



# Ultraviolet reflectance patterns of male guppies enhance their attractiveness to females

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In many groups of fish male colour patterns reflect in the ultraviolet, but little is known about female preferences for these components of male ornaments. We studied UV-reflective colour patterns in male guppies, *Poecilia reticulata*, and their importance in female choice. Using photographs taken with a filter transmitting only short wavelengths, we found that 4–24% of the area of a male's colour pattern reflects in the UV. We measured female visual responses to paired males placed, alternately, behind UV-blocking and UV-transmitting Plexiglas partitions. When pairs were matched for carotenoid (red), structural (white) and UV-reflective colour patterns, females spent significantly greater amounts of time inspecting a male when he was behind the UV-transmitting partition. These results show that UV-reflective components of male colour patterns enhance their attractiveness to females. To determine whether level of predation affects female response to UV-reflective colour patterns, we tested females from two populations differing in predation pressure. Females from both populations preferred males viewed through the UV-transmitting partition. When females were presented with male pairs that differed in the area of UV reflectance but were matched for carotenoids and structural pigments, difference in the time spent with the males was positively correlated with difference in the area of UV reflectance. Our results indicate that UV-reflective colour patterns enhance male attractiveness to females and thus may be elaborated through sexual selection.

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Ultraviolet patterns of reflectance may be an important component of visual signals, particularly those elaborated through sexual selection (birds: Maier 1993; lizards: Fleishman et al. 1993; butterflies: Brunton & Majerus 1995). The effect of UV reflectance of male plumage in influencing female choice has been particularly well studied in birds (Bennett et al. 1996, 1997; Andersson & Amundsen 1997). Visual receptors and pigments sensitive to UV wavelengths (360–380 nm) have been described for many groups of marine and freshwater fish living in shallow water habitats (Bowmaker 1995; Douglas et al. 1995; Losey et al. 1999). A role for UV reflectance patterns in intraspecific signalling and mate choice has yet to be demonstrated for any species of fish. UV reflectance patterns could enhance the attractiveness of male displays in at least two ways. They could draw a female's attention to particular combinations of colours or parts of a male's body by enhancing the contrast between the visible and UV reflectance components, or they could

enhance the attractiveness of the entire pattern (Losey et al. 1999).

Male guppies, *Poecilia reticulata*, have conspicuous colour spots and displays. The colours include red, yellow and orange carotenoid pigments, blue, green, violet and white structural pigments, and black melanins. The placement, size and combinations of pigment spots vary between males within a population as well as across populations (Houde & Endler 1990; Kodric-Brown 1993; Brooks & Caithness 1995; Endler & Houde 1995; Kodric-Brown & Nicoletto 1996). Sexual displays incorporating UV reflectance patterns should be favoured in fish inhabiting shallow, clear water environments, since detectability of wavelengths in the 300–400 nm range is greatest at depths less than 30 m (Levine & MacNichol 1979; Loew & McFarland 1990). Guppies have cones with a maximum sensitivity at 389 nm, so their colour vision extends into the near UV (UV-A: Archer & Lythgoe 1990; Bowmaker 1995). In Trinidad, guppies inhabit clear, shallow streams and experience various levels of predation, especially by cichlid fish, which lack UV-sensitive cones (Douglas & McGuigan 1989; Endler 1991; van der Meer & Bowmaker

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1995). These conditions should favour a signalling system that incorporates wavelengths in the UV range.

In this study we tested for UV-reflective colour patterns in males and response of females to these patterns. By comparing responses of females to the same males behind UV-transmitting and UV-blocking partitions, we were able to test directly for the effect of the UV reflectance component of the colour pattern on attractiveness to females. We asked the following questions.

(1) Does experimental manipulation of UV transmission affect female responses to male pairs matched for the area of all colours? Here we addressed the question of whether short wavelengths affect the overall appearance of males rather than individual components of a male's colour pattern (e.g. UV reflectance or carotenoids). If the UV-blocking partition affects the male's appearance, then females should spend less time with males when they are behind the UV-blocking partition.

(2) Do females respond to male patterns that reflect short wavelengths? If they do, then the effects of the UV-blocking partition should be greatest for males with large areas of UV reflectance. Females should find such males less attractive, and thus spend less time viewing them when they are behind the UV-blocking partition.

(3) Does manipulation of UV transmission affect female responses to male pairs differing in the area of carotenoids? This experiment is a control for the effect of the UV-blocking medium on female perception of non-UV colour patterns. If the UV-blocking partition blocks short wavelengths but has no effect on long wavelengths (carotenoids), then we do not expect any effect of the manipulation of UV transmission on female responses to males differing in the area of red colour spots.

