

# Environment-dependent use of mate choice cues in sticklebacks

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Human-induced environmental changes alter terrestrial and aquatic ecosystems worldwide. This influences also evolutionary processes, such as sexual selection, by constraining mate choice and mate competition. Organisms often use multiple cues in mate choice, with different cues indicating the same or different benefits. Because the assessment and information content of cues can vary with environmental conditions, changes in the environment could alter mate choice. Here we determined if increased phytoplankton turbidity influences the relative use of olfactory and visual cues in mate choice in the three-spined stickleback *Gasterosteus aculeatus*. In a mate choice experiment, we found that females relied more on visual than olfactory cues in clear water. However, in turbid water, the pattern was the opposite with olfactory cues being more important than visual cues. Interestingly, mate preferences based on visual and olfactory cues did not agree, which suggests that human-induced environmental change could shift mate choice. This could influence the direction and target of sexual selection and have further consequences for the viability of the population under the new conditions. *Key words*: environmental change, eutrophication, *Gasterosteus aculeatus*, mate preference, multiple cues, sexual selection. [*Behav Ecol* 20:1223–1227 (2009)]

Human activities are presently altering terrestrial and aquatic ecosystems. This can influence selection pressures and, hence, affect evolutionary processes. Sexual selection is one of the main forces of evolution, which drives the evolution of traits that increase mating and fertilization success (Andersson 1994). A growing number of studies find alterations of the environment to influence the strength and target of sexual selection (e.g., Järvenpää and Lindström 2004; Candolin et al. 2007). This could have long-term consequences for populations if it influences their viability and rate of adaptation to new conditions (Candolin and Heuschele 2008).

Changes in the environment can influence sexual selection through effects on mate choice. Previously favorable mating behaviors may become maladaptive under novel conditions and result in unfavorable mate choices. For example, mating preferences of male Buprestid beetles result in mating attempts with trashed beer bottles because the brown glass surface resembles the reflectance spectrum and the texture of females (Gwynne and Rentz 1983). Alterations of the environment can also interfere with species recognition and result in hybridization between closely related sister species. This has been documented in African cichlids where the ability to separate between species is impaired under increased water turbidity (Seehausen et al. 1997).

One way in which sudden changes of the environment may influence mate choice is by imposing restrictions on the use of mate choice cues. The choice of a mate is often based on multiple cues with different cues giving either the same or different information (Candolin 2003). Because the ability to assess the cues can vary with environmental conditions (Wiley 1994), changes in the environment could alter mate choice preferences. Whether this is adaptive or not depends on the reliability

of the cues in reflecting fitness benefits under different environmental conditions.

In the three-spined stickleback (*Gasterosteus aculeatus* L.), females use both visual and olfactory cues in mate choice. Olfactory cues are used to optimize offspring major histocompatibility complex allele number (Reusch et al. 2001; Aeschlimann et al. 2003) and increase immunocompetence (Milinski et al. 2005). Visual cues, like nuptial coloration and male size (e.g., Rowland 1989; Bakker and Milinski 1993; Kraak et al. 1999), are used to gain direct benefits in the form of parental care (Candolin 2000) and indirect benefits in the form of “good genes” (Milinski and Bakker 1990) or genes that code for attractiveness (Bakker 1993).

Recent research on a sympatric species pair of three-spined stickleback shows that the relative importance of olfactory cues to distinguish between mates differs depending on the habitat the fish live in. Benthic fish living in deeper water rely more than limnetic fish on olfactory cues for assessing conspecifics (Rafferty and Boughman 2006). However, the extent to which fish within a population can adjust the use of cues to different conditions is unknown.

Eutrophication and enhanced growth of algae and phytoplankton are currently changing aquatic ecosystems worldwide (Smith 2003). Eutrophication results in reduced visibility and in large algae mats that cover coastal water bottoms (Lehvo and Bäck 2001). In fishes, reduced visibility hampers the use of visual mate choice cues and relaxes sexual selection on visual traits (e.g., Järvenpää and Lindström 2004; Candolin et al. 2007; Wong et al. 2007), which in turn can influence adaptive mate choice and population viability (Seehausen et al. 1997). This emphasizes the importance of determining the effect of environmental change on the relative use of mate choice cues.

