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The relationship among swimming performance, courtship behavior, and carotenoid pigmentation of guppies in four rivers of Trinidad

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Synopsis

In the laboratory, courtship behavior and carotenoid pigmentation of male guppies are condition-dependent traits, since their expression is affected by physical vigor and environmental factors such as water velocity and diet. Whether these relationships exist in guppies under field conditions is yet to be determined. We compared the swimming performance, courtship behavior, and carotenoid pigmentation of guppies from headwater and downstream localities in four rivers of Trinidad. Swimming performance and courtship behavior of males differed among rivers and between headwater and downstream sites. Guppies from headwater sites swam significantly faster and had higher display rates than those from downstream sites. Mean swimming performance across sites was positively correlated with mean water velocity, but was correlated with the number of orange color spots (carotenoid pigment) in only one river. These results indicate that the courtship behavior of Trinidadian guppies is condition-dependent because the amount of display behavior is positively correlated to swimming performance, a measure of physical endurance. The proximal cause for this condition-dependence may be predator induced variation in microhabitat use by guppies in headwater and downstream locations.

Introduction

Many male secondary sexual characteristics and behaviors are influenced by social, genetic, and ecological factors (Endler 1983, 1987, 1995, Kodric-Brown 1989, Møller 1990, Zuk 1991). Such traits are thought to be favored by sexual selection, because they are indicators of the male's ability to survive and potentially reproduce in a given habitat (Andersson 1994 and references therein). These ornaments and behaviors are often called condition-dependent because the degree of their expression is positively correlated to various measures of an animal's overall health or physical condition (Zahavi 1975, Kodric-Brown & Brown 1984, Pomiankowski 1987). Thus, such traits may reflect both phenotypic vigor and adaptation to local environmental conditions. Condition-dependent ornaments and behavior may interact in complex ways to provide information about the short- and long-term condition of the male (Endler 1983, Kodric-Brown 1989, Nicoletto 1991, 1993). For example, courtship behavior and nuptial coloration reflect the animal's physical condition by showing its access to resources, health, and current motivational state (Trivers 1972, Searcy 1982, West-Eberhard 1983, Hill 1990, Møller 1990, Kodric-Brown 1993, Byers et al. 1994, Buchholz 1995). Such secondary sexual traits also vary with ecological circumstances such as predation intensity, population density, habitat productivity, and other environmental variables (Kodric-Brown & Brown 1984, Luyten & Liley 1985, Endler 1987, 1991, 1995, Magurran & Seghers 1994, Nicoletto 1996).

The numerous factors that can influence the inheritance, genetic divergence, development, and expression of sexually selected traits have been extensively studied in the guppy, *Poecilia reticulata*. Populations of guppies in the rivers of Trinidad are highly variable in social structure, color pattern, male courtship behavior, body size, and life history (Endler 1995). Much of this variation is influenced by predation. Guppies from headwater habitats experience less predation, are larger, have more complex color patterns, higher display rates, and less well developed anti-predator behavior than guppies from downstream habitats (Seghers 1974, Endler 1978, 1983, Reznick & Endler 1982, Luyten & Liley 1985, Magurran & Seghers 1994).

Physical conditions of the streams in which guppies live also vary and may influence the development and expression of secondary sexual characteristics (Luyten & Liley 1985, 1991, Winemiller et al. 1990, Endler 1991). Headwater streams are smaller, shallower, have steeper gradients, lower productivity, less suspended sediment, and lower light levels than downstream habitats (Luyten & Liley 1985, Endler 1991). Water velocities where guppies live also vary within and between rivers (Luyten & Liley 1985). In headwater habitats guppies occur throughout the stream and experience a variety of water velocities. In downstream habitats, the presence of predators restricts guppies to shallow areas near the edges of streams with low water velocities (Luyten & Liley 1985). Water velocity in different microhabitats can have a significant influence on the survivorship, size, shape, and swimming performance of fish (Burrows 1969, Cresswell & Williams 1983, Taylor & McPhail 1986). Experimental manipulation of water velocity has shown that male guppies raised in high water velocity conditions had deeper bodies, faster swimming speeds, more intense displays, and elicited more female sexual responses than males raised in low water velocity (Nicoletto 1996). Thus, an abiotic factor, water velocity, can influence the expression of male display behavior and potentially affect male mating success.

