenco, J. 1978. Plant species diversity in a marine rocky intertidal community: importance of herbivore food preference and algal competitive abilities. Amer. Naturalist 112: 23-29.

Luyten, P. H. and N. R. Liley. 1985. Geographic variation in the sexual behaviour of the guppy, *Poecilia reticulata* (Peters). Behaviour 95: 164-179.

Michod, R. E. 1979. Evolution of life histories in response to age-specific mortality factors. Amer. Natur. 113: 531-550.

Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62: 1370-1386.

__________. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65: 499-513.

__________. 1986. Predator-mediated habitat use: some consequences for species interactions. Environ. Biol. Fish. 16: 159-169.

Morin, P. J. 1983. Predation, competition, and the composition of larval anuran guilds. Ecol. Monogr. 53: 119-138.

O'Brien, W. J. 1987. Planktivory by freshwater fish: thrust and parry in pelagia. pp. 3-16 In: Predation: Direct and indirect impacts on aquatic communities, W. C. Kerfoot and A. Sih (eds). University Press of New England, Hanover, New Hampshire.

Paine, R. T. 1966. Food web complexity and species diversity. Amer. Naturalist 100: 65-75.

Peckarsky, B. L. 1980. Predator-prey interactions between stoneflies and mayflies: behavioral observations. Ecology 61: 932-943.

Pitcher, T. J. 1986. Functions of shoaling behaviour in teleosts. pp. 294-337 In: The behaviour of teleost fishes, T. J. Pitcher (ed.). Croom Helm, London.

Power, M. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. pp. 333-351 In: Predation: Direct and indirect impacts on aquatic communities, W. C. Kerfoot and A. Sih (eds). University Press of New England, Hanover, New Hampshire.

Pulliam, H. R. 1974. On the theory of optimal diets. Amer. Natur. 108: 59-75.

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

__________. 1982b. The genetic determination of offspring size in the guppy (*Poecilia reticulata*). Amer. Natur. 120: 181-188.

__________. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. Ecology 64: 862-873.

__________. 1989. Life-history evolution in guppies: repeatability of field observations and the effects of season on life histories. Evolution 43: 1285-1297.

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

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

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

Savino, J. F. and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Trans. Am. Fish. Soc. 111: 255-266.

Schlosser, I. J. 1988. Predation risk and habitat selection by two size classes of a stream cyprinid: experimental test of a hypothesis. Oikos 52: 36-40.

Schramm, H. L., Jr. and A. V. Zale. 1985. Effects of cover and prey size on preferences of juvenile largemouth bass for blue tilapias and bluegill in tanks. Trans. Am. Fish. Soc. 114: 725-731.

Seghers, B. H. 1973. An analysis of geographic variation in the anti-predator adaptations of the guppy, *Poecilia reticulata*. Ph.D. Thesis, University of British Columbia. 273 pp.

__________. 1974. Schooling behavior in the guppy (*Poecilia reticulata*): an evolutionary response to predation. Evolution 28: 486-489.

__________. 1978. Feeding behavior and terrestrial locomotion in the cyprinodontid fish, *Rivulus harti* (Boulenger). Verh. Internat. Verein. Limnol. 20: 2055-2059.

Sih, A. 1987. Predators and Prey Lifestyles: an evolutionary and ecological overview. pp. 203-224 In: Predation: Direct and indirect impacts on aquatic communities W. C. Kerfoot and A. Sih (eds.). University Press of New England, Hanover, New Hampshire.

Sih, A., P. H. Crowley, M. A. McPeek, J. W. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. Annu. Rev. Ecol. Syst. 16: 269-311.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3-47.

Stein, R. A. 1977. Selective predation, optimal foraging and predator-prey interaction between fish and crayfish. Ecology 58: 1237-1253.

__________. 1979. Behavioral response of prey to fish predators. pp. 343-353 In: Predator-prey systems in fisheries management, R. H. Stroud and H. Clepper (eds.). Sport Fishing Institute, Washington, D. C.

Stein, R. A. and J. J. Magnuson. 1976. Behavioral response of crayfish to a fish predator. Ecology 57: 751-761.

Strauss, R. E. 1990. Predation and life-history variation in *Poecilia reticulata* (Cyprinodontiformes: Poeciliidae). Environ. Biol. Fish. 27: 121-130.

Werner, E. E. and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15: 393-425.

Werner, E. E. and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55: 1042-1052.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548.

