

# Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait

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Although conspicuous visual sexual signals, such as bright colors, in males serve to attract females in numerous species, they may also attract the attention of potential predators and thus may be costly in terms of increasing individual risk of mortality to predation. Most models of the evolution of extravagant male sexual traits and female preferences for them assume that the sexually preferred male trait is costly to produce and maintain. However, there is surprisingly little empirical evidence for direct fitness costs associated with sexually selected visual traits that enhance male mating success. In the present study, we report a direct fitness cost for sexually selected, bright body-color patterns in males in the form of an associated greater risk of mortality to predation. By using the guppy (*Poecilia reticulata*) and the blue acara cichlid fish (*Aequidens pulcher*) as a model prey–predator system, we demonstrate experimentally that individual cichlids preferentially and consistently approached, attacked, and captured the more brightly colored of two size-matched male guppies presented simultaneously in staged encounters. This resulted in the brightly colored male incurring, on average, a significantly higher risk of mortality given an encounter with the predator than with the drabber male in matched pairs. Our results constitute strong behavioral evidence for a direct viability cost associated with bright coloration in male guppies, and they corroborate the generally accepted paradigm that directional predation by visual fish predators against brightly colored, adult male guppies underlies the evolution of the known divergent color patterns in natural guppy populations that experience different intensities of predation. The viability cost associated with bright conspicuous coloration in male guppies potentially reinforces for females the reliability of this sexually selected trait as an indicator trait of male quality. *Key words:* color, fish, fitness cost, guppy, ornament, *Poecilia reticulata*, predation risk. [*Behav Ecol* 14:194–200 (2003)]

Both Fisherian runaway and viability indicator (good genes) models of the evolution of elaborate male sexual traits, and female preferences for them, assume that the sexually preferred male trait is costly to produce and maintain (Andersson, 1994; Grafen, 1990; Johnstone, 1995; Kotiaho, 2001). For any such cost to be evolutionarily significant, however, it must decrease the male's fitness (Kotiaho, 2001). In theory, the average phenotypic relationship between the expression of sexually selected traits and male survival or longevity may either be positive or negative, depending on whether the expression of the sexual trait is condition dependent, that is, on whether males invest differentially in the sexual trait in relation to their ability to bear the associated costs (Jennions et al., 2001; Johnstone, 1995; Zeh and Zeh, 1988). A recent meta-analysis of data obtained from numerous studies and species (Jennions et al., 2001) revealed weak, but statistically significant, positive relationships between male survivorship or longevity and male ornaments or weapons, body size, and courtship rate; this result is consistent with sexual traits acting as honest advertisement of male genetic quality, as predicted by good-gene models of sexual selection (cf. Andersson, 1994; Johnstone, 1995). Notwithstanding the results of this meta-analysis and of other studies (for review, see Kotiaho, 2001; Zuk and Kolluru, 1998), there is surprisingly very little empirical evidence for direct fitness costs associated with sexually selected visual traits, such as

bright body coloration, that enhance individual mating success in males (cf. Kotiaho, 2001; Zuk and Kolluru, 1998).

Because visual sexual signals generally increase the visual conspicuousness of males to females, they may also concurrently and inadvertently increase the male's conspicuousness to eavesdropping predators and other natural enemies (Andersson, 1994; Endler, 1992; Kotiaho, 2001; Zuk and Kolluru, 1998). Therefore, conspicuous visual sexual signals in males may be associated with increased risk of predation and, as such, may be viability handicaps (sensu Grafen, 1990; Johnstone, 1995; Zahavi, 1977).

