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A receiver bias in the origin of three-spined stickleback mate choice

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Receiver-bias models of signal evolution predict that male sexually selected traits evolve through prior selection for other functions. Female three-spined sticklebacks (*Gasterosteus aculeatus*) in many populations show a mating preference for males with a red throat and jaw. It has been proposed that this preference evolved because the choice of males with red coloration confers direct and indirect benefits to females in accordance with the Fisher–Zahavi model of sexual selection. We present indirect evidence that the preference is an effect of a receiver bias in the perceptual or cognitive system of *G. aculeatus* for the colour red, which may have arisen in the context of foraging. In laboratory trials, male and female three-spined and nine-spined sticklebacks (*Pungitius pungitius*) responded most strongly to red objects outside a mating context. This result demonstrates a correlation between a sexually selected trait and an intrinsic attraction to red objects, and supports the sensory-exploitation model for the evolution of red nuptial coloration in three-spined sticklebacks.

Keywords: colour; Gasterosteidae; mate choice; sensory bias; sensory drive; sexual selection

1. INTRODUCTION

Sexual selection acts on a wide range of morphological and behavioural traits. Several hypotheses have been proposed to explain the mechanism underlying the evolution of these sexually dimorphic characters (see Andersson 1994 and references therein). Of these hypotheses, only the receiver-bias models (Ryan 1990; Ryan & Rand 1990; Endler 1992; Endler & Basalo 1998) propose that the origin of a preference and the origin of the sexually dimorphic trait are evolutionarily decoupled. According to this scenario, the perceptual or cognitive system in the receiver undergoes selection for other functions prior to the evolution of the sender's trait. Consequently, selection pressures other than in a mating response to the novel character must have been involved in the evolution of the receiver's sensory, perceptual or cognitive system. In the context of mate choice, the sensory-exploitation hypothesis predicts that sexually selected traits, usually expressed in males, are those most conspicuous to the perceptual or cognitive systems of females. Receiver-bias models may be central to the evolution of mate choice (Kokko *et al.* 2003) and can play a role in speciation through female choice (Boughman 2002).

Although numerous empirical studies have recognized the existence of receiver biases (e.g. Ryan *et al.* 1990; Proctor 1991, 1992; Christy & Salmon 1991; Fleishman 1992), few have explicitly addressed the reason for such a bias evolving in the receiver's perceptive or cognitive system (exceptions include Proctor (1992) and Ryan (1990)). In the guppy (*Poecilia reticulata*), a small tropical live-bearing fish, females generally prefer to mate with males with orange spots on their body and tail fin (Houde 1997). This preference for orange appears to have arisen as a bias in the context of foraging: both sexes have a feeding preference for orange fruits (Rodd *et al.* 2002). Among populations of guppies in Trinidad that have been tested, the strength of attraction to orange in a non-mating context explains 94% of the inter-population variation in female mating preferences for male orange traits (Rodd *et al.* 2002). Thus, female sensitivity to orange food items may have played at least as important a role as direct or indirect benefits in the origin of female mating preferences for males with orange spots. Beyond the origin of the orange preference, the continued elaboration of orange spots on males may have been influenced by direct and indirect benefits that accrue to females from selecting brightly coloured males in accordance with the Fisher–Zahavi model (Ryan 1991, 1997; Rodd *et al.* 2002).

In another fish, the three-spined stickleback (*Gasterosteus aculeatus*), in most populations females show a preference for mating with males that develop red pigmentation on their throat and jaw during the breeding season, termed nuptial coloration (Wootton 1976; Bakker 1993; Rowland 1994). In at least one population, male three-spined sticklebacks adorn their nests with red objects, when given the opportunity, which has the effect of increasing their reproductive success (Östlund-Nilsson & Holmlund 2003). Red breeding coloration in the three-spined stickleback correlates with male condition (Milinski & Bakker 1990), offspring parasite resistance (Barber *et al.* 2001), courtship effort (Bakker & Milinski 1991), nest defence during parental care (McKinnon 1996) and mating success (Bakker & Mundwiler 1994; Rowland 1994). Thus, the degree of red coloration of male sticklebacks appears to signal both direct and indirect benefits to females, at least in those populations where correlations exist. The stickleback family (Gasterosteidae) is relatively small, comprising only five genera (McLennan & Mattern 2001). Not all stickleback species exhibit distinctive nuptial coloration, but it is

