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Sensory exploitation and indicator models may explain red pelvic spines in the brook stickleback, *Culaea inconstans*

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ABSTRACT

Background: Sensory bias models explaining the evolution of sexually selected traits predict that trait preferences evolve as an artifact of a pre-existing preference for certain components of the environment such as specifically coloured prey. Indicator models, in contrast, predict that sexually selected traits indicate mate condition. We investigate the potential for sensory exploitation and condition indication models to explain the evolution of what appears to be a recently evolved sexually selected trait.

Question: Did red pelvic spine coloration in male Turnbull National Wildlife Refuge (TNWR) brook stickleback (*Culaea inconstans*) evolve to exploit a pre-existing sensory bias for red prey, thus helping males draw females to the nest? Or, did it evolve as an intersexual signal indicating male condition to females?

Methods: We recorded the frequency of red pelvic spine coloration in males versus females and in breeding versus non-breeding males. We measured the condition factor of males with and without red coloration on their pelvic spines. We presented fish with a paired choice between a red versus an orange, yellow, green, blue, or purple bead, and recorded the proportion of bites at each colour.

Results: Red coloration was significantly more common in males than in females and in males during the breeding season than outside the breeding season. Males with strongly red pelvic spines have a significantly higher mean condition factor than those with plain spines. TNWR brook stickleback prefer red to other colours in a predation context.

Conclusions: Our results suggest that TNWR brook stickleback red pelvic spine coloration is a secondary sexual character that may exploit a pre-existing sensory bias for red prey while also indicating condition to females.

Keywords: brook stickleback, *Culaea inconstans*, prey selection, sensory bias,
sensory exploitation, sexual selection.

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INTRODUCTION

Models currently used to describe the mechanisms of mate choice evolution include 'direct benefits', 'indicator mechanisms', 'Fisherian runaway sexual selection', and 'sensory bias'. The relative importance of these mechanisms remains controversial despite much theoretical and experimental work (for reviews, see Ryan, 1990; Kirkpatrick and Ryan, 1991; Andersson, 1994; Basolo, 1995; Møller and Alatalo, 1999; Kokko *et al.*, 2003; Fuller and Noa, 2010).

Direct benefit models hold that preferences evolve to favour cues in potential mates that may directly signal offspring chances of survival such as food, territory or parental care (e.g. Künzler and Bakker, 2000). Indicator mechanism models (Fisher, 1915; Williams, 1966; Zahavi, 1975; Hamilton and Zuk, 1982) predict that an individual can increase the success of its offspring by choosing mates with certain attributes indirectly indicative of 'good genes' (e.g. for superior physiological or immunological health). Fisherian runaway sexual selection (Fisher, 1930; O'Donald, 1967; Lande, 1981; Kirkpatrick, 1982) assumes an initial period in which those possessing a trait favoured slightly by natural selection are also favoured by certain mates, causing genes for the trait and those for the preference to increase simultaneously in succeeding generations. Over time, the frequency of the preference and the advantage of the preferred trait come to reinforce each other by positive feedback. The sensory bias model of sexual selection is a recently developed alternative to the direct benefits, indicator, and Fisherian runaway selection hypotheses (West-Eberhard, 1979, 1984; Ryan, 1990; Ryan and Rand, 1990; Ryan and Keddy-Hector, 1992; Basolo, 1996; Endler and Basolo, 1998; Fuller *et al.*, 2005). Sensory bias models predict that natural selection for changes in sensory and/or cognitive systems cause a preference for certain traits in some mates over others, generating sexual selection for those traits and causing them to increase in frequency. Sensory bias can be distinguished from other models in that it predicts the preference for a trait evolves prior to and/or in a different context than the preferred trait, for instance in the context of prey selection. However, it should be emphasized that any or all of the above mentioned potential mechanisms could act on the same population and contribute to the evolution of mate preferences (Andersson, 1994; Smith and Spence, 2013).

Red coloration is a common feature of male nuptial ornamentation in the stickleback family (Gasterosteidae). Threespine stickleback, *Gasterosteus aculeatus* (Bigelow and Schroeder, 1953; McLennan and McPhail, 1989), blackspotted stickleback, *Gasterosteus wheatlandi* (Bigelow and Schroeder, 1953; Östlund-Nilsson and Mayer, 2007), and fourspine stickleback, *Apeltes quadracus* (Bigelow and Schroeder, 1953; Reisman, 1963; Rowland, 1974; Bayer, 1980) all express red pigment as a component of their nuptial coloration.

