



UV wavelengths affect female mate choice in three-spined sticklebacks

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Recent behavioural studies on fish have emphasized the role of ultraviolet (UV) wavelengths in mate choice. We performed female mate choice experiments, focusing on the UV wavelength range, with the three-spined stickleback, *Gasterosteus aculeatus*, a species in which the role of visually guided behaviour in the human-visible wavelength range (400–700 nm) has been well studied. Ripe female sticklebacks were given the opportunity to watch courting males behind UV-transmitting (UV+) and UV-blocking (UV-) optical filters. We tested the hypothesis that a difference in viewing conditions, manipulated by the two optical filters, would affect male attractiveness, as indicated by the time that the female stayed near the males. Females significantly preferred UV+ males. They also became less selective with time. Control experiments, in which neutral-density optical filters were used, showed that the ability to perceive UV wavelengths is likely to be used for colour discrimination instead of detecting brightness differences.

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Based on the fact that many animals can perceive UV wavelengths in the range 300–400 nm (Tovée 1995), an increasing number of studies have taken this wavelength range into account. In UV vision in vertebrates a UV-sensitive cone type is often involved (Shi & Yokoyama 2003). Energetic shortwave light has a photo-oxidative effect on epithelia, and on the retinal tissue in particular (Collier & Zigman 1987). Furthermore, the perception of additional UV wavelengths may lead to a less focused retinal image because of strong chromatic aberration and scattering of shorter wavelengths (Lythgoe 1979). Consequently, a visual system sensitive to UV light bears physiological costs and thus must be favoured by selection compared to a system using only the human-visible spectrum.

Intraspecific UV signalling occurs in reptiles (Fleishman et al. 1993), insects (Arikawa et al. 1987) and especially birds (Bennett et al. 1996, 1997; Andersson & Amundsen 1997; Andersson et al. 1998) where UV signals are important in mate choice. In comparison, the evidence for UV signalling in fish is scarce. In mate choice experiments with guppies, *Poecilia reticulata*, Smith et al. (2002) measured a female preference for males viewed in light conditions containing UV light compared to light conditions lacking these shorter wavelengths. Furthermore, White

et al. (2003) found no effect of natural variation in male UV coloration on female choice behaviour in this species.

We studied female mating preference for UV signals in three-spined sticklebacks, *Gasterosteus aculeatus*. During the breeding season, males develop a carotenoid-based red belly coloration combined with blue eyes and blue-white dorsal coloration which are considered to be important courtship signals (McLennan & McPhail 1989a). Red belly coloration acts as a signal in male–male competition (Bakker & Sevenster 1983; Rowland 1984; Bakker 1986; Baube 1997) and, probably more importantly, in female mate choice (Bakker & Milinski 1993) with degrees of coloration varying with male behaviour (Bakker 1986; McLennan & McPhail 1989b; Candolin 2000). In particular, red nuptial coloration is positively correlated with physical condition (e.g. Milinski & Bakker 1990; but see Rush et al. 2003), courtship intensity (Milinski & Bakker 1990; Bakker & Milinski 1991) and female mating preference (e.g. Milinski & Bakker 1990; Bakker 1993).

Several behavioural studies on visual interactions in the three-spined stickleback have used dummies, video playback or computer animations (Rowland 1989; McKinnon 1995; Künzler & Bakker 2001). With regard to wavelengths between 400 and 700 nm, these methods have been based on the assumption that stickleback colour vision is similar to that of humans. However, there are differences, for example in the exact spectral positioning of photoreceptor absorbance maxima (Rush et al. 2003). Female sticklebacks become more sensitive to long

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wavelengths in the breeding season (Cronly-Dillon & Sharma 1968). McDonald & Hawryshyn (1995) used electrophysiological compound action potential recordings to compare spectral sensitivities of sticklebacks from different photic environments and found intraspecific variation in spectral sensitivity. There was a correlation between spectral sensitivity and the light conditions of the sticklebacks' habitat.

