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Human-induced water turbidity alters selection on sexual displays in sticklebacks

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Changes in the environment due to human activities are becoming increasingly common. A serious problem in aquatic environments is increased water turbidity due to phytoplankton algal growth. This may affect the breeding system of fishes, especially those with a visually based mating system. Here we show that increased turbidity affects sexual selection in the threespine stickleback (*Gasterosteus aculeatus*) through impaired possibility for visually based mate choice. In a laboratory mate preference and mate choice experiment on sticklebacks from the Baltic Sea, which is an area suffering from increased turbidity due to human activities, we found that females spent more time with and visited more often males in clear water than males in turbid water. For males in turbid water to receive the same amount of interest from females as males in clear water, they needed to court significantly more. Thus, turbid water induced selection for higher courtship activity. However, the final spawning decision of the females did not depend on water turbidity, which suggests that nonvisual cues determined the final spawning decision. Because visual cues are important in mate attraction, increased turbidity affects an important evolutionary force, sexual selection, which may have further consequences for the evolution of the sexual displays and preferences. Differences in visual conditions could hence be one factor that has lead to differences among stickleback population in the use of sexual signals. *Key words:* courtship, eutrophication, *Gasterosteus aculeatus*, mate choice, sexual selection, turbidity. *[Behav Ecol 18:393–398 (2007)]*

The environments of the earth are currently changing due to human activities. Intensive agriculture, forest management, fishing, and urbanization are disrupting nature and natural landscapes. These human-induced changes to the environment may have large impacts on reproduction and the breeding systems of different animals (Møller 2004; Gaston et al. 2005; Torti and Dunn 2005). Particularly sensitive to environmental changes are coastal aquatic ecosystems, due to their vicinity to agriculture and urban areas (reviewed by Karjalainen 1999). Factors such as chemical pollution and eutrophication affect reproduction of species inhabiting rivers, seas, and lakes (Flaherty and Dodson 2005) and interfere with sexual selection (Seehausen et al. 1997; van Doorn et al. 1998; Candolin 2004; Järvenpää and Lindström 2004; Genner and Turner 2005; Fisher et al. 2006; Candolin et al. forthcoming).

A widespread problem in coastal sea areas of today is eutrophication (Larsson et al. 1985; Cederwall and Elmgren 1990; Bonsdorff et al. 1997; Raateoja et al. 2005). Increased inflow of nitrogen and phosphorus in areas such as the Baltic Sea is increasing production (Perttilä et al. 1995), resulting in typical symptoms of eutrophication such as drifting algal mats, deepwater hypoxia, algal blooms, and turbidity (Bonsdorff et al. 1997). Algae-induced turbidity decreases the amount of light that can penetrate the water column and deteriorates the visual environment (Utne-Palm 2002). It can therefore affect mate choice based on visual signals, such as male coloration in littoral fish. The effect of turbidity on fish breeding systems has, however, been little studied. Luyten and Liley (1985, 1991) showed that guppy males are less conspicuous and display less often in turbid water than in clear water to gain access to females, whereas water turbidity had no influence on another sexually selected trait in a goodeid fish (*Xenotoca variatus*) (speckle number on the flank: Moyaho et al. 2004). Moreover, changes in water turbidity have been shown to interfere with visual mate choice in Lake Victoria cichlids (Seehausen et al. 1997), to reduce the time *Poecilia latipinna* males spend associating with females (Heubel and Schlupp 2006), and to relax sexual selection in the sand goby, *Pomatoschistus minutus* (Järvenpää and Lindström 2004).

The threespine stickleback (*Gasterosteus aculeatus*) is a littoral fish that breeds in early summer in the Baltic Sea. The males establish territories, build nests out of algae and sand, and attract females for spawnings (Wootton 1976). Breeding males in the present population develop a bright red belly and blue eyes and court females through a conspicuous courtship dance. They approach a female in a series of zigzag movements and then attempt to lead her to the nest. At the nest, the male engages in nest activities, principally fanning behavior. Courtship may last for several minutes before the female decides whether to lay her eggs. Females leave immediately after spawning, and the male alone cares for the eggs and newly hatched fry for 2 to 3 weeks (Wootton 1976). Earlier research shows that the female bases her mate choice on several cues, the intensity of the red nuptial coloration (reviewed by Rowland 1994), the major histocompatibility complex (MHC) diversity (Reusch et al. 2001), and the courtship activity of the males (Rowland 1995). However, the pattern varies among populations, and particularly, the use of red coloration as a signal and the preference for red differ from one population to another (reviewed in Braithwaite and Barber 2000). The variation may be related to environmental conditions and the efficiency of the red coloration as a signal of male quality because sticklebacks occur in areas that differ widely in turbidity.

The aim of the current study was to investigate if male sexual displaying and female mate preferences and choice in the threespine stickleback are affected by the increased turbidity of water such as those in the Baltic Sea, which is caused

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by increased phytoplankton growth due to human activities. Increased turbidity reduces visibility, which could influence the investment into visual displays and the use of visual cues in mate choice. This could have further consequences for sexual selection and for the evolution of sexual displays and preferences in populations subjected to different degrees of eutrophication.

METHODS

Collection and maintenance

We collected wild adult threespine sticklebacks by Plexiglas traps (Candolin and Voigt 2001) from the littoral zone in the surroundings of Tvärminne Zoological Station, SW Finland, Baltic Sea. They were collected at the beginning of May, before their breeding season. Males and females were held in different aquaria in an outdoor facility, with a constant flow through of brackish water (salinity 5.4 psu). Breeding behavior was prevented by the lack of appropriate nesting material and by keeping the fish density high in the holding aquaria. Sticklebacks were fed ad libitum with frozen chironomid larvae twice daily.