In the evolution of male stickleback red ornamentation, there exists empirical support for both the indicator model and Fisher's runaway model (Bakker, 1993; Boughman, 2007), which implies that the expression of red pigment co-evolved with the female preference for red. However, there is also evidence that the preference for red arose before the male expression of red nuptial features, in the form of a sensory bias for the colour red (Rowe *et al.*, 2004; Smith *et al.*, 2004). Such a bias may arise as an adaptation to the conditions of the local environment (Boughman, 2001).

We test for evidence that sensory bias and/or condition indication have played a role in the evolution of what appears to be a recently evolved secondary sexual character – red pelvic spine coloration in the Turnbull National Wildlife Refuge population of brook stickleback (*Culaea inconstans*). A preference for the colour red in this population in a non-sexual context (i.e. prey selection) would suggest a sensory bias origin for the trait.

Superior physical condition in individuals with the trait over those without would suggest the trait could be selected by females to increase their fitness.

MATERIALS AND METHODS

Fish collection

We collected brook stickleback for all studies using unbaited mesh-walled minnow traps and dip nets from the outflow of Winslow Pool into Middle Pine Lake, Turnbull National Wildlife Refuge, Spokane Co., Washington (47°24′45.45″N, 117°32′19.16″W). We set traps for one hour or less. The fish at this location were likely introduced to the watershed in the late 1990s by bait bucket transfer (Scholz *et al.*, 2003). We collected under a permit from the US Fish and Wildlife Service (#TBL–11–017r). The Eastern Washington University Institutional Animal Care and Use Committee approved our methods.

Pelvic spine and condition measurements

We collected fish for pelvic spine observations in November 2011, and April, May, and October 2012. Our estimate of the breeding season was based on the presence of gravid females and nuptially dressed (dark black) males, which were observed in April and May but not present in samples from October through February. Fish were killed (using cerebral percussion) and examined within 30 min of collection immediately before processing. It is possible that our results underrepresent coloration due to colour fading during the time elapsed between collection and processing. We scored pelvic spine coloration by eye through a dissection microscope. Coloration was confined to the posterior portion of the spines. Coloration scores were as follows: none (plain spines), mild (small patch of reddish-orange pigment droplets at the base of the spines), moderate (continuous coloration extending approximately half way up the spines), or strong (continuous coloration extending almost the full length of the spine). We did not use image analysis software for spine colour measurement because we could not obtain a sufficiently high-resolution image of the coloured areas of the spines due to their small size. For condition measurements we weighed each fish to the nearest 0.1 g and measured total length to the nearest millimetre. We calculated the condition factor (K) for each fish as:

$$K = 100 \times \text{weight}/\text{length}^{b}$$

where b is the slope of the linear least squares regression of $\log_{10}$ (weight) on $\log_{10}$ (length) (Bolger and Connolly, 1989; Milinski and Bakker, 1990; Bakker and Mundwiler, 1994). The sex of all fish was determined by the presence of ovaries or testes.

Colour preference tests

We collected fish for prey colour preference tests in January, February, November, and October 2011 and January 2013. They were transported in pond water and kept in groups of about 50 in a 200-litre tank filled with tap water for 1–4 weeks of training to feed in captivity. The training tank was covered on three sides with pond-like scenery. It included brown aquarium rocks and thick plastic macrophytes. A chiller held water temperature at 16 ± 2°C. Photoperiod was set to match the natural photoperiod. We fed fish brown-coloured dried chironomids (Penn-Plax® Pro Balance™ Blood Worms) or white-coloured frozen mysid shrimp (San Francisco Bay Brand®) several times a day. The food was soaked in tank water and injected into the centre of the tank through a modified transfer pipette. This procedure facilitated colour preference testing.

For the colour preference trials we transferred three fish at a time to a 38-litre testing tank. We covered the testing tank sides with scenery like that of the training tank, but on the back with a green shower curtain, which made beads and fish easier to distinguish. The testing tank included brown aquarium rocks but no artificial vegetation. Lighting for the training and testing tanks included a full spectrum Coralife® 14,000 K HQI lamp to emulate natural sunlight and the Sylvania Ecologic® 32 W fluorescent lighting of the room. After transfer to the testing tank we immediately presented fish with a pair of coloured beads suspended on 32 cm long fishing line from a Tiny Love® Take-Along Mobile™ for babies. Bead pairs hung 41 mm apart and revolved at 3 rpm around the tank's centre. Beads measured 4.21 mm in height and 2.34 mm in width. From videos taken behind a black shroud with a Nikon D5100 camera we recorded the colour of the first bead bitten by each fish. To quantify bead colours we averaged red, green, and blue (RGB) values for each bead using the selection tools and the 'average' blur filter in Adobe Photoshop® (Table 1). Colour measurements came from a single photograph taken with flash (Nikon D5100, exposure 0.05 s, aperture f/18.0, ISO speed 640) of all the beads used in the experiment. Stickleback vision corresponds to human vision (McKinnon, 1995) with a few exceptions (Rush *et al.*, 2003).