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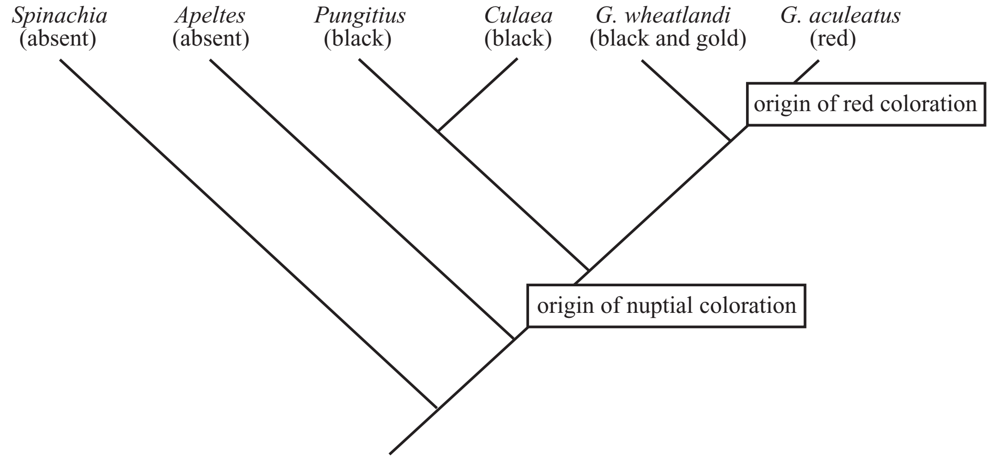

Figure 1. A phylogenetic tree of the family Gasterosteidae. Colours in parentheses under each species name indicate male nuptial coloration. Modified from McLennan (1996).

displayed in three genera: *Pungitius*, *Culaea* and *Gasterosteus* (figure 1). Although the hue of the nuptial coloration of the common ancestor of these genera is unknown, the colour is most probably black. Black is most probable because: (i) melanin-based pigments are an important part of the nuptial signal in all males in the three genera with nuptial coloration; and (ii) some members of the *G. aculeatus* species complex have black, not red, males (Reimchen 1989), thus it seems that black is the most likely plesiomorphic state for male nuptial colour (McLennan 1996; figure 1).

We test for a sensory bias for red coloration in the three-spined and nine-spined sticklebacks (*Pungitius pungitius*) outside a mating context. Nine-spined sticklebacks often occur sympatrically with *G. aculeatus* and exhibit black nuptial coloration (Wootton 1984). Specifically, we tested whether male and female three-spined sticklebacks show a feeding bias for red objects. We also tested whether there was evidence that *P. pungitius*, which belongs to a clade within the stickleback phylogenetic tree that does not exhibit red coloration, showed a response to red in a non-mating context. Thus, we used *P. pungitius* to test whether there was evidence for a red feeding bias in the sticklebacks that preceded the evolution of the red nuptial coloration in *G. aculeatus*.

2. MATERIAL AND METHODS

(a) *Experimental fishes*

Fishes for tests were collected on 26 March 2003 from an interconnected system of drainage ditches feeding into the River Cam at Upware, Cambridgeshire, UK (OS grid reference TL 537 705). Male *G. aculeatus* in this population show the typical red coloration during the spawning season. In laboratory trials, under conditions of male–male competition and female choice, males from this population with a high red index had the highest reproductive success (Le Comber 2003). Approximately 120 *G. aculeatus* and 90 *P. pungitius* were collected using a dip net and transported to the aquarium at Queen Mary College in ditch water. The samples of both species consisted predominantly of 1-year-old fishes and there were approximately equal numbers of each sex. Each species was housed separately, three-spined sticklebacks in an aquarium measuring 90 cm long × 44 cm wide × 47 cm high containing 160 l of freshwater and nine-spined sticklebacks in an aquarium measuring 90 cm × 30 cm × 50 cm containing 120 l of freshwater. All fishes were held under a light regime of 12 L : 12 D. Mean ± s.e. water temperature was 17.5 ± 0.33 °C. To avoid habituating fishes to food items of a particular colour before testing, all fishes were fed exclusively on the finely chopped adductor muscles of *Mytilus edulis*, which are white. Fishes were fed to satiation twice each day.

