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ORIGINAL ARTICLE

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Ultraviolet-based female preferences in a viviparous fish

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Abstract Studies on fish have demonstrated female-mating preferences based on dimorphic colours and colour patterns, but commonly focused on the 400–700 nm (visible) band. In experiment 1 we exposed females of the amarillo (*Girardinichthys multiradiatus*), a viviparous fish with visually based female mate choice, to two views of males either containing (UV+) or lacking (UV–) information in the 300–400 nm region. Experiments were conducted outdoors, and we found that females spent more time next to the male seen through the UV+ filter than the same seen through the UV– filter. Since the two images only differed in the content of UV radiation, we conclude that females of the amarillo can detect UV light. Experiments 2 and 3 were designed to test whether such an effect can be attributed to female preferences based on the males' UV-reflecting colour patterns. We first assessed which area(s) of the fish have UV-reflecting properties. Then, using an opaque gelatine powder to block skin reflectance, we found that, in the presence of environmental UV light, females spend more time close to the males with powder sprinkled outside the UV-reflecting area (control) than to the males with powder sprinkled over the UV-reflecting area (experiment 2). This could have been due to the concealment of signals in the visible spectrum, rather than in the UV spectrum; thus we repeated the same experiment indoors, in the absence of UV light (experiment 2b); here females failed to discriminate between males. Since we also found that females have UV-reflecting areas in their flanks, we conducted a third experiment to test whether the preferential association of females found in the first experiment was due to the tendency to school/associate with conspecifics, rather than to mate choice (experiment 3). We found no evidence of discrimination in this experiment. We conclude that the UV markings and vision in *G. multiradiatus* have a function in female mate choice. This is the first time that evidence has been found for the influence of UV for mate choice in fish.

Keywords Fish · Goodeidae · Mate choice · Ultraviolet light · Vision

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Introduction

Recent work has shown that the capability to detect ultraviolet (UV) light (below 400 nm) is both widespread among animals and phylogenetically conserved (Yokoyama and Shi 2000; Ebrey and Koutalos 2001; Hunt et al. 2001). In most cases, however, it is not known why this perception has evolved. Teleost fish have cone receptors in their retina containing pigments which absorb maximally at around 360 nm (Losey et al. 1999). This, coupled with the fact that many species possess ocular media which transmit UV light (Siebeck and Marshall 2001), indicates that many teleosts may have a UV component to their vision (see also Archer and Lythgoe 1990 ; Bowmaker et al. 1991; Hawryshyn and Harosi 1991 ; Beaudet et al. 1993; Muntz et al. 1996; Palacios et al. 1996). Short wavelength radiation such as UV light damages the retina (Collier and Zigman 1987); thus it is likely that UV vision bears a physiological cost. Nevertheless, organisms such as birds have lost, then reconstructed UV vision (Yokoyama and Shi 2000), which implies that UV vision conveys significant benefits. UV vision has been found to be implicated in mate choice in birds (Bennet et al. 1996,1997; Andersson and Amundsen 1997; Andersson et al. 1998; Hunt et al. 1998), reptiles (Fleishman et al. 1993) and insects (Arikawa et al. 1987), yet to date the possibility that there is a UV component to mate choice in fish, although suspected (Carleton et al. 2000), has not been studied.

As short-wavelength radiation is scattered more than long-wavelength radiation, predators may have to approach closer to detect prey species whose optical communication occurs largely within the UV band than would be necessary to detect prey with conspicuous colours outside the UV band. This would be an advantage during sexual selection as males should be able to display to females without substantially increasing the risk of being detected. Research has shown that many fish have skin pigments with reflectance peaks in the UV band (Marshall 1996, 2000) and it is possible that this coloration is used for social signalling. It has long been recognised that colour and colour patterns in fish are relevant in social (e.g. Barlow 1983a, b) and sexual contexts (Houde 1997; Galis and Metz 1998). Typically, the effect of optical display dimorphism (as perceived by humans) in sexual selection is investigated by measuring the responsiveness of females (or of territorial males) to dummies (Tinbergen 1951), or to live males that are (or are made to be) visually distinct (Basolo 1990, 1995). More recently, computer-generated video images have allowed the generation of stimuli that differ only in the attribute of interest, thus reducing the potentially confounding effects of other variables (see Rosenthal et al. 1996, Nicoletto and Kodric-Brown 1999; Trainor and Basolo 2000). However, most of this research had to ignore the UV component of light, as video systems cannot produce UV wavelengths comparable with natural stimuli.