(4) Does selection from predators influence female preferences for the UV-reflective component of male colour patterns? We compared the responses of females from two populations experiencing different predation pressure. No single prediction could be made regarding differences in the responses of females to the UV-reflective component of male colour patterns. Predators exert a strong selective pressure on male colour patterns. Males in high-predation environments have fewer and smaller carotenoid and iridescent spots, so they are less conspicuous to both predators and to receptive females than males from populations without piscivorous predators (Endler 1978; Houde & Endler 1990). However, if short wavelengths enhance the visibility of a courting male, then females should be particularly responsive to components of a male's colour pattern that reflect in the UV and are not detected by piscivorous predators. Therefore, females from the population experiencing predation should be more responsive to features of male colour patterns that are 'hidden' from the predator than females from the population experiencing no piscivore predation. However, since predators should exert a stronger selective pressure on male colour patterns than on the visual systems of females, females from different populations may not differ in their responses to experimental manipulation of the UV-reflective components of male colour patterns.

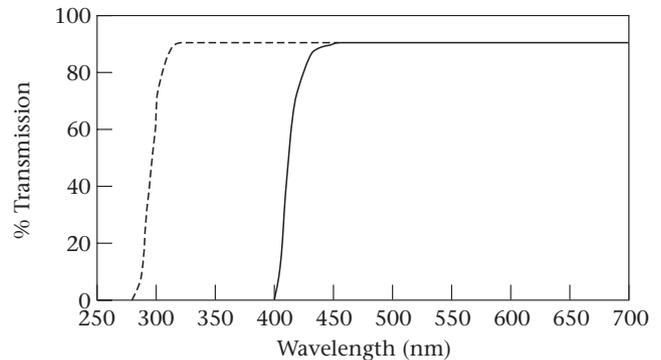


Figure 1. Spectral characteristics of the UV-transmitting partition (dashed line) and the UV-blocking partition (solid line).

## METHODS

### Male UV Reflectance Patterns

We anaesthetized males with MS222 and measured their standard length with calipers. We placed them in a petri dish with a 5-mm grid (for scale) and photographed them with a 35-mm camera with a 55-mm macro lens, mounted on a photographic stand and lit with a Phillips FD20X daylight spectrum fluorescent light. We took two photographs of each fish, a colour photograph (Kodak Ektachrome 200) and a black and white photograph (Ilford HP5). For the colour photograph we used a Wratten 2A filter that blocks short wavelengths below 400 nm. To visualize the UV reflectance of a male's colour pattern, we took a black and white photograph using a Wratten 18A filter that only transmits wavelengths under 400 nm. The photographs were digitized with an image analysis package (NIH image) on a Macintosh computer to determine the relative area of the carotenoid (red, orange, yellow) and iridescent (white, blue, green, violet) colour spots in both the visible and the UV range.

### Female Responses

We tested the visual preference of females with a binary choice design. All females were 4–5 months old and had previous mating experience. A week prior to testing, we removed females from the stock aquarium, where they could interact with the males, and placed them into one compartment of a 38-litre aquarium that was divided into two compartments by a clear glass partition. We placed males into the other compartment of this aquarium. Thus females had visual but not physical contact with males. Then we placed the females in the larger central compartment (30 × 25 cm) of a 38-litre aquarium with two removable 4-mm acrylic (Polycast) partitions. The ultraviolet-transmitting partition (UVT) transmitted wavelengths down to 250 nm. The ultraviolet-filtering partition (UVB) blocked wavelengths below 395 nm (Fig. 1). We placed two test males, matched for size ( $\bar{X} \pm SE = 17.9 \pm 0.03$  mm standard length; range 15.9–19.9 mm,  $N=75$ ), into the two small (10 × 25 cm) end compartments of the aquarium, one behind the UVT partition and the other behind the UVB partition. Thus a female could interact

visually but not physically with the two males. We measured female preference as the time she spent within 5 cm of a male's partition. Viewing time is a good indicator of a female's mating preference, because she usually mates with the visually preferred male (Kodric-Brown 1993).