To minimize the effects of learned food-colour choices under natural conditions, we also tested the responses of sticklebacks from the same population that were raised from an early juvenile stage under laboratory conditions to a size at which their responses could be tested. Early juveniles of both species were collected from the same location as adults using a fine-mesh hand-net on 18 May 2003. They were housed in two aquaria measuring 60 cm × 35 cm × 40 cm containing 75 l of freshwater. The same light, temperature and feeding regimes as for the adults were used.

Finally, we tested a group of 15 *G. aculeatus* that were obtained from laboratory spawnings and raised to the adult stage entirely in the laboratory. Parental fishes were obtained from Llyn Frongoch in mid-Wales. Throughout their lives, these fishes were fed predominantly on cultures of *Enchytraeus* spp. worms, which are white, though they were occasionally fed red *Tubifex*.

(b) *Laboratory experiment*

Tests on adult fishes began 5 days after they were collected and lasted 15 days. Tests were conducted in six plastic aquaria measuring 30 cm × 20 cm × 20 cm, containing 5 l of freshwater. Three sides of each test aquarium were covered with brown paper to prevent interactions between fishes in adjacent aquaria. Tests were conducted on the roof of the School of Biology in natural daylight. The mean ± s.e. photon flux density of incident light (400–700 nm) directly above the experimental aquaria during the trials was 944 ± 13.4 μmol m^{-2} s^{-1} (Skye Instruments, Quantum Sensor SKP 200). The mean ± s.e. water temperature was 17 ± 1.4 °C. Test aquaria were filled with aerated water from a holding tank in the aquarium to ensure that fishes did not experience a rapid change in water temperature or quality. To begin a trial, three individual three-spined or nine-spined sticklebacks of one sex were gently released into a test aquarium and allowed to adjust to conditions in the aquarium for at least 20 min. Males and females of each species could be visually

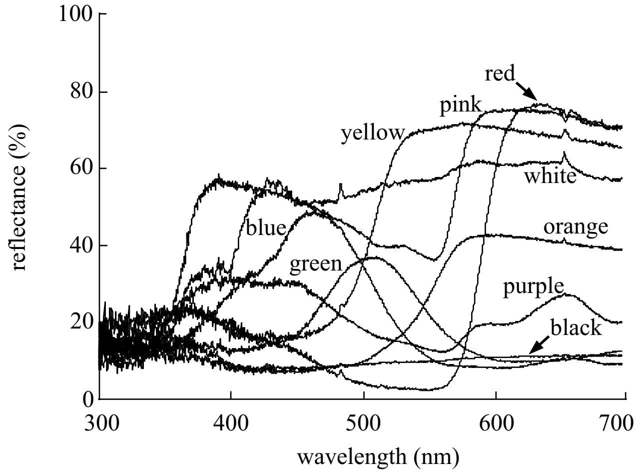

Figure 2. Reflectance spectra of the coloured plastic strips used in the experiments.

discriminated because males showed partial development of nuptial coloration, though in neither species were males in full nuptial coloration or females gravid. After 20 min, the fishes were consecutively presented with each of nine differently coloured strips of plastic (black, white, red, blue, green, orange, pink, purple, yellow) with a mean ± s.e. diameter of 1.4 ± 0.07 mm and a mean ± s.e. length of 12.3 ± 0.83 mm, in a randomly determined order. There was an interval of 3–4 min between consecutive presentations of plastic strips. The reflectance of the coloured plastic strips used in the trials was measured using a spectrometer (Ocean Optics, Dunedin, FL, USA, S2000 with a deuterium–halogen light source). Since the measurement area (diameter of 5 mm) exceeded the width of the plastic strips, several strips were glued side by side on black electrical isolation tape (for methods, see Chittka *et al.* (1994)). Reflectance spectra of plastic strips are shown in figure 2. The strips of plastic were tied to a *ca.* 150 mm length of 0.4 mm diameter monofilament fishing line, and when a plastic strip was presented to a group of fishes it was suspended, stationary, in the water column in the upper half of the test aquarium.