The amarillo fish (*Girardinichthys multiradiatus*) is a viviparous toothcarp (Cyprinodontoidei: Goodeidae) endemic to Central Mexico. This species is sexually dimorphic; males have larger and more colourful fins than females. These features have been shown to be important in female mate choice (Macías Garcia 1991). However, it is not known whether females use information in the UV spectrum when assessing male morphology. The aim of this study was to assess whether UV light is important to female *G. multiradiatus* when selecting mates. In experiment 1, we measured the responsiveness of females to males seen through filters (UV+ and UV–) under natural light. Experiment 2 was designed to determine whether *G. multiradiatus* females preferentially select males under UV light because of a direct effect of UV reflectance on their skin, or whether they are more visible due to the bright underwater background produced by UV radiance. Both of these would result in the male being more conspicuous to the female; however, a direct effect due to the male itself would indicate that UV perception (and UV reflecting skin areas) in these fish does have a direct role in intraspecific signalling, rather than only a role in habitat choice (for foraging or navigation). Experiment 3 explored whether UV vision in *G. multiradiatus* is used to differentially associate with males, rather than being used only for non-gender intraspecific signalling.

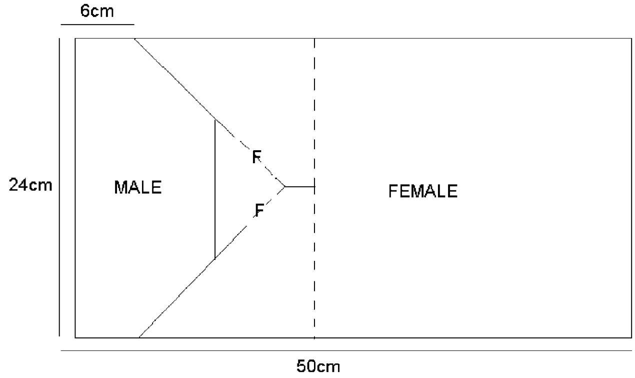

Fig. 1 Overview of the experimental tank. A 40-l aquarium was partitioned with a white, opaque plastic divide into a male (*left*) and a female (*right*) compartment. Two square windows 5 cm per side accommodated the UV+ and the UV– filters (*F*) in alternate positions each trial. A 5-cm-wide wall extending from the corner of the divide forced the female *Girardinichthys multiradiatus* to make unequivocal approaches to either window. We recorded as visits whenever the female remained between the filter window and the thin dotted line marked in the floor

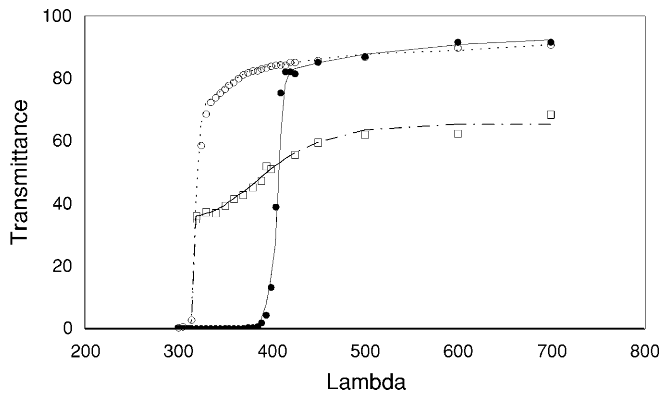

Fig. 2 We used as filters a sheet of acetate (*open circles*) and a LL 400 Corion filter (*closed circles*). *Open squares* show the reduction in the transmittance of the sheet of acetate when coated with a thin layer of Orahesive, a powder used in experiment 2. Transmittance *curves* shown here were obtained using a Perkin-Elmer Lambda 3A spectrophotometer. Note that the retinal UV sensitivity in the teleost fish where it has been measured usually peaks at about 360 nm (see Losey et al 1999)

Methods

Experiment 1: do females prefer males that are presented with, rather than without, UV light?