We allowed fish to acclimate to the test aquarium for 10 min before a 10-min trial. Each trial consisted of two 5-min periods. We recorded the time a female spent viewing each male during the first 5 min of the trial, then switched the partitions between compartments. The next 5-min period of the trial began as soon as the female began to inspect the males, usually less than 1 min after switching partitions. By switching partitions during a trial, each male acted as his own control, since a female could view the same male when he was behind the UV-blocking partition as well as when he was behind the UV-transmitting partition. If a female remained at the same side of her compartment during the entire 10-min trial, she either had a side bias, or a strong preference for one of the test males. We checked for female side preference by switching males between compartments and observing the female for an additional 5-min period. We discarded trials in which females showed a side preference. We tested each female only once with a single pair of males in each experiment.

We measured female visual responses to the UV reflectance patterns of males by manipulating viewing conditions with UV-transmitting and UV-blocking partitions, and by manipulating the area of UV reflectance and carotenoid patterns of male pairs. We tested each male pair with two females. We used average preference scores for the two females for all analyses. A few males were used more than once but were paired with different males (UV reflectance:  $N=4$  males; carotenoids:  $N=3$  males; colour matching:  $N=5$  males).

#### *Jemez females*

*Responses to male pairs matched for all colours.* We selected 20 male pairs carefully matched for size (standard length) and for the area of carotenoid, iridescent and UV reflectance from the digitized photographs. Males in each matched pair differed by less than 5% in area of carotenoid, iridescent and UV reflectance on the body. Differences among pairs in the proportion of these colours were as follows: carotenoid ( $\bar{X}=8.3\%$ , range 1.3–15%), UV reflectance ( $\bar{X}=17.6\%$ , range 6–28%) and iridescent ( $\bar{X}=16.6\%$ , range 4.6–24%). Paired males were also matched for colour pattern, although the colour patterns differed between male pairs.

*Responses to male pairs differing in UV reflectance area.* We selected 12 male pairs that differed in the area of UV reflectance from 6 to 16%, but were carefully matched for size (standard length, measured from the base of the tail to the tip of the snout) from the digitized photographs. Males in each paired set differed by less than 5% in area of carotenoid and iridescent colours. Differences in the area of UV reflectance among the pairs

of males used in this experiment ranged from 10 to 31% ( $\bar{X}=18\%$ ). Male pairs differed in the area of carotenoid and iridescent colour (carotenoid:  $\bar{X}=9\%$ , range 4–13%, iridescent:  $\bar{X}=17.3\%$ , range 9–26%).

*Responses to male pairs differing in carotenoid area.* We tested females with 13 male pairs, differing in the percentage of the body area covered by carotenoid pigment (5–16%). Again we used the 5% criterion for the area of the iridescence and UV reflectance when matching males. Male pairs differed in the area of iridescence and UV reflectance (UV reflectance:  $\bar{X}=16.8\%$ , range 6–24%; iridescence:  $\bar{X}=16.3\%$ , range 4–22%).

#### *Jemez versus Quare females*

*Responses to the UV-reflective components of male colour patterns.* To determine whether predation pressure affects female preference for males with UV-reflective colour patterns, we compared the responses of Jemez females with those of Quare females. The Jemez females were from a population of naturalized guppies in McCauley spring located in the Jemez Mountains of New Mexico, U.S.A. The Jemez population was introduced into the spring over 30 years ago, and since then has had no piscivorous predators. The Quare females used in this experiment were the offspring of first-generation guppies from the middle Quare River of Trinidad. Quare guppies experience predation from cichlids (Endler & Houde 1995). Because Jemez males show the widest range of both carotenoids and UV-reflective colours, we used them to test the responses of both Quare and Jemez females to UV-reflective components of male colour patterns. A description of the experiment measuring responses of Jemez females to pairs of males matched for the area of all colours is given above. Different sets of Jemez males were used to measure the responses of Jemez and Quare females to UV-reflective components of male colour patterns.

Quare females were tested with 15 pairs of Jemez males matched for standard length, area of carotenoid, iridescent and UV-reflective colours, as well as overall colour pattern. Males in each paired set differed by less than 5% in area of carotenoid, iridescent and UV reflectance on the body. Differences among pairs in the proportion of these colours were as follows: carotenoid ( $\bar{X}=7.9\%$ , range 2.0–14.8%), UV reflectance ( $\bar{X}=18.2\%$ , range 6.5–27.3%) and iridescent ( $\bar{X}=17.0\%$ , range 5.4–24.5%).