The behaviour of each group of three fishes was videoed for 90 s following the introduction of the plastic strip and later scored for the total number of bites directed at the strip by all three fishes in the test group. Fishes used for trials were fed 2 h before the trials began to standardize their motivation to feed. Fishes were used in trials only once, and each group of three represented a single replicate. Three fishes were tested together because only in a group of three or more did the fishes bite freely at the coloured strips.

Stickleback juveniles reached a size at which they could be tested after seven weeks. Tests on these juvenile fishes lasted 4 days. Protocols for husbandry and tests were the same as those for adults, with the exception that it was impossible to distinguish males and females because fishes were sexually immature and so the fishes were tested in groups in which the sex of the individuals was unknown. Laboratory-reared fishes were tested following the same protocols as for adult fishes, with the exception that tests were conducted in an aquarium facility, illuminated by artificial light. Tests took place over a period of 3 days.

3. RESULTS

The mean ± s.e. standard lengths (from the tip of the snout to the origin of the tail fin) of adult male and female three-spined sticklebacks were 43 ± 2.4 mm and 46 ± 3.1 mm, respectively. For nine-spined sticklebacks mean ± s.e. male standard length was 45 ± 3.8 mm and for females it was 48 ± 4.3 mm. The rate of biting at coloured strips by adult three-spined sticklebacks was tested for 15 groups of three fishes for each sex. Data for adult three-spined sticklebacks were not normally distributed and failed to respond to transformation. Consequently, a non-parametric test was used *in lieu* of parametric testing. There was a significant difference in biting rate among the nine colour treatments, with the highest rate directed at red strips (Friedman test, blocked by replicate: $S_8 = 84.4$, $p < 0.001$; figure 3*a*,*b*). The rank order of colour preference was red (most preferred), orange, pink, purple, yellow, white, blue, black, green (least preferred). There was no significant effect of sex on biting rate (Friedman test, blocked by replicate: $S_1 = 3.27$, $p = 0.071$; figure 3*a*,*b*).

Seven groups of three adult nine-spined sticklebacks of each sex were tested. Raw data were not normally distributed and were heteroscedastic, but responded to a $\log_e + 0.5$ transformation. The rate of biting of coloured strips by nine-spined sticklebacks was significantly different among colour treatments, again with the highest rate in both sexes directed at red strips (balanced two-way repeated-measures nested ANOVA: $F_{8,54} = 21.63$, $p < 0.001$; figure 3*c*,*d*). The rank order of preference was red, orange, pink, purple, yellow, white, black, green, blue. There was no significant effect of sex on biting rate ($F_{1,54} = 0.79$, $p = 0.384$; figure 3*c*,*d*), and there was no significant interaction between sex and colour ($F_{8,54} = 0.63$, $p = 0.749$).

For the laboratory-reared fry, seven groups of three juvenile sticklebacks of each species were tested. Data were square-root transformed to meet assumptions of normality and homoscedasticity. The rate of biting of coloured strips was significantly different among colour treatments, with the highest rate of biting directed, again, at red strips for both three-spined sticklebacks (repeated-measures one-way ANOVA: $F_{8,48} = 27.69$, $p < 0.001$; figure 4*a*) and nine-spined sticklebacks ($F_{8,48} = 14.03$, $p < 0.001$; figure 4*b*). For three-spined sticklebacks, the rank order of colour preference was red, orange, pink, yellow, white, purple, black, green, blue. For nine-spined sticklebacks, the rank order of preference was red, orange, yellow, pink, purple, white, blue, green, black.

