

## Courtship behavior, swimming performance, and microhabitat use of Trinidadian guppies

Astrid Kodric-Brown<sup>a</sup> & Paul F. Nicoletto<sup>b</sup>

<sup>a</sup>UNM Biology Department, University of New Mexico, MSC03 2020, Albuquerque, NM 87131, U.S.A.

<sup>b</sup>Department of Biology, Lamar University, P.O. Box 10037, Beaumont, TX 77710, U.S.A.

(e-mail: kodric@unm.edu)

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### Synopsis

We document differences in the use of microhabitats, male courtship behavior, and swimming performance of populations from headwater and downstream sites in two rivers of the Oropuche drainage in Trinidad. Guppies from headwater sites used microhabitats with higher water velocities, had a higher swimming performance, and were less patchily distributed than guppies from downstream sites. Although males from the headwater and downstream sites had similar display rates, males from headwater sites displayed in microhabitats with higher velocities (riffles) whereas males in downstream sites courted in still pools. Subtle effects of female choice maintain the honesty of male courtship behavior in various microhabitats. In downstream sites, where predators impose a survivorship cost on ornamental males, swimming performance was positively correlated with area of carotenoid ornamentation. In headwater sites, males frequently displayed in fast-flowing water, thus paid a higher metabolic cost of courtship. Interactions between characteristics of the physical habitat and predation pressure not only affect the distribution of guppies, but also have subtle effects on the types of condition-dependent traits favored by females.

### Introduction

Many sexually selected traits of males are costly to produce and maintain. The evolution of female preferences for such male traits has been modeled theoretically (Johnstone 1995) and tested empirically (reviewed in Andersson 1994, Houde 1997). Often male traits are condition-dependent and their expression varies with diet quality, social context, and the presence of parasites and pathogens (Candolin 2003). Female preferences for such male traits also vary (Forsgren 1992, Hedrick & Dill 1993). Physical attributes of the habitat, such as light conditions and water clarity (Endler 1995, Seehausen et al. 1997) may affect the expression of both male

secondary sexual traits and female preferences for these traits.

Both biotic and abiotic factors affect the distribution and behavior of guppies in streams in Trinidad. Intensity of predation is correlated with changes in social structure, life-history traits, and the expression of male secondary sexual traits, such as color patterns and courtship behavior (Endler 1995, Rodd & Reznick 1997). Interactions between predation and stream characteristics, especially water velocity, affect the distribution of guppies (Nicoletto & Kodric-Brown 1999). Water velocity affects the size, shape, and swimming performance of fish (Videler 1993). Experimental manipulation of water velocity in the laboratory not only affected the appearance and swimming

performance of male guppies, but also their display rates and attractiveness to females (Nicoletto 1996).

Here we examine how the physical features of the habitat interact with predation to determine the distribution of guppies in streams, and use of available microhabitats in courtship. (1) *Microhabitat use*. The distribution of guppies within streams reflects predation pressure. In the absence of piscivorous predators, guppies should occupy most available microhabitats, and experience a wide range of water velocities. In predator-rich communities, guppies are more patchily distributed. Their distribution should reflect selection of habitats, such as shallow, slow moving water, that minimize the risk of predation. This differential use of microhabitats by populations experiencing different levels of predation, should affect both physiological performance and courtship behavior.

(2) *Male display behavior and swimming performance*. Courtship should reflect a balance between risk of predation and the energetic constraints imposed by water velocities in different microhabitats. In the absence of predators, both sexes should utilize a greater range of microhabitats. Since swimming performance scales isometrically with body size (Domenici 2001) and adult females are larger than males, they can use microhabitats with water velocities that are not necessarily optimal for males. Thus females may impose an additional energetic cost on male displays. In high-predation environments, both sexes are restricted to microhabitats with slow-moving water, and males would not pay additional energetic costs of displays.

Although the importance of predators as a strong selective agent for reduced display rate, as well as expression of conspicuous coloration, is known (e.g. Endler 1980, Magurran & Seghers 1990), the importance of water velocity on courtship behavior, and especially choice of microhabitats by males has yet to be demonstrated.

In this study we (1) document interacting effects of physical factors (velocity and depth) and predation on the distribution of guppies at several sites in the Quare and Oropuche rivers; (2) describe differences in the display behavior and swimming performance of male guppies at these sites; and (3) document differences in courtship behavior in microhabitats that differ in water velocity and depth.