#### **Statistics**

For each of the three experiments (colour matching, UV reflectance, carotenoids), we analysed the time a female spent with a male when he was behind the UVT and the UVB partition, respectively, with a nonparametric Wilcoxon matched-pairs signed-ranks test using the following expression for each male of a pair: time (UVT – UVB)/time (UVT+UVB). We used a Spearman rank correlation test to analyse the relationship between

the difference in area of UV reflectance patterns (or carotenoids) of a male pair and the difference in time females spent viewing each male of the pair. We used the following expression to determine differences between paired males in the UV reflectance and the carotenoids experiments.  $\text{Male } 1_{(\text{UVT} - \text{UVB})} - \text{Male } 2_{(\text{UVT} - \text{UVB})} / \text{Male } 1_{(\text{UVT} + \text{UVB})} + \text{Male } 2_{(\text{UVT} + \text{UVB})}$ , where Male 1 was the more ornamented male for the trait in question (carotenoids or UV reflectance) and Male 2 the less ornamented male of the pair. We used a one-way analysis of variance (ANOVA) to test for differences in the responses of Quare and Jemez females to the experimental manipulation of male colour patterns.

## RESULTS

### Male UV Reflectance Patterns

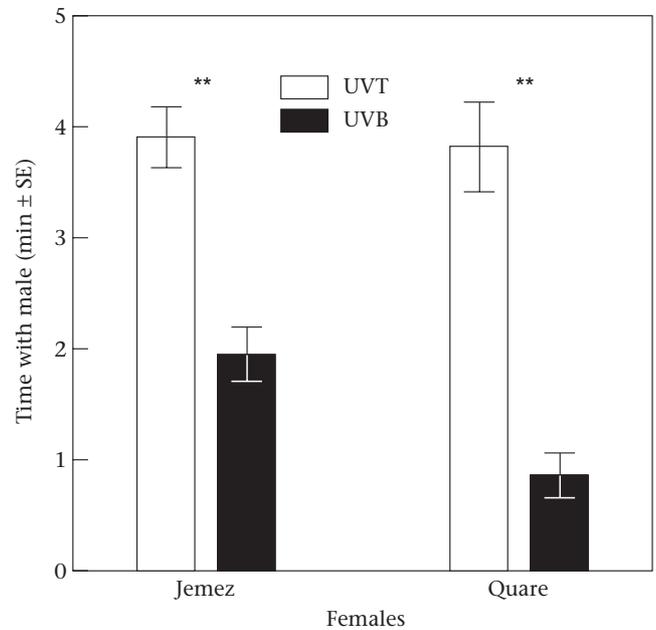
Colour patterns of Jemez males showed UV-reflective components that covered 4–31% ( $\bar{X}=16.6\%$ ,  $N=72$ ) of the body area. Most, but not all, of the iridescent colours also reflected below 400 nm (near UV and UV). Among the iridescent colours, white and purple strongly reflected below 400 nm, but green and blue did not. Gold (yellow–orange) also showed a UV component. Generally, the area of UV reflectance closely matched the area of iridescence visible in longer wavelengths (iridescence:  $\bar{X} \pm \text{SE} = 15.2\% \pm 0.90$ , range 4–28%; UV reflectance:  $\bar{X} \pm = 16.6\% \pm 0.92$ , range 5.5–31,  $N=72$ ). Although the overall colour pattern was the same when viewed in the visible and the short wavelengths, certain aspects of the pattern were more noticeable in the UV wavelengths. Melanin (black) spots surrounded, either completely or partially, by a ring of iridescent white, and gold spots next to black areas provided a striking contrast in the UV.

### Female Responses

#### Jemez females

*Responses to male pairs matched for all colours.* Females spent almost twice as long observing a male behind the UVT partition as they did the same male viewed behind the UVB partition (Wilcoxon matched-pairs signed-ranks test:  $Z=4.70$ ,  $N=20$ ,  $P<0.001$ ; Fig. 2). These results suggest that females not only respond to the UV-reflective components of the male colour patterns, but that these components contribute to the overall attractiveness of a male.

*Responses to male pairs differing in UV reflectance area.* Females, when given a choice between pairs of males that were matched for carotenoids and iridescence but differed in UV reflectance, consistently chose the male of the pair behind the UVT partition (Wilcoxon matched-pairs signed-ranks test:  $T=4.579$ ,  $N=12$ ,  $P<0.001$ ). Difference in the time females spent with the more ornamented male of the pair was positively correlated with the difference in the area of UV reflectance between the pairs (Spearman rank correlation:  $r_s=0.767$ ,  $N=12$ ,  $P=0.015$ ; Fig. 3). These results indicate that females



**Figure 2.** Preference of Jemez and Quare females for males that were placed behind a UV-transmitting (UVT) partition, and for the same males when they were placed behind a UV-blocking (UVB) partition.  $**P<0.001$ . We measured preference as the time the female spent within 5 cm of a male's partition during two 5-min choice tests. Paired males were matched for size and area of carotenoid, iridescent and UV-reflective spots. The Jemez population has no piscivore predators, the Quare population experiences some piscivore predation.