Little is known about stickleback perception outside the human-visible spectrum. In addition to the three types of retinal cone cells that absorb maximally at short (435 nm), medium (530 nm) and long (605 nm) wavelengths (Lythgoe 1979), a fourth cone type, maximally sensitive in the UV (360 nm), has recently been found (Rowe et al. 2004). Furthermore, reflectance spectrophotometry of reproductively active male sticklebacks indicates that they possess UV-reflective regions on their sides (Rick et al. 2004; Rowe et al. 2004). These findings suggest a possible role of UV signalling during social and particularly sexual interactions in the three-spined stickleback as described for some other fish (Smith et al. 2002; Macias Garcia & Burt de Perera 2002; Cummings et al. 2003). Our aim in the present study was to assess female preference for courting males under UV-present and UV-absent conditions.

METHODS

Experimental Subjects

Adult three-spined sticklebacks were caught with minnow traps on 3 June and 23 July 2002 from a shallow pond near Euskirchen, Germany (50°38'N, 6°47'E), with permission of the landowner, J. Wittler. The pond is located in a small woodland, with sparse vegetation along the shoreline and shallow banks with few macrophytes. The fish were transported to the institute by car, in plastic containers filled with pond water. In the laboratory, two samples, each consisting of about 200 individuals, were maintained in two separate outside stock tanks (volume 700 litres; temperature 15°C with a freshwater flow rate of 3 litres/min and air ventilation). Males and females were held in separate halves of the stock tanks, separated by an opaque partition. To allow full penetration of UV-rich daylight, the tanks were regularly cleaned. Males were fed to excess once daily and females were fed to excess twice daily with frozen chironomids.

One week later, males that showed conspicuous courtship coloration (i.e. an intense red throat and blue eyes) were moved individually into aquaria (30 × 20 × 20 cm, 12 litres) in the laboratory. Black partitions between the aquaria prevented males seeing each other. Each aquarium contained a petri dish filled with fine gravel to provide males with a nesting site and 150 threads, each 4 cm long, of green cotton twine (100% cotton, Patricia, Karstadt, Germany), as nesting material. The fish were maintained at 17 ± 2°C under a 16:8 h light:dark illumination cycle provided by fluorescent tubes (True Light, Aura Light, Germany, Natural Daylight 5500, 36 W, 1200 mm) hanging 20 cm above the water surface. These fluorescent tubes

produce a proportion of UV similar to natural skylight. Fish were fed ad libitum with chironomids once daily. Females were also transferred into the laboratory and placed in group tanks (45 litres) with 10 individuals each. Females and single males were held under similar conditions.

We stimulated all males once a day for 5 min by presenting a ripe female in a 500-ml jar in front of the holding aquarium. Males that showed no nest-building activity after 2 weeks were replaced by new males with courtship coloration from the outside stock tanks. Males with completed nests were matched by colour intensity (saturation) and extension of their red belly coloration as well as by the colour intensity (saturation) of the blue eye. A human observer matched the fish, as we wanted only to avoid marked variation in male colour traits other than UV within male pairs used in the following choice experiment. Matching was done by ranking colorations within randomized groups of four males. To that aim we put males into four aquaria that stood side by side and that were covered on three sides by grey plastic partitions. Each colour parameter was ranked 1–4 and summed for each male. Red extension was rated in half points from 0.5 to 2 (0.5, 1.0, 1.5, 2.0). Males within a group that differed by less than 1.5 points were used as a pair in the mate choice experiment if their standard length also differed by less than 2 mm and their body mass by less than 200 mg.

We selected ripe females with extended bellies from the group tanks, and measured standard length and body mass before using them in the mate choice experiment. After the experiment, we allowed females to spawn in the nest of a reproductively active male.

Choice Experiment

Our experimental set-up consisted of a dichotomous choice design similar to that used by Smith et al. (2002). We used an 80-litre aquarium (80 × 40 cm and 40 cm deep) which was filled with tap water up to 21 cm. The aquarium was divided in half by a UV-transmitting and visible-light-transmitting Plexiglas partition (GS-2458, Röhm, Darmstadt, Germany). One half formed the female's compartment and the other was further divided into two sections for the two courting males. Between these two sections there was a space of 4 cm so that the female was unable to see the males side by side. An opaque plastic partition in the space prevented the two males seeing each other. The waterproof isolation between the sections also prevented olfactory influences on the choice behaviour (Smith et al. 2002). The male sections were of similar size to the males' holding aquaria. Between the male sections and the female section we inserted two changeable optical filters. One was UV-opaque (GS-233, Röhm, Darmstadt) and the other one transmitted UV-A wavelengths (GS-2458), so that the female could see one male in the human-visible wavelength range and the other male in an extended wavelength range including UV-A. The experimental aquarium was placed on a polystyrene tile on which we marked two preference zones (9 × 16 cm, 0.3-cm-wide line) in front of the male sections. The