Results for laboratory-reared fishes were not normally distributed and failed to respond to transformation, so data were tested using a non-parametric test. Also, because the sample size for these fishes was small, results for males and females were pooled. There was a significant difference in biting rate among the nine colour treatments, with the highest rate directed at red strips (Kruskal–Wallis test: $H_8 = 23.5$, $p = 0.003$). The rank order of preference was red, pink, orange, white, purple, black, blue = green = yellow (the last three colours received no bites in tests and scored an equivalent lowest ranking).

4. DISCUSSION

Four criteria have been proposed to determine whether a male trait is likely to have evolved in accordance with the receiver-bias model (Ryan & Rand 1990; Ryan 1997; Endler & Basalo 1998): (i) the species has the trait and a

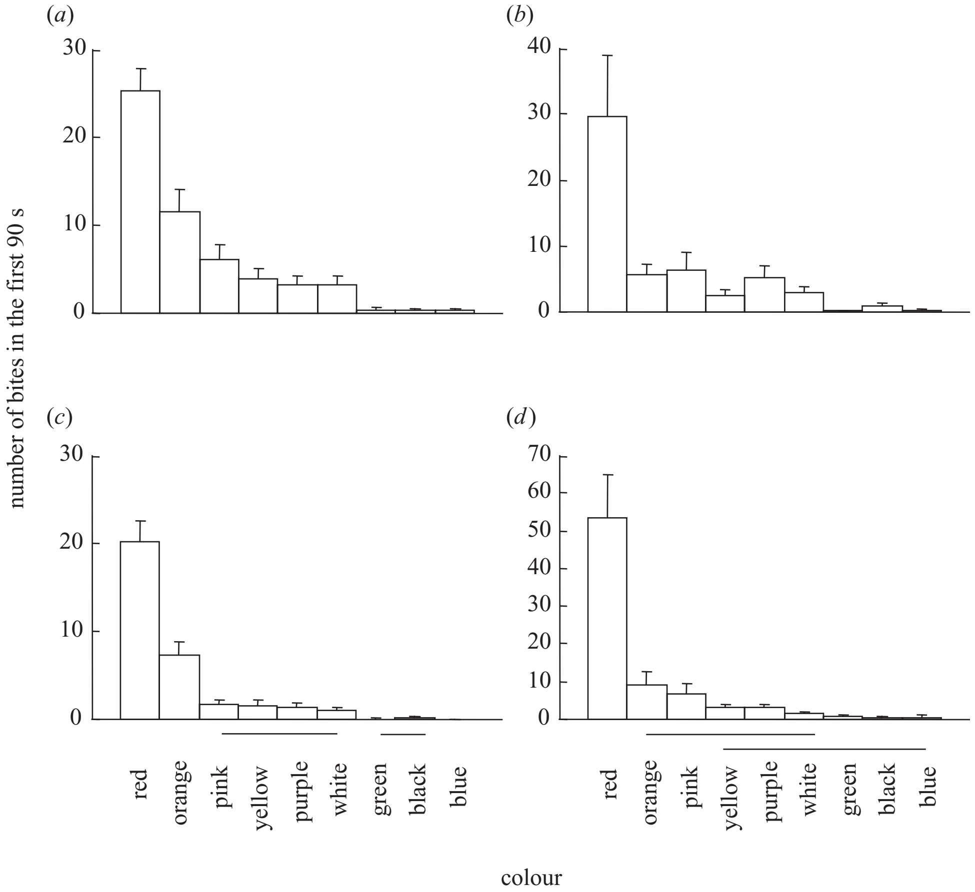

Figure 3. Mean responses to coloured plastic strips, measured as number of bites in the first 90 s for adult (*a*) male three-spined, (*b*) female three-spined, (*c*) male nine-spined and (*d*) female nine-spined sticklebacks. Error bars are one standard error. Because data were non-parametric, *post hoc* tests were not completed for three-spined sticklebacks. (*c*,*d*) Black bars under the *x*-axis indicate where significant differences lie: where bars overlap, bite rates were not significantly different using a Tukey *post hoc* test.

