

Feeding under predation hazard: response of the guppy and Hart's rivulus from sites with contrasting predation hazard

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Summary. Populations of guppies, *Poecilia reticulata*, and Hart's rivulus, *Rivulus harti*, in Trinidad experience different levels of predation hazard from piscivorous fish. Those from the larger rivers ("downstream sites") experience chronically high predation hazard, while those from headwater streams ("upstream sites") have few predators. Guppies and Hart's rivulus, collected from downstream and upstream sites, were assayed for their feeding rate in the presence and absence of predators. We defined *tenacity* as the ratio of the feeding rates in the presence and absence of a predator stimulus. Thus, *tenacity* expresses the degree to which the forager maintains its feeding rate when a predator stimulus is present. Previous work by Seghers (1973) showed that non-feeding guppies from downstream sites responded more strongly to predators than did guppies from upstream sites. Based on this, we initially hypothesized that fish from downstream sites would show lower tenacities than fish from upstream sites. However, we found the opposite in every case. When confronted with a predator stimulus, guppies and Hart's rivulus from downstream sites fed at consistently greater rates and displayed greater tenacities than did those from upstream sites. These differences were found in experiments using both live and model predators. The results suggest that upstream fish readily trade off feeding for hiding and avoiding predation hazard, a likely response when predators appear infrequently, while downstream fish appear to be selected for boldness and tenacity while foraging under chronically high hazard.

Introduction

Foraging under predation hazard has been the subject of numerous recent studies. Most have been

concerned with how foragers trade off or balance the potentially conflicting demands of needing to forage while simultaneously avoiding predators (e.g. Milinski and Heller 1978; Gilliam and Fraser 1987), but little attention has been paid to the origins or previous experience of the foragers. Here, we measure the response to hazard by individuals that were derived from populations with contrasting predation pressure.

Fraser and Huntingford (1986) used a laboratory assay for characterizing the response towards hazard of feeding fish. They pointed out that there is a continuum of response, varying from complete risk-avoidance (shut down when a predator is present) to complete risk-recklessness (ignore predator, feed maximally). In the present study we use the term *tenacity* as a way of explicitly addressing the concept of a continuum of responses. The tenacity index expresses the forager's attitude towards hazard in terms of the degree to which it maintains its feeding rate when a predator is introduced. Thus, we define the tenacity index (T) as:

$$T = F_p / F_{np}$$

where F = feeding rate, p = predator, np = no predator.

We chose the guppy, *Poecilia reticulata*, as a suitable subject for studying attitude towards hazard, because other aspects of its behavior, as well as morphology and life history characteristics, are known to vary with the level of predation pressure to which it is exposed (Haskins et al. 1961; Seghers 1973; Seghers 1974a, b; Liley and Seghers 1975; Farr 1975; Endler 1978; Reznick and Endler 1982; Goodey and Liley 1986). Seghers (1973) found that guppies collected from certain populations which had experienced low predation pressure responded to predatory threat with less appropriate antipredator responses than did guppies from populations with a history of chronically high predation pres-

sure. Fish from sites with low predation allowed predators to approach more closely before reacting and schooled less tightly than did guppies from sites with high predation. Giles and Huntingford (1984) found similar patterns when comparing populations of three-spined sticklebacks, *Gasterosteus aculeatus*.

Based on these findings, we hypothesized that guppies from a low predation regime would be naïve about predators, relative to those derived from high predation sites. Thus, an assay for tenacity while feeding would be predicted to show guppies from high predation sites to be significantly less tenacious when presented with a predator than those from low predation sites.

We tested these predictions in a preliminary experiment (see below), conducted in Trinidad, on freshly caught guppies. The results of this test were the opposite of the prediction; guppies from high predation sites were more tenacious than those from low predation sites.

In this paper we report the results of the preliminary study, and a second, more extensive study of tenacity, in which we assayed guppies and a second species, Hart's rivulus, *Rivulus harti*. The fish were obtained from two localities in two river systems, one being upstream and experiencing relatively low predation pressure, the other downstream and experiencing chronically high predation pressure.