Wootton, R. J. 1990. Ecology of teleost fishes. Chapman and Hall, London. 404 pp.

Yamamoto, T. 1975. The medaka, *Oryzias latipes*, and the guppy, *Lebistes reticularis*. pp. 133-149 In: Handbook of Genetics, Vol. 4, R. C. King (ed.), Plenum Press, New York.

Zaret, T. M. 1980. Predation and freshwater communities. Yale Univ. Press, New Haven, Connecticut. 187 pp.

Zaret, T. M. and A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52: 336-342.

Appendix 1. Experiment 1: Small-tank tests to evaluate size-selective predation by ***Rivulus harti*** and ***Crenicichla alta*** on guppies. Prey densities ranged from 0.07 to 0.39 guppies/L for ***Crenicichla*** and were 0.68 guppies/L for *Rivulus*. In Trials 1 and 2, each ***Rivulus*** individual was offered a total of six domestic guppies, two in each of three size classes (6-10 mm, 10-14 mm, and 14-18 mm). Also in Trials 1 and 2, eight *Crenicichla* were each offered 15 guppies, five in each of the same size classes. The values reported in the last six columns are the numbers of guppies eaten by the predators in each size class in each of the two trials (Trials 1 and 2 are labelled "1" and "2" below). The testing dates for the trials were as follows: Trial 1, *Rivulus* = 11 Jan 1991; Trial 2, *Rivulus* = 17 Jan 1991; Trial 1, *Crenicichla* = 30 Jan 1991; Trial 2, *Crenicichla* = 04 Feb 1991.

		Number of Guppies Eaten					
		6-10 mm		**10-14 mm**		**14-18 mm**	
***Rivulus* Individual**	**Predator Length (SL mm)**	**1**	**2**	**1**	**2**	**1**	**2**
R-1	49	1	2	0	1	0	0
R-2	47	2	2	0	1	0	0
R-3	59	1	0	0	1	0	0
R-4	55	1	0	0	0	0	0
R-5	65	2	2	1	0	0	0
R-6	75	2	2	2	2	2	2
R-7	60	0	0	1	0	0	1
R-8	53	2	2	1	2	0	0
R-9	65	2	2	2	2	1	2
R-10	59	1	2	1	1	1	1
R-11	66	0	2	0	0	0	0
R-12	58	2	2	2	2	1	1
R-13	55	2	2	1	1	0	0
R-14	58	1	2	0	0	1	0
R-15	41	0	0	0	0	0	0
R-16	49	0	1	1	1	0	0
R-17	63	0	1	0	0	0	0
R-18	56	1	1	1	1	0	0
Rivulus Sums	Mean Length=57.4	20	25	13	15	6	7
***Crenicichla* Individual**							
C-6	138	1	4	4	3	5	2
C-5	131	0	1	4	2	4	3
C-10	155	1	2	1	1	2	3
C-4	129	0	0	0	1	0	0
C-1	101	0	0	2	1	3	2
C-3	106	1	1	4	1	3	2
C-9	155	1	2	3	2	4	1
C-2	104	3	2	3	2	3	3
Crenicichla Sums	Mean Length=127.4	7	12	21	13	24	16

Appendix 2. Chi-square tests of independence to determine significant prey-size selection by *Crenicichla* and *Rivulus* on immature (< 14 mm) versus mature (> 14 mm) guppies in Experiments 1 and 2. The deviations from equal selection of the two size classes (denoted "imm" for < 14 mm and "mat" for > 14 mm guppies) are shown along with appropriate X^2 statistics. $P < .01$ is indicated by **, $P < .05$ is indicated by *, and NS indicates no significant deviation from equal selection ($P > .05$). When multiple analyses were conducted on the same experiment, the experiment-wise error rates were adjusted accordingly. Tests were conducted in small (Experiment 1) and large (Experiment 2) tanks. Equal numbers of immature and mature guppies were not present in the tests; therefore, observed and expected values for the Chi-square analyses were adjusted accordingly.