We conducted at least 12 trials for each colour pair (red vs. orange, red vs. yellow, red vs. green, red vs. blue, red vs. purple). Lone brook stickleback are rarely bold enough to bite beads. Therefore, we used three fish in each trial. From among the three fish, we recorded the colour of the bead that was first bitten by the first fish. All subsequent selections from this fish and from the other two fish were not used in the analysis. Thus, each individual three-fish trial produced a single colour selection and was considered a single trial replicate.

Statistical analyses

We used binomial tests (Howell, 2007) with an alpha of 0.05 to determine male versus female and breeding versus non-breeding season differences in the frequency of red pelvic spine coloration. Data from fish sampled during the breeding season were pooled for analysis, as were those from outside the breeding season.

Table 1. Mean levels of red, green, and blue measured in coloured beads

	Hue		
Bead colour	Red	Green	Blue
Red	136	24	31
Orange	210	68	24
Yellow	178	155	4
Green	83	143	87
Blue	29	38	138
Purple	74	52	80

We used analysis of variance (ANOVA) with Tukey HSD (Quinn and Keough, 2002) *post-hoc* comparisons to test for condition factor differences between groups with different degrees of red pelvic spine coloration during the breeding season.

We analysed the frequencies of bites at beads of different colours using binomial tests in which expected bite frequency at each colour was 0.5 and alpha varied according to the Holm-Bonferroni sequentially reflective multiple test procedure (Holm, 1979).

RESULTS

Frequency of pelvic spine coloration peaked in males during May and was lowest in mid-winter (Fig. 1). Frequency of red/orange pelvic spine coloration was greater ($Z = 18.5$, $P < 0.0002$) in males (mean ± S.E.: 0.61 ± 0.02, $n = 429$) than females (0.03 ± 0.01, $n = 440$) during the breeding season. Frequency of red spines, with mild, moderate, and strong coloration combined, was greater ($Z = 4.5$, $P < 0.01$, $n = 369$) among males during the mid-summer breeding season (0.29 ± 0.03, $n = 345$) than in non-breeding males (0.09 ± 0.04, $n = 140$) sampled in November 2011 and October 2012.

Condition increased with the level of pelvic spine coloration (ANOVA: $F_{3,148} = 3.47$, $P = 0.017$; Table 2, Fig. 2). Males with strong coloration had a higher condition factor (1.23 ± 0.03, Tukey HSD, $P = 0.026$) than those with plain spines (1.15 ± 0.02). All other *post-hoc* pairwise comparisons were non-significant.

Fish bit red beads significantly more frequently than yellow, green, blue, and purple but not orange beads (Table 3, Fig. 3).

DISCUSSION

To our knowledge, red pelvic spine coloration in brook stickleback has not been previously reported. With the possible exception of fifteenspine stickleback, *Spinachia spinachia* (Östlund-Nilsson, 2000), all stickleback genera exhibit some kind of breeding coloration.

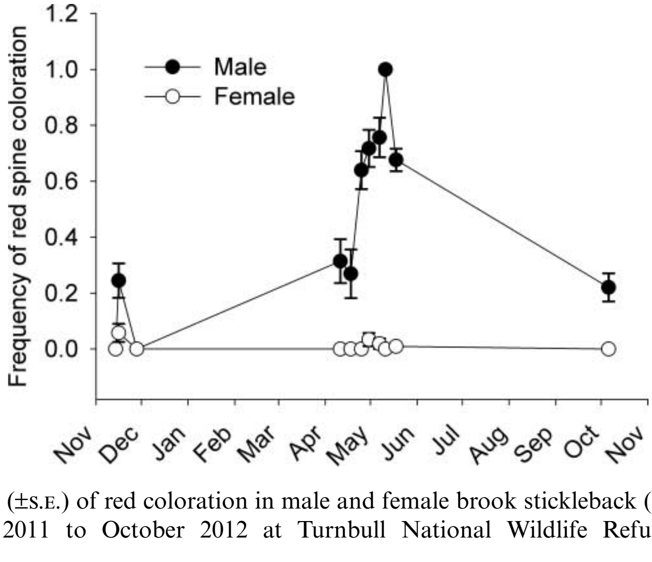

Fig. 1. Frequency (±S.E.) of red coloration in male and female brook stickleback (*Culaea inconstans*) from November 2011 to October 2012 at Turnbull National Wildlife Refuge, Spokane Co., Washington.