In the current study, we investigated experimentally whether bright coloration, a known sexually selected trait (Houde, 1997), in males of the guppy (*Poecilia reticulata*) incurs an inherent increased risk of mortality from predation by quantifying the behavior of one of its natural diurnal fish predators toward males varying in color pattern. The guppy is sexually dichromatic, with males being genetically polymorphic for color patches that vary in hue, chroma, reflectivity, size, number, and location on their body (Endler, 1978, 1983, 1991; Grether, 2000; Houde, 1997). The amount and brightness of orange color (carotenoid pigments), in particular, in the color pattern of male guppies reveals individual boldness toward predators (Godin and Dugatkin, 1996) and condition, as males possessing more orange color are more vigorous behaviorally (Kennedy et al., 1987; Kodric-Brown, 1993; Nicoletto, 1991, 1993), are less likely to be parasitized (Houde and Torio, 1992), and are better foragers (Endler, 1978, 1980; Grether, 2000; Grether et al., 1999; Kodric-Brown, 1989) than are drabber conspecifics. Bright coloration in male guppies thus appears to be an honest indicator trait of their quality, and female guppies generally tend to prefer to mate with brightly colored males than with drabber ones (for review, see Houde, 1997).

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Although bright coloration is sexually selected and confers a potential mating advantage to males (Houde, 1997), several lines of evidence at the population level suggest that diurnal visual fish predators select against conspicuous color patterns in male guppies in nature. First, in natural populations in Trinidad where they experience high predation intensity from diurnal fishes, male guppies are less colorful (i.e., more cryptic) on average than are males in populations experiencing weaker predation intensity (Endler, 1978, 1982, 1983, 1995; Houde, 1997). Second, Endler (1980, 1983) has shown that an experimental addition of natural fish predators to artificial stream populations of guppies resulted in a gradual reduction in the number and size of color patches in adult males, on average, over only a few generations compared with control populations experiencing little predation on adults. Third, an experimental transfer of adult guppies originating from a high-predation (control) population into a nearby low-predation population devoid of guppies in Trinidad resulted in a gradual increase over only a few generations in the number and size of color patches in males in the introduction sites compared with those in the control sites (Endler, 1980, 1983). Last, in nature, adult males have higher mortality rates than do similar-sized females and juveniles that lack conspicuous body color patterns (Reznick et al., 1996).

It is implicitly assumed in the aforementioned studies that observed evolutionary changes in male color patterns within and between populations were caused by direct, differential visual fish predation on conspicuous (colorful) adult males. Alternatively, the aforementioned observed evolutionary patterns at the population level (cf. Endler, 1978, 1980, 1983, 1995; Houde, 1997) could potentially have resulted from indirect selection on adult male color patterns through the following: (1) selective predation on juvenile male offspring of brightly colored males (cf. Brooks, 2000), resulting in a correlated shift in the frequency of bright males at the adult stage over time; (2) selective predation based on other male phenotypic traits (e.g., body size; Mattingly and Butler, 1994) that may be correlated with color pattern; (3) a predator-mediated reduction in female mate choosiness (Godin and Briggs, 1996; Gong and Gibson, 1996) that could reduce the mating advantage of bright males, and thereby their relative frequency, in the population over time (Houde, 1993); and/or (4) variation in the water color, background substrata, and productivity of the stream in which the guppies live, among other environmental factors, that are correlated with local predation risk (Endler, 1992, 1995). To support the assumption of differential fish predation on adult males, direct behavioral observations of preferential predator attractiveness to, and attack on, brightly colored males are required, but are generally lacking. A notable exception is the laboratory experiment of Haskins et al. (1961), in which they exposed male guppies of three distinct color morphs to predation from a single cichlid fish (*Crenicichla saxatilis*) in an aquarium over a 3-week period. Although their experiment was not replicated and apparently did not control for other potential phenotypic differences between male guppies, their limited data nonetheless indicate that the more colorful guppies suffered a higher mortality rate to predation than the less colorful ones.

The objective of the current study was therefore to rigorously and experimentally test the general assumption, derived from the previous studies of Endler (1978, 1980, 1982, 1983), that the diurnal visual fish predators of the guppy possess intrinsic behavioral preferences for the more brightly colored (and more visually conspicuous) of available male guppies as prey. More specifically, we predicted that individual fish predators would be preferentially attracted to, and preferentially attack and capture, the more brightly colored

of simultaneously available male guppies, when controlling for other potential differences in phenotype between males. We used the blue acara cichlid (*Aequidens pulcher*) as a model diurnal predator species. This species is a known natural predator of the guppy in Trinidad (Endler, 1978, 1983; Houde, 1997; Liley and Seghers, 1975), although it is not considered to be as dangerous a predator as the pike cichlid, *Crenicichla alta* (Endler, 1978, 1983, 1991; Mattingly and Butler, 1994). The latter species was not available to us in sufficient numbers to adequately replicate our experiments, but the blue acara was.