Test Situation	Prey Size Classes	No. Prey Eaten Per Class	n	X^2	df	P
Exp. 1; *Crenicichla*; Trial 1	imm:mat	28/80:24/40	8	3.85	1	NS
Exp. 1; *Crenicichla*; Trial 2	imm:mat	25/80:16/40	8	0.60	1	NS
Exp. 1; *Crenicichla*; Sum of Trials 1 and 2	imm:mat	53/160:40/80	8	3.92	1	*
Exp. 1; *Rivulus*; Trial 1	imm:mat	33/72:6/36	18	5.65	1	*
Exp. 1; *Rivulus*; Trial 2	imm:mat	40/72:7/36	18	7.20	1	*
Exp. 1; *Rivulus*; Sum of Trials 1 and 2	imm:mat	73/144:13/72	18	12.85	1	**
Exp. 2; *Crenicichla*; No Structure	imm:mat	32/180:102/540	15	0.09	1	NS
Exp. 2; *Crenicichla*; Structure	imm:mat	9/96:39/288	8	1.00	1	NS
Exp. 2; *Rivulus*; No Structure	imm:mat	7/80:0/240	8	7.00	1	**
Exp. 2; *Rivulus*; Structure	imm:mat	1/80:0/240	8	1.00	1	NS

Appendix 3a. Large-tank (350 L) tests (Experiment 2) with *Crenicichla alta* and guppies from Trinidad. Water temperatures ranged from 19.5 to 25.5 C, but typically were between 22 and 24 C. Prey densities were approximately 0.14 guppies/L. Roman numerals indicate the following columns: I = *Crenicichla* individual; II = *Crenicichla* length; III = Test date; IV = Duration of the test in hours; V = Total number of guppies eaten in the test; VI = Predation Intensity, or the number of guppies eaten per 24 h; VII = Mean(± 1 S.E.) prey size consumed; VIII = Number of guppies eaten in each of the size classes B (10-14 mm), C (14-18 mm), D (18-22 mm), and E (>22 mm). (i) Tests with no structure present in tanks. (ii) Tests with structure present. Superscript "a" indicates those tests which were included in the analysis of habitat effects (no-structure versus structure tests).

I	II	III	IV	V	VI	VII	VIII			
(i)							B	C	D	E
C-1	73	06 Aug 90	62	6	2.32	13.0(0.9)	5	1	0	0
C-2	78	18 Sep 90	93	3	0.77	13.1(2.1)	2	1	0	0
C-3	81	08 Sep 90	99	6	1.45	15.2(1.4)	2	3	1	0
C-4	116	06 Aug 90	96	8	2.00	20.1(3.0)	3	1	0	4
C-5	118	19 Aug 90	62	6	2.32	17.4(2.0)	1	2	1	2
C-6	125	28 Jul 90	96	6	1.50	20.3(1.9)	0	2	2	2
C-7	126	28 Jul 90	96	5	1.25	17.9(2.9)	2	0	2	1
C-8	126	13 Sep 90	93	8	2.04	19.8(1.9)	1	2	3	2
C-9	148	08 Sep 90	76	12	3.79	23.0(1.2)	0	1	5	6
C-10	148	30 Jul 90	24	8	8.00	23.5(2.5)	0	2	1	5
C-11	127	17 May 91^{a}	20	11	13.20	17.4(0.9)	1	3	7	0
C-12	130	26 May 91^{a}	24	14	14.00	15.7(0.8)	4	6	4	0
C-13	155	21 May 91^{a}	45	8	4.27	22.4(2.8)	2	1	1	4
C-14	157	08 May 91^{a}	24	13	13.00	20.6(1.6)	2	2	5	4
C-15	162	13 May 91^{a}	20	20	24.00	16.9(1.3)	7	7	3	3
C-1	118	02 May 91^{a}	41	7	4.10	19.0(1.6)	1	3	2	1
C-2	120	01 Apr 91^{a}	71	8	2.70	21.5(2.5)	2	1	2	3
C-5	139	24 Apr 91^{a}	90	14	3.73	18.0(1.4)	4	3	5	2
	n=18	(i) Mean	62.9	9.1	5.80	18.6(0.7)	2.2	2.3	2.4	2.2
	n=8	(i)^{a} Mean	41.9	11.9	9.88	18.9(0.8)	2.9	3.3	3.6	2.1
(ii)										
C-11	127	26 May 91^{a}	88	6	1.64	18.0(3.0)	2	2	1	1
C-12	130	03 Jun 91^{a}	71	3	1.01	17.6(1.1)	0	1	2	0
C-13	155	27 May 91^{a}	65	7	2.58	24.8(3.0)	1	0	2	4
C-14	157	02 May 91^{a}	42	16	9.14	17.5(1.6)	6	4	3	3
C-15	162	30 Apr 91^{a}	24	7	7.00	22.9(2.1)	0	1	4	2
C-1	118	25 Apr 91^{a}	122	3	0.59	21.6(3.6)	0	1	1	1
C-2	120	23 Mar 91^{a}	117	3	0.62	20.2(2.5)	0	1	1	1
C-5	139	06 Mar 91^{a}	94	3	0.77	20.5(1.2)	0	0	2	1
	n=8	(ii)^{a} Mean	77.9	6.0	2.92	20.4(0.9)	1.1	1.3	2.0	1.6