preference for that trait, and the trait is used in mate choice; (ii) the trait is absent or primitive in ancestors; (iii) preference for the trait originated prior to the appearance of the trait in its rudimentary or elaborated condition; (iv) there is a bias in the perceptual or cognitive system of receivers that predicts the direction of preferences. All four criteria are met in the case of red nuptial coloration in sticklebacks. Male sticklebacks exhibit red nuptial coloration in most populations, and female three-spined sticklebacks show a mating preference for red males. Our study demonstrates that in both three-spined and nine-spined sticklebacks, irrespective of sex or age, there is a strong response to red objects. Red coloration is derived in the three-spined stickleback, though a red preference in a foraging context exists in the nine-spined stickleback. Finally, sticklebacks have visual systems that are highly sensitive to long wavelengths. Cronly-Dillon & Sharma (1968) measured the optomotor responses of three-spined sticklebacks and demonstrated that they have a peak spectral sensitivity to stimuli close to 600 nm (in the red region of the light spectrum). Notably, the threshold response to this wavelength was shown to be lower among females during the spawning season (Cronly-Dillon & Sharma 1968); females are more sensitive to red during the period when males exhibit red nuptial coloration, suggesting coevolution between the red male sexual signal and female perception of it.

Diet studies of three-spined sticklebacks have also shown a preference for red food items. For example, Ibrahim & Huntingford (1988) observed that red coloration was the principal visual property of natural food items that were positively selected by three-spined sticklebacks. The preference for red food items shown by three-spined and nine-spined sticklebacks may be related to a requirement in their diet for carotenoid-rich food items. Carotenoids cannot be synthesized by animals and instead must be obtained in the diet. Important physiological functions appear to require carotenoids: liver function, immune response, cancer prevention, water balance, growth and cell differentiation are examples (Olsen & Owens 1998). The red pigment of three-spined sticklebacks is principally derived from the carotenoid pigments astaxanthin and tunaxanthin/lutein (Wedekind *et al.* 1998), with the degree of redness of males correlating with the amount of carotenoids in the diet (Frischknecht 1993). Because sticklebacks inhabit a wide range of habitats, their diet is varied. However, under natural conditions the most prominent prey are microcrustaceans: copepods, cladocerans and ostracods (Wootton 1984). It is from these food items that sticklebacks may acquire carotenoids in their diet (Ronnestad *et al.* 1998).

A receiver bias may favour one trait over another as a sexual signal by reducing mate search costs. However, a trait is unlikely to be maintained under sexual selection