## METHODS

### Fish and holding conditions

Blue acara cichlids and guppies were obtained from a local aquarium fish supplier and were therefore of unknown origin. These two species were held in separate glass aquaria. Each aquarium contained continuously filtered aged well water (24°C–26°C), a gravel substratum, and a plastic plant, and was exposed to a 12-h light : 12-h dark illumination cycle provided by Sun-Glo fluorescent tubes (R.C. Hagen, Montréal), which simulate the energy spectrum of sunlight. Guppies were fed ad libitum flake food (NutraFin) three times daily, supplemented with live brine shrimp nauplii. The cichlids were fed in their holding aquaria twice daily with freeze-dried euphausiid shrimps, occasionally supplemented with live female guppies (selected haphazardly from the stock aquaria) so as to maintain high motivation to attack guppies as prey, for at least 1 month before being used in the following experiments. Female guppies are drab olive-grey in color and do not possess the complex color patterns of males. The male guppies used in the current study qualitatively resembled wild Trinidadian male guppies in morphology, coloration (i.e., possessed yellow-orange-red and black color spots and iridescent structural colors), and antipredator behavior. The stock guppies were free of ectoparasites; the latter are known to affect male coloration (Houde and Torio, 1992).

### Experiment 1: predator preference of stationary guppies

In this experiment, individual blue acara cichlids ( $n = 22$ , mean  $\pm$  SE = 68.7  $\pm$  1.6 mm total length) were presented with a simultaneous choice to approach and attack either of two stationary male guppies, located equidistant from them. The paired guppies were similar in body length but different in their body-color pattern, with one of the paired males being more brightly colored than the other. Therefore, this experiment controlled for any differences in body size, activity, and proximity to the predator between the paired stimulus guppies.

The experimental choice arena consisted of a 16-l aquarium, divided into two unequal compartments by a removable opaque Plexiglas partition located 10 cm from the end containing the guppies (Figure 1). The aquarium was covered externally on three sides with tan paper, with the fourth side (the end furthest from the removable partition) covered with a cardboard blind equipped with a small screened opening for observations. The aquarium had a gravel bottom, contained aged well-water maintained at 24°C–25°C, and was illuminated overhead with a Sun-Glo fluorescent tube (28  $\mu$ E/m<sup>2</sup>/s) on a 12-h light : 12-h dark illumination cycle. The larger compartment housed a predatory cichlid fish and had a plastic plant anchored to the substratum near the end of the aquarium covered by the blind. The smaller compartment was used to present the cichlid with a pair of guppy males, each constrained within a small clear plastic cylinder

(33 mm long  $\times$  7 mm inside diameter) attached to a clear plastic rod (2-mm diameter), mounted 7 cm apart (center to center) on an overhead clear Plexiglas plate. This plate rested on top of the aquarium, such that the tubes were suspended in the water column 5 cm above the substratum and against the end wall of the small compartment. Because the dimensions of these cylinders closely approximated the body length and depth of the males, the latter could hardly move at all within the cylinders. For any given trial, a pair of stimulus male guppies was chosen from a pool of 12 individuals. Paired males were intentionally chosen to differ in their overall color patterns, but otherwise matched for body length (less than 1-mm difference). The brighter male ( $20.1 \pm 0.2$  mm, total length) in a pair ( $n = 22$ ) always possessed more numerous and relatively larger and more saturated color patches than did the drabber male ( $20.2 \pm 0.2$  mm), and thus was more visually conspicuous (cf. Endler, 1991) against the uniform tan background, at least to our eyes.