## Methods

We studied microhabitat use and behavior of guppies in the Quare and Oropuche Rivers for the following reasons. (1) The two rivers are part of the same drainage system (the Oropuche), and both guppies and their predators share a similar microevolutionary history (Fajen & Breden 1992). (2) Guppies at the Quare sites are subjected to low to moderate levels of predation, primarily from predators such as *Rivulus hartii*, *Aequidens pulchur*, and the freshwater prawn, *Macrobrachium crenulatum*, which pose little threat to adults (Endler 1995). Guppies at the Oropuche sites experience high levels of predation. Predators such as *Hemibrycon dentatum*, and especially the pike cichlid, *Crenicichla cardiostigma* (Ploeg 1991), are major predators of guppies (Table 1; Endler 1978, Matingly & Butler 1994).

Table 1. Sampling site, grid reference, predation intensity, and types of predators in the Quare and Oropuche rivers of Trinidad.

Sampling site	Grid reference*	Predation rate**	Predators at sampling sites***
Quare 1	PS 971 813	Low	<i>Rivulus</i> , <i>Aequidens</i> , <i>Macrobrachium</i>
Quare 2	PS 973 808	Low	<i>Rivulus</i> , <i>Aequidens</i>
Quare 3	PS 973 805	Low	<i>Rivulus</i> , <i>Aequidens</i>
Quare 4	PS 973 800	Medium	<i>Rivulus</i> , <i>Crenicichla</i> , <i>Hemibrycon</i>
Oropuche 1	QS 036 800	High	<i>Rivulus</i> , <i>Crenicichla</i> , <i>Hemibrycon</i>
Oropuche 2	QS 039 794	High	<i>Rivulus</i> , <i>Aequidens</i> , <i>Crenicichla</i> , <i>Hemibrycon</i>
Oropuche 3	QS 041 791	High	<i>Rivulus</i> , <i>Crenicichla</i> , <i>Hemibrycon</i>

\* Grid references from Universal Transverse Mercator Grid, Zone 20, 1:25000 topographical maps (Land and Surveys Division, Trinidad and Tobago Government, 1978).

\*\* Predation categories obtained from Endler and Houde (1995), and from personal observations.

\*\*\* *Rivulus hartii*, *Aequidens pulchur*, *Macrobrachium crenulatum*, *Crenicichla cardiostigma*, *Hemibrycon dentatum*.

### *Sites*

The study was conducted between 19 May and 2 June 1997, before the arrival of the wet season, when water levels were low and visibility was excellent. We sampled four sites on the Quare River and three sites on the Oropuche River. We did not find a suitable fourth site on the Oropuche River. The pike cichlid was abundant at all three sites in the Oropuche River, but was absent at three of the four sites in the Quare River (Table 1). At the fourth site it was present, but occurred in low numbers (2 individuals compared to 10–15 per site in the Oropuche River). The sampling sites were spaced approximately 1 km apart, and were chosen because they were accessible and representative of the aquatic habitats of these streams. Each site consisted of a 50 m section of the river with a transect placed every 10 m. Along each of the six transects we measured velocity, depth, and presence/absence of guppies at 1 m intervals across the width of the river. Water velocity was measured with a flow meter (Swoffer 2100), and depth with a meter stick held vertically in the water column. We determined presence or absence of guppies by scanning the area within 1 m radius of the point location where we recorded water velocity and depth. We controlled for inter-observer bias in detection ability by independently scanning the same area and recording the presence or absence of guppies. Upon arrival at each site, and before we began taking measurements, we quantified the number and type of predators by visually scanning each 10 m section of the site from shore.

### *Male courtship*

At each site between 8:00 and 11:00 h, we recorded the display behavior of randomly selected focal males from shore, and measured depth and water velocity at each display site. We observed each male for 1–5 min and recorded the number of courtship displays. The duration of each observation depended on the length of time the male was courting and his mobility. The display rate for each focal male was calculated by dividing the number of displays by the time the male was observed. Courtship consists of a series of sinusoidal movements of the body when the male is

perpendicular to, or in front of a female (Clark & Aronson 1951, Baerends et al. 1955). We minimized the probability of repeatedly observing the same male by choosing males differing in color patterns as well as different locations within each site. We recorded the display rate of 49 males (9–14 per site) in the Quare River and 42 males (12–17 per site) in the Oropuche River.