Methods

Study area

Guppies, *Poecilia reticulata*, and Hart's rivulus, *Rivulus harti*, were seined in May 1986 from up- and downstream sites in the Turure and Oropuche Rivers which drain portions of the southern versant of Trinidad's northern mountain range. At 150–185 m elevation, the upstream sites were above the waterfall line for each river; downstream sites were at about 45 m (Fig. 1).

Turure collection sites

The upstream Turure sites were located along a series of waterfalls, 3–6 m high (Table 1). Rivulus were rare above the first waterfall, but guppies were found in the pools at the base of several waterfalls beyond. Guppies were seined from one of these pools that contained only guppies (Site 1). Rivulus were collected at the base of the first waterfall (Site 2).

Downstream, both guppies and rivulus were seined from shallow and backwater areas of the main river (Site 3).

Oropuche collection sites

Three upstream sites were seined in the Oropuche. Sites 4 and 5 were located along a series of falls, which, as in the upstream Turure, separated the two species. At site 4 rivulus was the only species taken above a large barrier fall, 4 m high, while

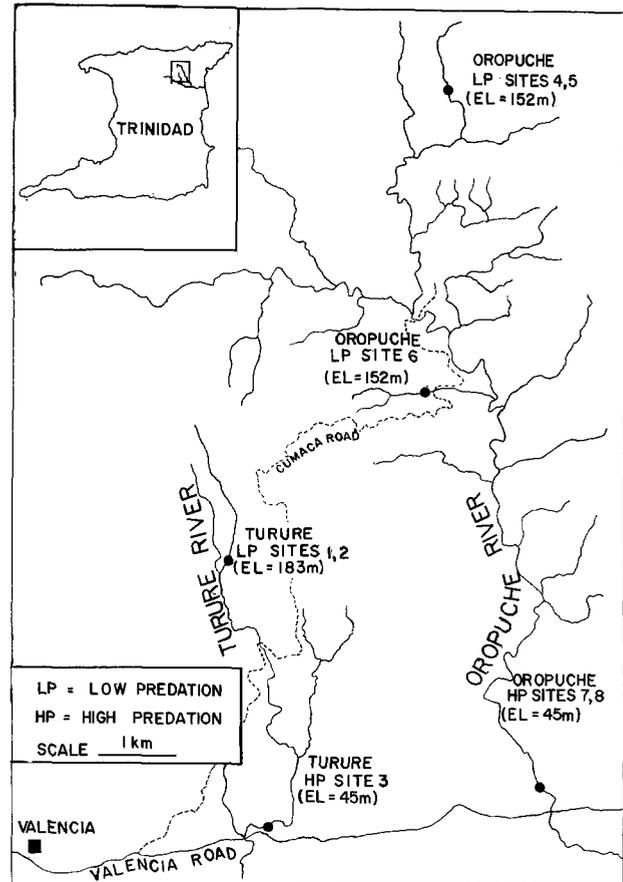


Fig. 1. Location of up- and downstream collection sites for *Poecilia reticulata* and *Rivulus harti* in the northern mountain range of Trinidad

guppies were seined at site 5, just below the falls, where rivulus were also present (Table 1). Site 6 was a small tributary, 4 km, airline, from sites 4 and 5, where only rivulus were present. No guppies were found anywhere along this tributary.

At the downstream site guppies were seined from the edge of the main river (Site 7), while rivulus were taken from a pool connected to the main river by a drainage ditch (Site 8). Rivulus were abundant in the drainage ditch, but relatively scarce in the main river where we occasionally found them in shallow pools.

Predation pressure

Predators were present at some of the collection sites (Table 1). The predators can be ranked in order of severity: *Crenicichla alta* > *Rivulus harti* > *Astyanax bimaculatus* > *Aequidens pulcher* (Endler 1978). Levels of predation from terrestrial sources are unknown, but assumed to be low (Endler 1978). The freshwater prawn, *Macrobrachium crenulatum*, a potential predator of the guppy, was found in pools at the rivulus and guppy collection sites in the upper Turure.

