

# Colour perception in three-spined sticklebacks: sexes are not so different after all

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**Abstract** Sexual selection theory implies a tight coupling between the evolution of male sexual display and the sensory capabilities of the female. In sexually dimorphic species it is proposed that this might lead to sex differences in a species' perceptive abilities. However, supporting evidence for this is rare, and to date there is only one example; three-spined sticklebacks, *Gasterosteus aculeatus*. Here, the female's visual system is reported to become more red-sensitive during the summer breeding season; a time when sexually mature males display a red throat and belly to potential mates. In contrast, a shift in sensitivity is not apparent in males. These results, although commonly quoted, are surprising because previous observations suggest that both sexes may benefit from the detection of the male's red colour patch; in females the intensity of red coloration can influence the choice of mate, and in males the conspicuous red colouration can aid the detection of rival males. To investigate this paradox we repeated the original optomotor experiment using a fully controlled design. In contrast to the earlier result, we found that both males and females exhibit a shift in their sensitivity to red during the reproductive period. These new data therefore do not support the hypothesis that sex differences in perceptual abilities occur in sexually dimorphic species.

**Keywords** Vision · *Gasterosteus aculeatus* · Stickleback · Receiver bias · Sensory drive

## Introduction

In a natural environment overloaded with information it is necessary for sexually active males to communicate their availability to potential mates (Tinbergen 1951; Andersson 1994). Accordingly, sexual selection favours signals that most effectively

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stimulate the recipient: that is, those that are noticed more quickly, give an indication of male quality, or are simply able to advertise the male's presence over a greater distance (Sargent et al. 1998). To achieve such an outcome, signallers and receivers should maximise the strength of the signal relative to background noise. Viewed in this way, sexual selection theory predicts coevolution between male sexual ornamentation and female preference (Fisher 1915; Lorenz 1970; Kirkpatrick 1982). Moreover, biases in the perceptual process will influence preference, and this will ultimately influence the direction of selection (Ryan 1990a). A number of empirical studies have successfully demonstrated tight coupling between the male signal and a female receiver in a variety of species (e.g., frogs, Capranica 1976; crickets, Hoy 1978; lizards, Fleishman 1988; and fireflies, Cronin et al. 2000).

The key visual tasks performed by an animal often alter over the course of its life-history. For example, in several species of fish, changes in the ambient light environment caused by seasonal changes in dissolved organic material or by migration into different waters often coincide with movements in the wavelength sensitivity of the visual system (Beatty 1966; Muntz and Wainwright 1978). Nevertheless, such shifts may represent a compromise, with the organism trading-off divergent optical requirements of biologically significant visual tasks (Partridge and Cummings 1999). Given the prominent role which sensory systems play in the assessment of sexual display, in species that display seasonal secondary sex traits we might predict that such animals might also experience seasonal shifts in their visual system. Furthermore, in those species where sexual dimorphism is evident, we might expect that only the sex which is subject to this display will undergo this shift. To date, only one such finding has been reported and this is in the three-spined stickleback, *Gasterosteus aculeatus* (Cronly-Dillon and Sharma 1968). During spring, reproductively active male sticklebacks exhibit considerable sexual dimorphism, developing an intensely red throat and belly, with the degree to which this signal is expressed influencing female preference (McLennan and McPhail 1990; Bakker and Mundwiler 1994; Braithwaite and Barber 2000). Work carried out by Cronly-Dillon and Sharma in 1968 suggests that the onset of the breeding season also coincides with an increase in the red-sensitivity of females relative to that of males, producing a seasonal sex difference in spectral sensitivity. In doing so, it is thought that the female maximises her chance of detecting a mate without compromising the efficacy of her visual system outside the breeding season.

The existence of such a clear example of the coevolution of signal and receiver supports the receiver bias models of sexual selection, bringing with it the possibility that such a bias in receiver physiology may further drive the evolution of the male sexual characteristic apparent in sticklebacks. The findings presented by Cronly-Dillon and Sharma (1968) are unique in the field of sensory ecology. However, their results seem surprising given that males also perform similar visual tasks to females in an identical optical environment. Moreover, since the red patch of rival males serves to advertise the presence of an intruder to the territory, it is likely that territorial males would also find it beneficial to easily detect such a signal. Whether the red colour of the male *per se* also plays an important role in the initiation and control of agonistic behaviour (Ter Pelkwijk and Tinbergen 1937; Rowland 1994) is, however, unclear (McKinnon and McPhail 1996).