### *Male swimming performance*

We collected 43 males from the four sites of the Quare River and 54 males from the three sites of the Oropuche River. At each site we caught males with dip nets, took them back to the laboratory, and placed them in 75 l holding tanks for 24 h to acclimate them. The next day we measured their swimming performance in a flow chamber. Swimming performance was measured by determining a male's critical swimming speed, which is the maximum speed that a male can sustain for a given time period in a flow chamber (Brett 1964, Kolok 1999). Critical swimming speed is a common measure of swimming performance and is correlated with health, active metabolism and endurance (Martinez et al. 2003). Swimming performance was measured by placing each fish into a 1.2 m long, 1.8 cm in diameter transparent PVC pipe (the swimming chamber), with an initial water velocity of 7.8 cm s<sup>-1</sup> for 5 min, then the velocity was increased 2.9 cm s<sup>-1</sup> every 5 min until the guppy contacted a screen placed over the outflow end of the chamber for 3 s. A collimator was placed at the inflow end of the swimming chamber to ensure that the water velocity profile was rectilinear and microturbulent. We recorded the highest velocity and the time the fish spent at that velocity, and calculated critical swimming speed (Brett 1964). A complete description of the swimming chamber and methodology is given in Nicoletto (1991). We cannot exclude the possibility that some of the males used in the swimming performance trials might have been the same ones that were observed displaying to females, but it was unlikely that many males were reused, because collection for the swimming performance trials were made over several days following courtship observations.

Each male was anesthetized with MS-222, measured for standard length with a pair of digital calipers accurate to 0.01 mm, then photographed

with a 35 mm camera with a 50 mm macro lens and 400 ASA slide film (Kodak) under a GE 'Plant and Aquarium F20T12-PL- AQ' fluorescent light. Male color pattern was quantified by projecting a slide onto a computer digitizing tablet and recording the area and the number of carotenoid spots (Nicoletto & Kodric-Brown 1999). The proportion of the body covered by carotenoids was determined by dividing the total area of spots by body area, thereby standardizing for variation in body size. Analysis of color pattern revealed that swimming trial samples contained both showy (15–25% area of carotenoids) and dull males (2–5% area of carotenoids), and represented the diversity of male color patterns at these sites.

#### *Statistical analyses*

Data on water depth and velocity between sites and microhabitat preferences of guppies were analyzed with a two-way analysis of variance on rank-transformed data (Conover & Iman 1981). The factors used in the analyses were the point location (at each m) along a transect and the presence or absence of guppies. The water depth and velocity data were rank-transformed because they were not normally distributed. Differences between sampling sites were analyzed with a Tukey mean separation procedure.

Differences in swimming performance of guppies from the Quare and Oropuche rivers were evaluated with a one-way analysis of covariance on rank-transformed data. The standard length of males was used as the covariate. Differences in area of carotenoid pigment and display rate of males in the Quare and Oropuche Rivers were evaluated, respectively, with a Mann–Whitney-rank-sum test and a Kruskal–Wallis one-way analysis variance on ranks. Data on display rates were analyzed with a two-way nested analysis of variance, with sites nested within rivers. The relationships between display rate and water depth and velocity, and between swimming performance and percent carotenoid coloration were evaluated with Spearman rank correlations for each river. Velocities at which guppies displayed and those at the point locations where they were present were compared with a Mann–Whitney rank sum test for the Quare and the Oropuche Rivers.

## **Results**

### *Physical features of rivers and guppy distributions*

In both rivers at the sites we sampled, microhabitats of guppies varied in depth and water velocity. The sites at the Oropuche River were deeper than those at the Quare River when we combined all point locations sampled within rivers (Mann–Whitney U test  $T = 33,518.5$ ,  $p < 0.0001$ ). Depth varied between sites within each river (Kruskal–Wallis one-way ANOVA, Quare:  $H = 8.20$ ,  $df = 3$ ,  $p = 0.042$ ; Oropuche:  $H = 18.35$ ,  $df = 2$ ,  $p < 0.001$ ). The two rivers did not differ in water velocity when all point locations were combined (Mann–Whitney U test,  $T = 42,819.5$ ,  $p = 0.143$ ). Water velocity varied between sites in the Oropuche River (Kruskal–Wallis one-way ANOVA,  $H = 11.53$ ,  $df = 2$ ,  $p = 0.003$ ), but not in the Quare River (Kruskal–Wallis one-way ANOVA,  $H = 1.435$ ,  $df = 3$ ,  $p = 0.697$ ). Velocity and depth were not positively correlated in the Quare River ( $r_s = -0.035$ ,  $p = 0.65$ ,  $n = 173$ ), or the Oropuche River ( $r_s = -0.19$ ,  $p = 0.72$ ,  $n = 297$ ).