This study had two objectives. First, we wanted to determine whether the degree of expression of the carotenoid pigmentation and display behavior of wild-caught Trinidadian guppies is condition-dependent. We predicted a positive relationship between male swimming endurance and the development of orange color spots because carotenoid pigments are acquired from the diet, and thus reflect a male's physical condition (Endler 1983, Kodric-Brown 1989). We also predicted that swimming performance, water velocity, and display rate should be positively correlated with each other at the population level because laboratory data indicate that increased water velocity enhances muscle development which in turn may affect swimming performance and display behavior (Nicoletto 1996).

The second objective was to compare the swimming performance, carotenoid pigmentation, and display behavior of guppies from headwater and downstream habitats and among rivers. We hypothesized that the swimming performance of guppies should differ between localities and among rivers. We predicted that guppies from headwater localities would not only have higher display rates and more carotenoid pigmentation (Endler 1983, Luyten & Liley 1985), but also have significantly greater swimming performances. Variation in behavior, coloration, and morphology among rivers is well documented (reviewed in Endler 1995). We wished to determine if there was similar variation in swimming performance and if so, if there was parallel variation in carotenoid pigmentation and display. We were primarily interested in display behavior and swimming performances because of the links established between these two variables in the laboratory (Nicoletto 1996).

Materials and methods

Study sites and water velocity

We visited a headwater and a downstream site on the Limon (upper Yarra), Yarra, Quare, Guanapo, and Oropuche rivers between 17 and 31 May 1995. Sites were chosen because they were accessible, representative of the stream at that geographic location, and they had the abiotic characteristics of either headwater or downstream habitats that were described in the introduction (Table 1). At all but one site (lower Quare) we took multiple measures of flow rates using the floating canister method (Robins & Crawford 1954). We used a half-empty film canister and a meter stick and recorded the time that it took the float to travel a distance of 1 m. At each of these sites we took four (Yarra and Quare) or six (Oropuche and Guanapo) water velocity measurements across the entire stream at regular intervals. We did not measure water velocity at the lower Quare site, because the fish were located in small pools that had virtually no flow. This site was located in an area with a steep grade and near the head of a waterfall. Thus, the

Table 1. Location, elevation, predation intensity, and elevation drop of eight sites on four rivers in Trinidad.

Locality	Location	Elevation (meter)	Predation*	Elevation drop (meters)
Lower Guanapo	PS 910 787	58	Medium	64
Upper Guanapo	PS 901 818	122	Medium	
Lower Oropuche	QS 038 795	38	High	62
Upper Oropuche	QS 024 851	100	High	
Lower Quare	PS 975 794	69	Medium	68
Upper Quare (Campo River)	PS 971 813	137	Low	
Lower Yarra	PS 801 938	15	High	76
Upper Yarra (Limon River)	PS 833 875	91	Low	

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

fish at this site probably periodically experience high water velocities.

The water velocity of headwater and downstream sites was compared using a Mann-Whitney *U* test. Comparisons of water velocity among rivers were made with a Kruskal-Wallis test and differences between river were evaluated with Dunn's method. Guppies from the lower Quare were collected from pools with zero flow, therefore we did not compare the water velocity at headwater and downstream sites in this river.

Display behavior

At each site we observed focal males between 8:00 and 12:00 h and recorded the number of courtship displays and copulation attempts. We observed each male for no more than five minutes but the duration of observations varied depending upon the male's mobility and the sunlight and wind conditions. Male guppies display in front of and perpendicular to the female. The courtship display consists of rapid waves of lateral muscle contraction which results in a rapid head to tail flexing of the male's body (Baerends et al.1955). The display rate was calculated by dividing the number of courtship displays by the length of time that the male was observed and was analyzed as displays per minute. Copulation attempts occur when the male swims beside the female and attempts to insert his gonopodium into the female's urogenital pore. The focal males were selected arbitrarily. When the focal male swam from view another male was observed. Care was taken not to observe the same male twice; individuals could be distinguished easily by their unique color patterns.