The Cronly-Dillon and Sharma result (1968) has been receiving increasing attention because visual evolutionary ecology has become a focal research area for a number of research groups (Douglas and Hawryshyn 1990; Ryan 1990b; Boughman

2001; Ostlund-Nilsson and Holmlund 2003, Rowe et al. 2004, Smith et al. 2004, Rick et al. 2006). Given this current interest, and the importance of this result to sexual selection theory and signal-receiver evolution, we repeated the Cronly-Dillon and Sharma (1968) study and investigated sensitivity to red in male and female three-spined sticklebacks. We designed the study to permit the comparison of spectral sensitivity across sexes and seasons.

## Materials and methods

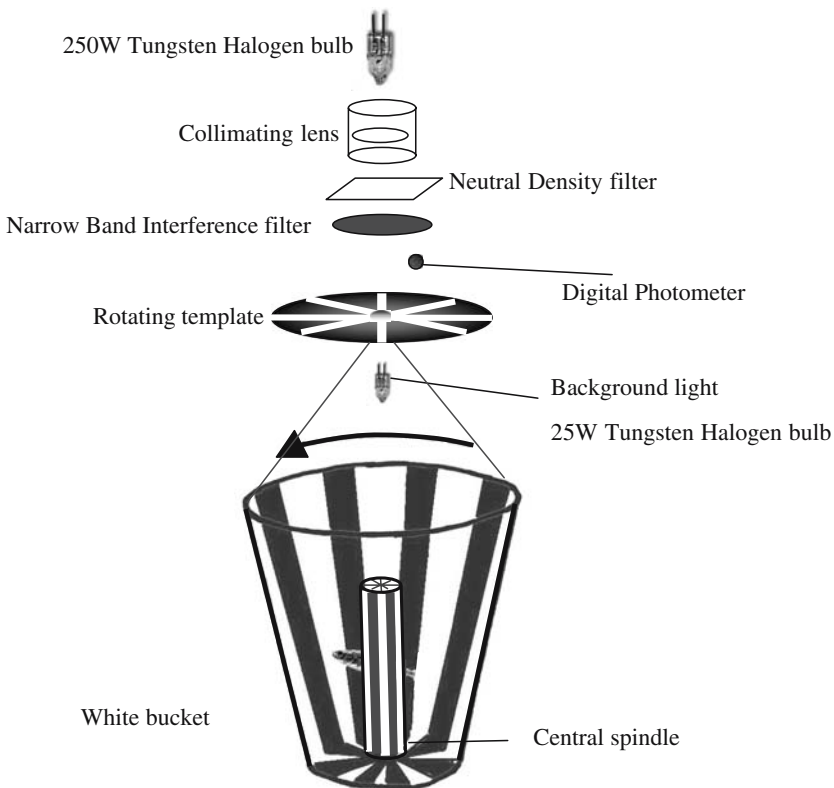
### Subjects

We analysed the spectral sensitivity of 82 sticklebacks sampled from a freshwater pond adjacent to Loch Lomond, Scotland, during periods of non-breeding (October, 2001,  $n = 22$ ; February 2002,  $n = 20$ ) and sexual activity (June 2001,  $n = 20$ ; April 2002,  $n = 20$ ). Observations taken from the study site over the past 10 years has revealed that the population is effectively semelparous, with very few reproductively active adults surviving the winter following the breeding season, and it is likely that considerable changes in the age structure of the population occur after the breeding season. To maximise the likelihood that fish selected belonged to a similar age demographic, and were likely to reproduce that year, only fish that were greater than 35 mm in the non-reproductive samples were selected for study. This size range was found to be consistent with maturation occurring in this slow growing population. The replication of our study during 2002 allowed us to collect samples at a time in the year when only very small changes in the age structure of the population occur (Wootton and Smith 2000); permitting us to sample from what was effectively a closed population. Once in the laboratory, fish were housed in aquaria which were lit by two full-spectrum fluorescent bulbs (Arcadia Ltd), each with a colour temperature of 5600°K, suspended 40cm above the holding tanks. To minimise the effect of holding conditions on visual sensitivity and reproductive state, fish were held under ambient temperatures and light cycles, and were only kept for a maximum period of two weeks prior to experimentation (Kröger et al. 2003). All fish were fed once daily on a diet of bloodworm, *Chironomid*.