Here, we investigated if phytoplankton-induced water turbidity influences the relative use of olfactory and visual cues in mate choice in three-spined sticklebacks. The use of visual cues is impaired in turbid water (Engström-Öst and Candolin 2007; Wong et al. 2007), but it is unknown if sticklebacks can compensate for the reduction in information by increasing the use of nonvisual cues, like olfactory cues. We further determined if a possible switch in the relative use of the cues

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could influence mate choice. If olfactory and visual cues give different information, then a reduction in the number of cues could reduce information gain and influence mate choice.

## MATERIALS AND METHODS

### Fish collection and maintenance

Adult three-spined sticklebacks were caught with minnow traps from a shallow bay in the Baltic Sea, close to Tvärminne Zoological Station in southern Finland (60°N, 23°E). The fish were caught in early May before the breeding season, and the choice experiment was conducted in June and early July. All trials were performed between 9 AM and 5 PM.

Males were housed in individual flow-through aquaria (10 l) that contained a nesting dish (11 cm in diameter) filled with sand and *Cladophora glomerata* as nesting material (Candolin 1997). To stimulate nest building, a gravid female enclosed in a transparent Plexiglas cylinder was presented daily to each male for 30 min. Females were housed in large holding tanks (150 l) at a density of 0.25 fish/l. All fish were fed frozen bloodworms, chironomid larvae, and ad libitum. They were kept in an outdoor facility under natural light conditions (transparent plastic roof).

### Mate preference experiment

To determine if the relative use of visual and olfactory cues depends on water turbidity, we allowed a female that was ripe for spawning (i.e., with ovulated eggs) to choose between 2 nesting males in the presence of visual cues, olfactory cues, and both visual and olfactory cues in either clear or turbid water. Two randomly chosen males, which had completed nest building and were in the courtship phase, were transferred together with their nesting dishes to a Y-maze fluvium in the outdoor facility (Lautala and Hirvonen 2008, Figure 1). Water was constantly flowing through the fluvium at a speed of  $\sim 190 \text{ ml min}^{-1}$ . The males were transferred in the evening before the experiment was carried out to give them time to acclimatize. The 2 males were separated by opaque dividers and could not see or smell each other.

We allowed 2 gravid females to sequentially choose between the 2 males (see Figure 1). Each female was used in 3 consec-

utive runs with access to visual cues, olfactory cues, or both cues in either clear or turbid water (Figure 1). The order of the 2 first runs, visual or olfactory cues, was randomized, whereas the run with both cues present was always last. In the visual cue run, the males and the females were separated by a transparent divider, and the water flow was directed past the males so that there was no olfactory contact between the fish. In the olfactory run, the divider was replaced with a perforated opaque divider and the flow of water was passing the males so that olfactory cues but no visual cues were transmitted. In the both cues run, a perforated transparent divider was used so that the female could both see and smell the males (Figure 1).

Each female exposure lasted for 20 min, including a 5-min acclimatization period when the female was enclosed in a Plexiglas cylinder (diameter 12 cm) at the front of the fluvium. The female was released by gently lifting and removing the cylinder, which lacked a bottom, so that the female could swim out under the cylinder. The observer was hidden behind a curtain. The time that the female spent in close proximity, within 5 cm, to either male's compartment was recorded. Relative time spent with males has been found to indicate female preferences and predict female mate choice (Milinski et al. 2005).

Five minutes after the first female had been removed, the second female was placed in the fluvium and exposed to the same treatment as the first female for 20 min. There was then a 15-min break before the first female was presented the other cue. Thus, each female was allowed to rest for 40 min (5 + 20 + 15 min) between exposures. Females were kept under the same water conditions as in the experiment, clear, or turbid water.