Twenty-five sexually receptive females and 25 males of *G. multiradiatus* were collected from sites in central Mexico. Fish were allocated to pairs of one female to one male from the same population. Each pair was placed in the experimental tank (Fig. 1) in a random order over 6 consecutive days. In each trial, the female was presented with only one male. The experiment was performed outdoors under natural light conditions to obtain biologically relevant results. All the experimental sessions were performed between 1000 and 1300 hours and on clear days; thus photic conditions were very similar over the entire experiment. The male was placed in a holding area and was visible to the female through two filters. The LL-400 (Corion) filter prevented most of the light of wavelengths below 400 nm from passing, whereas the acetate filter allowed most UV light to pass (Fig. 2). These filters were deemed adequate for this experiment because the retinas of the closely related Poeciliids are known to maximally absorb UV light at about 360 nm (Archer and Lythgoe 1990; Muntz et al. 1996). We tested the hypothesis that the filters would affect attractiveness of the male, as indicated by approaches by the female.

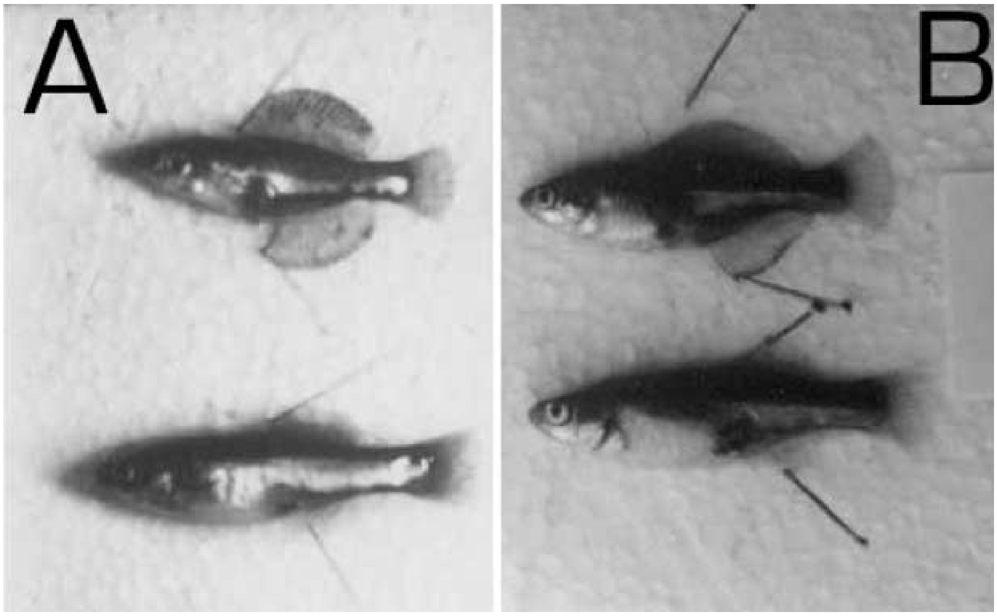

Fig. 3 **A** Male (*top*) and female (*bottom*) *G. multiradiatus* under an ultraviolet light source (245 nm). **B** Male (*top*) and female (*bottom*) *G. multiradiatus* under normal fluorescent white light. Photographs taken with black and white Kodak T400CN film

Before every trial, a male was introduced into the male holding area, a female was placed in the female compartment, and the filters were placed in the filter windows, in alternate positions for each consecutive trial. A white lid with an observation window was then placed over the female compartment. Both fish were left to acclimate in the experimental tank for 20 min prior to the start of each trial. The female was allowed to see the male through both filters during acclimation; she was therefore aware that a male was visible through each window, and it was always oriented towards the male once the trial began. During the trial, the observer recorded the time (in seconds) spent in the vicinity of the male at each filter for a 15-min period. "Vicinity" was defined as crossing a line from which she could closely observe the male (ca. 3 cm). On completion of the trial, both fish were removed and the entire procedure was repeated with another pair.

Experiment 2a: female choice between UV+ and UV– males: does UV vision function in non-gender intraspecific signalling?

Twenty sexually mature males and 10 females of *G. multiradiatus* were collected from sites in central Mexico. Before the experiment began, photographs were taken of the fish under normal fluorescent white light and under UV light from a 245 nm 115 V lamp (Mineralight UVG-54, Upland, Calif.), using Kodak T400CN film. The fish were anaesthetised with 2 g of benzocaine in 5 ml of pure acetone per 300 ml water. These photographs revealed that both male and female fish have an area on their heads and a strip along their flank that reflects UV light (Fig. 3A). These areas appear silvery under visible light (Fig. 3B).