Experimental design

To assay for attitude towards hazard, we tested adult guppies and juvenile rivulus (sizes in Table 2) in the presence and absence of a predator stimulus in a cross-classified, factorial design (upstream or downstream location cross-classified with

Table 1. Characteristics of up- and downstream sites in the Turure and Oropuche Rivers

River	Site	Description	Elevation, m	Species	Micro-habitat
Turure					
Upstream					
	1	3rd order tributary	183	<i>Poecilia</i> ^a	Main stream
	2	3rd order tributary	180	<i>Rivulus</i> ^a	Main stream
Downstream					
	3	Main river	45	<i>Poecilia</i> ^a <i>Rivulus</i> ^a <i>Crenicichla</i> <i>Astyanax</i>	Along edge Along edge Main stream Main stream
Oropuche					
Upstream					
	4	2nd order tributary	152	<i>Rivulus</i> ^a	Main stream
	5	3rd order tributary	150	<i>Rivulus</i> <i>Poecilia</i> ^a	Main stream
	6	2nd order tributary	150	<i>Rivulus</i> ^a	Main stream
Downstream					
	7	Main river	45	<i>Poecilia</i> ^a <i>Rivulus</i> <i>Crenicichla</i> <i>Astyanax</i>	Side pools Side pools Main stream Main stream
	8	Pool connected to main stream by drainage ditch	50	<i>Rivulus</i> ^a	Pool

^a Used in behavioral assay

predator present or absent). Each treatment combination was replicated eight times. Subjects were allowed to choose between a location that always contained food and sometimes a predator, and a safe refuge without food.

The Preliminary Experiment was done in Trinidad in January 1986 using only guppies. Tenacity of each fish was measured by counting the number of bites taken in the absence of a predator and then in the presence of a live predator, *Aequidens pulcher*, on a subsequent day.

The Main Experiment was conducted in June and July 1986 using both guppies and Hart's rivulus collected in May 1986 and transported to Loudonville, New York. In these tests, each fish was tested only once: either in the presence or in the absence of a predator. Both species were tested each day, and the order of treatments was randomized.

Details of the experimental protocol

Prior to testing the fish were maintained at 21° C in laboratory aquaria under a 10 L–14 D light cycle. They were fed commer-

Table 2. Total length, mm (range, mean, 1 standard error), of subjects used in behavioral assay

Turure upstream	Oropuche upstream	Oropuche upstream	Turure downstream	Oropuche downstream
Guppies				
Site 1	Site 5		Site 3	Site 7
Males				
20–25 21.69 (0.39)	20–24 21.81 (0.34)		19–22 20.57 (0.48)	18–22 20.19 (0.30)
Females				
18–30 25.00 (1.13)	20–31 25.25 (1.03)		18–23 20.00 (0.56)	20–32 25.75 (1.13)
Hart's rivulus				
Site 2	Site 4	Site 6	Site 3	Site 8
27–48 35.38 (1.59)	30–46 34.87 (1.15)	28–41 33.06 (0.85)	30–40 33.19 (0.66)	25–38 29.56 (1.04)

cial flake food. The aquaria were housed behind black plastic so as to minimize disturbance.

Tests were done in aquaria, 50 × 25 × 25 cm deep, divided into two compartments: a refuge 10 cm long, and a test compartment 40 cm long, separated by an opaque partition. The upper third of the partition was cut to provide a rectangular opening (8 × 10 cm), screened with mesh of a size that allowed the fish to pass through easily. The sides and bottom of the aquaria were opaque. The tank was viewed by means of a mirror that was placed behind an opaque screen, keeping the observer out of view of the fish.

In preliminary testing we found that it was not practical to use live predators. Unacclimated *Crenicichla*, the principal predator of guppies, tended to remain motionless in a corner at the bottom, while acclimated ones, if hungry, ate the subject instantly. *Aequidens pulcher*, used in the Preliminary Experiment, tended to behave erratically in that it was active during some tests and quiet in others. To circumvent these problems and to properly standardize the assay, we used a realistic model predator, made of wood, and carved to the likeness of a *Crenicichla*. Facial features, a red eye, and a lateral line were painted on the model. The model predator, 11 cm long, was weighted internally and suspended from a stick by clear, monofilament fishing line. The model was maneuvered through the water by the experimenter, from behind the screen. Except during chases, described below, the model predator "resided" 3 cm above the bottom, along the side opposite the refuge.