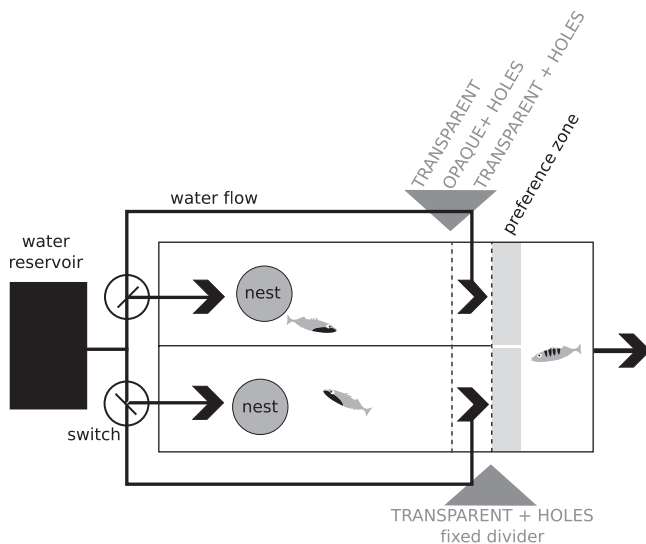
The trials, with 2 females judging paired males during 3 consecutive runs, were performed in clear and turbid water. Different males and females were used in the 2 water treatments. In the turbidity treatment, turbid water was flowing through the fluvium. To obtain turbid water, a fast-growing nontoxic flagellate algae *Isochrysis* sp., which is part of the phytoplankton community of the Baltic Sea, was cultivated in 60 l tanks containing sea water and nitrogen (0.046 g/l) and phosphorus (0.036 g/l; Järvenpää and Lindström 2004). Turbidity in the fluvium was  $6.1 \pm 1.3 \text{ NTU}$  in the turbid treatment and  $2.0 \pm 0.7 \text{ NTU}$  in the clear water treatment, measured using a portable nephelometer (Hach 2100P Portable Turbidimeter). Turbidity in the Baltic Sea can vary between 0.5 and 45 NTU (Granqvist and Mattila 2004).

Females which spawned before the end of the 3 runs were excluded from the analysis, leaving 96 females, which were tested with 51 pairs of males.

### Male traits

To determine the extent of the red nuptial coloration of the males, the left lateral side of each male was photographed immediately after the last run (Candolin 1999). The male was placed into a small glass box containing a black sponge that fixed him in position and then placed in a nonreflective dark box containing a camera, Canon EOS D350. The male was photographed under standardized settings (aperture f10.0, shutter speed 1/200, ISO 200) using the inbuilt flash. The use of the integrated white balance for flash and the absence of other light sources ensured a constant color representation. The similarity between human and stickleback vision allowed the use of the camera's trichromatic color system to analyze the nuptial red coloration of the males (Rowe et al. 2006).

We cropped each image so that the fish were presented against a white background. To measure both absolute and relative area of red color on each male, we used image analysis



**Figure 1** Schematic presentation of the experimental fluvium. Light gray areas indicate the 5 cm preference zones.

software (ImageJ version 1.38w [http://rsb.info.nih.gov/ij/]) with the plug-in “Threshold Color” (http://www.dentistry.bham.ac.uk/landinig/software/software.html). We chose the HSB color model and selected red areas using the following values: hue = 0–21 and 238–255, saturation = 83–255, and brightness = 0–255. The images were converted to 8-bit gray scale, and the selected area was measured using the “Image/Adjust/Threshold” and the “Analyze/Measure” commands. We also measured the total area of the fish to calculate the percentage of red area of the male ( $R_{\text{male}}$ ). We omitted 2 males and the corresponding females from the analyses due to missing images. Male red coloration covered on average  $7 \pm 7\%$  standard deviation (SD) of the body surface.