Fish were caught using wire minnow traps (Eagle Claw Ltd.). The collection site at Balmaha is a sizeable, natural pond which supports a large population of three-spined sticklebacks. Accordingly, the number of individuals sampled in this study (40 fish per year) represents only a very small proportion of the adult breeding stock. Sticklebacks have been sampled annually from this site at this level for the past six years with no discernable change in the density or number of breeding fish produced each year being apparent. Following capture, fish were transported by road to the laboratory in aerated aquaria. After the completion of each experimental trial fish were euthanized by over-anaesthesia (using MS222). We do not release fish after they have been held in the laboratory because of the risk of introducing pathogens to wild stocks. Euthanized fish which were tested during non-reproductive periods were also dissected to ascertain their sex. No procedure carried out in this study required Home Office Licence.

## Quantifying sensitivity

To assess sensitivity, we used an optomotor technique that exploits the innate following behaviour of the stickleback in response to a revolving stimulus light. In order to generate such a response, we devised a method of projecting a pattern of moving coloured stripes onto the side of a white cylindrical tank (Fig. 1). Sticklebacks are known to respond behaviourally to a wide range of wavelengths light, including ultraviolet wavelengths (Boulcott and Braithwaite 2005), with the four cones receptors in the retina maximally sensitive at 360, 445, 530, and 605 nm (Rowe et al. 2004). By projecting the stimulus stripes at suitable intensity and visual angle we were able to elicit a following-response from a subject placed within the apparatus. Stimulus illumination was produced by passing light produced from a 250W tungsten bulb (colour temperature approximately 3050°K) through a collimating lens before altering its spectral content using a narrow band interference filter (Edmund Optics Inc.). In addition to the stimulus light, diffuse background illumination was provided by a 20 W tungsten halogen bulb (approximate colour temperature 2900°K) positioned directly above the tank. Preliminary trials were run to establish that these background conditions provided sufficient light necessary to



**Fig. 1** Schematic diagram of the optomotor apparatus used to estimate photopic sensitivity in the three-spined stickleback. Subjects were exposed to stimulus wavelengths descending in intensity by 0.2 log units across each trial. Wavelengths tested were: 590, 620, 650, 680 nm

maintain photopic vision; a situation signified by the production of two characteristic peaks (one green, one red) in the spectral sensitivity curve of a test subject (Cronly-Dillon and Sharma 1968). The absolute energy transmitted by both the stimulus and background lamps was measured using a Tektronix J16 digital photometer operated in conjunction with a Tektronix J6502 probe. Using this apparatus it was possible to calibrate each lamp prior to each test, thereby ensuring that the intensity of the stimulus and background light remained constant. No other illumination was present in the laboratory during the experiment, allowing the observer to remain in relative darkness whilst viewing the behaviour of the subject.

Once fish were found to exhibit a clear optomotor response to the rotating stimulus, the intensity of the stimulus light was then presented at an intensity 0.2 log units lower. Stimulus intensity was controlled using a series of neutral density filters (Edmund Optics Inc.). In each instance the direction of stimulus rotation was assigned at random, and the process repeated until no following response from the subject evident. When a subject finally failed to respond to the stimulus, the test was repeated a further time at the previous, higher intensity to ensure that the null response could not be attributed to a general loss in motivation. By testing for the lowest intensity of light that produces a response across four wavelengths in the orange-red region of the spectrum - 590, 620, 650 and 680nm - we were able to construct spectral sensitivity curves according to sex and reproductive status. The four stimulus wavelengths were presented to fish in pseudo-random order with the caveat that adjacent wavelengths were not tested one after another. In combination with a 5 min rest period between trials, this precaution was used to prevent subjects from becoming selectively adapted to a particular region of the spectrum.