One female was allocated to a pair of males of comparable size from the same population. Prior to each trial, one of the males in each pair (selected at random) was subjected to the UV– treatment and one to the UV+ (control) treatment. UV– males had a coating of Orahesive protective powder applied to the UV reflecting areas on the head and along the flank, whereas UV+ males had the same powder applied to the dorsal and upper surfaces, which contain no UV reflecting areas. This powder was not harmful to the fish and washed off in approximately 30 min. Photographs taken under UV light (245 nm) previously showed that the powder blocked UV reflecting areas when applied to the fishes' skin after the fish had been allowed to swim in the tank for 15 min. In addition, transmittance of a thin layer of this product applied to an acetate demonstrates that Orahesive has a greater impact in blocking UV than in blocking wavelengths above 400 nm (Fig. 2).

During stage A of each trial, the two males in each group (UV+ and UV–) were placed in the end sections of the tank (same dimensions as experiment 1) behind acetate screens. These screens allow approximately 80% of UV and visible light to pass. Positions of the males were selected at random. The female was placed in the central area of the tank and all three fish were left to habituate for 10 min prior to the start of each trial. This allowed the female to see both males at either end of the tank. The observer then recorded the time (in seconds) that the female spent in the vicinity of the male at either end of the tank. "Vicinity" was defined as crossing a line from which she could closely observe the male (ca. 5 cm). On completion of the trial, all fish were removed and held in a recovery tank for 1 h. The fish were then subjected to stage B of each trial. This was identical to stage A except that the treatment of each male was reversed. This procedure was repeated with all the fish over 5 consecutive days. As in experiment 1, the entire experiment was performed outdoors under natural light conditions.

Experiment 2b (control)

Experiment 2a was repeated with the same fish, but indoors under normal white fluorescent lamps. These lamps emit virtually no UV light. The aim of this control experiment was to ascertain whether the result obtained from experiment 2a was due to UV reflectance on the fish's skin, or to an important cue in the visible spectrum being blocked by the powder (see Fig. 2).

Experiment 3: sexual selection or species recognition?

Experiment 2a was repeated, but using only female fish. We hypothesised that females would preferentially associate with UV+ individuals if the effect displayed in experiment 2a was due to species recognition rather than female choice.

Results

Experiment 1

Females frequently approached and stood by the filter windows during the trials. On average they remained for 258 s±161 SD on the side of the UV+ filter and

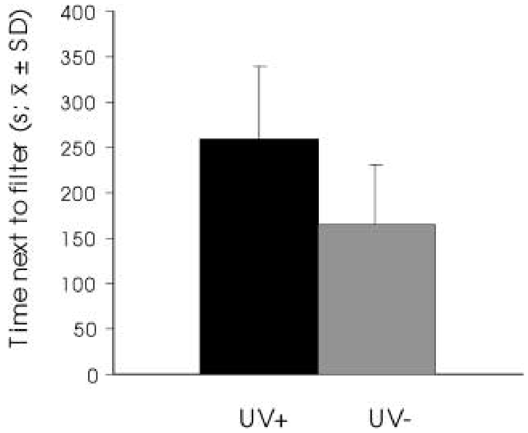

Fig. 4 Average time spent by females next to the image containing (UV+) or lacking (UV–) information in the 300–400 nm range