The wet mass and standard length of all males and females were measured after the experiment. Male condition was estimated using Fulton’s condition factor ( $[\text{weight}/\{\text{standard length}^3\}] \times 10\,000$ ), Ricker 1975). Males were on average  $52 \pm 5$  mm (SD) long, weighted  $1.74 \pm 0.53$  g (SD), and mean male condition was  $1.21 \pm 0.12$  (SD). Females were on average  $50 \pm 8$  mm (SD) and weighted  $1.98 \pm 0.9$  g (SD).

### Statistical analysis

All statistical analyses were done using the statistical software R v 2.5.1 (R Development Core Team 2009), using the lme function for linear mixed-effect models with normally distributed data (nlme package; Pinheiro et al. 2008). Because each female was used in 3 consecutive runs and 2 females were tested with the same pair of males, females were included as a random factor nested within male pairs. The initial models included all interactions between fixed effects. The models were then reduced to the minimum adequate models using stepwise backward deletion. When an interaction was statistically significant, all included main effects and lower order interactions were retained in the model without testing their statistical significance (Sokal and Rohlf 1995). The distribution of the residuals was checked visually (q–q plot, histogram of residuals) and statistically (Shapiro–Wilk) after the final analysis to confirm the reliability of the chosen test.

To determine the use of different cues in clear and turbid water, we analyzed if the relative time spent with a male when both cues were present  $T_{\text{BothCues}}$  covaries with the relative time spent with the male when only visual or only olfactory cues were present  $T_{\text{SingleCue}}$ , using a mixed-model nested analysis of covariance (ANCOVA) with  $T_{\text{SingleCue}}$  as dependent factor,  $T_{\text{BothCues}}$  as covariate, and water turbidity and cue type as fixed factors. Because the times spent with the 2 males were dependent, we used only the relative time spent with the male on the left side in the analysis. Relative time is defined as the time spent with the focal male divided by the total time spent with the 2 males.

We tested for a possible side bias in female preferences using a separate mixed-model nested analysis of variance (ANOVA) with  $T_{\text{BothCues}}$  as dependent factor and “male side” (left/right) as fixed factor. Only one randomly chosen male from each experimental trial was used in this analysis.

To determine if the motivation of females to inspect males depended on water turbidity and the type of cue, we used a mixed-model nested ANOVA with total time spent with both males as dependent factor and cue type and water turbidity as fixed factors. To investigate if visual and olfactory cues convey the same information, we determined the congruence between female preferences with olfactory and visual cues. A mixed-model nested ANCOVA was used with relative time spent with olfactory cues as dependent factor and relative time spent with visual cues as covariate and water turbidity as fixed factor.

To determine if female preferences depended on differences between the 2 males in body size and red coloration and the

influence of the type of cue and water turbidity, we used a mixed-model nested ANCOVA with the relative difference in length ( $[\text{length}_{\text{focal}} - \text{length}_{\text{other}}]/\text{length}_{\text{focal}}$ ) or the relative difference in red area ( $[(R_{\text{male1}} - R_{\text{male2}})/(R_{\text{male1}} + R_{\text{male2}}])$ ) between the males as the covariate and type of cue and water turbidity as fixed factors.

## RESULTS

### The use of cues in clear and turbid water

The relative use of visual and olfactory cues was affected by water turbidity, as indicated by the 3-way interaction between preference with both cues, type of single cue, and water turbidity. The interaction demonstrates that the covariance between times spent with a male when only one cue is present and when both cues are present depends on water turbidity and the type of cue ( $T_{\text{BothCues}} \times \text{Turbidity} \times \text{CueType}$ :  $F_{1,91} = 5.40$ ,  $P = 0.022$ ). In clear water, females relied more on visual cues than on olfactory cues when choosing between 2 males, whereas in turbid water, the pattern changed and females paid more attention to olfactory cues (Figure 2). There was no side bias in female preferences ( $F_{1,43} = 0.002$ ,  $P = 0.97$ ).

### Attraction toward cues under different water turbidity levels

The total time a female spent inspecting the 2 males depended on both the type of cue and water turbidity, as shown by a significant interaction between type of cue and water turbidity ( $F_{2,187} = 5.59$ ,  $P = 0.004$ ). In clear water, females showed more interest in the males when visual cues rather than olfactory cues were present, but in turbid water, the difference between the 2 cues in stimulating females disappeared (Figure 3).