The distribution of guppies differed between the two rivers. In the Quare River guppies were widely distributed, and were present at 105 (61%) of the 173 point locations sampled. They showed microhabitat selection only for velocity (Table 2,  $p < 0.001$ ), and occurred at lower velocities (in all four sites Figure 1b) than were available at the sites sampled. Depth had no overall effect on the distribution of guppies in the Quare River (Table 2,  $p = 0.136$ ; Figure 1a). In contrast, in the Oropuche River guppies were much more restricted, and were present in only 45 (15%) of the 297 point locations sampled. They showed microhabitat selection for both velocity and depth (Table 2, velocity  $p < 0.001$ , depth  $p = 0.005$ ), and occurred in a narrower range of both variables than were available in the river (at all sites for velocity Figures 1b and 2 of 3 sites for depth Figure 1a). In the Oropuche the highly significant restricted guppy distribution relative to availability for both velocity and depth (Table 2) rejects the null hypothesis that the low frequency of occupied point locations is due to chance and low overall abundance; i.e., the distribution cannot be attributed simply to random sampling.

Table 2. Results of two-way ANOVAs of the presence/absence of guppies and the depth and velocity at four sites in the Quare River and three sites in the Oropuche River of Trinidad Quare River.

Variable	Source of variation	DF	MS	F	p
Quare River Velocity (cm s <sup>-1</sup> )	Guppy	1	105,734.78	58.94	<0.001
	Site	3	94.93	0.05	0.984
	Guppy*Site	3	3863.24	2.15	0.095
Depth (mm)	Guppy	1	4923.36	2.24	0.136
	Site	3	9345.49	4.25	0.006
	Guppy*Site	3	11,097.83	5.05	0.002
Oropuche River Velocity (cm s <sup>-1</sup> )	Guppy	1	153,340.89	24.28	<0.001
	Site	2	23,211.84	3.67	0.027
	Guppy*Site	2	569.75	0.09	0.914
Depth (mm)	Guppy	1	54,147.04	8.03	0.005
	Site	2	51,255.28	7.60	<0.001
	Guppy*Site	2	1825.66	0.27	0.763

In both rivers sites differed in depth. There was a significant interaction between guppy presence/absence and site in the Quare River (guppy\*site interaction,  $p = 0.002$ ), but not in the Oropuche River ( $p = 0.763$ ). There was significant variation in water velocity between sites in the Oropuche ( $p = 0.027$ ) but not in the Quare River ( $p = 0.984$ ), and lack of a guppy by site interaction in both rivers (Table 2). In both rivers guppies occurred in microhabitats with slow-moving water and were absent in velocities exceeding 8 cm s<sup>-1</sup> (Figure 1b).

#### Male courtship

Although male display rates did not differ between rivers ( $F_{1,90} = 0.06$ ,  $p = 0.80$ ) and were not correlated with depth ( $r_s = 0.04$ ,  $p = 0.66$ ,  $n = 91$ ), there were differences in the water velocities in which males displayed (Figure 2). In the Quare River males displayed in a wide range of velocities, from 0 to 20 cm s<sup>-1</sup>, and display rate was positively correlated with velocity  $r_s = 0.31$ ,  $p = 0.01$ ,  $n = 50$ ). In the Quare River, 86% of courtship was observed in flowing water, especially in riffles. Males were frequently swept several meters downstream and had to swim back upstream to resume their courtship of a female. Males in the Oropuche River displayed in lower velocities from 0 to 5 cm s<sup>-1</sup>, 78% of displays occurred in still water, and display rate was not correlated with velocity ( $r_s = 0.11$ ,  $p = 0.45$ ,  $n = 41$ ).

