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The role of ultraviolet wavelengths in the mate-choice decisions of female three-spined sticklebacks

P. D. Boulcott*, K. Walton and V. A. Braithwaite

The University of Edinburgh, Institute of Cell and Animal Population Biology, West Mains Road, Edinburgh EH9 3JT, Scotland

*Author for correspondence (e-mail: pip.boulcott@virgin.net)

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Summary

Female three-spined sticklebacks have been found to use visual cues when responding sexually towards courting males, often preferring more intensely red-coloured males, and males with blue rather than silver irises. However, traditionally the literature has failed to test preference across the full spectral range to which females might be sensitive, limiting analysis to the human-visible wavelengths of the electromagnetic spectrum. We studied the effects that the addition of ultraviolet wavelengths has on the mate-choice preferences of female sticklebacks using a two-choice paradigm. We found that females preferred males that were viewed across the full spectrum to males whose display lacked an ultraviolet component. Using suitable controls we were able to establish that female preference was sexually motivated and was not caused by a general preference for the manipulated light conditions. Our results indicate that female preference may be due to an enhancement in visual contrast when males are viewed in full spectrum conditions.

Key words: mate choice, three-spined stickleback, *Gasterosteus aculeatus*, ultraviolet, UV, light vision.

Introduction

More than 60 years have passed since Niko Tinbergen and co-workers first drew attention to the use of sign stimuli in the courtship rituals of the three-spined stickleback (ter Pelkwijk and Tinbergen, 1937). This work provided clear evidence that reproductively active females during the breeding season respond to the conspicuous red area around the throat and belly displayed by sexually mature males. In the intervening years, it has become clear that the male's colourful body pattern plays a central role in the sexual selection of this species (Semler, 1971; Kirkpatrick, 1987; Rowland, 1994). Whilst comprehensive, this body of work is incomplete, as the role of colour and vision in the courtship of the three-spined stickleback has been examined only across the region of the electromagnetic spectrum to which humans are sensitive (400–700 nm).

Under competition for potential mates, whilst controlling for factors such as courtship vigour and size, female three-spined sticklebacks have been found to prefer males displaying blue rather than silver irises, and in particular, more intensely coloured red throats (McLennan and McPhail, 1990). Yet, the function of the red signal should not be regarded as a universal feature across the *Gasterosteus aculeatus* species complex since black-throated populations are found to exist (Fitzgerald, 1993). Even in those populations where red-throated males are present there exists considerable room for ambiguity, with female preference for one male over another depending on the degree of difference in the signals displayed by two competing males (Braithwaite and Barber, 2000), her motivational state (Rowland, 1995), or prior experience of the female (Bakker and Milinski, 1991). Evidence also suggests that female choice may not be related to the specific optical properties of the red colour patch *per se*, but may instead relate to the high contrast appearance of the red signal when viewed in some environments (Baube et al., 1995). Hence, whilst the red throat of the male may be utilised in the mate-choice decisions of the stickleback, its importance may be overstated. In contrast, relatively little is known about the role that the ultraviolet waveband plays in the visual communication of the stickleback despite growing evidence that this region of the spectrum is used by many vertebrates (for a review, see Tovée, 1995).

Data suggesting that the three-spined stickleback is sensitive to ultraviolet light does exist. As early as the 1930s, Merker, using a single population of three-spined sticklebacks, found that each of the optical components of the stickleback's eye – cornea, vitreous humour and lens – were found to be transparent to ultraviolet wavelengths (Merker, 1932, 1934, 1937). Given the absorption characteristics of the three widely acknowledged cone pigments in the stickleback retina (peak absorptions 445, 530, 605 nm), it is possible that ultraviolet sensitivity is mediated by a secondary (beta) absorption peak belonging to pigments that are maximally sensitive in the human-visible region of the spectrum (Dyer, 2001). However, in addition to the possibility of beta peak sensitivity, recent microspectrophotometric evidence suggests that the stickleback also possesses a fourth, independent cone photoreceptor, maximally absorbent in the UV region of the spectrum at 360 nm (Rowe et al., 2004). That such a visual system is capable of perceiving ultraviolet light is supported by behavioural experiments carried out under high intensity ultraviolet illumination (Merker, 1939), and under full-spectrum conditions (P. D. Boulcott and V. A. Braithwaite, manuscript submitted for publication).