### Light adaptation

The degree of light adaptation an individual is subjected to during the optomotor technique is critical to the production of accurate spectral sensitivity curves. Indeed, failure by Cronly-Dillon and Sharma (1968) to maintain background illumination at a constant intensity meant that experimentally derived threshold levels could not be compared statistically across season in their experiment. Whilst the energetic output of the background lamp in our study remained fixed throughout the duration of the experiment, it was not possible to rule out the chance that the colour composition of its light had drifted. The effect of a gradual change in colour composition of background conditions will give the impression that subjects becomes more/less sensitive to red light over time, with this effect potentially increasing as the lamp gets older. To control against such problems we ran our experiment twice using the same apparatus: once during the transition from sexual activity in late summer 2001 (when females are expected to become less red-sensitive) and again during the spring of the next year (when females are expected to become more red-sensitive). Since changes in spectral sensitivity caused by gradual changes in the background light would be expected to only occur in one direction, such shifts would be easily discernable from the hypothesised changes in spectral sensitivity.

### Statistical analysis

Owing to the repeated measure of visual threshold for each fish under different spectral conditions a repeated measures ANOVA was used to analyse the data.

Whilst the stimulus and background lamps used in both years were the same, due to unavoidable differences in the positioning of our apparatus between the 2001 and 2002, data from these two years were analysed separately. The initial model described threshold response as the dependent variable and included sex, season, wavelength, and their interactions as factors. The minimum adequate model was then derived by a process of stepwise deletion of all non-significant terms. A plot of residuals against fits was plotted to confirm that the data complied with homogeneity of variance. Data was also tested for normality using an Anderson–Darling test.

## Results

### 2001

As expected, spectral sensitivity in the three-spined stickleback was found to vary across the four wavelengths tested (Repeated measures ANOVA:  $F_{3,38} = 155$ ,  $P < 0.0001$ ), recording a peak sensitivity at 620 nm (Fig. 2, 2001). A statistically significant interaction term describing the relationship between wavelength and season (Repeated measures ANOVA:  $F_{3,38} = 3.44$ ,  $P = 0.02$ ) indicated that the shape of this red peak changed with season (Table 1). A significant difference in visual sensitivity associated with season was also found, with subjects sampled in winter being less sensitive to red light (Repeated measures ANOVA:  $F_{1,38} = 28.6$ ,  $P < 0.0001$ ). However, we were unable to find any differences in spectral sensitivity according to sex (Repeated measures ANOVA:  $F_{1,38} = 0.23$ ,  $P = 0.63$ ) or its interaction with season (Repeated measures ANOVA:  $F_{1,38} = 3.70$ ,  $P = 0.06$ ).