Testing procedure

Prior to testing, fish were acclimated to the test tank until they fed readily and moved freely between compartments. Usually this took 2–3 days. All subjects were starved for 24 h prior to testing, and all testing was done between the hours of 0900 and 1500.

At the beginning of each trial 75 pieces of commercial flake food, cut into 1 mm² pieces, were added to the test side of the aquarium. The subject was taken from the community tank and placed in the refuge side of the test tank. The 5 min test

period began when the subject crossed over to the test side, usually within 2 min. Subjects that did not cross over within 20 min were returned to the community tank. The number of bites taken in each minute interval was recorded.

The following procedure was followed for treatments that required a predator stimulus. Prior to putting the subject in the tank, the model predator was lowered into position. When the subject crossed over to the test side, the model was made to "chase" the subject, which usually executed escape responses. The chases lasted 5–10 s, and were done once each minute, at the beginning of the minute interval. The model was maneuvered every minute regardless of the location of the subject. All tests were conducted under normal laboratory lighting.

We followed a similar procedure when a live predator was required in the Preliminary Experiment. The predator, *Aequidens pulcher*, was placed in the tank prior to the addition of the subject and allowed to acclimate. The subject was then introduced into the refuge side.

Analysis

Tenacities were tested for significance in two ways, depending upon the experiment. In the Preliminary Experiment, each subject was tested both with and without a predator stimulus present. Thus, an individual tenacity index (F_p/F_{np}) could be computed for each subject, enabling us to directly compare up- and downstream fish by a Mann-Whitney Test (two-tailed, $\alpha=0.05$). In the Main Experiment different subjects were tested in the with and without predator treatments; no subject was ever tested twice. Here, individual tenacity indices could not be computed for each fish, only a single tenacity index for a population, in which the numerator and denominator are the mean number of bites taken by the 8 subjects under the two treatments. This is a ratio of two random variables, and the expected value and variance of such a ratio are not estimable analytically from the means and sample variances of the two random variables. Thus, we made such estimates with the bootstrap technique (Efron 1982; Meyer et al. 1986). This method, which is easily implemented on microcomputers, provides such estimates by randomly resampling the original data. Given 8 experimental replicates for each treatment, the number of bites by the 8 fish receiving the predator treatment were placed in a pool, and the number of bites by the 8 fish receiving the no predator treatment were placed in a second pool. Eight values were then drawn randomly with replacement from each pool and a bootstrap replicate of tenacity was then calculated by dividing the mean of the values drawn for the first pool by the mean of the values drawn from the second pool. This resampling was repeated 1000 times to obtain 1000 bootstrap replicates. The bootstrap estimate of tenacity is the mean of the 1000 bootstrap replicates, and the standard error of the estimate is the square root of the variance in the 1000 replicates (the variance is not first divided by 8 before taking the square root, because the sample size is already implicitly included in the resampling procedure). The number of bootstrap replicates chosen (1000) was sufficiently large that the estimates converged by the law of large numbers (Efron 1982). Tenacity indices were compared by means of *t*-tests (two-tailed, $\alpha=0.05$).

In the Main Experiment, main effects of the independent variables (site, predator stimulus, sex for guppies) on number of bites were analyzed by an analysis of variance. We also tested for an effect of fish length on bites by using length as a covariate. Data were log-transformed for statistical tests (untransformed data are reported in the text). Two planned, orthogonal comparisons were made: (1) the mean number of bites

taken by fish from up- and downstream locations in the presence of a predator stimulus, and (2) the mean number of bites by fish from these two locations in the absence of the predator stimulus. These contrasts were analyzed by means of a *t*-test, two-tailed with degrees of freedom equal to that of the error mean square of the ANOVA ($\alpha=0.05$).