Comparisons of depths and velocities of microhabitats in which guppies were seen (presence/absence data) with those where males courted females, showed that guppies did not necessarily use the same microhabitats to court as they did for other activities, such as foraging (Figure 3a, b). In the Quare River males displayed at higher velocities than they utilized for other activities (Mann–Whitney Rank Sum:  $T = 12,442$ ,  $p < 0.001$ ). This was not the pattern seen for males in the Oropuche River. Courtship as well as other activities took place in microhabitats with the same narrow range of velocities. Because of the limited variation of velocities in which males displayed (Figure 3, mostly in still water), we could not perform a similar analysis for the Oropuche males as we did for the Quare males. Comparisons of depths of microhabitats in which males displayed and where they performed other activities showed that in the Quare River males displayed at similar depths as those where they performed other activities ( $T = 15,469$ ,  $p = 0.206$ ), while in the Oropuche River males displayed in deeper water than they utilized for other activities ( $T = 1604.5$ ,  $p < 0.001$ ).

#### Male swimming performance

Males from the two rivers differed in their swimming performance ( $F_{2,95} = 17.94$ ,  $p = 0.001$ ). Males from the Quare River swam at higher velocities than males from the Oropuche River

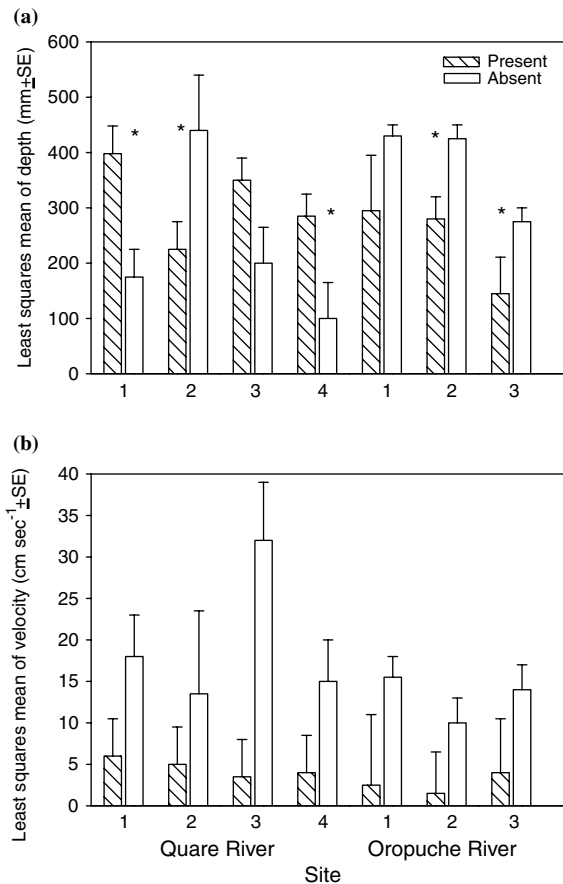


Figure 1. (a) Distribution of depth (least squares mean  $\pm$  SE mm) and (b) velocity (least squares mean  $\pm$  SE  $\text{cm s}^{-1}$ ) of guppies present (open bars) and absent (hatched bars) at four 50 m reaches of the Quare River and three 50 m reaches of the Oropuche River in Trinidad. Depths at which guppies were present differed from those where they were absent in the Quare River (sites 1, 2, 4; Dunn's multiple comparison test,  $p < 0.05$ ) and in the Oropuche River (sites 2, 3; Dunn's multiple comparison test,  $p < 0.05$ ). In the Quare River guppies were found in deeper water at sites one and four and in shallower water at site two. In the Oropuche River guppies were found in shallower water at sites two and three. Presence or absence of guppies was not affected by depth at site three in the Quare River and site one in the Oropuche River. In both rivers guppies occurred in microhabitats with slow-moving water.

( $F_{1,96} = 6.00$ ,  $p = 0.01$ ). Although males in the two rivers did not differ in the area of body covered by carotenoid spots ( $T = 2139$ ,  $p = 0.82$ ,  $n = 97$ ), swimming performance was positively correlated with carotenoid ornamentation in Oropuche ( $r_s = 0.27$ ,  $p = 0.04$ ,  $n = 54$ ) but not in Quare males ( $r_s = 0.05$ ,  $p = 0.76$ ,  $n = 43$ ). Males