aquarium was surrounded by opaque grey plastic partitions up to a height of 30 cm. In addition, a black plastic curtain encased the whole set-up. Illumination was provided by a fluorescent tube (True Light, Natural daylight 5500, 36 W, 1200 mm) positioned 35 cm above the water surface.

Before each trial of the experiment ($N = 18$) we transferred the two males' nests from the holding aquaria to the experimental tank and placed them centred in front of the wall opposite to the optical filters. We thereafter transferred the males to the male sections and put a female in the female section. After closing the black curtain we started recording (see below). Each experimental trial was divided into three phases. During the 10-min acclimation phase before the observation phase we placed an opaque partition between the female and the male sections. This phase enabled the males to accept their nests in the new environment; acceptance was evident from distinct courtship behaviour during the choice phase (I. P. Rick, personal observation).

The following observation phase lasted from the removal of the dividing partition to when the female had entered both preference zones. We then started the test phase. After 10 min, we replaced the opaque partition and exchanged the optical filters in front of the male sections. In the second half of the experiment, the female viewed the same males but behind exchanged optical filters. This was done to control for a potential side bias of the female that is dependent on the stimulus fish. The exchange of filters should resolve whether a potential UV trait of the stimulus males has more impact on female choice behaviour than a possible variation in non-UV traits. The experimental design was identical, including acclimation, observation phase and test phase. Males and females were used only once. We filmed the trial from above with a CCD-camera (Provitek CCTV camera black-and-white, 400 tv lines), observed it on a control monitor and recorded it on videotape. Videotapes were analysed blind, that is, without knowledge of the positions of the UV+ and UV- filters. We measured the time that the female (at least half of the body) spent in the two preference zones in front of the UV+ and UV- males during the test phases. We replaced the tank water after each trial and conducted the next one a day later. All trials were done in normal daylight hours.

Since males may change their behaviour when seeing a female in a UV+ environment, we also measured male courtship activity by counting how many times males crossed a line marked on the monitor which divided the male section into a back half containing the nest and a front half directed to the female section.

Control Experiment

The two optical filters, UV+ and UV-, differed in their spectral transmission and consequently also in quantal flux, so females in the UV experiment will have perceived the males in different brightness conditions. We therefore measured transmission properties of the two filters using a spectrophotometer (Avantes AVS-USB2000, Eerbeek, Netherlands). Illumination was provided in the

range 215–1700 nm by a deuterium-halogen lightsource (Avantes DH-2000). We determined transmission by measuring reflectance relative to a 98% white standard with the reflection probe attached at a 90° angle to the measured filter located on the white standard. In a wavelength range of 300–700 nm the spectra we obtained showed a distinct difference in quantal flux between the two optical filters (UV+ to UV-: mean 18% reduction; Fig. 1).

To test whether UV wavelengths are used for hue or for brightness discrimination, we performed a control experiment with the UV+ and UV- filters being replaced by two neutral-density filters, ND2 (Cotech 298, Zilz, Germany) and ND1 (Lee 209, Zilz, Germany), respectively. These filters alter luminance independent of hue between 300 nm in the UV waveband and 700 nm in the human-visible waveband. In this wavelength range, the difference in quantitative transmission between the two treatment filters (ND1 and ND2) was nearly twice as large as that between the UV treatment filters (ND2 to ND1: mean 34% reduction; Fig. 1). The control experiment was performed and analysed as described for the UV treatment. The fish were sampled from the same population as those used in the choice experiment and treated similarly.

After the study, all fish were kept in the laboratory as breeding stock for future experiments.