Results

Preliminary experiment (*Turure guppies*)

Subjects derived from downstream populations had significantly higher tenacities than did those from upstream populations: mean tenacity of 0.76 ± 0.13 SE for the downstream fish versus 0.24 ± 0.06 for the upstream fish (Mann-Whitney Test, $U=79$, $n_1=8$, $n_2=12$, $P<0.05$). This held for both sexes: males, 0.80 ± 0.16 downstream and 0.24 ± 0.03 upstream; females 0.70 ± 0.27 downstream and 0.25 ± 0.11 upstream. Further, in the presence of a predator stimulus, subjects from downstream sites took significantly more bites than did those from upstream: 23.4 ± 4.4 bites by downstream fish versus 3.1 ± 1.0 by upstream fish ($U=90$, $P<0.01$). In the absence of the predator, downstream subjects also fed at a greater absolute rate than did upstream fish: 31.0 ± 4.9 downstream versus 10.8 ± 1.6 upstream ($U=95$, $P<0.01$). Thus, the relationship between up- and downstream populations of *Turure guppies* persisted in both the presence and absence of a predator stimulus.

Main experiment

Effect of size. In all within-species comparisons, body size did not affect the number of bites (total length analyzed as a covariate, all $P>0.10$). Therefore, body size was not considered further in the statistical analysis.

Tenacity. In every case but one (female guppies, Oropuche River) the tenacity of downstream subjects was significantly greater than the tenacity of upstream subjects of the same species, from the same river system (*t*-test, $P<0.05$, Table 3). Thus, in both species from both river systems, the upstream populations showed a greater proportional reduction in feeding rate under the predator stimulus (i.e. lower tenacity) than did the downstream fish. Tenacities of downstream populations ranged from 0.40 to 0.91, but upstream populations showed tenacities of only 0.04 to 0.39.

The tenacity indices of male and female guppies, considered separately, showed the same pattern of downstream tenacity > upstream tenacity

Table 3. Tenacity indices, mean (± 1 SE), calculated by the bootstrap method, for each population

	Upstream		Downstream
Turure River			
Guppies			
All	0.22 (0.056)	<*	0.51 (0.074)
Males	0.29 (0.065)	<*	0.60 (0.071)
Females	0.19 (0.073)	<*	0.41 (0.073)
Rivulus	0.26 (0.100)	<*	0.65 (0.104)
Oropuche River			
Guppies			
All	0.10 (0.034)	<*	0.50 (0.148)
Males	0.04 (0.022)	<*	0.75 (0.044)
Females	0.14 (0.050)	<*	0.40 (0.178)
Rivulus	0.04 (0.025) ^a	<*	0.91 (0.139)
	0.39 (0.109) ^b	<*	0.91 (0.139)

^a Site 6^b Site 4* $P < 0.05$

(Table 3). Despite small sample sizes ($n=4$), the means were significantly different in 3 of 4 comparisons (t -test, $P < 0.05$, Table 3).

Absolute feeding levels. First considering the data without regard to sex, Table 4 shows that in both rivers for both species, downstream fish fed at higher absolute rates in the presence of the predator stimulus than did upstream fish. However, the

feeding rates in the absence of a predator stimulus did not always show this relationship. In two cases (Turure rivulus and Oropuche rivulus site 6, Table 4) downstream fish continued to feed at a greater rate than upstream fish when no predator was present. In one case downstream fish (Oropuche guppies) fed more slowly than did upstream guppies in the absence of a predator. In the other two cases (Turure guppies and Oropuche rivulus site 4) there was no significant difference between upstream and downstream fish in the absence of a predator.

Considering each guppy sex separately, in both sexes the downstream fish tended to feed at a higher rate than did upstream fish in the presence of a predator stimulus (Table 4). The differences were significant for males from both river systems, but not for females (planned orthogonal contrasts, t -tests, $n=4$, Table 4). In the absence of the predator stimulus, downstream males from the Turure River fed at a significantly greater rate than did their upstream counterparts. This relationship was reversed in the other three cases (Oropuche males and females from each river), but the differences were not significant.