Swimming performance

Twenty five male guppies were collected by dip netting at each site, taken back to the Simla Research Station and placed in holding tanks for 24 h. We were careful to collect a representative sample of male color patterns at each site. Analysis of color pattern revealed that all samples contained both bright and pale males, suggesting that we did not inadvertently collect only the visually conspicuous individuals. The next day we measured their swimming performance in a flow chamber. Swimming performance was measured by determining the male's critical swimming speed which is the maximum speed that a fish can sustain for a given time period in a laboratory flow chamber (Brett 1964). Critical swimming speed is a common measure of swimming performance in other species, and is correlated with a fishes' health, active metabolism and endurance (Smit 1965, Brett & Glass 1973, Webb 1975, Beamish 1978).

Swimming performance was measured by placing each fish into the swimming chamber with an initial water velocity of 7.8 cm sec^{-1}. After 5 min at the initial velocity the water velocity was increased 2.9 cm sec^{-1} every 5 min until the guppy contacted a screen placed over the outflow end of the chamber for three seconds. A collimator was placed at the inflow end of the swimming chamber to make water velocity profile micorturbulent and rectilinear. The highest velocity and the time that the fish spent at that velocity were recorded and critical swimming speed was calculated (Brett 1964). A complete description of the swimming chamber and methodology is given in Nicoletto (1991).

Carotenoid pigments

Each male was then photographed and its standard length measured with a pair of digital calipers accurate to 0.01 mm. Male color pattern was quantified by projecting the slide onto a computer digitizing tablet and recording the area and the number of orange-colored spots (Kodric-Brown 1989). The area of orange was divided by the body area making it relative to body size.

Statistical analyses

Two-way analyses of variance were used to test for differences in display rate and coloration between rivers and sites. Color data and display rate were rank-transformed, because they were not normally distributed (Conover & Iman 1981). The relationship between swimming performance and coloration was evaluated with a Spearman rank correlation for each river since our sample sizes were not large enough to separately analyze the relationship between swimming performance and coloration at headwater and downstream sites.

Swimming performance data were analyzed for differences among rivers and between sites with a two-way analysis of covariance. Standard length was used as the covariate to remove the linear effect of differences in male body size from the analysis. Thus, the analysis of covariance statistically controlled for differences in body size among rivers and between sites.

The relationship between mean swimming performance and water velocity at each site was evaluated with a linear regression. The relationship between mean display rate, mean swimming performance, and mean water velocity at each site was evaluated with Spearman rank correlation.

Results

Water velocity

Water velocity differed significantly among rivers ($H = 18.14$, df $= 3$, $p < 0.001$). This difference was due to the much lower water velocity in the Yarra River, since there were no significant differences in water velocity for the Guanapo, Oropuche, and Quare rivers (Table 2). Water velocities at headwater and downstream sites did not differ significantly for any of the four rivers.

Display behavior

The display rates of guppies differed among rivers (Table 3). The display rates of Quare guppies were significantly greater than display rates of guppies from the other rivers. Guanapo and Oropuche males had intermediate display rates that were not significantly different from each other and Yarra males had the lowest display rates (Figure 1). The display rates of guppies from headwater sites were significantly greater than those from downstream sites (Tables 3, 4).