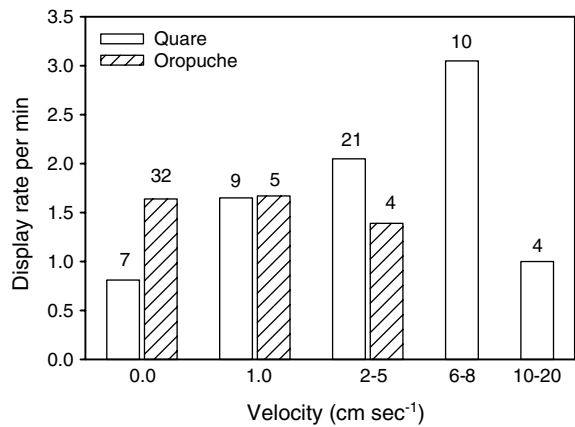


Figure 2. Display rates of male guppies at different velocities in the Quare River (open bars) and Oropuche River (hatched bars) in Trinidad. Numbers above bars indicate sample sizes. Note that Quare River males displayed in a greater range of water velocities than Oropuche males. Display rate was positively correlated with water velocity in the Quare River ( $r_s = 0.32$ ,  $p = 0.01$ ,  $n = 50$ ), but not in the Oropuche River ( $r_s = 0.11$ ,  $p = 0.45$ ,  $n = 41$ ).

from the two rivers also differed in size ( $F_{1,96} = 10.09$ ,  $p = 0.002$ ). Quare males were larger (standard length  $\pm$  SE;  $23.76 \pm 0.53$  mm) than Oropuche males ( $21.56 \pm 0.24$  mm). The higher swimming performance of Quare males was not due to their larger size, since we standardized swimming performance by male size by using size as a covariate in our analyses.

## Discussion

Both population density and the presence of predators contribute to the observed differences in the distribution of guppies in the two rivers. Guppies occur at higher densities in headwater streams where piscivorous predators are absent than in lowland streams with diverse communities of piscivorous predators (Endler 1995, Reznick et al. 2001). Our data indicate that across all sites in each river incidence of guppies was approximately four times higher in the Quare than in the Oropuche. These values are not densities, since we did not record the number of individuals encountered at each point location. In the Quare River, where guppies had fewer piscivorous predators they were more widely distributed, and occupied a greater diversity of habitats, including the faster-flowing

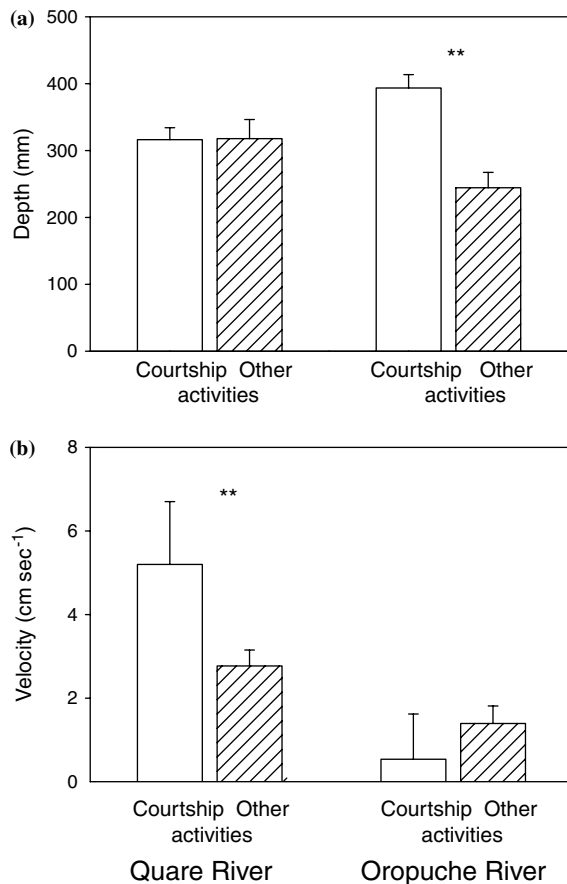


Figure 3. Comparisons of (a) depth (mean  $\pm$  SE mm) and (b) velocity (mean  $\pm$  SE cm s<sup>-1</sup>) of microhabitats where males courted and those guppies utilized for other activities in the point location census (presence or absence data). In the Quare River males courted in microhabitats with higher velocities than they utilized for other activities ( $p < 0.001$ ). In the Oropuche River males courted in deeper water than they utilized for other activities ( $p < 0.001$ ).

riffles. In the Oropuche River guppies were restricted to shallow, calm water. So, predators have two effects on guppy distribution. They increase patchiness and reduce the diversity of microhabitats used by guppies. Fraser et al. (1995) showed a similar effect of predators on the distribution of prey species (*Rivulus hartii*) in two Trinidadian streams. Differences in the choice of microhabitats by guppies in these two populations suggest an interaction between biotic factors (predation pressure and intraspecific competition), and abiotic factors (velocity and depth).