### Mate preferences

There was no congruence between the preferences of females for the 2 males with olfactory and visual cues ( $F_{1,43} = 1.91$ ,  $P = 0.17$ ), regardless of water turbidity ( $F_{1,42} = 0.029$ ,  $P = 0.87$ ).

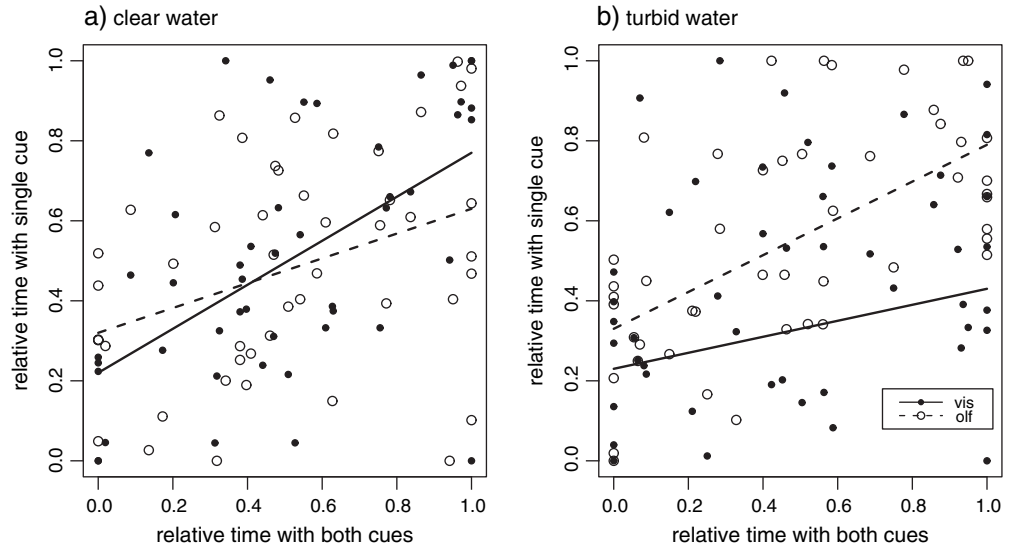
### Female preference for male traits

Differences in redness between the 2 males (mean  $\pm$  SD:  $0.01 \pm 0.44$ ) did not influence female preferences ( $F_{1,48} = 2.35$ ,  $P = 0.13$ ), independent of water turbidity (interaction between turbidity and difference in redness;  $F_{1,46} = 0.86$ ,  $P = 0.36$ ), and cue type (interaction between cue type and difference in redness;  $F_{2,183} = 0.29$ ,  $P = 0.75$ ).

Differences in male size influenced female preference depending on the type of cue (interaction between cue type and relative length difference between the 2 males:  $F_{2,187} = 3.60$ ,  $P = 0.029$ ) but not water turbidity ( $F_{1,48} = 0.01$ ,  $P = 0.93$ ). When testing the cues separately, females preferred smaller males with visual cues ( $F_{1,49} = 4.37$ ,  $P = 0.042$ ), but there was no clear preference in the presence of olfactory cues ( $F_{1,49} = 0.75$ ,  $P = 0.39$ ) or both cues ( $F_{1,49} = 0.039$ ,  $P = 0.84$ ).

## DISCUSSION

Phytoplankton-induced water turbidity influenced the relative use of visual and olfactory cues in mate choice in three-spined sticklebacks. When gravid females were allowed to inspect 2 courting males in clear water, they relied more on visual cues than on olfactory cues. However, the pattern changed under turbid conditions and female paid more attention to olfactory



**Figure 2**  
The relationship between relative time spent with a male with one cue and both cues present in (a) clear and (b) turbid water. Lines are based on model estimates from the mixed-model analysis.

cues. Because the use of visual cues is constrained under poor visibility (Seehausen et al. 1997; Candolin et al. 2007; Engström-Öst and Candolin 2007; Wong et al. 2007), the turbidity-dependent switch in the use of cues is most likely due to females relying more on the cue that is most easily judged in each environment. This is further supported by the fact that increased algal photosynthesis increases the pH of the water, which facilitates the use of olfactory cues (Heuschele and Candolin 2007). Thus, the use of the cues was flexible and adjusted to environmental conditions.