Observations on behavior while feeding. In addition to quantifying bites, we made qualitative observations on the behaviors of the foragers. In general,

Table 4. Mean (± 1 SE) number of bites in the presence and absence of a predator stimulus. Significance determined by orthogonal contrasts on log-transformed data

	Turure River		Oropuche River		
	Upstream	Downstream	Upstream	Downstream	
Predator present					
Guppies					
All	5.1 (1.0)	<*	13.5 (1.9)	7.5 (2.7) <*	24.4 (5.7)
Males	5.0 (1.1)	<*	17.5 (2.1)	3.3 (1.8) <*	22.8 (5.6)
Females	5.3 (1.8)	<	9.5 (1.2)	11.8 (4.2) <	26.0 (11.2)
Hart's rivulus	1.8 (0.7)	<*	17.5 (2.8)	0.5 (0.3) ^a <*	32.4 (3.6)
				16.4 (4.5) ^b <*	32.4 (3.6)
Predator absent					
Guppies					
All	23.4 (4.4)	<	26.8 (2.2)	79.9 (9.4) >*	50.3 (10.5)
Males	17.3 (2.0)	<*	29.5 (1.9)	75.0 (13.1) >	31.3 (6.5)
Females	29.5 (7.8)	>	24.0 (3.7)	84.8 (14.9) >	69.3 (15.4)
Hart's rivulus	6.8 (0.9)	<*	27.0 (1.3)	12.1 (2.8) ^a <*	36.0 (3.9)
				42.5 (5.3) ^b >	36.0 (3.9)

^a Site 6^b Site 4* $P < 0.05$

fish from downstream sites fed more "boldly" than did those from upstream sites. The downstream fish maintained a distance of several centimeters from the predator stimulus, but did not completely cease activity. In contrast, when confronted with the predator stimulus, upstream fish were more likely to cease feeding, and swim to the surface, move to the refuge, or become motionless in a corner of the tank.

Discussion

Tenacity

Seghers (1973) found that guppy populations showed geographic variation in their tendency to school, the distance at which they reacted to the presence of a predator, and the kind of motor-patterns displayed upon encountering a predator (diminished movement of body and increased skulling with pectoral fins, rapid dart away, swimming at the surface, breaking the surface with a jump). In most cases the variation correlated with predation pressure; guppies from areas that contained the predators *Crenicichla alta* and *Hoplias malabaricus* schooled more tightly, reacted to disturbance at a greater distance and displayed stronger motor patterns than did guppies from areas lacking these species. These characteristics persisted across generations in laboratory stocks, suggesting that the observed geographic variation is caused by genetic differences. Based on these findings, we might have predicted that guppies from low predation sites should have fed recklessly (predator naive), while those from high predation sites should have been risk-avoiders. Our results are opposite to this prediction in every case.

Recently, Magurran (1986) studied two populations of minnows, *Phoxinus phoxinus*, one that had long been sympatric with the pike, *Esox lucius*, and one that presumably had never experienced pike predation. Like Seghers, she found that experienced minnows behaved more cautiously towards the pike than did the inexperienced minnows. However, unlike Seghers' study, food was also present in the test arena, so that the response of the minnows involved both the value of food and the risk of predation. In Seghers' study, the guppies could respond to the threat of predation without losing food. In this respect, our study was closer to Magurran's, yet our most salient finding was a consistently greater tenacity of the downstream fish, irrespective of species or river system, in spite of the fact that upstream sites were always less dangerous than downstream sites.

We do not know why the downstream populations are "bolder" than upstream ones. Indeed, one can identify a suite of selective forces that could result in the differences in tenacity that we found. For example, when hazard levels are not likely to diminish in time, as in downstream areas, waiting for safe conditions could be a costly solution. Chronically high mortality rates can also place a premium on rapid growth by juveniles (Werner and Gilliam 1984). Under such circumstances selection might modify response to hazard in ways that raise the level of tenacity; it may favor boldness while foraging under hazardous conditions. In addition, it is possible that downstream fish "feel" safer, because they can detect predators at relatively long distances, are more cryptic (male guppies, Endler 1978) or normally school.

Since we observed the same results with both the live and model predator, in both species and both rivers, we feel that the differences in tenacity reflect real and consistent differences in the response of the up- and downstream populations to predation threat and/or the value of food. However, perception of predatory threat can be imperfect (e.g. Thorpe 1963; Otis and Cerf 1963; Karpus and Algom 1981; Fraser and Mottolose 1984), and we cannot dismiss the possibility that upstream fish were reacting especially strongly to novel predator stimuli, given their lack of information on the stimuli, since neither *Aequidens* nor *Crenicichla* occurs in the upstream areas. Thus, the contrast between the up- and downstream fish might disappear, or even reverse, if different predator stimuli were used or if the subjects were given different experiences with predators.