Statistical Analyses

Before statistical analyses we tested female behaviour for normality using the Kolmogorov-Smirnov test. Normally distributed data were tested with parametric statistical tests; otherwise nonparametric statistics were used. We analysed female preference for UV+ and UV- males with a sign test and analysed the relative amount of time they spent near the two males with parametric t tests. With regard to trends in female choice behaviour during the experimental period, we used a linear regression to analyse female preference index and a Pearson correlation test to analyse overall female activity. We used a Wilcoxon signed-ranks test and a parametric t test to analyse male activity. All statistical tests were two tailed.

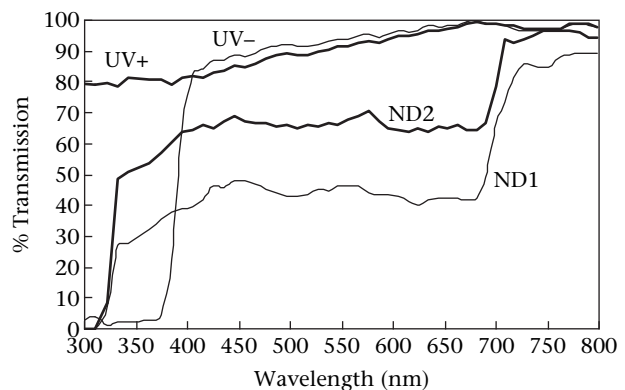


Figure 1. Transmission spectra of the filter types (UV+, UV- and ND2, ND1, respectively). Spectra were measured with an Avantes AVS-USB2000 spectrophotometer and an Avantes DH-2000 deuterium-halogen lightsource.

RESULTS

Mate Choice and UV Vision

Of 18 females only one did not assess both males and was therefore excluded from statistical analyses. All females spawned within 24 h of the end of the experimental trials and thus were regarded as reproductively active. When given a choice between matched pairs of males that differed only in UV reflectance, ripe females significantly preferred the male behind the UV+ filter with respect to both the number of females that spent more time near the UV+ filter than near the UV- filter (sign test: $N_1 = 13$, $N_2 = 4$, $P = 0.049$) and the relative amount of time spent near the UV+ filter ($\bar{X} \pm \text{SD} = 58.7 \pm 16.5\%$) and UV- filter ($41.3 \pm 16.5\%$; paired t test: $t_{16} = 2.172$, $P = 0.045$; Fig. 2).

During the experimental period of 77 days (22 July–7 October 2002), females became increasingly less selective: the preference index (the difference in the relative amount of time spent near the UV+ and UV- filters) was significantly negatively correlated with the number of days after the start of the first trial (Fig. 3). The overall female responsiveness towards male stimuli did not change with ongoing trials since no significant correlation was found between the total time females spent in the preference zones during the trials (UV+ + UV-) and the number of days after the start of the first trial (Pearson correlation: $r_{16} = 0.034$, $P = 0.894$).

Activity of males in the left-hand section did not differ significantly between the UV+ and the UV- settings (Wilcoxon signed-ranks test: $Z = -1.505$, $N = 18$, $P = 0.132$); nor did the activity of males in the right-hand section (paired t test: $t_{17} = -1.500$, $P = 0.152$).

In the later trials we predominantly used females from the second catch conducted later in the breeding season. These females had a significantly lower preference index than females from the first catch (t test: $t_{15} = 2.529$, $N_1 = 12$, $N_2 = 5$, $P = 0.023$), so we analysed mate assessment of females from the first catch separately. Early

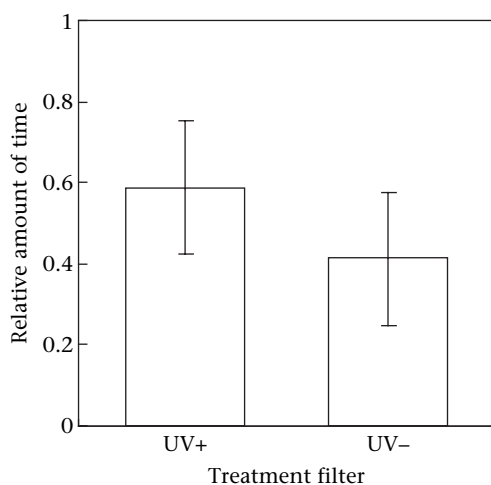


Figure 2. Mean relative time \pm SD spent by 17 females within the preference zone of 9 cm in front of each filter during the mate assessment phase. The filters blocked (UV-) or transmitted (UV+) UV radiation between 300 and 400 nm.