Despite growing evidence that sticklebacks can perceive ultraviolet wavelengths, our understanding of their mate-choice decisions has been exclusively derived from experiments using techniques appropriate to the human visual system. In adopting such an approach, it is likely that colour choice has been misclassified in this species, and the functional significance of the ultraviolet waveband overlooked (Bennett et al., 1994). Moreover, it has become apparent that the use of ultraviolet wavelengths during mate choice may be quite a common behaviour amongst vertebrates. Ultraviolet reflectance has been found to influence the mate-choice decisions of birds (Bennett et al., 1996), lizards (Fleishman et al., 1993), butterflies (Arikawa et al., 1987) and fish (Kodric-Brown and Johnson, 2002; Smith et al., 2002). Given that the three-spined stickleback is capable of responding behaviourally to ultraviolet wavelengths, and that colour plays an important part in the mate-choice decision of this species, we hypothesised that females may use ultraviolet-based cues in their selection of a mate.

Materials and methods

General experimental protocol

To assess female preference during mate choice we employed a simple two-choice technique that examined the time a female apportioned to the courtship display of two reproductively active males. Such a technique has been used successfully by Smith et al. (2002) in their ultraviolet mate-choice experiments with the guppy *Poecilia reticulata*, and by mate-choice experiments in general (Houde, 1987). However, as the use of visual cues by the stickleback is not restricted to inter-sexual communication, it was necessary to establish that any preference for one male over another reflected sexually motivated decisions. By way of a control, a series of four experiments were conducted to assess female choice when: two empty choice compartments were presented to sexually immature females (Exp. 1), two sexually immature shoals were presented to sexually immature females (Exp. 2), empty compartments were presented to sexually receptive females (Exp. 3), and when two sexually responsive males were presented to sexually receptive females (Exp. 4).

Experimental set-up

The experimental apparatus consisted of five rectangular tanks (50 cm×40 cm×30 cm), each divided by an opaque plastic partition into three sections: a central viewing chamber and two adjacent choice chambers (Fig. 1). In each experiment, the presentation of the two choice-chambers to the test fish

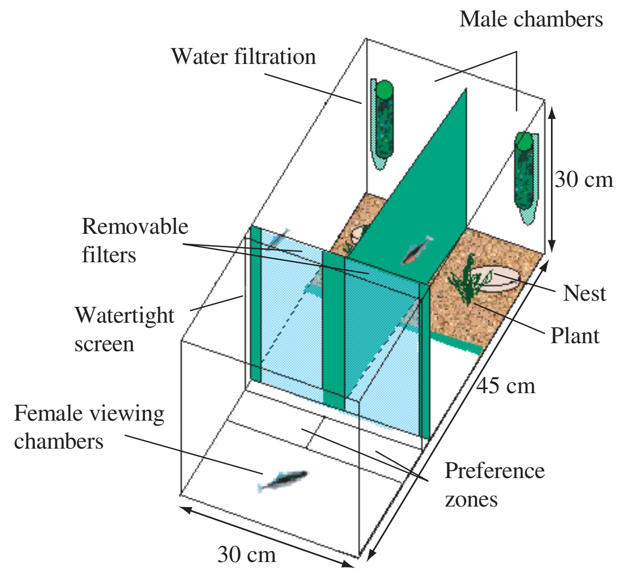

Fig. 1. Schematic diagram of the two-choice apparatus used in Exps 2–4.

differed in terms of two interchangeable light-filter treatments placed in front of each viewing chamber. These filters were either ultraviolet transmitting (UV+) or blocking (UV–); Fig. 2A. For an animal with the appropriate visual system, identical objects viewed through these filters will differ in terms of their hue and brightness.

To prevent the use of olfactory cues during the trials, the two choice chambers were sealed from the viewing chamber by a single sheet of UV transmissive Perspex. The tank walls were then covered with black plastic screen to minimise outside disturbance. Test tanks were illuminated by a single 5500°K full spectrum fluorescent tube (Arcadia Ltd, UK) suspended 40 cm above the tank (Fig. 2B).