Carotenoid pigments

The percent area of orange coloration did not differ among rivers (Table 3, Figure 2). The percent area of orange coloration of guppies from headwater sites was significantly greater than those from downstream sites (Tables 3, 4). The number of orange spots on guppies differed among rivers. Male guppies from the Quare river had significantly more orange color spots than males from the other three rivers. There were no significant differences in the number of orange color spots of male guppies from the Yarra, Oropuche, and Guanapo rivers. The number of orange spots of guppies from

Table 2. Mean water velocity (cm sec^{-1}) and standard deviation for the four Trinidadian rivers and the headwater and downstream sites for three of the rivers. The *z*-score and *p*-value are given for Mann-Whitney *U* tests for differences in water velocity at upstream and downstream sites of three rivers.

River	River		Upstream		Downstream		Mann-Whitney *U* tests	
	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.	*z*-score	*p*
Guanapo	14.5	3.14	14.0	3.99	14.9	2.29	0.06	0.87
Oropuche	19.2	8.13	19.3	9.08	20.5	6.88	0.01	0.99
Quare	19.6	3.35	19.6	3.35				
Yarra	6.42	2.47	7.9	1.63	4.9	2.32	1.73	0.083

Table 3. The results of two-way analyses of variance on display rate, orange area, and orange number and a two-way analysis of covariance on swimming performance (with standard length as a covariate) for guppies from two locations from four rivers in Trinidad.

Variable	River			Location		
	F	DF	*p*	F	DF	*p*
Display rate	95.70	3, 138	0.0001	5.28	1, 138	<0.02
Orange area	1.77	3, 171	0.16	6.17	1, 171	<0.01
Orange number	3.31	3, 171	0.021	7.31	1, 171	<0.008
Swimming performance	30.51	3, 171	0.0001	38.70	1, 171	0.0001

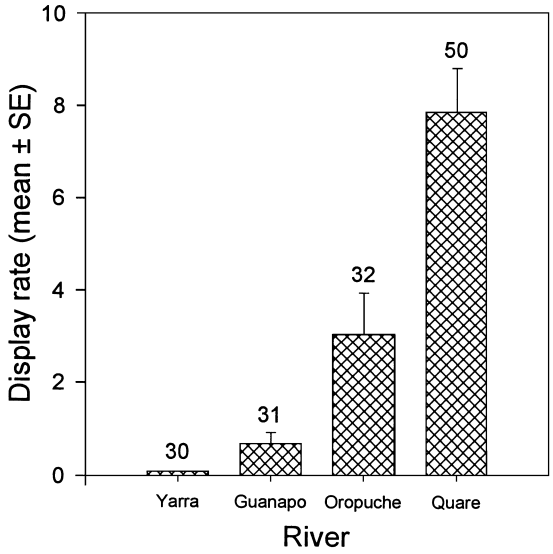

Figure 1. Mean display rates (displays per min) ± standard errors of male guppies from four rivers in Trinidad. All means were significantly different ($p < 0.001$, for all pairwise *t*-tests on neighboring means). Sample sizes of the fish observed in each river are shown above the bar.

headwater sites was significantly greater than those from downstream sites.

Swimming performance

The swimming performance of males differed among rivers as well as between headwater and downstream sites (Table 3). Quare males swam significantly faster and Yarra males swam significantly slower than the males from other rivers. The swimming performances of Guanapo and Oropuche males were intermediate in value and were not significantly different from each other (Figure 3). Guppies from headwater localities had significantly higher swimming performances than those from downstream localities (Table 4).

Table 4. Means and standard errors for display rate, orange area, orange number, and swimming performance of guppies from headwater and downstream habitats in four rivers in Trinidad.

Variable	Headwater		Downstream	
	Mean	SE	Mean	SE
Display rate	3.86	0.663	3.31	0.697
Orange area	0.081	0.006	0.066	0.0054
Orange number	1.96	0.11	1.56	0.11
Swimming performance	29.01	0.434	25.31	0.415

Swimming performance was positively correlated with the number of orange color spots in males from the Oropuche and Yarra rivers, but not for those from the Guanapo or Quare rivers (Table 5). However, after a sequential Bonferroni adjustment, the relationship between swimming performance and coloration remained significant only for the Oropuche river. Swimming performance and the percent area of orange were not correlated for any of the four rivers. The coefficients of variation indicate that there was little variation within a population for swimming performance, but that both the percent of orange area and number were highly variable. These differences in variation are probably the reason that the correlations are either weak or not significant. The power of the correlations in Table 5 is low, indicating that the probability of detecting a relationship, if one exists, is also low. Sample size analyses indicated that a sample size of over 100 males would be required to detect a statistically significant relationship between swimming performance and male coloration.

