Environmental Deterioration Compromises Socially Enforced Signals of Male Quality in Three-Spined Sticklebacks

Bob B. M. Wong, Ulrika Candolin, and Kai Lindström

1. Department of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, FI-00014 Helsinki, Finland; 2. School of Biological Sciences, Monash University, Melbourne, Victoria 3800, Australia; 3. Department of Ecology and Evolution, Uppsala University, Box 573, SE-752 37 Uppsala, Sweden; 4. Environmental and Marine Sciences, Åbo Akademi University, FI-20500 Turku, Finland

Submitted July 12, 2006; Accepted February 5, 2007; Electronically published June 5, 2007

ABSTRACT: Social costs are often important in promoting the honesty of sexually selected traits. What happens, then, when social costs are relaxed? In species that breed in shallow coastal waters, increases in the frequency and severity of phytoplankton blooms may undermine the value of visual signals by reducing visibility and, in so doing, lead to dishonest signaling by relaxing the social consequences of high signaling effort for poor-quality individuals. Here, we experimentally test the effects of algal induced water turbidity on the role of male-male competition in facilitating reliable sexual displays in three-spined sticklebacks. We found that males in poor condition reduced their courtship effort in the presence of competition in turbid water. This reduction, however, was to a much lesser extent than that observed in clear water. Thus, courtship under conditions of algal turbidity did not reflect male condition as honestly as courtship in clear water. Algal turbidity also influenced breeding coloration, with males in poor condition reducing their area of red nuptial coloration in turbid conditions. Our findings suggest that anthropogenic disturbance to the signaling environment can potentially reduce the evolutionary potential of sexual selection by diminishing the efficacy of visual displays and weakening socially enforced signals of male quality.

Keywords: environmental disturbance, eutrophication, sexual selection, signal honesty, turbidity, Gasterosteus aculeatus.
is believed to communicate a host of male traits ranging from good genes to superior male parental abilities (Barber et al. 2001). The latter is especially important because males alone are responsible for looking after the developing embryos and defending the brood from potential predators. Candolin (1999b) previously showed, however, that male sexual signals are not always reliable indicators of male quality. Specifically, because of a life-history trade-off between present and future signaling effort, males in poor physical condition tend to invest heavily in current signaling when future prospects of survival and reproduction are grim (Candolin 1999b). Such males make poor choices for females because they are also more likely to cannibalize the female’s eggs (Candolin 2000a). Candolin (1999a, 2000a), however, demonstrated that male-male competition facilitates female choice by preventing poor-quality suitors from dishonestly signaling their condition to females. In the Baltic Sea, the socially imposed costs responsible for maintaining signal honesty are likely to be compromised by a deterioration of the stickleback’s visual environment as a result of water turbidity from algal blooms. Specifically, because males display close to their nests, turbidity may, in turn, make it more difficult for males to see one another, thus allowing poor-quality individuals to establish territories and to signal dishonestly. In light of this, we predicted that algal turbidity, by reducing visibility, should relax male competition and, in so doing, promote dishonest sexual signaling and reduce the evolutionary potential of sexual selection (Järvenpää and Lindström 2004; Candolin et al. 2007).

Methods
Collecting, Maintenance, and Conditioning
Sticklebacks were collected from the Baltic Sea in southern Finland and housed in separate-sex aquaria under natural light and temperature conditions at the Tervamme Zoological Research Station. Females were maintained on frozen chironomid larvae. Males, on the other hand, were assigned randomly to one of two feeding regimes (fed and unfed) for 3 weeks to manipulate condition (Candolin 1999b, 2000a). It is worth noting that male sticklebacks, in this regard, often encounter long periods of food deprivation in nature: males often do not feed for up to 3 weeks at a time (e.g., during the parental phase), and energy reserves often decrease during the course of the breeding season (Candolin 1999b). At the end of the 3-week-long conditioning period, males were allowed to construct nests in individual aquaria containing a shallow sand-filled nesting dish and tufts of Cladophora as nesting material. After they had finished constructing their nests, males were measured and weighed to quantify body condition using the Fulton index (body mass/length; Ricker 1975) and spine-clipped for identification (Candolin 2000a, 2000b).

Experimental Setup
One fed and one starved male (size matched to within 1 mm standard length) were randomly assigned, along with their nests, to each of two adjoining compartments of an experimental aquarium. Males were separated by an opaque partition to prevent visual and olfactory contact. Stimulus females were housed in a third compartment separated from the two males.