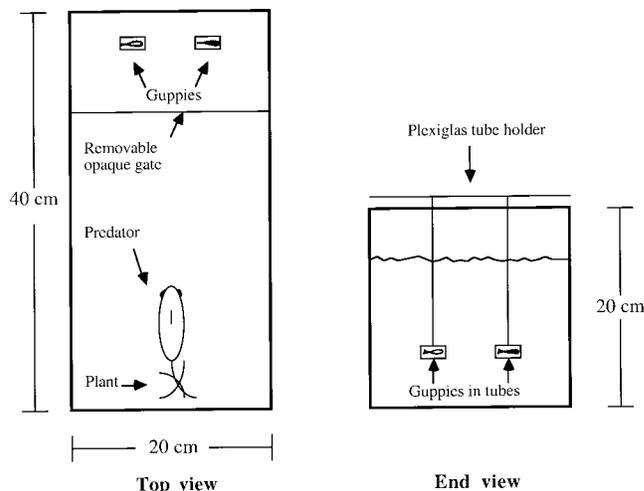
A trial consisted of placing an individual cichlid into the larger compartment of the aquarium and allowing it to adjust undisturbed for 24 h. At the end of this acclimatization period, a pair of constrained male guppies was placed into the smaller compartment of the aquarium (as described above), behind the opaque partition, and allowed to acclimatize for 5 min. The particular position (left or right tube) of the paired bright and drab males was randomized for each trial. The opaque partition was then raised remotely by using a pulley system, allowing the predator to view both males in their respective tubes located about 30 cm away and thus within the attack range of cichlid fish on guppies in nature (Endler, 1991; Godin JGJ, personal observations). A standardized 10-min trial began when the cichlid approached either guppy. We noted which one of the two guppies was first approached and first attacked (i.e., bite at the tube containing the guppy) by the cichlid fish. To determine the consistency of the preference of the cichlid for either the paired bright or drab male guppy, the preference of each of 22 cichlid fish was determined twice daily as described above, once in the morning and once in the afternoon of the test day.

For each of the paired daily preference trials, we compared separately the numbers of cichlids that initially approached and initially attacked the bright or the drab male guppy by using the binomial test. The consistency of the predator's preference for either of the paired male guppies across the two daily trials was compared by using the  $G$  test for approach and attack behavior separately.

### Experiment 2: predator choice of free-swimming guppies

Given the nonrandom predatory behavior of the cichlids in the first experiment (see Results), we performed a corollary experiment in which individual cichlid fish were presented with a simultaneous choice of similar-sized, free-swimming bright and drab male guppies in a larger aquarium. This experiment thus simulated natural encounters between guppies and their natural cichlid fish predators, during which male guppies differing in color patterns may simultaneously occur within the visual field of a predator but not necessarily at the same distance from it (Godin JGJ, personal observations, Quaré River, Trinidad).

The experimental choice arena consisted of a glass aquarium (120  $\times$  50  $\times$  50 cm, length  $\times$  width  $\times$  height), covered externally on three sides with tan paper, with the fourth side left open for observations. The aquarium had a gravel bottom, contained aged well-water maintained at 24–25°C, and was illuminated overhead with a Sun-Glo fluorescent tube (26  $\mu\text{E}/\text{m}^2/\text{s}$ ) on a 12-h light : 12-h dark cycle. A group of rocks, located at one end of the aquarium, provided a potential