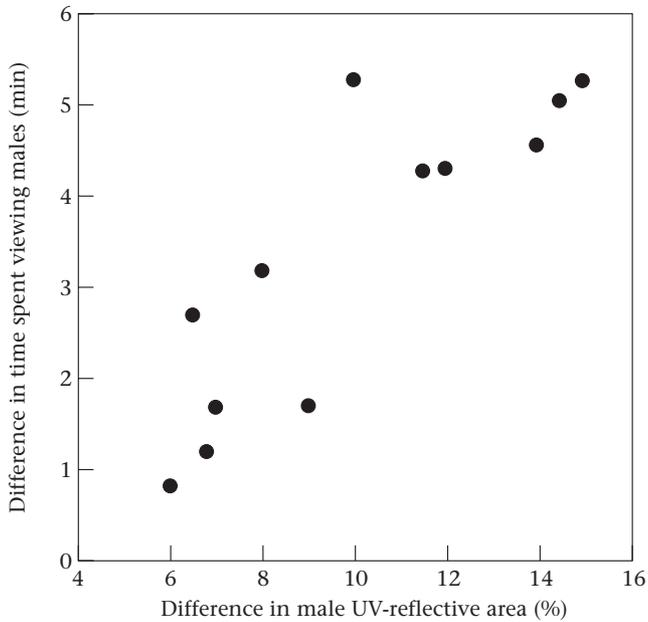
respond to the area of a male's colour pattern that reflects UV wavelengths.

#### *Responses to male pairs differing in carotenoid area.*

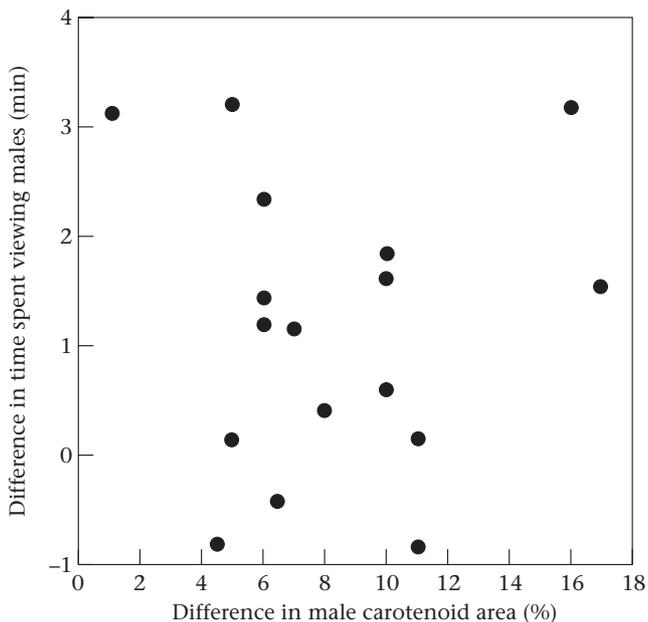
There was no effect of treatment (UVT versus UVB) on female responses to male pairs that differed in the area of carotenoids but were matched for area of iridescence and UV reflectance. (Wilcoxon matched-pairs signed-ranks test:  $T=1.048$ ,  $N=13$ ,  $P=0.295$ ). Similarly, there was no positive correlation between the time females spent with the more ornamented male of the pair when he was behind the UVT partition ( $r_s=0.213$ ,  $N=13$ ,  $P=0.425$ ; Fig. 4).

#### Jemez females

*Responses to the UV-reflective components of male colour patterns.* Females from both populations spent longer viewing males when the males were placed behind the UVT partition than when the same males were placed behind the UVB partition (Quare females: Wilcoxon matched-pairs signed-ranks test:  $T=3.61$ ,  $N=15$ ,  $P<0.001$ ; Jemez females:  $Z=4.70$ ,  $N=20$ ,  $P<0.001$ ; Fig. 2). Jemez and Quare females responded in a similar way to manipulations of the UV-reflective component of male colour patterns (ANOVA:  $F_{1,33}=0.478$ ,  $P=0.50$ ) Predation level thus does not seem to affect female responses to UV-reflective components of male colour patterns.