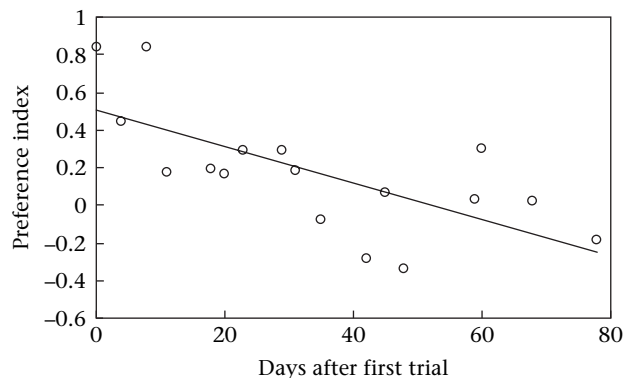


Figure 3. Relation between the preference index and the number of days after the start of the first experimental trial. Positive values indicate a preference for the male behind the UV+ filter, negative values for the UV- male. The line is the least-square regression: $Y = -0.0097X + 0.5038$, $r^2 = 0.470$, $N = 17$, $F_{1,15} = 13.266$, $P = 0.002$.

females had a greater preference for males under UV+ conditions ($\bar{X} \pm \text{SD} = 64.3 \pm 14.6\%$) than for males under UV- conditions ($35.7 \pm 14.6\%$; paired t test: $t_{11} = 3.397$, $P < 0.01$; Fig. 4).

Mate Choice and Achromatic Brightness

Differences in achromatic brightness did not affect female responses towards male stimuli under UV+ conditions. Test females showed no significant preference for males behind the ND1 ($\bar{X} \pm \text{SD} = 51.6 \pm 15.9\%$) or ND2 treatment filter ($48.4 \pm 15.9\%$; paired t test: $t_{13} = 0.388$, $P = 0.705$).

DISCUSSION

The results of the UV mate choice experiment show that female three-spined sticklebacks prefer to assess a male

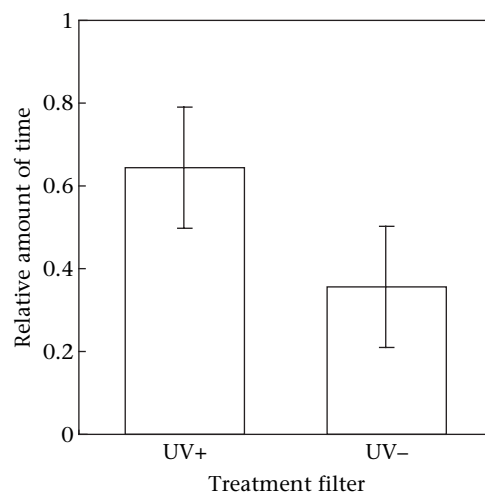


Figure 4. Mean relative time \pm SD spent by 12 females from the first catch within the preference zone of each filter during the mate assessment phase. UV+ and UV- filters transmitted and blocked UV radiation, respectively.

that is in a light environment including UV-A (UV+: 300–700 nm) compared to a male presented in conditions lacking these wavelengths (UV–: 400–700 nm). Thus, we conclude that female three-spined sticklebacks are able to discriminate between UV and non-UV stimuli, especially in a mate choice context. Owing to the filtering of UV wavelengths on the UV– side it is possible that species or sex recognition on this side was prevented, causing females to prefer males behind the UV+ treatment filter (Bennett et al. 1997). However, females courted males with the typical head-up posture on both the UV+ and UV– side (I. P. Rick, personal observation).

In some other vertebrates, UV cues do have a function in social interactions. Numerous well-documented studies on birds deal with UV signalling in mate choice (Bennett et al. 1996, 1997; Andersson & Amundsen 1997; Hunt et al. 1998) and foraging (Viitala et al. 1995; Church et al. 1998). Recent studies on fish have investigated the role of UV light in mate selection by using UV-transmitting and UV-blocking optical filters in dichotomous choice experiments (Kodric-Brown & Johnson 2002; Macias Garcia & Burt de Perera 2002; Smith et al. 2002).