Appendix 3b. Large-tank tests (Experiment 2) with *Rivulus harti* and *Poecilia reticulata*. Prey densities were approximately 0.11 guppies/L. Roman numerals indicate the following columns: I=*Rivulus* individual; II=*Rivulus* length (SL mm); III=Test date; IV=Origin of test population, "T" represents guppies from Trinidad and "D" represents domestic feeder guppies; V=Duration of the test in hours; VI=Total number of guppies eaten in the test; VII=Predation Intensity, or the number of guppies eaten per 24 h; VIII=Mean (± 1 S.E.) prey size consumed, "(----)" indicates no standard error where fewer than two guppies were consumed; IX=Number of guppies eaten in each of the size classes A (6-10 mm), B (10-14 mm), C (14-18 mm), and D (18-22 mm). (i) Tests with no structure in tanks. (ii) One test with four *R. harti* in an unstructured tank. (iii) Tests with structure present in tanks. Superscript "a" indicates those tests which were included in the analysis of habitat effects (no-structure versus structure tests).

I	II	III	IV	V	VI	VII	VIII	IX			
(i)								A	B	C	D
R-6	78	29 Jan 91^a	T	120	3	0.60	8.0(0.4)	3	0	0	0
R-8	53	12 Mar 91^a	T	123	0	0.00	0.0(----)	0	0	0	0
R-9	69	29 Jan 91^a	D	120	0	0.00	0.0(----)	0	0	0	0
R-10	62	06 Jun 91^a	T	113	0	0.00	0.0(----)	0	0	0	0
R-12	61	20 Feb 91^a	T	122	3	0.59	8.4(0.7)	3	0	0	0
R-13	55	16 Jun 91^a	T	120	1	0.20	9.6(----)	1	0	0	0
R-19	92	11 Jan 91^a	T	119	0	0.00	0.0(----)	0	0	0	0
R-20	73	16 Jan 91^a	D	144	0	0.00	0.0(----)	0	0	0	0
R-19	92	16 Jan 91	D	142	2	0.34	10.6(1.5)	1	1	0	0
R-20	71	11 Jan 91	T	120	0	0.00	0.0(----)	0	0	0	0
R-21	77	17 Mar 91	T	140	0	0.00	0.0(----)	0	0	0	0
		(i)^a Mean	n=8	122.6	0.9	0.17	3.3(1.6)	0.9	0.0	0.0	0.0
(ii)											
R-6, R-9, R-12, R-19	see above	03 Feb 91	D	119	4	0.81	9.0(0.8)	3	1	0	0
(iii)											
R-6	78	08 May 91^a	T	120	0	0.00	0.0(----)	0	0	0	0
R-8	53	06 Jun 91^a	T	114	0	0.00	0.0(----)	0	0	0	0
R-9	69	14 May 91^a	T	96	0	0.00	0.0(----)	0	0	0	0
R-10	62	12 Mar 91^a	T	122	0	0.00	0.0(----)	0	0	0	0
R-12	61	12 May 91^a	T	117	0	0.00	0.0(----)	0	0	0	0
R-13	55	11 Jun 91^a	T	120	0	0.00	0.0(----)	0	0	0	0
R-19	92	20 Feb 91^a	D	121	1	0.20	9.3(----)	1	0	0	0
R-20	73	18 May 91^a	T	119	0	0.00	0.0(----)	0	0	0	0
		(iii)^a Mean	n=8	116.1	0.1	0.03	1.2(1.2)	0.1	0.0	0.0	0.0

Appendix 4. Male and female guppies consumed by *Crenicichla alta* in large-tank tests (Experiment 2). In the Habitat Type column, "N" indicates tests with no structure in tank and "S" indicates tests where structure was present. Superscript "a" denotes those tests which were included in the analyses to evaluate the effects of habitat differences. The fequencies of males to females eaten (males:females) are given in the final three columns, where the guppy size classes C (14-18 mm) and D (18-22 mm) contained equal numbers of male and female guppies. The test dates and lengths of the individual *Crenicichla* are presented in Appendix 2a.