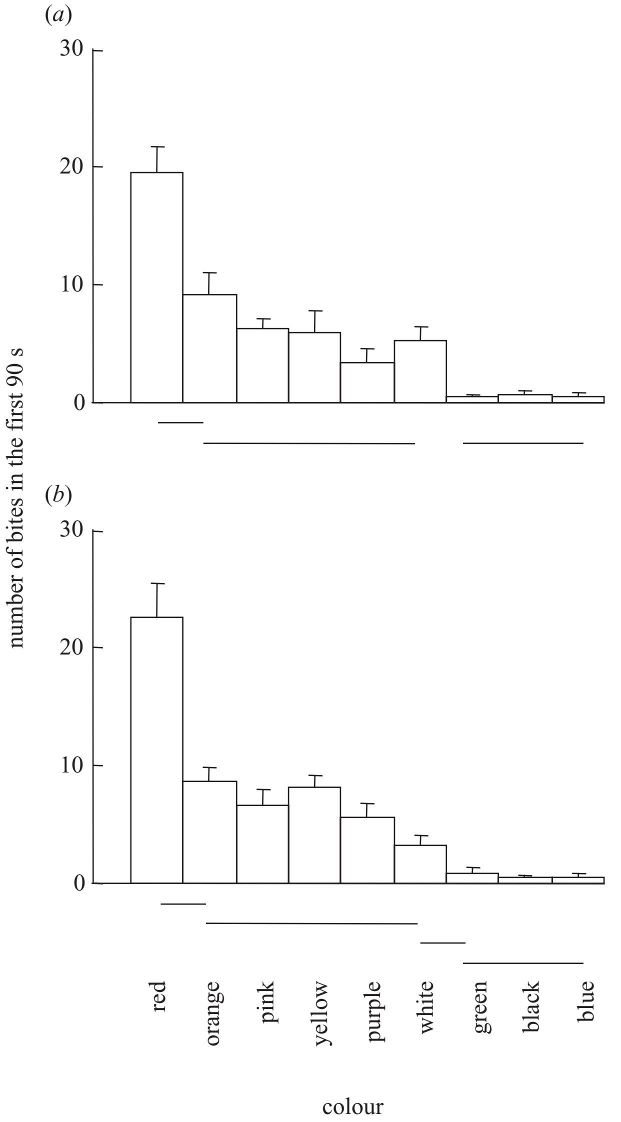

Figure 4. Mean responses to coloured plastic strips, measured as number of bites in the first 90 s for juvenile (*a*) three-spined and (*b*) nine-spined sticklebacks. Error bars are one standard error. Black bars under the *x*-axis indicate where significant differences lie: where bars overlap, bite rates were not significantly different using a Tukey *post hoc* test.

unless it correlates with a fitness benefit to the choosing females (Kirkpatrick 1996). As discussed previously, red coloration in male sticklebacks appears honestly to signal direct and indirect fitness benefits to female receivers (e.g. Milinski & Bakker 1990; Barber *et al.* 2001; but see Candolin 1999). Zahavi (1975) proposed that a sexual signal must impose a fitness cost on the signaller to be reliable. In three-spined sticklebacks, the vivid red coloration imposes a cost in the form of increased conspicuousness to predators (Whoriskey & FitzGerald 1985). In addition, foraging for carotenoids may be costly: their availability in the environment can be limited and prey items rich in carotenoids may not be ideal from an energetic perspective (Olsen & Owens 1998). Thus, while red nuptial coloration in three-spined sticklebacks seems likely to have initially evolved through a receiver-bias mechanism, the signal conforms to the predictions of the Fisher–Zahavi model of sexual selection. In consequence, it is likely that sexual selection on male nuptial hue in the three-spined stickleback has involved a variety of mechanisms in the evolution of the signal.

One alternative possibility is that females are attracted to red objects as a side effect of a female mate preference for red coloration. However, this interpretation of our results raises two objections. First, both males and females, rather than only females, were attracted to red objects though male attraction to red objects could be the result of a genetic correlation between the sexes or an aggressive response to a potential rival. A second difficulty is that nine-spined sticklebacks of both sexes showed a strong attraction to red objects. Given the black nuptial coloration of male nine-spined sticklebacks, the prediction would be for an attraction to black not red in this species, if the response evolved in a mating context. Consequently, the most parsimonious interpretation of our results is that a sensitivity to red functions in a feeding context in both three-spined and nine-spined sticklebacks. In our tests on adult wild fishes, a learned response to red food items could also explain the red bias we observed. However, laboratory-reared juveniles and adults showed similarly strong preferences for red, suggesting that the response might not depend on learning from direct experience with red prey. It is unclear how widespread the sensory bias we detected in the present study might be among stickleback populations, and further studies will be needed to test the ubiquity of the response to red.

Sticklebacks of all species so far tested (including *G. aculeatus* and *G. wheatlandi*) have four types of visual pigments, with maximum spectral sensitivities in the ultraviolet (*ca.* 360 nm), blue (*ca.* 445 nm), green (*ca.* 530 nm) and red (*ca.* 605 nm) (Lythgoe 1979; Rowe *et al.* 2004). In the present study, all sticklebacks, irrespective of sex and species, preferred those items that stimulated their red receptors most strongly, i.e. the red plastic strips with reflectance at *ca.* 620 nm. At the same time, it is clear that their choice is not based on the red signals alone, since the pink and yellow strips have almost equally high reflectances at *ca.* 605 nm (figure 2) yet they are chosen infrequently (figures 3 and 4). By contrast, orange strips, which have a comparatively low red reflectance, were chosen second only to red. These observations suggest that the neuronal pathway in sticklebacks underlying the observed colour preferences in our tests must be based on a spectrally opponent mechanism, whereby red receptor signals are matched against those of shorter-wavelength receptors, such as those for blue or green.