Table 2. Numbers of female and male *Culaea inconstans* sampled from Turnbull Wildlife Refuge, Spokane Co., Washington, with plain spines or spines with mild, moderate or strong coloration

	Female coloration				Male coloration			
Date	Plain	Mild	Moderate	Strong	Plain	Mild	Moderate	Strong
12 July 2011	36	2	1	0	28	6	11	3
21 July 2011	34	3	2	0	31	5	0	0
14 November 2011	17	0	0	0	16	0	0	0
16 November 2011	49	3	0	0	37	11	1	0
28 November 2011	8	0	0	0	7	0	0	0
11 April 2012	34	0	0	0	24	7	4	0
18 April 2012	40	0	0	0	14 (1.13 ± 0.03)	2 (1.12 ± 0.25)	3 (1.20 ± 0.15)	1
25 April 2012	31	0	0	0	18 (1.15 ± 0.04)	19 (1.19 ± 0.02)	10 (1.22 ± 0.06)	3 (1.25 ± 0.09)
30 April 2012	57	1	1	0	13 (1.18 ± 0.06)	14 (1.17 ± 0.04)	12 (1.30 ± 0.06)	7 (1.30 ± 0.07)
7 May 2012	52	1	0	0	9 (0.97 ± 0.05)	11 (1.02 ± 0.02)	12 (1.11 ± 0.06)	5 (1.10 ± 0.03)
11 May 2012	40	0	0	0	0	6 (1.12 ± 0.04)	7 (1.14 ± 0.04)	2 (1.22 ± 0.01)
18 May 2012	104	0	1	0	44 (1.17 ± 0.02)	23 (1.22 ± 0.03)	41 (1.20 ± 0.02)	28 (1.21 ± 0.04)
6 October 2012	78	0	0	0	53	13	1	1

Note: The mean (±S.E.) condition factor for males is given in parentheses for samples with condition data. See text for calculation of condition factor.

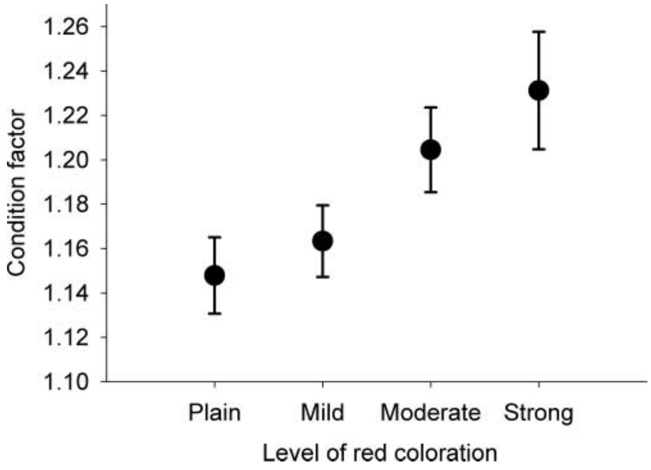

Fig. 2. Mean condition factors (±S.E.) of male brook stickleback *Culaea inconstans* from Turnbull National Wildlife Refuge, Spokane Co., Washington, with different levels of red coloration of their pelvic spines during the breeding season April–May 2012.

Table 3. Sample sizes, *P*-values, and Holm-Bonferroni-corrected alpha values for differences between observed and expected frequencies of first bites per trial directed at differently coloured beads by *Culaea inconstans*, Turnbull National Wildlife Refuge, Spokane Co., Washington

Paired comparison	*n*	*P*	alpha
Orange vs. red	14	0.7905	0.0500
Yellow vs. red	12	0.0004	0.0100
Green vs. red	12	0.0063	0.0167
Blue vs. red	16	0.0212	0.0250
Purple vs. red	16	0.0041	0.0125