The importance of visual and olfactory cues in raising and maintaining the interest of females was similarly dependent on water turbidity. In clear water, visual cues were more stimulating than olfactory cues, but in turbid water, the stimulating effect of the 2 cues did not differ. This was due to the stimulating effect of olfactory cues increasing to the same level as visual cues in turbid water.

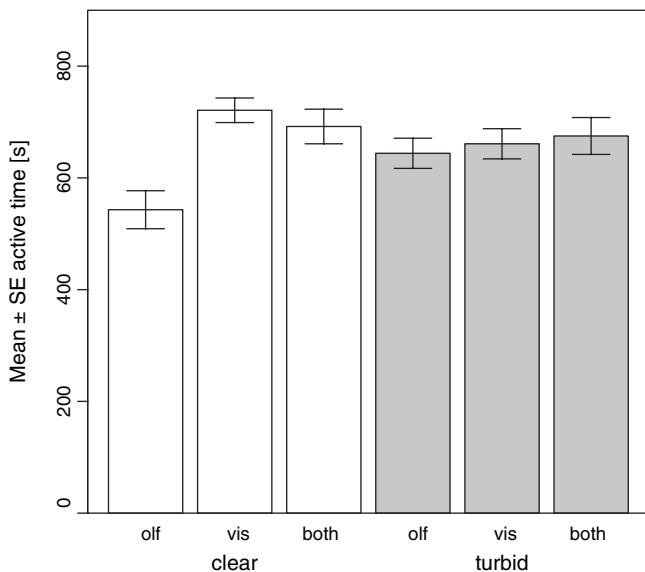
Interestingly, female preferences with visual and olfactory cues did not agree, and females could hence make slightly

different choices depending on the cue available. This suggests that visual and olfactory cues convey different information and are multiple messages and not backup cues (Candolin 2003). This is supported by earlier studies that have found different mate choice cues to code for different aspects of male quality in three-spined sticklebacks; visual cues have been found to indicate direct benefits and good genes (Bakker and Milinski 1993; Frischknecht 1993), whereas olfactory cues appear to code for the compatibility of the genomes (Aeschlimann et al. 2003; Kurtz et al. 2004). This suggests that information on mate quality can be lost when one or a few cues cannot be assessed or are more difficult to assess. This could result in suboptimal mate choices if information crucial for adaptive mate choices in the new environment is lost.

An increasing number of studies find female choice to be context dependent and adjusted to social and ecological conditions (Jennions and Petrie 1997; Qvarnström 2001). In the fish *Rhinogobius brunneus*, the preference for courtship display depends on the nutritional condition of the female (Suk and Choe 2008), whereas in the green swordtail *Xiphophorus helleri*, mate preferences of females depend on the social composition, leading to a rare male effect (Royle et al. 2008). There are, however, surprisingly few studies that find context-dependent female choice to influence offspring fitness. One rare example is the flagfish *Jordanella floridae* where a salinity-dependent female preference for male behaviors improves offspring hatching rates (Hale and St Mary 2007; Hale 2008).

Whether the turbidity-dependent switch in the use of cues in the three-spined stickleback ensures adaptive mate choice is unknown. The fish appear to pay most attention to the cues that are most easily assessed in each habitat, visual cues in clear water, and olfactory cues in algae-rich water. This may reduce mate searching costs and the time until mate choice. However, whether the mates chosen under the new conditions are the ones that are most adapted to the new conditions and will father most offspring of high quality remains to be determined.