In the three-spined stickleback, the function of male courtship coloration in inter- and intraspecific interactions in human-visible light is well understood. Several behavioural studies focusing on sexual selection have shown that an increase in male red belly coloration is particularly associated with greater female preference (e.g. Milinski & Bakker 1990; Bakker & Milinski 1991, 1993; Bakker 1993) and higher levels of male aggression (Rowland 1984) and dominance (Bakker & Sevenster 1983). However, conspicuous coloration might also be accompanied by an increased risk of being detected by predators. This can lead to decreased conspicuousness of reproductive traits (Endler 1980; Zuk & Kolluru 1998). For the three-spined stickleback, information on the effect of predation on male coloration patterns is scarce. Candolin (1998) described a decrease in male breeding coloration either as a direct reaction to predator presence or as an effect of greater investment in antipredator behaviour.

Increased predation can also lead to elaboration of traits that are difficult to detect by predators (Endler 1991). For example, colour patterns reflecting in the UV could serve as secret signals since UV light is scattered strongly in water. Thus, UV signals may be useful for intraspecific signalling over short distances while eliminating the risk of being detected by others (Losey et al. 1999). Cummings et al. (2003) described the use of a phenotypically diverse UV signal in private communication in northern swordtails (*Xiphophorus malinche*, *X. nigrensis*); the signal is almost imperceptible to predators and its development and importance in courtship depend on predator density.

Further investigations should thus concentrate on intraspecific variation in UV coloration and signalling with regard to varying predatory influences and spectral conditions of the habitat. For example, McDonald & Hawryshyn (1995) showed intraspecific variation in the spectral sensitivity of three-spined sticklebacks originating from different photic environments. Since three-spined sticklebacks have a UV-sensitive cone type (Rowe et al.

2004) this wavelength range should be considered in future experiments dealing with vision in this species.

In our choice experiment, females became less choosy in the later trials although overall female responsiveness towards the presented males did not change significantly. A decrease in UV reflectivity in males used in later trials could be responsible for the reduced choosiness of the females. However, in reflectance measurements on males from the same population that were taken during the courtship season we did not find such a decrease (I. P. Rick, personal observation).

Kynard (1978) observed a shift to a female-biased sex ratio later in the breeding season in a lacustrine population of three-spined sticklebacks. In our study, female sticklebacks that were used in the later trials predominantly derived from the second catching date almost 2 months after the first. Therefore, it is conceivable that these females experienced a female-biased operational sex ratio in the field which could have reduced female choosiness (reviewed in Jennions & Petrie 1997). Furthermore, females may be less capable of viewing UV wavelengths outside the breeding season. Cronly-Dillon & Sharma (1968) found in optomotor tests that female sticklebacks became more sensitive to long wavelengths during the breeding season, which suggests a shift in visual pigment spectral sensitivity brought about by either a change in chromophores or the expression of a new opsin (Archer et al. 2001). Our results suggest that a seasonal shift in UV sensitivity in sticklebacks cannot be excluded, although the potential mechanisms and functions need to be investigated.

A photoreceptor maximally absorbing in UV light can contribute to extended colour vision as well as simply enhance achromatic brightness discrimination (Smith et al. 2002). In the experiment with neutral-density filters, females showed no significant preference for males appearing in either high or low brightness conditions independent of hue. We may therefore assume that the UV component of stickleback coloration is involved in mate choice. Furthermore, although the mechanisms involved in brightness discrimination in sticklebacks are unknown, our experiment indicates that hue rather than brightness influences the mate choice behaviour of female sticklebacks.

In conclusion, we found for the first time that female mate choice in the three-spined stickleback is influenced by a visual component outside our human perceptual range. Future research should take into account this component which has been disregarded in previous studies on stickleback behaviour and ecology. Finally, it would be interesting to discover how the UV wavelength range is related to currently known visual mechanisms working in mate choice and intraspecific interactions in general.

Note added in press: Recently, Boulcott et al. (2005, *Journal of Experimental Biology*, 208, 1453–1458) also assessed an effect of UV in female mate choice in another stickleback population.

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