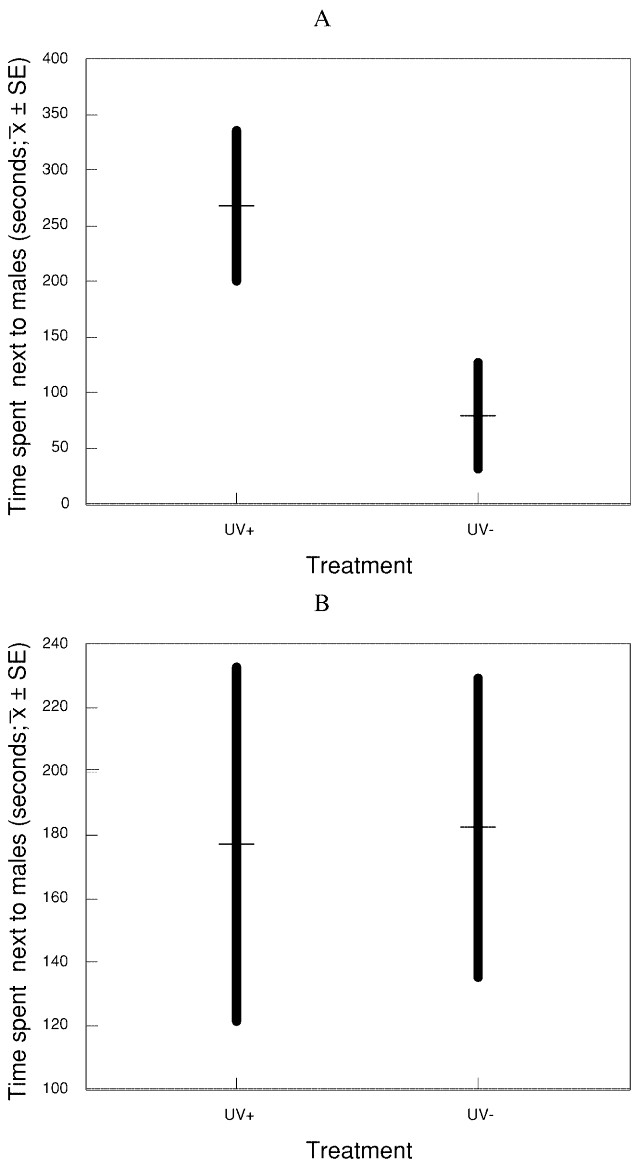

Fig. 5 **A** Mean time spent by females with males in each condition (UV+ and UV–), presented outdoors. **B** With no UV light present in the environment

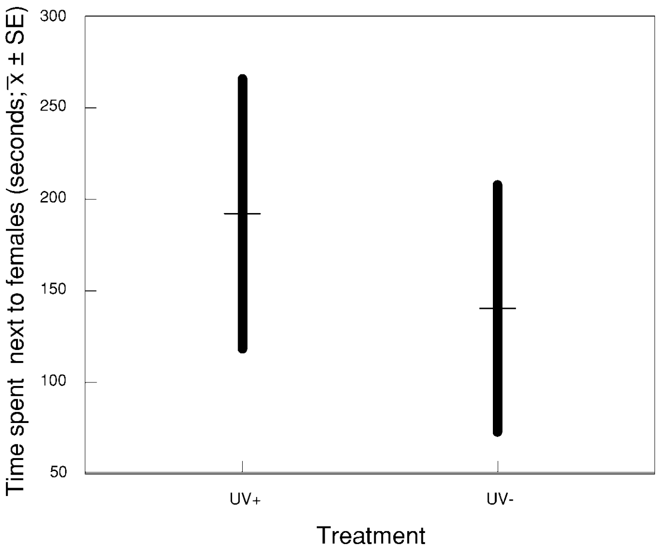

Fig. 6 Mean times spent by females with females in each condition (UV+ and UV–) presented outdoors

165 s±133 SD on the side of the UV– (Fig. 4). Hence, female *G. multiradiatus*, on average, preferred the male image seen through the UV+ filter to that seen with the UV component blocked (paired *t*-test; t=2.14; n=25; P=0.02). The fact that responsiveness to the male seen through the UV– filter was not zero suggests that male features other than UV reflecting skin are attractive to females, but it is still possible that the UV cones were stimulated in the UV– condition, since they are also sensitive to photons outside the UV.

Having discovered that the female fish preferred the image of the male in the presence of UV light we wished to ascertain whether this effect could be attributed to female preferences based on the males' UV-reflecting colour pattern.

Experiment 2a

The times spent by each female with each male in the UV+ and UV– conditions were obtained. As the males in a pair were not independent, mean values were calculated for each pair of males in both conditions (Fig. 5A). The results show that female *G. multiradiatus* preferred to approach males in the control condition rather than the same males with UV reflecting areas blocked (paired Wilcoxon signed-ranks test t=9; n=10; P=0.03).

Experiment 2b

There was no difference in female preference for UV+ and UV– males when no UV light was present in the environment (paired Wilcoxon signed-ranks test t=27; n=10; P=0.50; Fig. 5B).

Experiment 3

There was no difference in female preference for UV+ and UV- females (paired Wilcoxon signed-ranks test t=15; n=10; P=0.37; Fig. 6). These results show that species recognition is not the only function of UV vision in these fish and that the most likely function is in sexual selection.