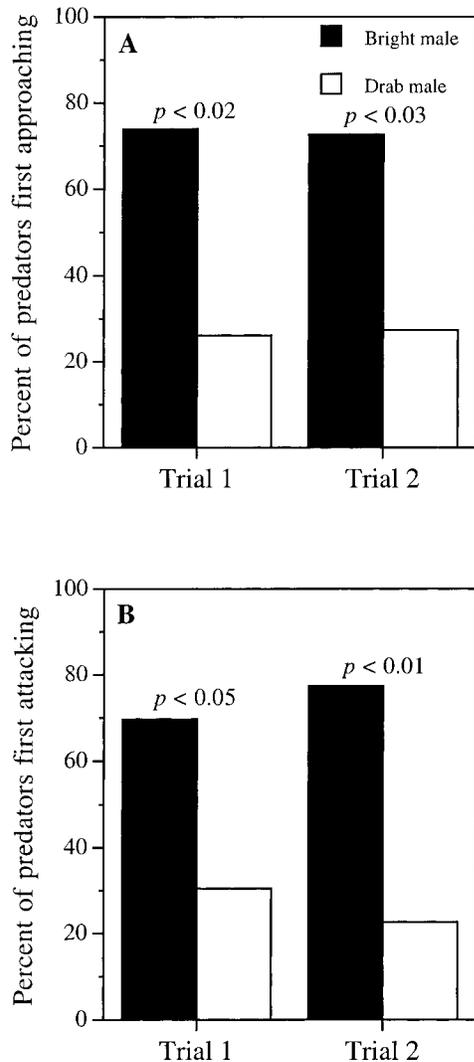
**Figure 1**

Binary-choice apparatus for testing the preferences of individual cichlid fish predators for either brightly colored (dark silhouette) or drabber (open silhouette) paired male guppies of similar body length, each constrained in a clear Plexiglas tube. The tubes were separated by 7 cm from center to center. Fish silhouettes are not to exact scale.

hide for the cichlid. A plastic plant, which the guppies could use as a refuge, was anchored into the substratum at the opposite end of the aquarium.

We introduced a blue acara cichlid in this aquarium 3 days before experimentation. The fish was fed daily with one juvenile female guppy and freeze-dried euphausiids, but otherwise was left undisturbed to acclimatize until tested. The cichlid typically spent most of its time near the rocks or in a crevice between the rocks. Twice daily (once in the morning and once in the afternoon), for 5 consecutive days, we simultaneously introduced into the aquarium a pair of male guppies ( $n = 120$  pairs total) that differed in body color pattern, but otherwise matched for total body length (paired brighter male,  $20.3 \pm 0.2$  mm; drabber male,  $19.9 \pm 0.2$  mm). For a given trial, a pair of guppies was placed in a small beaker of water, which was then poured into the aquarium near the plant, at the end opposite where the cichlid was located. Once both guppies began to swim about the aquarium, either solitary or as a pair, we recorded which one of them was first attacked and first captured by the cichlid predator. We also recorded concurrently the relative distances of both guppies to the predator at the instant of its initial attack. To standardize the hunger level of the cichlid between trials, we allowed it to eat both guppies during each trial (i.e., four guppies consumed per day). Therefore, an individual test cichlid was presented with a different pair of male guppies as prey on each of 10 such trials (i.e., two trials per day  $\times$  5 days). The preference of 12 different blue acara cichlids ( $78.6 \pm 2.3$  mm) for either brightly colored or drabber male guppies was similarly tested.

For each cichlid predator separately, we expressed the recorded numbers of bright and drab male guppies that were first attacked and first captured as proportions out of 10 trials (e.g., nine first attacks on the bright male during 10 trials, 0.90; 1 first attack on the drab male during 10 trials, 0.10). We then compared separately the relative (percentage) frequencies of first attacks and first captures on paired bright and drab guppies by the 12 cichlids by using the Wilcoxon matched-pairs signed-rank test. To account for the possibility that a cichlid might simply attack the guppy that is closest to it regardless of color pattern, we also compared, by using the



**Figure 2**  
Percent frequency of cichlid predators ( $n = 22$ ) that initially approached (A) and initially attacked (B) either the bright or drab stimulus male guppies, which were constrained in clear tubes, in each of two consecutive trials. Individual cichlids were each tested repeatedly in the paired morning and afternoon trials (trial 1 and trial 2, respectively).  $p$  values were obtained by using the binomial test.

Wilcoxon test, the observed relative frequencies of first attacks on paired bright and drab males with expected frequencies based on the proximity of the guppies to the predator at the instant of its initial attack. The latter frequencies were obtained for each cichlid predator separately by noting the number of times (over the 10 trials) the bright or drab guppy in a given pair was closest to the predator on first attack.

Probability of death on an initial attack was calculated separately for bright and drab males as the product of the probability of being attacked first and the conditional probability of being captured given an attack. This product was obtained separately for each predatory cichlid and then averaged over all 12 cichlids. The average probabilities of death for paired bright and drab guppies were compared by using the Wilcoxon test.