Subjects

Adult three-spined sticklebacks *Gasterosteus aculeatus* L. were collected from the Balmaha Pond, Loch Lomond, in March 2002. Whilst in the laboratory, fish were held in two main stock tanks (92 cm×39 cm×30 cm), each illuminated by a full spectrum fluorescent tube in addition to eight ceiling 80 W fluorescent tubes, and were fed twice daily on a diet of live and frozen *Tubifex* worms. To encourage the onset of reproductive condition for subjects in Exps 3 and 4, the ambient temperature of these two stock tanks was maintained at approximately 20°C. For similar reasons the light regime was set to a 16 h:8 h light/dark cycle (Hoar, 1962). Once the fish had reached a sexually reproductive condition, males were temporarily removed to smaller holding tanks (30 cm×22 cm×20 cm) prior to testing. Temperature and light regimes in these smaller tanks, and the test tanks, were the same as the stock aquaria.

Assessing preference

Preference was quantified in terms of the proportion of time

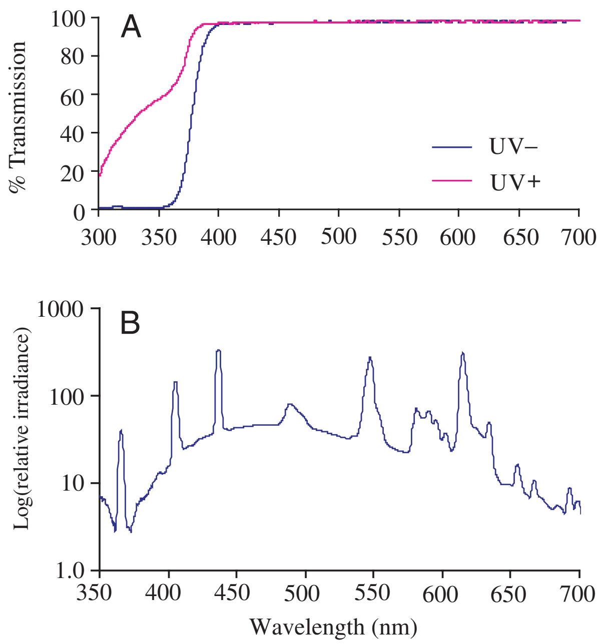

Fig. 2. (A) Transmission curves for the UV+ and UV– filters (300–700 nm). (B) Relative irradiance (log quantal flux) of full spectrum fluorescent tubes (Arcadia Ltd, UK) used in all four experiments (350–700 nm).

the fish spent orientated towards the choice chambers within a 5 cm zone of either of the two filter types. Each test fish was only judged to have entered a new zone once its head and pectoral fins had crossed the zone boundary. For the data to be included in any subsequent analysis, the test fish must have entered both test zones during the first 2 min of the trial period. Such a measure of preference has proved a useful estimate of preference in previous mate-preference experiments (Rowland, 1995).

At the outset of each trial all test individuals were allowed a 10 min settling period. During this period the two choice chambers were screened off using an opaque screen. This screen could be raised remotely, signifying the beginning of a trial, and was only lifted when the test fish was situated centrally in the non-preference zone. Each trial lasted 20 min, during which observations were recorded *via* a video camera (JVC, GX-NFE) suspended 1 m above the tank. All trials were carried out between 10:00 h and 16:00 h.

Experiment 1 – filter preference of non-reproductive individuals

Exp. 1 was designed to determine if fish in non-reproductive condition exhibited a preference for either filter type. Ten test fish were screened individually. A fish was selected at random from either of the two stock tanks and placed centrally in the non-preference zone for a 10 min period of acclimation, after which fish preference was recorded for 20 min.

Experiment 2 – ultraviolet perception and shoaling behaviour

Exp. 2 examined whether ultraviolet wavelengths are used in the visually mediated shoaling decisions of the three-spined stickleback. This experiment was identical to Exp. 1, with the exception that two groups of non-reproductive stimulus shoals, each containing three individuals, now occupied the two choice chambers. Both shoal fish and test fish used in each of the ten trials were naïve to the set-up. Shoal members were size matched in order to minimise size selection bias during the shoaling. All fish in any given trial had been pooled in the same stock tank for a minimum of 14 days and had, therefore, a similar degree of familiarity with each other. This time period has been found to be sufficiently long for the stickleback to establish shoaling preferences (Barber and Wright, 2001).