Discussion

The results of experiment 1 show that female *G. multiradiatus* preferentially associate with a male which is presented with UV light rather than the same male presented with the UV section of the spectrum blocked. Since the only difference between the two male images was that one contained visual information in the UV range and one did not, we conclude that females of this species can detect UV light.

In other animals it has been shown that UV light can be used for a number of different behaviours. It is thought that salmonids use the UV component of polarised light to navigate (Hawryshyn 1992; Parkyn and Hawryshyn 1993). It has also been demonstrated that yellow juvenile perch (*Perca flavescens*) use the bright underwater background UV light when foraging for plankton (Loew and Wahl 1991; Loew et al. 1993). UV wavelengths have also been implicated in visually guided/released behaviour in vertebrates and invertebrates (Bennet and Cuthill 1994; Bennet et al. 1994; Goldsmith 1994). In addition, there has been a recent surge in studies that seek to explain the relevance of UV light in mate choice. Hunt et al. (1998) showed that blue tits, traditionally regarded as sexually monomorphic, are in fact dimorphic under UV light, and Andersson et al. (1998) found that blue tits mate assortatively in relation to the amount of UV reflectance. Experiments 2 and 3 in the current paper aimed to ascertain whether UV vision is also relevant in mate choice in *G. multiradiatus*.

Experiment 2a showed that female *G. multiradiatus* preferred to approach a male in the control condition rather than the same male with UV reflecting areas on the skin blocked. This shows that females preferentially select males under UV light because of a direct effect of UV reflectance on their skin and not because the male was more conspicuous against the bright underwater background caused by UV radiance, which might have explained the results of experiment 1. This effect was not due to signals in the visible spectrum being blocked, as the same result was not found when the experiment was repeated indoors with no available UV light (experiment 2b). Slight caution must, however, be shown as removing UV reduces the total amount of light present; thus the avoidance of UV– fish in either experiment 1 or 2 might be due to a reduction in overall brightness.

The fact that fish in this species have UV markings on their skin to which females are attracted implies that a function of UV vision is in intraspecific communication. UV reflecting areas would presumably be costly due to an increased risk of detection during short-range encounters with predators. The most important underwater predator of *G. multiradiatus* is the visually guided garter snake *Thamnophis melanogaster* (Macías Garcia et al. 1994, 1998). Since garter snakes are capable of perceiving UV radiation (Sillman et al. 1997) it is likely that UV markings would result in a heightened salience to this predator. A cost implies that there must be a benefit to having UV reflecting patterns on the skin. Since such patterns would not be useful for either foraging or orientation, neither of these hypotheses explain the adaptive significance of the UV patterns present on the fish's surfaces, and it is likely that a function of UV vision is in intraspecific signalling. The most likely hypotheses are that females in this experiment were preferentially attracted to the UV+ males either because they recognised the particular colour patterns of their own species or because some feature(s) of the UV reflecting areas is (are) in some form associated with the phenotypic quality of potential partners.

Experiment 3 aimed to separate these two hypotheses and to determine whether a function of UV markings in *G. multiradiatus* is to act as a signal in sexual selection or whether UV markings are involved solely in species recognition. We repeated the experiment with females alone and we hypothesised that females would preferentially associate with UV+ individuals if the effect were purely based on species recognition. The results showed no difference in preference for females with or without UV reflecting areas blocked, thus species recognition is not the only function of UV markings and we conclude that an adaptive significance of UV vision and markings in *G. multiradiatus* is in mate choice.

Male *G. multiradiatus* display to females in such a way that the UV reflecting areas are apparently orientated to the females during courtship displays. When courting, a male exhibits either a lateral (side-to-side) or a perpendicular approach to the female. He also hides the dorsal and ventral fins in the flank that is not exposed to the courted fish (Macías Garcia 1991). This has the effect of displaying the UV reflecting stripes to the female. This behavioural observation further implicates these areas in female mate choice.

In conclusion, these experiments have shown that *G. multiradiatus* possess UV vision and that this vision influences female mate choice. Our finding that females of the Goodeidae (Cyprinodontoidei) can use information in the UV band to direct behaviour adds to a growing body of evidence. Carp (Bowmaker et al. 1991; Hawryshyn and Harosi 1991), trout (Beaudet et al. 1993), perch (Loew and Wahl 1991) and danios (Palacios et al. 1996) have all been shown to possess UV sensitivity. However, this is the first study to show that a function of UV vision and markings in fish is in intraspecific signalling, specifically in mate choice.

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