Mean swimming performance of males was positively correlated ($r_p = 0.81$, $n = 7$, $p < 0.026$) with the mean water velocity across all sites (Figure 4). The line was fitted with least squares linear regression to

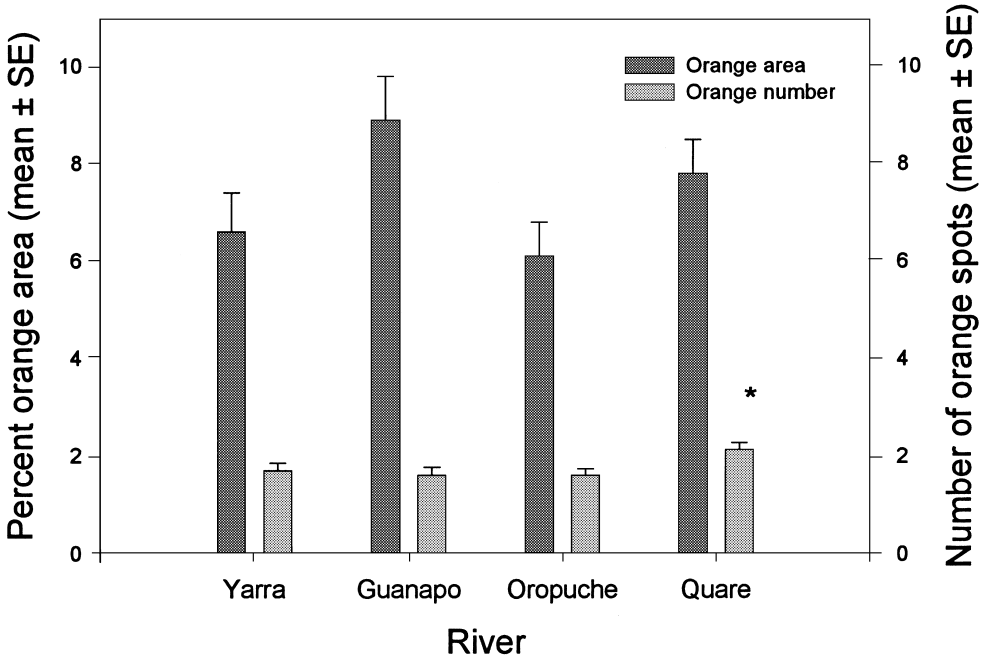

Figure 2. Mean percent area of the body covered by orange coloration and the mean number of orange spots ± standard errors of male guppies from for rivers in Trinidad. The only mean that was statistically different was the number of orange color spots on males from the Quare River ($p < 0.05$).

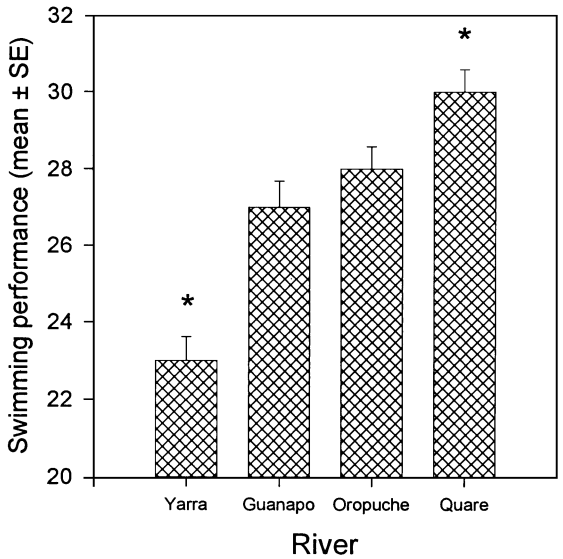

Figure 3. Least squares means (cm per sec) ± standard error comparing the swimming performances of male guppies from four rivers in Trinidad. Means that were significantly different are indicated by an asterisk ($p < 0.008$, for all pairwise *t*-tests on neighboring means).