The experiment consisted of two treatments: trials were run either in clear water (control treatment, n = 23) or in water that was made turbid to simulate the algal blooms that occur in the Baltic Sea during the stickleback breeding season (algal treatment, n = 23). The latter was achieved by adding Brachionus submillina, a unicellular planktonic alga, to the treatment tanks, as done by Järvenpää and Lindström (2004). Experimental aquaria were randomly assigned to control and algal treatments. The standard length (mean ± SE) and body mass (mean ± SE) of males did not differ between treatments (length of males in control = 51.64 ± 0.30 mm, algal = 51.63 ± 0.42 mm; t-test: t = 0.02, df = 22, P = .98; body mass of males in control = 1.68 ± 0.037 g, algal = 1.70 ± 0.057 g; t = 0.29, df = 22, P = .77). In the algal treatment, a mixture of algae and water was added 1 day after males were introduced into the experimental aquarium to achieve the desired turbidity. To control for any possible effects caused by introducing water into the treatment tanks, an equivalent amount of clear seawater was also added to control tanks (Järvenpää and Lindström 2004). Turbidity, measured in nephelometric turbidity units (NTU; mean ± SE), was higher in algal tanks (10.35 ± 0.99 NTU, n = 23) than in control tanks (0.66 ± 0.24 NTU, n = 23; two-sample t-test: t = 9.78, df = 22, P < .0001). These levels are well within the range recorded in the Baltic Sea during the stickleback breeding season (which may vary between 0.5 and 45 NTU; Granqvist and Mattila 2004). Turbidity did not differ significantly between the 2 days that male courtship and color were measured (control treatment: t = 0.69, df = 22, P = .49; algal treatment: t = 0.22, df = 22, P = .83).

Male Signaling Effort in Absence of Competition
One day after adding algae to the treatment tanks and clear sea water to the control tanks, a gravid female was placed into a clear Plexiglas tube (diameter of 10 cm) positioned in the middle of the female compartment in front of the opaque divider separating the two males. Con-
control and treatment tanks received females of the same length (control = 55.20 ± 0.72 mm, algal = 54.61 ± 0.64 mm; \( t = 0.61, df = 22, P = .54 \)) and body mass (control = 2.26 ± 0.087 g, algal = 2.26 ± 0.085 g; two-sample \( t \)-test: \( t = 0.01, df = 22, P = .99 \)). We then recorded, over a 10-min period, the number of times each male attempted to lead the female to the nest to spawn, which, in this population, has previously been shown to reflect male courtship intensity and attractiveness to females (Candolin 1997). We also measured total courtship activity by tallying the number of courtship behaviors observed over the same 10-min period (i.e., zigzag movements, leads, bites, fanning displays, and swimming through the nest; sensu Candolin 1997). Male nuptial coloration was measured immediately after female exposure by photographing his left lateral side under standardized conditions described by Candolin (1999b). After photography, the male was returned immediately to the aquarium. The area of red coloration was later determined using the image analysis software ImageJ, version 1.34s (http://rsb.info.nih.gov/ij/). Because the color vision of sticklebacks does not differ greatly from that of humans (reviewed by Frischknecht [1993]), we used a system for defining color space in ImageJ that was based on human visual perception, namely, the YUV color model, which decomposes color into three components: \( Y \) = luminance, \( U \) = blue chroma, and \( V \) = red chroma. For the purpose of color analyses, we first cropped each image so that the fish was presented against a white background. All areas that ranged in color from yellow to red to purple were then selected in YUV mode (corresponding to the following YUV values: \( Y = 32–255, U = 0–143, \) and \( V = 141–255 \)). Following this, the image was converted to 8-bit gray scale, and a color threshold was applied (using the plug-in “ThresholdColour,” available at http://www.dentistry.bham.ac.uk/landing/software/software.html). This was done to remove from the image all pixels that were outside the selected values (i.e., the nonred areas on the male’s body). The area of the remaining pixels was then measured, and this, in relation to the total area of the male’s body in the original image, was used to determine the percent of the lateral side that was red colored, yielding a red-area value.

Male Signaling Effort in Absence of Competition

When both males had been photographed and returned to their respective compartments, the opaque divider was removed so that males could interact. A clump of artificial vegetation positioned in the middle of the aquarium provided a boundary marker separating the two male territories (Candolin 1999a). After the partition was removed, both males continued to take care of, and defend, their nests. One day after the partition was removed, we again measured the courtship activity and color of males exposed to a gravid female using procedures identical to the ones described above. Stimulus females used here were size matched (±1 mm standard length) with those presented to males in the absence of competition.

Within each male pair, the relative amount of courtship activity and area of red coloration was calculated as \( a(a + b) \), where \( a \) is the value for the poor-condition male and \( b \) the value for the good-condition male. All data were checked for normality and homogeneity of variances before analyses.

Results

Male Signaling Effort in Absence of Competition

On the basis of their lower body condition index (paired \( t \)-test: \( t = 6.99, df = 45, P < .0001 \)), food-deprived males were clearly in poorer physical condition than their well-fed counterparts. Despite this, in the absence of competition, food-deprived males actually courted more intensively than well-fed males (repeated-measures ANOVA, leads: \( F = 5.48, df = 1, 45, P = .024 \); total activity: \( F = 4.28, df = 1, 45, P = .044 \); fig. 1). In the absence of competition, food-deprived males in clear water also expressed relatively larger areas of red nuptial coloration than did well-fed males (repeated-measures ANOVA: \( F = 7.70, df = 1, 22, P = .011 \); fig. 2). By contrast, the difference in red area between good-and poor-condition males was reduced under turbid conditions (within-subjects interaction between male condition and water turbidity: \( F = 4.35, df = 1, 44, P = .043 \); fig. 2).