The red nuptial dress of the threespine stickleback typically includes red pelvic spines as well as a red jaw and belly (Bigelow and Schroeder, 1953). Non-territorial male threespine stickleback (McLennan and McPhail, 1989), as well as females in some populations (Bigelow and Schroeder, 1953; Nordeide, 2002; Yong *et al.*, 2013), develop red coloration in their pelvic spines. Blackspotted stickleback males have red pelvic spines (Bigelow and Schroeder, 1953; Östlund-Nilsson and Mayer, 2007). Breeding fourspine – or 'bloody' – stickleback males have bright red pelvic spines (Bigelow and Schroeder, 1953; Reisman, 1963; Rowland, 1974; Bayer, 1980). Breeding male ninespine stickleback, *Pungitius pungitius*, sister species to the brook stickleback, have no red coloration (but see Bigelow and Schroeder, 1953). Rather, they develop a black ventral surface, which contrasts with bright white pelvic spines. In a study of a brook stickleback population from New York, Reisman and Cade (1967) report similar breeding ornamentation: breeding males possess a black body and the ventral spines are white as in *P. pungitius*.

McLennan (1993a) leaves red pelvic spine membrane presence/absence criteria out of her behaviour-based Gasterosteidae phylogenetic reconstruction citing a lack of information

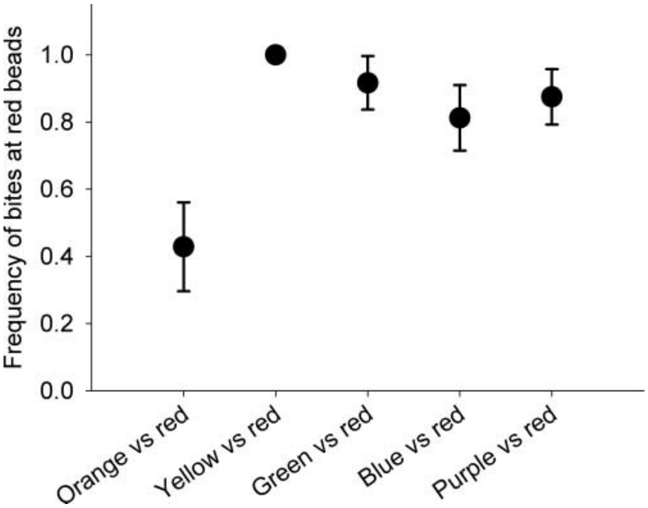

Fig. 3. Frequencies (±S.E.) of bites directed at red beads versus beads of other colours by *Culaea inconstans* from Turnbull National Wildlife Refuge, Spokane Co., Washington.

on the subject at the time for the brook stickleback. McLennan (2011, personal communication) has indicated that red pelvic spines in the brook stickleback would represent a return to the ancestral stickleback condition. This, together with a general lack of reports in the literature of red pigment being expressed at all in this species, suggests that the Turnbull National Wildlife Refuge brook stickleback (hereafter TNWR stickleback) are unusual in this respect.

Red pelvic spine coloration in TNWR stickleback meet Darwin's suggested criteria (Darwin, 1871; Andersson, 1994) for sexual selection in a visual display, in that it is developed in males almost exclusively and only during the mating season. Another of Darwin's criteria for invoking sexual selection is that the trait is used in displays directed at potential mates or same-sex rivals. Although the function of red pelvic spine pigmentation in TNWR stickleback remains unknown, pelvic spines are important in both male–male agonistic and male–female sexual interactions in all the stickleback genera, with the possible exception of the fifteenspine stickleback, for which we found no information. Blackspotted (Van Iersel, 1953; McInerney, 1969), fourspine (Rowland, 1974), and ninespine (Morris, 1958) stickleback erect their pelvic spines during various threat displays. Brook stickleback commonly erect their pelvic spines during S-displays and flare them during broadside displays, head-down displays, and circle fights (McKenzie, 1969; McLennan, 1993b; Ward and McLennan, 2006). Pelvic spines are also very important in courtship interactions. In blackspotted (McInerney, 1969), fourspine (Reisman, 1963; Rowland, 1974), ninespine (Morris, 1958), and brook (McKenzie, 1969) stickleback, the female follows the male to the nest to spawn from behind and below, where she has a view of his erect pelvic spines, sometimes nudging the male between them.