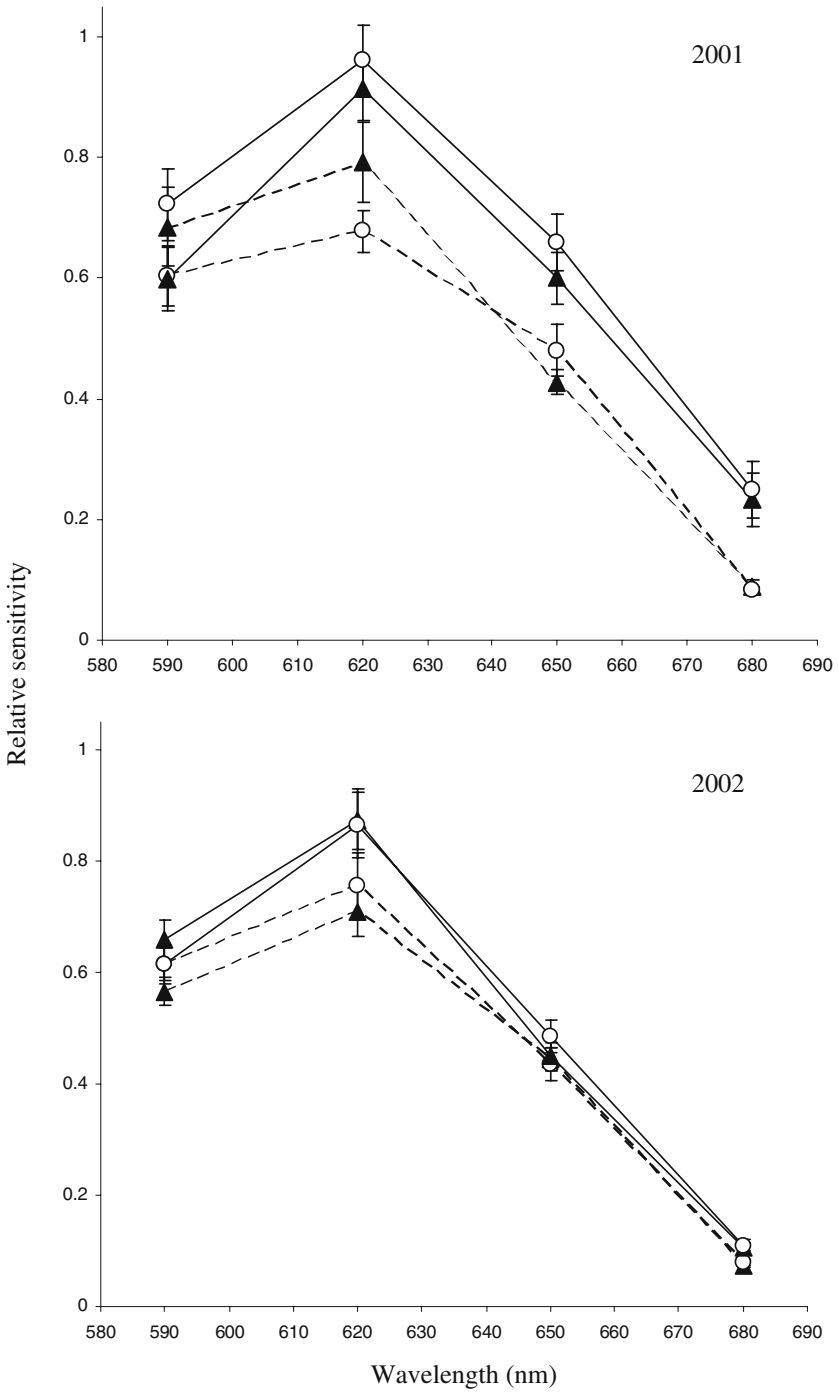
### 2002

Our results obtained in 2002 replicate those of the previous year (Fig. 2, 2002), confirming that the 2001 results were not produced by a change in the light adapted state of the subjects brought about by a progressive reddening of background illumination. Again, we found a significant difference in red-sensitivity associated with season, with subjects sampled in spring being more sensitive to red light ( $F_{1,35} = 15.2$ ,  $P < 0.001$ ). No statistical difference in spectral sensitivity according to sex ( $F_{1,35} = 0.33$ ,  $P = 0.57$ ) or its interaction with season ( $F_{1,35} = 0.70$ ,  $P = 0.41$ ) was found. All individuals tested during the winter samples in both years were found to be outside breeding condition, with the opposite being true during summer, 2001 and spring, 2002.

## Discussion

The onset of the breeding season in the three-spined stickleback is accompanied by an increase in sensitivity to red light by both males and females. Thus, in contrast to

**Fig. 2** The relative spectral sensitivity of the three-spined stickleback to four wavelengths of long-wavelength light according to sex and reproductive condition in 2001 and 2002. Males (closed triangles) and females (open circles) were tested during summer (solid line) and winter (dashed line) when the fish were in full reproductive and non-reproductive condition, respectively. Vertical bars denote standard error from the mean



**Table 1**

	d.f.	<i>F</i> -value	<i>P</i> -value
2001			
Wavelength	3	155	<0.0001
Sex	1	0.23	0.63
Season	1	28.6	<0.0001
Sex * season	1	3.7	0.06
2002			
Wavelength	3	263	<0.0001
Sex	1	0.33	0.57
Season	1	15.1	<0.001
Sex * season	1	0.7	0.41

the earlier work by Cronly-Dillon and Sharma (1968), both sexes show an increase in sensitivity. That males also become more red-sensitive seems reasonable given the fact that males may use the conspicuous red signal to assist the detection of rival males entering their territory. Indeed, one implication of sexual selection theory is that ornaments such as the stickleback's red throat act as signals to sexually active females, rival males, or both (Sargent et al. 1998). Male three-spined sticklebacks set up territories during the breeding season, guarding their nests from encroaching males, and it is likely that an increase in red-sensitivity during this time may improve detection of intruders.