#### Ethical considerations

In line with generally accepted ethical standards for behavioral predation experiments (Huntingford, 1984), appropri-

ate measures were taken to minimize any stress and suffering to the guppies and the number of fish used in this study.

More specifically, in experiment 1, the guppies were placed inside plastic cylinders and thus physically separated from the cichlid predators. Although no guppy was killed in this experiment, they likely experienced some stress when the predator approached and contacted the cylinders. Any stress was minimized by keeping trials relatively short (10 min). Experiment 2 was performed only as a consequence of the positive results obtained in experiment 1, and because an unequivocal test of our hypothesis of differential risks of predator attack and mortality based on differences in body color pattern in male guppies requires that predator and prey physically encounter each other (cf. Kotiaho, 2001). In experiment 2, the guppies were relatively small compared with the size of cichlids used; this ensured that if caught by the predator, they would be quickly swallowed and not chewed, thus minimizing any postcapture suffering. The numbers of guppies and cichlids used were kept to the minimum necessary for rigorous statistical testing of the hypothesis. Finally, the experiment had no impact on wild guppy populations because only laboratory-bred, commercially available fish were used.

This research received prior approval from the institutional Animal Care Committee at the authors' home university and, thus, adheres to the guidelines for the care and use of experimental animals of the Canadian Council on Animal Care and to legal requirements in Canada.

## RESULTS

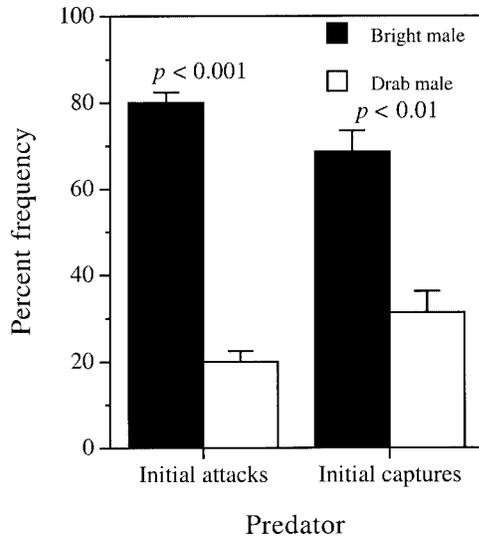
### Experiment 1: predator preference of stationary guppies

For each of the paired daily preference trials, significantly greater proportions of the cichlid predators first approached (Figure 2A) and first attacked (Figure 2B) the more brightly colored of the paired male guppies than expected by chance (all  $p < .05$ , binomial test). The results of these two consecutive trials did not differ statistically for both approach ( $G_{\text{adj}} = 0.01$ ,  $df = 1$ ,  $p > .80$ ) and attack ( $G_{\text{adj}} = 0.33$ ,  $df = 1$ ,  $p > .40$ ) behavior. Individual cichlids were therefore consistent in their preference for the bright male guppy over the drabber one when the body length, movement, and distance to the predator were held constant.

### Experiment 2: predator choice of free-swimming guppies

When paired male guppies were allowed to interact freely with individual cichlid fish predators, the more brightly colored male was attacked first ( $T = 78$ ,  $n = 12$ ,  $p < .001$ , one-tailed Wilcoxon test) and captured first ( $T = 64$ ,  $n = 12$ ,  $p < .01$ , significantly more often than was the drab male (Figure 3). The predators did not necessarily attack and capture the nearest guppy, irrespective of its color pattern. On the contrary, the more brightly colored guppy in a pair was initially attacked significantly more often ( $T = 78$ ,  $n = 12$ ,  $p < .001$ , two-tailed Wilcoxon test), and the drabber male significantly less often ( $T = 78$ ,  $n = 12$ ,  $p < .001$ ), than expected if it was the one closest to the predator at the instant of the attack (Figure 4). Therefore, the cichlid predators preferentially attacked the more brightly colored male guppy when given a choice, regardless of the distance of the latter to the predator relative to that of the paired drabber male.