Differences related to sex

Farr (1975) found that downstream male guppies courted more intensely than did upstream males, and our data suggest that differences in tenacity between upstream and downstream populations are stronger for male guppies than for females. It is possible that these two traits, boldness in feeding and in courting, have motivating factors (e.g. hormone levels) in common. For example, downstream males are more cryptic than upstream males, because sexual selection has been overridden by predator selection for crypsis (Endler 1978, 1983), and it is possible that, given the dull coloration of downstream males, compensatory selection for boldness may have occurred in downstream males, where boldness is reflected in both tenacity while feeding and aggressiveness in courting (Farr attributes the aggressiveness to accentuated male-

male competition in schooling downstream populations). Indeed, Huntingford (1976) found that two aspects of boldness, antipredator behavior and aggression towards conspecifics co-varied in the three-spined stickleback, *Gasterosteus aculeatus*. She suggested that the two traits depended, in part, on common internal factors. Our findings and those of Farr (1975) suggest yet another instance of this phenomenon which deserves further study.

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References

- Efron B (1982) The jackknife, the bootstrap and other resampling plans. Society for Industrial and Applied Mathematics. Philadelphia, Pennsylvania, USA
- Endler JA (1978) A predator's view of animal color patterns. *Evol Biol* 11: 319–364
- Endler JA (1983) Natural selection on color patterns in poeciliid fishes. *Envir Biol Fishes* 9: 173–190
- Farr JA (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
- Fraser DF, Mottolese TN (1984) Discrimination and avoidance reactions towards predatory and nonpredatory fish by blacknose dace, *Rhinichthys atratulus* (Pisces: Cyprinidae). *Z Tierpsychol* 66: 89–100
- Fraser DF, Huntingford FA (1986) Feeding and avoiding predation hazard: the behavioral response of the prey. *Ethology* 73: 57–68
- Giles N, Huntingford FA (1984) Predation risk and inter-population variation in anti-predator behaviour in the three-spined stickleback, *Gasterosteus aculeatus* L. *Anim Behav* 32: 264–275
- Gilliam JF, Fraser DF (1987) Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* (in press)
- Goodey W, Liley NR (1986) The influence of early experience on escape behaviour in the guppy (*Poecilia reticulata*). *Can J Zool* 64: 885–888
- Haskins CP, Haskins EF, McLaughlin JJA, Hewitt RE (1961) Polymorphism and population structure in *Lebistes reticulatus*, a population study. In: Blair WF (ed) *Vertebrate speciation*. University of Texas Press, Austin, pp 320–395
- Huntingford FA (1976) The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Anim Behav* 24: 245–260
- Karplus I, Algom D (1981) Visual cues for predator face recognition by reef fishes. *Z Tierpsychol* 55: 343–364
- Liley NR, Seghers BH (1975) Factors affecting the morphology and behavior of guppies in Trinidad. In Baerends GP, Beer C, Manning A (eds) *Function and evolution in behaviour*. Oxford University Press, Oxford, pp 92–118
- Magurran AE (1986) Predator inspection behaviour in minnow shoals: differences between populations and individuals. *Behav Ecol Sociobiol* 19: 267–273
- Meyer JS, Ingersoll CG, McDonald LL, Boyce MS (1986) Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. *Ecology* 67: 1156–1166
- Milinski M, Heller H (1978) Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* 275: 642–644
- Otis LS, Cerf JA (1963) Conditioned avoidance learning in two fish species. *Psychol Rep* 12: 679–682
- Reznick DN, Endler JA (1982) The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* 36: 160–177
- Seghers B (1973) An analysis of geographic variation in the antipredator adaptations of the guppy, *Poecilia reticulata*. PhD Thesis, University of British Columbia
- Seghers B (1974a) Schooling behavior in the guppy (*Poecilia reticulata*): an evolutionary response to predation. *Evolution* 28: 486–489
- Seghers B (1974b) Geographic variation in the response of guppies (*Poecilia reticulata*) to aerial predators. *Oecologia (Berl)* 14: 93–98
- Thorpe WH (1963) *Learning and instinct in animals*, 2nd ed. Harvard University Press
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Ann Rev Ecol Syst* 15: 393–425