In contrast to the findings of Cronly-Dillon and Sharma (1968), our study did not reveal any sex differences in red-sensitivity during either reproductive or non-reproductive periods. Whilst sex was not found to be a significant factor affecting red-sensitivity in our two studies, the interaction between sex and season in the first of our two data sets (2001) suggested that there is a trend for females to show a larger shift than males. It is possible, however, that differences in the age demographic between the summer and autumn samples could also account for such an effect. Such age related changes in sensitivity could be mediated by changes in the concentration of retinal photopigments due to developmental changes in diet or hormone level (e.g. Knowles and Dartnall 1977), or by changes in the light transmissive properties of the cornea with time (e.g. Thorpe and Douglas 1993). If true, a differential loss of older females shortly after reproduction, or a differential increase in the number of fast-growing, age-0 females entering the selected size range in autumn sample, would account for the observed interaction effect. Indeed, the first year of our study dealt with the transition from summer into winter; a time in which the age structure of the population changes greatly in this short-lived species (Wootton and Smith 2000). Such an interaction effect was not apparent in 2002 when the study sampled from what was effectively a closed population.

It should be emphasised that seasonal shifts in visual sensitivity in both males and females are found in several teleosts, and possible adaptive explanations are numerous and varied. For example, they have been attributed to changes in the photic environment, temperature, behavioural patterns, and developmental life-history (Bridges 1972; Knowles and Dartnall 1977; Muntz and Northmore 1973). Smith and colleagues (2004) present indirect evidence that the preference of female sticklebacks for the colour red in the nuptial signal may have arisen from biases in the visual system specific to the requirements of foraging. Such an evolutionary mechanism may also underpin the summer shift in spectral sensitivity found in our



study. Nevertheless, as our study examines only a single population of red throated stickleback, it is important to note that the function of the red throat over the entire species complex is not universal (Braithwaite and Barber 2000). Indeed, the existence of black-throated populations suggests that different evolutionary pressures or time-scales may operate across the species complex. The evolution of these signals is not random, and could be largely driven by the optical conditions of the habitat in combination with the visually mediated behaviour of the animal, with particular conditions favouring particular sensory and signalling characteristics (Endler and McLellan 1988; Endler 1992). Examining the spectral sensitivity of three-spined stickleback populations originating from three different photic regimes, McDonald and Hawryshyn (1995) found that populations living in red-shifted, peat-stained waters were more sensitive to longer wavelengths of light. It is in such waters that uncoloured or black throated populations of male stickleback are often found (Reimchen 1994; Scott 2001), and it is possible that this nuptial coloration is adaptive as the more usual red signal provides low chromatic contrast in such waters (Reimchen 1989). In support, McDonald and colleagues (1995) found that female sticklebacks selected males on the degree of colour contrast relative to the background rather than any specific spectral quality associated with the nuptial signal.

The results presented in this paper show that shifts in the receiver physiology of the stickleback vary seasonally, with sticklebacks becoming more red-sensitive at a time when both male colouration and ambient light changes. That both sexes undergo this shift means that the three-spined stickleback is no longer an example of a species where there are sex differences in perceptual abilities. The physiological processes which initiate the change in red colour sensitivity are, as yet, unknown and need to be addressed if we are to understand spectral tuning in this species. Nevertheless, given the range of optical environments in which the three-spined stickleback reside, it is likely that the visual conditions prevalent in the immediate habitat, taken in combination with their effect on key visually mediated behaviours, could be important for understanding the considerable variation in the standard red response apparent in this species.

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