Experiment 3 – filter preference of gravid females

The experimental procedure in Exp. 3 replicated Exp. 1, except that ten gravid females were selected as test individuals. As it was important to ensure that these gravid females were sexually responsive, females were chosen only if they exhibited the characteristic ‘head-up’ display in response to a sexually reproductive male. To avoid the problems associated with prior experience, the stimulus male used in this procedure was not used in the later mate-choice experiment.

Experiment 4 – ultraviolet perception and mate choice

Exp. 4 examined the role that ultraviolet wavelengths might play during mate-choice decisions of the female three-spined stickleback. Sexually responsive males were placed in each of the two choice chambers, which were furnished with suitable nesting materials, and encouraged to build nests. Once both males had constructed a nest and were observed to court a stimulus female vigorously, they were judged ready for test trials. To minimise any influence of the male’s nest on the female’s assessment, the water filter in each viewing chamber was placed in front of the nest (Braithwaite and Barber, 2000; Barber et al., 2001). Preference measures were made with ten gravid females, all of whom were naïve to the test apparatus. In order to assess male behaviour, the number of zig-zag displays performed by each male during the trial was recorded. Such display rates have been found to be a useful measure of male sexual tendency in this species (Rowland, 1984).

Pairing stimulus males

Males used in the trial did not develop the same intensity of nuptial colouration, despite being reared in identical conditions. Evidence suggests, however, that females may select males based on their degree of colouration and also on the extent of the differences between two males (Braithwaite and Barber, 2000). In view of this, each pair of males was matched for size, general morphology and, as far as practicably possible, colour. To obtain an estimate of the degree of intensity of the red belly of each fish, males were scored from 1–5 for colour by two observers, and the average score taken (Rowland, 1984). No trials were undertaken where the males differed in redness by more than one point. Whilst this technique is necessarily subjective, it does reduce the influence of factors other than ultraviolet content that are known to affect female choice. Once paired, males were then randomly assigned to one of the two filter treatments: UV transmitting or UV blocking.

Statistical analyses

Female preference, measured as the proportion of time spent within either of the two preference zones, was analysed using a General Linear Model (GLM). A GLM was initially fitted to the data and included all explanatory variables and their interactions. Terms were then removed by stepwise deletion. Where possible, minimal models for the main factor are reported for each of the four experiments in the form of a student *t*-test. Prior to analysis, all proportional data was arcsine square-root transformed. An Anderson–Darling test was performed on the data to assess normality. Male display rates in Exp. 4 were analysed using a Wilcoxon matched signed-pairs ranked test.

Results

Experiment 1

Female sticklebacks were not found to show a preference for either filter type (two-tailed *t*-test: t=–0.26, d.f.=17, P=0.80; see Fig. 3). Similarly, no holding tank effect was found (GLM: $F_{4,5}$=1.36, P=0.365).

Experiment 2

Females did not prefer to shoal with conspecifics viewed through either the UV+ or UV– filter (two-tailed *t*-test: t=–1.27, d.f.=15, P=0.22; see Fig. 3). No effect of the holding tank was found (GLM: $F_{4,5}$=0.96, P=0.503). When comparing the time each female spent in the preference zones across Exps 1 and 2, there were no differences (two-tailed *t*-test: t=–1.88, d.f.=12, P=0.08).

Experiment 3

Gravid females did not exhibit a preference for either the UV+ or UV– filter (two-tailed *t*-test: t=–1.52, d.f.=17, P=0.15; see Fig. 3). Similarly, no effect of the holding tank was revealed (GLM: $F_{4,5}$=2.09, P=0.219). Hence, gravid females, in common with their non-gravid counterparts in Exp. 1, did not express a preference for either filter type.

Experiment 4

Throughout all mate-choice trials, males were seen to perform the zig-zag display. The rate of this display was not found to differ significantly according to the filter type (Wilcoxon matched signed-pairs ranked test: Z=–0.255, P=0.79). Similarly, all females were seen to display the classic head-up posture while in the preference zone. No effect of the holding tank was found (GLM: $F_{4,5}$=0.41, P=0.79). Gravid