visualize the relationship (swimming performance = 20.33 + 0.45 water velocity). Mean display rate was positively correlated with mean swimming performance across all sites ($r_s = 0.89$, $n = 8$, $p < 0.002$, Figure 5), but was not correlated with mean water velocity across all sites ($r_s = 0.54$, $n = 7$, $p < 0.21$).

Discussion

Courtship displays of male guppies are affected by a variety of social conditions such as the operational sex ratio and group size, and environmental factors such as presence and abundance of predators and parasites, ambient light conditions, and water turbidity (reviewed in Endler 1995). Intensity of courtship is a conditionally expressed trait that has evolved by means of intersexual selection, since females prefer to mate with colorful, vigorously displaying males (Clark & Aronson 1951, Farr 1980, Liley 1966, Kodric-Brown 1993, Nicoletto 1993, 1996).

Comparisons of guppy populations in the four rivers of Trinidad suggest that prevailing water velocity may have a strong effect on the swimming performance of

Table 5. Coefficients of variation for orange coloration and swimming performance, Spearman rank correlations between swimming performance and orange coloration, and power analyses for the males collected from four rivers in Trinidad.

Variable	River			
	Guanapo $N = (34)$	Oropuche $N = (49)$	Quare $N = (50)$	Yarra $N = (44)$
CV orange area	83.8	78.7	54.4	64.8
CV orange number	70.6	65.8	43.3	58.8
CV swimming performance	16.4	16.3	11.7	20.8
r_s orange area vs. swimming performance	−0.25	0.22	0.02	0.17
p-value	0.14	0.14	0.85	0.27
r_s orange number vs. swimming performance	−0.24	0.35	0.04	0.30
p-value	0.17	0.01	0.74	0.05
Power	0.28	0.39	0.40	0.35

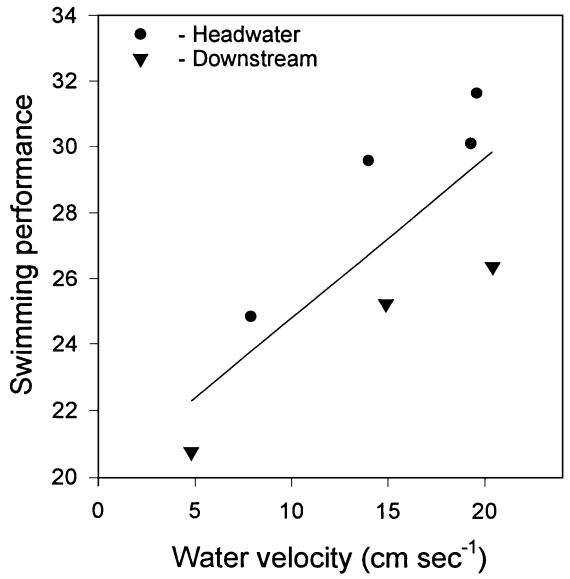

Figure 4. The relationship between mean water velocity and the mean swimming performance (cm per sec) of male guppies from headwater and downstream sites from four rivers in Trinidad.