Crenicichla Individual	Habitat Type	C	D	C+D
C-1	N	0:1	0:0	0:1
C-2	N	1:0	0:0	1:0
C-3	N	2:1	1:0	3:1
C-4	N	1:0	0:0	1:0
C-5	N	0:2	1:0	1:2
C-6	N	2:0	1:1	3:1
C-7	N	0:0	0:2	0:2
C-8	N	1:1	1:2	2:3
C-9	N	1:0	3:2	4:2
C-10	N	0:2	1:0	1:2
C-11	N^a	1:2	4:3	5:5
C-12	N^a	2:4	3:1	5:5
C-13	N^a	0:1	1:0	1:1
C-14	N^a	0:2	2:3	2:5
C-15	N^a	4:3	0:3	4:6
C-1	N^a	2:1	0:2	2:3
C-2	N^a	1:0	0:2	1:2
C-5	N^a	3:0	2:3	5:3
Sum of "N"	(n=18)	21:20	20:24	41:44
Sum of "N^a"	(n=8)	13:13	12:17	25:30
C-11	S^a	1:1	1:0	2:1
C-12	S^a	1:0	1:1	2:1
C-13	S^a	0:0	1:1	1:1
C-14	S^a	3:1	1:2	4:3
C-15	S^a	1:0	0:4	1:4
C-1	S^a	1:0	0:1	1:1
C-2	S^a	1:0	0:1	1:1
C-5	S^a	0:0	1:1	1:1
Sum of "S^a"	(n=8)	8:2	5:11	13:13

Appendix 5. Two other Trinidadian freshwater predatory species, (i) *Hoplias malabaricus* and (ii) *Gobiomorus dormitor*, were collected in April 1991 and were offered various-sized guppies in the large tanks in June 1991, under conditions similar to those described for *Crenicichla alta* and *Rivulus harti* in Experiment 2.

(i) A small (approximately 20 mm) juvenile wolffish (*Hoplias malabaricus*) was collected with a hand-held net in the El Cedro River (southern slope of Northern Range) in April 1991 and was tested on 14 Jun 1991, at a length of 57 mm, in a structured large tank with 30 Trinidadian guppies, ten guppies in each of three size classes (10-14 mm, 14-18 mm, and 18-22 mm). The wolffish was previously observed to consume adult guppies (> 14 mm) in a small tank (8.8 L) by the time it had reached a length of about 50 mm. In the large-tank test beginning 14 Jun 1991, it consumed one guppy (10.2 mm) in three days of testing; unfortunately, the wolffish jumped out of the tank and died sometime between the third and fourth test day.

(ii) On the northern slope of the Northern Range Mountains, several rivers, including the Yarra, the Damier, the Marianne, and the Paria, drain relatively small basins before emptying into the ocean along Trinidad's northern coast. Some of these rivers, including the Paria and the Yarra, contain *Poecilia reticulata*; however, most of the predatory species common to the southern slope rivers, including *Crenicichla*, are not present in the northern slope rivers (J. Endler unpubl. ms.). The piscine predators on the northern slope include gobies that migrated upstream from the ocean and have adapted to freshwater conditions. These northern slope fishes are not well studied and include *Gobiomorus dormitor* (Eleotridae) and the more common *Eleotris pisonis* (Eleotridae). We collected three *Gobiomorus* in mid-April 1991 using small fishing rods with natural and artificial lures in the Yarra and Damier Rivers. One *Gobiomorus* from the Yarra River, 255 mm SL, was sacrificed to examine its stomach contents. Only one food item was present, a freshwater prawn approximately 40 mm in length. Another *Gobiomorus*, a 174 mm individual from the Damier River, was tested in a non-structured large tank on 14 Jun 1991 with 48 Trinidadian guppies; 12 in each of four size classes (10-14 mm, 14-18 mm, 18-22 mm, and >22 mm). This 174 mm predatory eleotrid exhibited noticable prey size selection, consuming mostly large adult guppies. The test results are given below.

						Number of Guppies Eaten in Each Size Class			
Predator Length	Test Date	Test Duration (h)	Number of Guppies Eaten	Predation Intensity (guppies eaten/day)	Mean (± 1 S.E) Prey Length Consumed	10-14 mm	14-18 mm	18-22 mm	>22 mm
174 mm	14 Jun 1991	20	24	28.8	22.8 ± 1.3	1	5	7	11