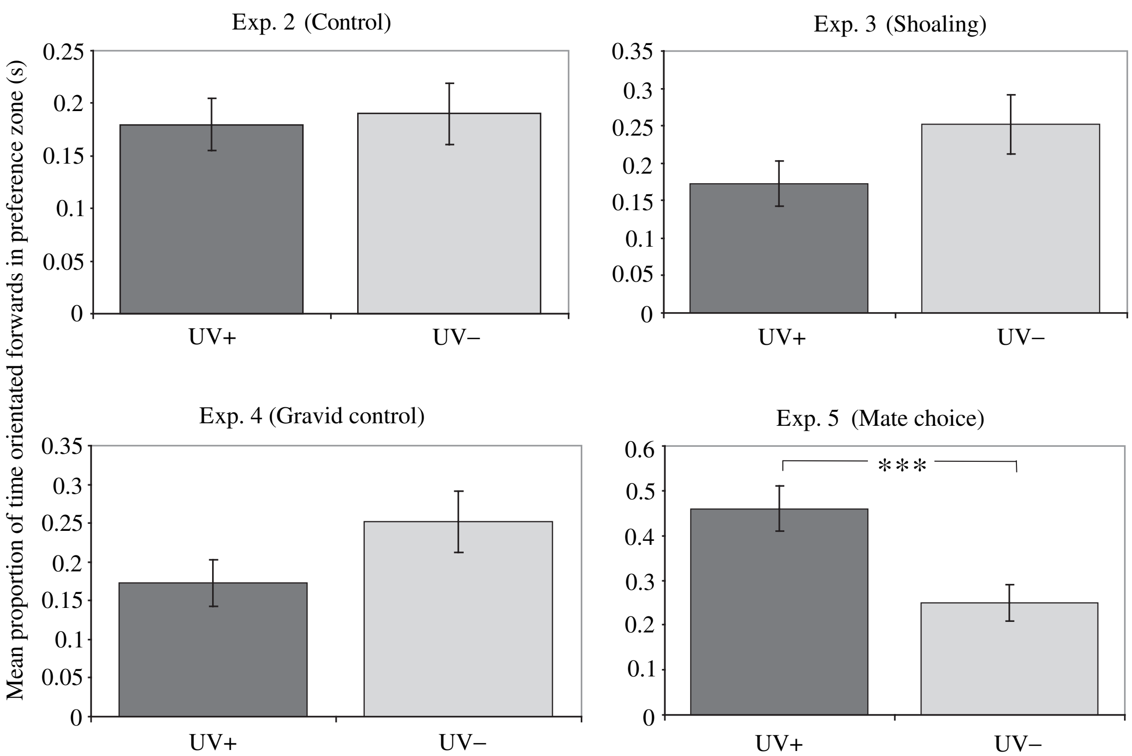

Fig. 3. Comparison of female preference according to light-filter type. Exps 1 and 3 were control experiments conducted in the absence of other conspecifics, and tested the preferences of non-reproductive and sexually receptive females, respectively. Exp. 2 tested when small shoals of conspecifics could be viewed through the two filter types. Exp. 4 tested preference when sexually responsive males could be viewed (***P<0.01). In all four experiments, preference is denoted by the proportion of time each individual spent in either of the two preference zones (UV+/UV–) where the fish was facing towards the choice compartments during the 20 min test. Values are means ± S.E.M. (N=10).

females did, however, exhibit a significant preference for those males viewed through the UV+ filter compared to those viewed through the UV– filter (two-tailed *t*-test: $t=3.88$, d.f.=12, $P=0.002$; see Fig. 3). Gravid females in Exp. 4 also spent more time facing the preference zone when males were present compared to Exp. 3, where no conspecifics were present (two-tailed *t*-test: $t=-4.46$, d.f.=17, $P<0.001$).

Discussion

Female three-spined sticklebacks use ultraviolet cues during mate assessment. When given a choice between two similarly sized and coloured males, females preferred to spend more time with a male that could be seen with ultraviolet cues. That no such preference was found in experiments 1 and 3, where conspecifics were absent from the two choice chambers, suggests that the female's choice is not based on general preference for filter type. Females performed clear head-up responses to both males during the experiments, confirming that females were sexually responsive to both males and did not view either individual as unsuitable. In addition, gravid females were found to spend more time in the two preference zones adjacent to the displaying males in comparison to the time they spent in the same preference zones during experiment 3 when no males were present.

The two ultraviolet treatments used in this experiment did not influence shoaling choice. Given that previous studies have shown three-spined sticklebacks prefer to associate with conspecifics with a familiar appearance (Barber and Ruxton, 2000), it would seem that the females we tested did not regard the individuals viewed through the ultraviolet blocking filter as abnormal. Furthermore, this indicates that preference decisions taken by the female in experiment 4 were based on a sexually motivated mate preference, rather than a natural tendency to associate with individuals, male or female, displaying across the ultraviolet and human-visible region of the spectrum.