A receiver bias must originate before the trait it eventually favours (Ryan 1990). In the context of the sticklebacks, it is unclear at what point the red preference detected in the present study in three-spined and nine-spined sticklebacks arose. Our tentative conclusion is that it appears to have evolved with, or prior to, the evolution of nuptial coloration in the *Pungitius–Culaea* + *Gasterosteus* clade (figure 1). It would be informative to test the responses of *Apeltes* and *Spinachia* using the protocol in the present study, to establish whether the red preference arose in the gasterosteids, or is more basal in the Gasterosteiformes as a whole.

Our results indicate that nine-spined as well as three-spined sticklebacks show a strong intrinsic attraction to red objects outside a mating context. Despite the existence of this preference, male nine-spined sticklebacks do not appear to have exploited this female sensory bias for red in their sexual signal. One explanation for this 'failure' might be that nine-spined sticklebacks lack the genetic basis for red nuptial coloration. Alternatively, nine-spined sticklebacks, which possess less robust spines and bony body armour than three-spined sticklebacks, may be too vulnerable to predation to evolve bright nuptial coloration. Bright nuptial colours attract the attention of predators in guppies (Godin & McDonough 2003). Under high predation levels, nuptial coloration is quickly lost through natural selection even though females may retain the preference for more extensively coloured males (Endler 1980). Certainly, three-spined sticklebacks behave more boldly than nine-spined sticklebacks under a threat of predation, and this difference has been ascribed to their more robust defences (Godin & Clark 1997). However, in populations where predation pressure is relaxed, red nuptial coloration in nine-spined sticklebacks would be expected to spread through sexual selection, yet this appears not to be the case. Thus, a genetic constraint, rather than one imposed by natural selection, is more likely to account for the absence of red coloration in nine-spined sticklebacks. It also remains to be demonstrated that female *P. pungitius* have a mating preference for male *P. pungitius* exhibiting red nuptial coloration.

Receiver biases are environment dependent (Ryan *et al.* 1990, 1996). Consequently, a receiver bias can lead to a divergence in sexual signals among populations under different environmental conditions (the 'sensory drive' of Endler & McLellan (1988)). Just such a sensory drive appears to have led to a divergence in the sexual signals of three-spined sticklebacks along the Pacific coast of North America. Here, males in some populations exhibit black rather than red nuptial coloration (Reimchen 1989). Black males occur in tannin-stained lakes, in which the water colour is red-shifted, with the result that black males are more conspicuous than red males to females (Boughman 2002). Without a phylogeny of these populations, it is impossible to determine whether black nuptial coloration in any given population represents a reversal to the ancestral character state or a retention of that plesiomorphic state. In some populations of black males, females have retained the plesiomorphic preference for red males (McKinnon 1995), whereas in others that preference appears to have been lost (Boughman 2001). Notably, the spectral sensitivities of three-spined sticklebacks in populations in North America do appear to have undergone adaptive evolutionary change in response to local photic regimes (McDonald & Hawryshyn 1995). Once again, a robust phylogeny coupled with environmental and mate-choice data could help us to determine how many times in these populations the preference for red has been lost, and under what conditions. The present study supports the assumption of Boughman (2001) that sexual selection in the three-spined stickleback is underpinned by a sensory bias, and provides an explanation for the origin of the bias. However, it is not known whether sticklebacks in populations with black nuptial coloration have retained a red feeding bias, and it would be valuable to test for a response in these populations. Among some populations of guppies at least, the loss of male orange nuptial coloration has been found to correlate with the loss of a mating preference by females, while a response to orange in a feeding context is retained (Endler & Houde 1995; Rodd *et al.* 2002).

In summary, the results of this study suggest that the red nuptial coloration of male three-spined sticklebacks may have evolved as a consequence of a receiver bias for red (carotenoid-rich) food items. Further tests on other stickleback species will indicate where in the gasterosteid clade the sensory bias arose, while tests on black three-spined sticklebacks will provide information about the role of sensory exploitation in the context of divergent sexual selection.

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