**Figure 3.** Difference in the time females spent viewing males placed behind a UV-transmitting partition (UVT) and a UV-blocking partition (UVB) as a function of the differences in the percentage of UV-reflective area of male pairs. Male pairs differed in the area of UV reflectance, but were matched for size and area of carotenoid and iridescent spots. Difference in time females viewed males (UVT–UVB) was calculated using the following expression (Male 1<sub>(UVT–UVB)</sub>–Male 2<sub>(UVT–UVB)</sub>/Male 1<sub>(UVT+UVB)</sub>+Male 2<sub>(UVT+UVB)</sub>).



**Figure 4.** Difference in the time females spent viewing males placed behind a UV-transmitting partition (UVT) and a UV-blocking partition (UVB) as a function of the differences in the percentage of the area of carotenoids of male pairs. Male pairs differed in the area of carotenoids, but were matched for size and area of UV reflectance and iridescence. Difference in time females viewed males (UVT–UVB) was calculated as in Fig. 3.

## DISCUSSION

The importance of the UV-reflective component of secondary male traits in intraspecific and interspecific communication has been shown in other groups of vertebrates (lizards: e.g. Fleishman et al. 1993) and insects (butterflies: e.g. Brunton & Majerus 1995). The best evidence that UV reflectance of secondary sexual traits is used by females to discriminate among potential mates comes from research on birds (e.g. red-billed *Leiothrix*: Maier 1993; zebra finches, *Taeniopygia guttata*: Bennett et al. 1996; starlings, *Sturnus vulgaris*: Bennett et al. 1997; bluethroats, *Luscinia svecia*: Andersson & Amundsen 1997; blue tits, *Parus caeruleus*: Hunt et al. 1998). Females discriminate among males based on the degree of UV reflectance of male plumage and prefer to mate with males showing greater iridescence. Also, fine-grain discrimination is possible, because male attributes, such as feather wear, which often reflect age or physical condition, may be 'amplified' (Hasson 1990) in the UV, either by enhancing the contrast between the visible and the UV component of colours, or by changing the overall extent of iridescence.

One advantage of studying guppies is that experiments with UV-transmitting and UV-blocking partitions allow stronger and more direct tests of the role of the UV component of signals. The results of our experiments suggest that females respond to aspects of a male's colour pattern, primarily structural pigments, that reflect in the UV (Fig. 3). The attractiveness of colours and colour patterns is enhanced when viewed in light that transmits across a wider spectrum of wavelengths and extends into the UV (Fig. 2). However, the attractiveness of carotenoid pigments, such as red and orange, that reflect long wavelengths, is not affected by manipulating the UV transmission of viewing conditions (Fig. 4). The responses of females to males with UV-reflective patterns when viewed in the full light spectrum suggests that the UV-reflective component enhances the overall attractiveness of males, and affects mate choice.

The role of sexual selection in the elaboration of UV reflectance patterns in fish may be especially important in species where the sexes are permanently dichromatic, or in those where males develop bright coloration only during the breeding season, because male colour patterns are not only conspicuous to females but often to their predators as well (Kodric-Brown 1998). In guppies, piscivorous predators exert strong selection in shaping many aspects of the colour patterns of males (Endler 1978, 1991; Endler & Houde 1995). Unlike their cichlid predators, which are insensitive to short wavelengths (Muntz 1973; Douglas & McGuigan 1989; van der Meer & Bowmaker 1995, but see Carleton et al. 2000), guppies have UV-sensitive receptors (Archer & Lythgoe 1990). Selection should favour signalling in these short 'private' wavelengths (Endler 1991), because the displays are attractive to females but relatively inconspicuous to their predators. Iridescent colour spots, such as white, although highly reflective in the UV, also are visible in longer wavelengths and are detectable by guppy predators (Endler 1978, 1991). Thus cichlid predators

exert strong selection on the visible (longer wavelength) components of guppy colour patterns, but should have very little effect on the UV-reflective component of these colour patterns. Predation pressure should not affect female preferences for the UV-reflective component of male colour patterns, unless there is a correlated response between expression of male colour patterns and female preference (Houde & Endler 1990). Females from a predator-free population (Jemez) and a population from Trinidad (Quare), which experiences intermediate levels of predation, responded in a similar way to the UV component of male colour patterns. These results suggest that piscivorous predators do not seem to exert strong selection in shaping levels of female responses to signals that use 'private wavelengths' (Endler 1991). Whether sexual selection enhances the UV-reflective component of male colour patterns under high predation pressure has yet to be determined.

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