Male behaviour

Female sticklebacks, following the onset of sexual receptivity, develop a dark bar-like melanated pattern down their silver flanks (Wootton, 1976). Reflectance spectra obtained from these colour patches reveal that the silver flanks possess a peak in the ultraviolet region of the spectrum, providing a contrast with the relatively low UV reflectance of the flanks (Boulcott, 2003). Since the addition of the ultraviolet waveband will serve to enhance the contrast of this signal, it is possible that this characteristic pattern might be used by males when assessing female receptivity (Rowland et al., 1991). Furthermore, as female mate choice in the stickleback has been found to be affected by the vigour of the displaying male's courtship (Rowland, 1995), it could be argued that the female's choice in experiment 4 is driven by the two males responding to the female differentially, since they viewed her under different spectral conditions. Such a mechanism would operate despite the random assignment of filter type to each pair of males. Our results, however, suggest that male display rate does not differ significantly with filter, and that each male courts the female vigorously throughout the period. It is, therefore, likely that female preference in experiment 4 was driven by the visual appearance of the males alone, and not by a difference in display activity. This finding differs from similar mate-choice studies carried out in the guppy *Poecilia reticulata*, where the addition of the ultraviolet waveband was found to enhance the attractiveness of potential mates in both males and females (Kodric-Brown and Johnson, 2002; Smith et al., 2002).

Mate choice and signal display

Work carried out by Rowe et al. (2004) suggests that the red throat colour of the reproductively active male is encoded by an orthogonal opponent mechanism that is largely insensitive to input from the ultraviolet photoreceptor. Hence, the addition of ultraviolet wavelengths to the appearance of the displaying male in our experiment would not alter the red signal appreciably. However, as the mosaic pattern – red throat, blue iris and dark green melanted flank – of the male is a high-contrast signal (Milinski and Bakker, 1990), females viewing a displaying male under full spectral conditions may find that both hue and luminance contrast are enhanced – thereby increasing total contrast. Both the silver flanks (Boulcott, 2003) and the blue iris of coloured males (Rowe et al., 2004) reflect short wavelength light strongly, and would contrast against the red throat and dark flank, which only weakly reflect light in the ultraviolet waveband. This will be true even if the ultraviolet photoreceptor does not contribute to the colour visual system because differences in contrast can be detected by brightness perception alone (Kevan et al., 2001). Furthermore, if a displaying male is viewed against a background reflective to ultraviolet light, a situation which is likely if the fish is viewed against a sandy substrate, visual contrast would be increased given the relatively poor ultraviolet reflectance of the cryptic flank (Rowe et al., 2004).

The addition of the ultraviolet region would seem to enhance total contrast of the male's nuptial signal and might, therefore, be responsible for the manipulated change in female preference observed during experiment 4. Indeed, the importance of red colouration in this species complex may be overstated, and there is increasing evidence to suggest that female preference for the male signal is more likely to be related to its efficiency in generating visual contrast. In an elegant series of experiments, Baube and coworkers found that 100% red dummies used to elicit mate-choice behaviour in females brought no greater reaction than 100% beige coloured dummies (Baube et al., 1995). However, dummies that possessed some degree of visual contrast produced the greatest reaction, and this response was found to be independent of the area of shading. Such findings suggest that not only are abnormal signals disregarded, and that key stimuli must have context (Tinbergen, 1951), but that the stickleback's visual system is tuned to detect signals in terms of form and colour that produce a high contrast target within the aquatic environment. The function of the mosaic signal as a high-contrast optical signal is supported in the field by studies investigating mate choice in populations of black-throated three-spined sticklebacks (McDonald et al., 1995). In this instance signal contrast, rather than the red throat colour itself, was found to be the important determining factor of female choice during courtship.

Although our results show that females utilise ultraviolet wavelengths during their mate-choice decision, key questions relating to the evolutionary implications of this finding arise. Given the diversity of the three-spined stickleback species in terms of evolutionary history and habitat, it is unclear as to what extent the ability to perceive ultraviolet wavelengths varies. If variation exists, it may lead to selective pressure on male colouration in this species.

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