Altered mate choice could change the target and strength of sexual selection and influence the evolution of traits. Phenotypically, plastic changes in behavior could hence be followed by genetic changes and influence the further evolution of the populations (Yeh and Price 2004). When it comes to selection on male traits, no preference for red coloration was detected. This has been found in earlier studies on sticklebacks (reviewed in Braithwaite and Barber 2000) and could be due to a preference for red being masked by preferences



**Figure 3**  
The total time that a female spent inspecting the 2 males with visual (vis) and olfactory (olf) cues in clear or turbid water.

for other visual traits, such as courtship. A preference for small males occurred with visual cues but not with olfactory cues. This probably arose from small males courting more intensively than larger males when not suppressed by larger competing males and this attracting the attention of females (Candolin and Salesto 2009).

To summarize, the results show that changed environmental conditions can induce a shift in the use of mate choice cues and influence mate preferences. Because various mate choice cues can indicate different benefits, the shift could influence the benefits of choice and ultimately the genetic quality and the further evolution of the population.

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## REFERENCES

- Aeschlimann P, Haberli M, Reusch T, Boehm T, Milinski M. 2003. Female sticklebacks *Gasterosteus aculeatus* use self-reference to optimize MHC allele number during mate selection. *Behav Ecol Sociobiol.* 54:119–126.
- Andersson M. 1994. *Sexual selection*. Princeton (NJ): Princeton University Press.
- Bakker T. 1993. Positive genetic correlation between female preference and preferred male ornament in sticklebacks. *Nature.* 363: 255–257.
- Bakker T, Milinski M. 1993. The advantages of being red—sexual selection in the stickleback. *Mar Behav Physiol.* 23:287–300.
- Braithwaite AI, Barber I. 2000. Limitations to colour-based sexual preferences in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behav Ecol Sociobiol.* 47:413–416.
- Candolin U. 1997. Predation risk affects courtship and attractiveness of competing threespine stickleback males. *Behav Ecol Sociobiol.* 41:81–87.
- Candolin U. 1999. The relationship between signal quality and physical condition: is sexual signalling honest in the three-spined stickleback? *Anim Behav.* 58:1261–1267.
- Candolin U. 2000. Changes in expression and honesty of sexual signalling over the reproductive lifetime of sticklebacks. *Proc R Soc Lond Ser B Biol Sci.* 267:2425–2430.
- Candolin U. 2003. The use of multiple cues in mate choice. *Biol Rev.* 78:575–595.
- Candolin U, Heuschele J. 2008. Is sexual selection beneficial during adaptation to environmental change? *Trends Ecol Evol.* 8:446–452.
- Candolin U, Salesto T. 2009. Does competition allow male mate choosiness in threespine sticklebacks? *Am Nat.* 173:273–277.
- Candolin U, Salesto T, Evers M. 2007. Changed environmental conditions weaken sexual selection in sticklebacks. *J Evol Biol.* 20:233–239.
- Engström-Öst J, Candolin U. 2007. Human-induced water turbidity alters selection on sexual displays in sticklebacks. *Behav Ecol.* 18: 393–398.
- Frischknecht M. 1993. The breeding coloration of male 3-spined sticklebacks (*Gasterosteus aculeatus*) as an indicator of energy investment in vigor. *Evol Ecol.* 7:439–450.
- Granqvist M, Mattila J. 2004. The effects of turbidity and light intensity on the consumption of mysids by juvenile perch (*Perca fluviatilis* L.). *Hydrobiologia.* 514:93–101.
- Gwynne D, Rentz D. 1983. Beetles on the bottle—male burprestids mistake stubbies for females (Coleoptera). *J Aust Entomol Soc.* 22:79–80.
- Hale R. 2008. Evidence that context-dependent mate choice for parental care mirrors benefits to offspring. *Anim Behav.* 75:1283–1290.