Although the more brightly colored guppy in a test pair was significantly more likely to be attacked first (Figure 3), the mean ( $\pm$  SE) conditional probabilities of the bright ( $P_r = 0.137 \pm 0.52$ ) and drab ( $P_r = 0.103 \pm 0.32$ ) males being captured on the predator's initial attack did not differ



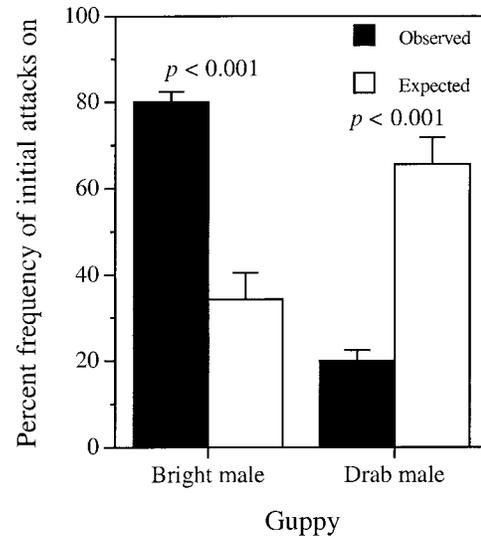
**Figure 3**  
Mean (+ SE) percent frequency of initial attacks and initial captures by cichlid predators ( $n = 12$ ) on paired free-swimming bright and drab male guppies.  $p$  values were obtained by using the Wilcoxon matched-pairs signed-rank test.

significantly ( $T = 27.5$ ,  $n = 9$ ,  $p > .30$ , one-tailed Wilcoxon test). However, largely because of their differential probability of being initially attacked (Figure 3), the probability of death given an initial encounter with a cichlid predator ( $P_r$  [attack]  $\times P_r$  [capture|attack]) was significantly greater ( $T = 39$ ,  $n = 9$ ,  $p < .05$ , one-tailed Wilcoxon test), on average, for the brightly colored male ( $P_r = 0.107 \pm 0.040$ ) than for his paired drabber counterpart ( $P_r = 0.023 \pm 0.007$ ). In nature, an individual guppy that escapes a predator's initial attack is likely to either find refuge nearby or to distance itself from the predator, thereby likely avoiding any repeated attack by the same predator (Godin JGJ, personal observations, Quaré River, Trinidad).

## DISCUSSION

Our study clearly demonstrates that one of the guppy's natural diurnal predators, the blue acara cichlid, possesses a marked visual bias towards brightly colored, adult, male guppies as prey. Such preferential predatory behavior, and resulting differential risk of mortality in the prey, cannot be explained by differences in the body length, general activity, and proximity of the paired guppies available to the predator, but rather is more likely the result of differences in their body-color pattern and visual conspicuousness (cf. Endler, 1991) against the standardized tan background of the test aquaria.

Our experimental behavioral results indicate that bright and conspicuous body coloration, a known sexually selected trait (Houde, 1997), in male guppies incurs a direct fitness cost, in terms of an increase in individual risk of mortality to predation (cf. Kotiaho, 2001), and is thus a viability handicap (sensu Grafen, 1990; Johnstone, 1995; Zahavi, 1977). Although our model predator, the blue acara cichlid, is a relatively minor predator on the guppy compared with the larger pike cichlid (Endler, 1978, 1983, 1991; Liley and Seghers, 1975) in Trinidad, these two fish species are members of the same family (Cichlidae) and have evolved in similar environments as they both commonly co-occur in rivers in Trinidad (Endler, 1978; Houde 1997; Liley and Seghers, 1975). The blue acara likely possesses at least as good



**Figure 4**  
Observed mean (+ SE) percent frequency of initial attacks directed by cichlid predators ( $n = 12$ ) towards paired free-swimming bright and drab male guppies compared with initial attack frequencies expected if the cichlids simply first attacked the nearest of the two guppies (calculated based on which one of the paired guppies presented was closest to the predator at the instant the initial attack occurred).  $p$  values were obtained by using the Wilcoxon matched-pairs signed-rank test.

and probably better color vision than that of the pike cichlid (Endler, 1991; Endler JA, personal communication). Therefore, it seems reasonable to assume that these two cichlid fish species perceive the color patterns of male guppies in a qualitatively similar manner under the same lighting conditions, and like the blue acara cichlid (the present study), the pike cichlid also possesses a visual bias toward, and a predatory preference for, the most colorful of male guppies present in its visual field.