Our results are consistent with other findings regarding stickleback red coloration and preferences for red. In threespine stickleback there is evidence that both the preference and the trait have become exaggerated through an indicator mechanism (Boughman, 2007). The magnitude of red expressed is often positively condition dependent (e.g. Milinski and Bakker, 1990), but this varies among populations. Boughman (2007) found that red colour was strongly condition dependent in limnetic stickleback, weak in anadromous forms, and non-existent in benthic forms. Bakker and Mudwiler (1994) found that in males from two sites with limited inter-migration, males with more intense red received more eggs from females, but redder males were in better condition at only one of the sites. Candolin (1999) reports a curvilinear relationship with condition as measured by lipid stores. Red coloration was most intense in males of high and low condition, and lower for males of intermediate condition. Frischknecht (1993) found red coloration correlated with current, short-term condition while intensity of blue eye colour indicated long-term, overall condition and development. Barber *et al.* (2001) found offspring of redder stickleback fathers grew more slowly than those of dull fathers, but they were more resistant to parasitic infection. Red coloration in stickleback is often, but not always, associated with better condition.

Sexual signals can evolve to indicate condition even if they evolved originally because they exploit the sensory system of mates (Garcia and Ramirez, 2005). This scenario has been suggested for threespine stickleback (Boughman, 2007) based on findings that the colour red is preferred in non-mating contexts. For example, threespine stickleback bit red plastic strips at a higher rate than other colours (Smith *et al.*, 2004). Ninespine stickleback have been observed to do the same (Smith *et al.*, 2004), even though this species does not exhibit any red coloration. Ibrahim and Huntingford (1989) found that threespine stickleback use the colour red as a cue in predation. Rowe *et al.* (2004) showed that the spectral sensitivities of the threespine stickleback are optimized for representing its red breeding colours. They found similar spectral sensitivities in ninespine, blackspotted, and fourspine stickleback. Based on these results, the authors suggest a sensory bias origin of red sexual colours (Rowe *et al.*, 2004). Threespine stickleback females prefer to spawn with males who decorate the entrances to their nests, and males have a habit of using red objects to do so (Morris, 1958; Östlund-Nilsson and Holmlund, 2003). Östlund-Nilsson and Holmlund (2003) suggest conspicuous nest decorations may indicate low levels of nest predation or male dominance to females, and that the male use of red reflects a preference for their own nuptial colours. However, it is also possible that a pre-existing bias for red has played a role in male and female nest material preferences.

Colour sensitivity can depend upon water clarity (Levine and MacNichol, 1979; Endler, 1992). Species residing in shallower waters tend to be relatively sensitive to red, and those in more coloured waters to blue. The ponds at TNWR are shallow and the water has a brownish coloration when filtered from the pond and viewed in a fish tank. Thus environmental light conditions may partly explain the apparent sensitivity to red in TNWR stickleback, as they do in threespine stickleback (Boughman, 2001). This assumes that the fish either experienced similar conditions before their introduction in the late 1990s or adapted visually to the new conditions by way of phenotypic plasticity or evolution (Bell and Aguirre, 2013). Fish with a greater sensitivity to red may have been at an advantage because red coloration is common in invertebrate prey, or due to the health benefits of consuming carotenoids. The TNWR ponds contain numerous blood-red chironomids, pink and red branchiopods, red copepods, and pink amphipods. These taxa are a good source of carotenoids (Tanaka *et al.*, 1976; McLennan, 2007), which cannot be synthesized by animals but are important for maintaining health (Smith *et al.*, 2004 and references therein).

Red pelvic spines in the TNWR population of brook stickleback may represent an opportunity for research into the mechanisms behind the evolution of a derived sexually selected trait. However, we do not know whether the trait or the preference is currently under selection or whether males with redder spines receive more eggs and sire more offspring than those without. If so, it remains to be determined whether this occurs by way of female choice or competition among males. The importance of direct and/or genetic benefits and Fisherian runaway sexual selection has also not yet been established. The bias for red may extend back to or beyond the common ancestor of the sticklebacks. The closest extant stickleback relative is probably the yellow tubesnout (McLennan, 1991; Mattern, 2004; Mattern and McLennan, 2004; Kawahara *et al.*, 2009). Breeding male yellow tubesnouts exhibit bright red pelvic fin coloration (Hart, 1973; Akagawa *et al.*, 2004), which might be homologous to the red in pelvic spines of sticklebacks. Yellow tubesnouts would be a good subject for a colour preference study, as would the Japanese tubesnout, *Aulichthys japonicas*, which does not express red coloration (Akagawa *et al.*, 2004). In general, our results are consistent with a scenario in which red breeding colours in stickleback arose in response to a pre-existing sensory bias for red and are also maintained as an honest signal of condition.

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