Although males from the Quare and Oropuche Rivers had similar display rates, they differed in

the types of microhabitats in which they displayed. An interesting pattern emerges when we compare the microhabitats in which males displayed and those in which guppies performed other activities. In the Oropuche River, where predators restrict guppies to calm water, males courted in deeper water than expected on the basis of their occurrence (Figure 3). Male color patterns, especially the carotenoids, which are preferred by females but also are conspicuous to guppy predators, increase the predation risk to males (Haskins et al. 1961, Endler 1980, Matingly & Butler 1994, Godin & McDonough 2003). Courting females in deeper water imposes a greater predation risk to conspicuous males than to drab, cryptic females. In the Quare River, where predation pressure on adults is low, males displayed in microhabitats with much faster flowing water than expected based on their occurrence (Figure 3). Since energy expenditure decreases with size, while swimming speed increases with size (Videler 1993), the smaller males pay a disproportionate cost relative to the larger females for courting in fast-flowing water. Thus female choice may select for energetically costly displays in microhabitats with higher flow rates (e.g. Takahashi & Kohda 2001). An alternative, but not mutually exclusive explanation for this pattern is that females attempt to escape harassment by courting males and seek microhabitats, such as riffles, visited only by males in good physical condition.

Differences in the swimming performance between guppy populations in the Quare and the Oropuche reflect differences in habitat use and the water velocities encountered (Nicoletto 1996, Nicoletto & Kodric-Brown 1999). Swimming performance is also a measure of endurance, which reflects physical condition (Nicoletto 1991, 1996). In high-predation environments, where ornamented males are especially likely targets for predators, one measure of a male's quality is his ability to avoid predators. In the Oropuche River, where predators such as the pike cichlid are abundant and exert a strong predation pressure on ornamented males, we show a positive correlation between males' showiness and their swimming performance. A meta-analysis by Jennions et al. (2001) showed a positive interaction between ornament size and survivorship for a number of taxa, suggesting that males with maximum

expression of ornaments are better at avoiding predators. Both laboratory experiments by O'Steen et al. (2002) and field observations (Magurran et al. 1992) showed rapid evolution of escape ability in Trinidadian guppies subjected to different rates of predation. Thus guppies in high-predation environments would be better at escaping predators than those in low-predation environments. In a series of laboratory experiments, Godin & Dugatkin (1996) showed a positive correlation between the conspicuousness of a male's color pattern (especially the area of carotenoid pigment), the willingness to approach and inspect a potential predator and escape distance from the predator. No such correlation between male showiness and swimming performance was shown for males in the stretches of the Quare River we sampled, where predation rates by piscivorous fish on adult guppies are low.

Several studies to date have shown that female choice is condition-dependent and is often based on multiple criteria such as ornamentation and display rate (Kodric-Brown 1993, Andersson, 1994 and references cited therein; Godin & Dugatkin 1996). Our results on habitat use and display rates of male guppies suggest that female choice is not only condition-dependent, but subtle as well. Thus females may select not only for differences among males in courtship behavior and color patterns, but also for differences in the use of microhabitats that would impose additional costs for males during courtship. In downstream habitats where predation on showy males by piscivorous predators is intense (Haskins et al. 1961, Endler 1978, 1980, Rodd & Reznick 1997, Reznick et al. 2001), both sexes seek microhabitats with slow moving water, that maximize survival. Nevertheless, females impose an additional cost by 'forcing' males to display in deeper water, where predation risk is greater. In upstream habitats, females may impose an additional cost by 'forcing' males to display in microhabitats with faster flow rates. Positive correlations between courtship displays in high-velocity microhabitats in low-predation environments suggest that: (1) female choice of males is condition-dependent and selects for male traits that are costly (thus honest), (2) females may take advantage of environmental conditions that impose additional energetic costs on male courtship, and (3) the types of traits that are selected often

depend on the interaction between abiotic and biotic environmental conditions.

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