If the above assumptions regarding the similarities in the color vision and visually guided predatory behavior of the blue acara and pike cichlids are valid, then our results strongly corroborate the generally accepted paradigm that directional predation by visual fish predators against brightly colored, adult, male guppies underlies the evolution of the known divergent color patterns in natural and experimental guppy populations that experience different intensities of predation (Endler, 1978, 1982, 1983, 1995; Haskins et al., 1961; Houde, 1997). Given that the blue acara cichlid readily preyed on guppies in the current study, but that it attacks guppies at a much lower rate than the pike cichlid and characins in nature (Endler, 1978, 1983, 1991; Liley and Seghers, 1975), the latter, more dangerous fish predators probably exert an even stronger natural selection intensity than does the blue acara than hitherto believed. Directional selection by visual predators against bright conspicuous color patterns in guppy populations has important implications for the maintenance of observed color polymorphism in males within populations (Endler, 1978, 1991; Haskins, et al. 1961; Houde, 1997), for constraints on the further evolution of bright colors as sexual signals in males through sexual selection (Houde, 1997), and for the evolution of threat-sensitive behavior in males (Houde, 1997).

The visual bias toward, and predatory preference for, brightly colored male guppies in the blue acara cichlid, and presumably in the pike cichlid, may have arisen through at

least three potential evolutionary mechanisms: (1) predator preference for bright colors may have co-evolved with sexual selection for bright coloration in guppy populations (cf. Houde, 1997), a process known as “sensory drive” (Endler and McLellan, 1988); (2) the cichlids may have evolved a “preexisting sensory bias” toward bright colors from selection in a separate context or from other perceptual tasks than predation (Rosenthal et al., 2001; Ryan, 1998); or (3) predator preference for brightly colored prey may be an evolved adaptive sensory preference if individual cichlid fish that preferentially eat brightly colored guppies have, on average, higher fitness than those that do not, perhaps through a greater net energy intake rate (cf. Stephens and Krebs, 1986), and(or) greater acquisition of carotenoid pigments from brightly colored prey as carotenoids have a number of putative health-related benefits (Lozano, 1994; Olson and Owens, 1998). Which one of these evolutionary mechanisms best explains the observed predatory preference of the blue acara cichlid for brightly colored male guppies is presently unknown.

Bright coloration is thus a costly trait (Haskins et al., 1961; this study) that appears to be a reliable condition-dependent signal of male quality in the guppy (Endler, 1978; Grether, 2000; Houde and Torio, 1992; Kennedy et al., 1987; Kodric-Brown, 1989, 1993; Nicoletto, 1991, 1993), which increases male attractiveness to females (Brooks, 2000; Brooks and Endler, 2001a,b; Grether, 2000; Houde, 1997). The greater sensitivity to perceived predation hazard and associated stronger antipredator behavioral responses in brightly colored male guppies (Endler, 1987; Godin, 1995; Godin and Dugatkin, 1996; Magurran and Seghers, 1990) compensate for their greater conspicuousness to visual predators and, along with sexual selection for bright coloration, likely contribute to the maintenance of different color phenotypes (and genotypes) in natural populations.

To ascertain with greater certainty whether bright coloration in the guppy evolved as a costly indicator trait of male genetic quality, it would be particularly important to demonstrate experimentally whether the fitness cost (i.e., increased risk of mortality to predation) associated with this sexual trait is smaller for males in good condition than for males in poor condition (cf. Grafen, 1990; Johnstone, 1995; Kotiaho, 2001; Zeh and Zeh, 1988). This type of study remains to be done with the guppy and, in fact, has been performed in only a couple of species, with the male sexual trait being one other than coloration, to date (for review, see Kotiaho, 2001).

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