- Hale R, St Mary C. 2007. Nest tending increases reproductive success, sometimes: environmental effects on paternal care and mate choice in flagfish. *Anim Behav.* 74:577–588.
- Heuschele J, Candolin U. 2007. An increase in pH boosts olfactory communication in sticklebacks. *Biol Lett.* 3:411–413.
- Järvenpää M, Lindström K. 2004. Water turbidity by algal blooms causes mating system breakdown in a shallow-water fish, the sand goby *Pomatoschistus minutus*. *Proc R Soc Lond Ser B Biol Sci.* 271:2361–2365.
- Jennions MD, Petrie M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev.* 72: 283–327.
- Kraak S, Bakker T, Mundwiler B. 1999. Sexual selection in sticklebacks in the field: correlates of reproductive, mating, and paternal success. *Behav Ecol.* 10:696–706.
- Kurtz J, Kalbe M, Aeschlimann P, Haberli M, Wegner K, Reusch T. 2004. Major histocompatibility complex diversity influences parasite resistance and innate immunity in sticklebacks. *Proc R Soc Lond Ser B Biol Sci.* 271:197–204.
- Lautala T, Hirvonen H. 2008. Antipredator behaviour of naive Arctic charr young in the presence of predator odours and conspecific alarm cues. *Ecol Freshw Fish.* 17:78–85.
- Lehvo A, Bäck S. 2001. Survey of macroalgal mats in the Gulf of Finland, Baltic Sea. *Aquat Conserv.* 11:11–18.
- Milinski M, Bakker T. 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature.* 344: 330–333.
- Milinski M, Griffiths S, Wegner K, Reusch T, Haas-Assenbaum A, Boehm T. 2005. Mate choice decisions of stickleback females predictably modified by MHC peptide ligands. *Proc Natl Acad Sci USA.* 102:4414–4418.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, and the R Core team. 2008. nlme: linear and nonlinear mixed effects models. R package version 3.1–92.
- Qvarnström A. 2001. Context-dependent genetic benefits from mate choice. *Trends Ecol Evol.* 16:5–7.
- R Development Core Team. 2009. R: a language and environment for statistical computing [Internet]. Vienna (Austria): R Foundation for Statistical Computing. Available from: <http://www.R-project.org>.
- Rafferty N, Boughman J. 2006. Olfactory mate recognition in a sympatric species pair of three-spined sticklebacks. *Behav Ecol.* 17: 965–970.
- Reusch T, Haberli M, Aeschlimann P, Milinski M. 2001. Female sticklebacks count alleles in a strategy of sexual selection explaining MHC polymorphism. *Nature.* 414:300–302.
- Ricker WE. 1975. Computation and interpretation of biological statistics of fish populations. *Bull Fish Res Board Can.* 191:1–382.
- Rowe M, Baube C, Phillips J. 2006. Trying to see red through stickleback photoreceptors: functional substitution of receptor sensitivities. *Ethology.* 112:218–229.
- Rowland W. 1989. Mate choice and the supernormality effect in female sticklebacks (*Gasterosteus aculeatus*). *Behav Ecol Sociobiol.* 24:433–438.
- Royle NJ, Lindström J, Metcalfe NB. 2008. Context-dependent mate choice in relation to social composition in green swordtails *Xiphophorus helleri*. *Behav Ecol.* 19:998–1005.
- Seehausen O, Alphen JJ, Witte F. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science.* 277: 1808–1811.
- Smith V. 2003. Eutrophication of freshwater and coastal marine ecosystems—a global problem. *Environ Sci Pollut Res.* 10:126–139.
- Sokal RR, Rohlf FJ. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd ed. New York: W.H. Freeman.
- Suk H, Choe J. 2008. Dynamic female preference for multiple signals in *Rhinogobius brunneus*. *Behav Ecol Sociobiol.* 62:945–951.
- Wiley RH. 1994. Errors, exaggerations and deception in animal communication. In: Real LA, editor. *Behavioural mechanisms in evolutionary ecology*. Chicago: University of Chicago Press. p. 157–189.
- Wong B, Candolin U, Lindström K. 2007. Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. *Am Nat.* 170:184–189.
- Yeh PJ, Price TD. 2004. Adaptive phenotypic plasticity and the successful colonization of a novel environment. *Am Nat.* 164:531–542.