Male Signaling Effort in Presence of Competition

In clear water, males in poor condition decreased the intensity of their courtship activity when interacting with good-condition males. As a result, males in good condition ended up courting more (repeated-measures ANOVA on the effect of competition on the difference between males in leads: \( F = 30.76, df = 1, 22, P < .001 \); total activity: \( F = 25.06, df = 1, 22, P < .001 \); fig. 1A). The effect of competition on difference in courtship activity, however, was weakened under turbid conditions (within-subjects interaction between water turbidity and competition on difference in leads: \( F = 3.85, df = 1, 44, P = .056 \); total activity: \( F = 5.21, df = 1, 44, P = .027 \); fig. 1). The difference in red color expression between paired males was unaffected by the presence of competition (within-subjects effects: \( F = 0.99, df = 1, 45, P = .32 \)). This was true irrespective of whether males were tested under clear or turbid conditions (within-subjects inter-
Discrimination between water turbidity and competition: $F = 2.02, df = 1, 44, P = .16$. However, when the two male groups were analyzed separately, we found that the presence of algae reduced the red color expression of poor-condition males (between-subject effects in repeated-measures ANOVA: $F = 4.35, df = 1, 44, P = .043$) but had no effect on the color expression of males in good condition ($F = 0.11, df = 1, 44, P = .74$; fig. 2) regardless of whether a competitor was present (within-subject effects for males in poor condition: $F = 0.11, df = 1, 44, P = .74$; good condition: $F = 1.82, df = 1, 44, P = .18$; fig. 2).

**Discussion**

The results of our study suggest that any regulatory effects that competition may have on the honesty of male sexual displays in sticklebacks may be compromised under turbid conditions. Although males in poor condition reduced their courtship effort in the presence of competition in turbid water, this reduction was to a much lesser extent than that observed in clear water. Consequently, there was no difference in courtship effort between poor-condition males and those in good condition. Thus, courtship under conditions of algal turbidity did not reflect male condition as honestly as did courtship in clear water. This is likely due to a reduction in visibility that would otherwise permit males to inhibit one another’s courtship attempts. As a result, increased water turbidity seems to weaken some of the social costs that keep courtship displays honest.

Algal turbidity also appears to influence red breeding coloration. Although the area of red displayed by good-condition males did not differ between turbid and clear water conditions, males in poor condition expressed less red coloration in turbid water. This was true irrespective of whether a competitor was present. It would seem that poor-condition males are more sensitive to the lower payoffs of expressing large areas of red breeding coloration under algal turbidity. Decreased visibility, in this regard, likely diminishes the effectiveness of visual signals. Earlier studies have previously shown, for example, that female preference for red males disappears under green light, which masks the color difference between prospective suitors (Milinski and Bakker 1990), and under dense growth of filamentous algae, which reduces visibility (Candolin et al. 2007).

The results of our study have important implications for the reliability of sexual signals in human-altered environments. Increased turbidity of coastal waters in the
breeding areas of sticklebacks could allow males in poor condition to signal at a higher level than they would otherwise. Previous studies have demonstrated that poor-quality males with a high signaling effort are also more likely to cannibalize their own broods (Candolin 2000a). Thus, increased turbidity is likely to have dire consequences for females relying on the honesty of these displays to select high-quality suitors with superior parental qualities.

In the longer term, it is important to bear in mind that some degree of dishonesty is permitted in an evolutionarily stable signaling system (Johnstone and Grafen 1993; Kokko 1997). However, if dishonesty becomes pervasive under algal turbidity, the current signaling system of Baltic sticklebacks could become unstable. If this were to occur, traits that yield very little, if any, benefit under turbid conditions could, eventually, be diminished or lost. Such a situation appears to have occurred among the rift-valley cichlids of Lake Victoria, with males living under turbid conditions expressing duller coloration than those living in clearer waters (Seehausen et al. 1997).

It remains to be seen whether Baltic sticklebacks can adapt to the increasingly turbid conditions afflicting their environment. Certainly, from an evolutionary perspective, sticklebacks appear to be highly adaptable organisms, with evidence from several North American populations suggesting a proclivity for exploiting novel habitat (Schluter and McPhail 1992; Boughman 2001; McKinnon et al. 2004). Adjustment to turbidity could involve a switch to alternate cues that more accurately convey male condition or a relaxation of social costs that keep signals honest, it is conceivable that human-induced changes to the signaling environment might lead to a decrease in population viability (Fisher et al. 2006).

Acknowledgments

We thank J. Engström-Öst and T. Salesto for help collecting fish, M. Järvenpää for assistance culturing algae, H. Sasi for processing our images, and J. Heuschele for advice on the image analysis software. This project was supported financially by a Centre for International Mobility Fellowship (to B.B.M.W.), the Academy of Finland, and the Australian Research Council. Experiments were approved by the animal care committee of the University of Helsinki (approval 53-05).

Literature Cited


Associate Editor: Robert Montgomerie
Editor: Monica A. Geber