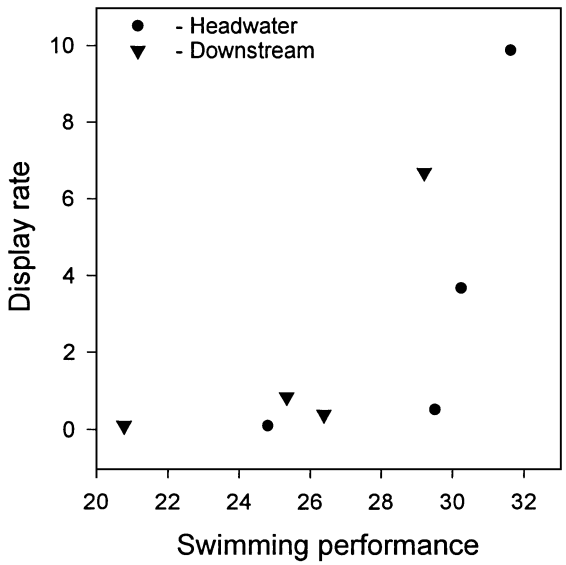

Figure 5. The relationship between the mean swimming performance (cm per sec) of male guppies and the mean display rate (displays per min) of other males observed in the field from the same location.

males and may indirectly affect their courtship behavior. Selection for swimming performance in habitats with high water velocity may favor increased muscle development and condition (Nicoletto 1996, Figure 4). Display behavior may be condition-dependent largely because guppies probably use the same muscles to swim and to display (Nicoletto 1996). High display rates in such environments may be a byproduct of selection to enhance performance related to survival. Alternatively, high display rates may be favored by selection, because they are energetically costly thus honestly advertise a fit male's physical condition (Kodric-Brown & Brown 1984). Females choosing vigorously displaying males would obtain mates that are, on average, in better physical condition and are better adapted to local environmental conditions. Thus sexual selection would reinforce natural selection. In many species of fish swimming performance is

positively correlated with active metabolism, health, and endurance (Brett 1964, Webb 1975, Beamish 1978).

Since mean water velocity did not differ between headwater and downstream sites for three of the four rivers (Table 2), it cannot explain the differences in swimming performance and display behavior of males between sites. However, variation in water velocity in microhabitats where guppies occur was greater at headwater sites in three of the four rivers (Table 2). In general, at headwater sites fish were distributed across the entire stream, including areas of high flow rates. At downstream sites they were restricted by predators, that occur in deeper waters, to vegetated areas near the stream banks with low water velocities (Luyten & Liley 1985, personal observation).

Predators at downstream sites may affect guppies both directly and indirectly. Males are directly affected, because their conspicuous color patterns and courtship behavior render them particularly vulnerable to predators (Haskins et al. 1961, Endler 1978, 1983, Reznick et al.1996, Winemiller et al. 1990). Predators also indirectly affect the athletic ability of males by restricting them to protected microhabitats. Without continual swimming in high-velocity currents, aerobic condition may not be maximally developed. This factor probably contributes to the reduced swimming performance and perhaps also to lower display rates of these males.

The general pattern reported here, namely that males from headwater localities were more ornamented (carotenoid pigment spots) and engaged in a greater number of courtship displays than males from downstream localities, is consistent with that reported in previous studies (Luyten & Liley 1991, Endler & Houde 1995). These studies suggest that epigamic selection for conspicuous color patterns and high display rates is more intense in populations under low predation pressure.

Differences in the diets of guppies may contribute to the observed differences in swimming performance, carotenoid pigmentation, and display rate between headwater and downstream localities. Diet quality has been shown to influence the development of carotenoid pigmentation in the laboratory (Kodric-Brown 1989). Aquatic insect larvae, a more nutritious food, form an important component of the diet of guppies from headwater localities, whereas benthic algae, a lower-quality food, are the major component of the diet of guppies from downstream localities (Dussault & Kramer 1981). Diet quality may also be related to swimming performance. For example, swimming speed was positively correlated with food availability in the Atlantic cod (Björnsson 1993).

A variety of factors, such as genetic differences, predators, and historical events in the watersheds, all contribute to the observed variation in the reproductive biology and life history of guppies (Endler 1992, Luyten & Liley 1985, Magurran et at. 1993). However, these factors may not explain all of the variation observed among rivers and between sites. Other factors, such as water velocity, may affect the expression of such sexually selected, condition-dependent traits as courtship displays and patterns of carotenoid pigmentation, which indicate a male's health and vigor.

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