Males in breeding condition, which had blue eyes and started to turn red on the ventral side, were moved to individual 20 l aquaria to build nests. Each aquarium contained a plastic plant saucer (diameter: 12 cm) filled with 1 cm sand and some *Cladophora glomerata* as nesting material. The males were placed into the aquaria 2–3 days before being used in the experiment.

Algal culture

Brachiomonas submarina (cell size: ~7.5 μm; Koski et al. 1999) was obtained from a pure monoculture maintained by the Tvärminne Zoological Station, University of Helsinki (Hällfors G and Hällfors S 1992). The algal cultures needed for the experiment were grown outdoors under natural light conditions in 45-l uncovered containers, using 10-μm-filtered seawater and aquatic fertilizer (Kemira) at a concentration of 0.75%. The culture was diluted daily and nutrients added to favor rapid algal growth. The cultures were supplied with air continuously. Turbidity was measured daily with a nephelometer (Hach 2100P Portable Turbidimeter). Turbidity in the Baltic Sea may vary between 0.5 and 45 NTU (Granqvist and Mattila 2004) and coincides with the stickleback reproductive season.

Experimental setup

We allowed 2 stickleback males, one in turbid seawater (L_S: 47.2 ± 0.8 mm; mean ± standard error [SE]) and the other in clear seawater (L_S: 48.4 ± 0.7 mm), to simultaneously court 3 sequential females in a Plexiglas fluviarum (120 × 34 × 12 cm). The fluviarum was a selection test arena (Figure 1) and is based on the design by Hirvonen et al. (2000). It was located in an outdoor facility with natural light and temperature conditions. The inflow of water into the 2 arms of the fluviarum came from two 10-l tanks at the back end of the fluviarum, one containing clear water (1.1 ± 0.2 NTU), the other concentrated turbid water (51.4 ± 9.4 NTU). Both tanks were aerated constantly during the experiment. The clear water tank contained 10-μm-filtered seawater, whereas the turbid water tank contained a *B. submarina* algae solution. The algae concentration was 400 μg C l^{-1} and was mixed with 10-μm-filtered seawater in the 10-l tank. The speed of the water flow into the fluviarum was ~164 ml min^{-1}. This corresponded to approximately 10–15 NTU in the turbid treatment in the fluviarum. The clear water treatment was 1 NTU.

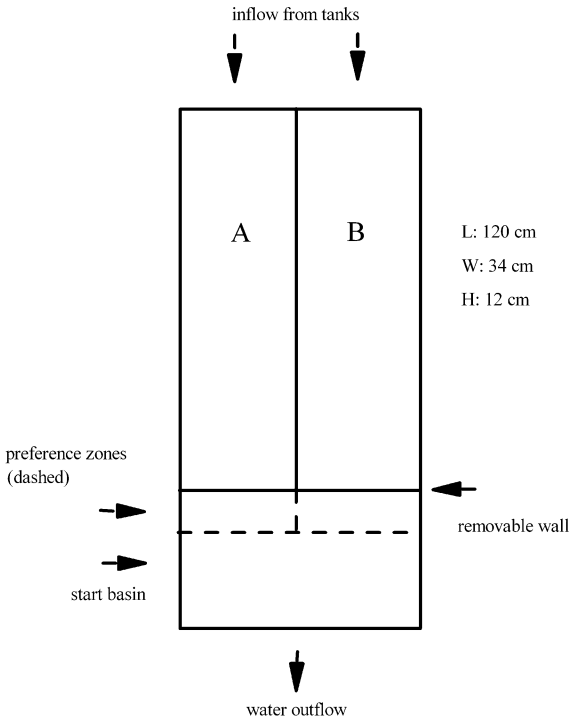

Figure 1
A schematic drawing of the fluviarum. L = length, W = width, H = height. Female preference (for male A or B) was measured only in the preference zones as time and times visited.

One day before the experiment, 2 randomly selected males, who had completed nest building, were carefully moved to the fluviarum together with their nesting dishes. One male was placed into each lateral half, or arm, of the fluviarum (Figure 1). The nesting dish was placed at the back end of the arm. A removable wall with small holes that allowed water flow prevented the males from leaving their side of the fluviarum and entering the other male's side. The males could not see each other.

Three egg-bearing randomly chosen females were sequentially exposed to the 2 males. One female at a time was placed on the other side of the removable Plexiglas wall. She was acclimated for 5 min inside a Plexiglas tube (diameter: 12 cm) and then carefully allowed to swim out of the tube. The tank taps were opened to allow the water to flow through. We measured the time that the female spent in front of each male's lateral half (area: 5 × 17 cm) and the number of visits to these preference zones. Further, we monitored courtship behavior of both males, by recording the number of zigzag dances toward the female, leads to the nest, the number of fanning bouts, and the time spent fanning. Only females that displayed the head-up posture and that spawned the eggs within the same day were included in the analyses, to assure that the females were expressing mate preference and not shoaling preferences.

Each session with a single female lasted 15 min after which the taps were closed and the female was removed. Fifteen minutes later, the next female was acclimated and the same procedures were repeated. When all 3 females had been presented to the males, the same procedures were repeated, with the same 3 females in the same order, but this time without the separating Plexiglas wall. The females were allowed to spawn with the males, and we observed which nest the female first inspected and which male she eventually spawned with. If the female did not spawn within 30 min, the session was terminated. The same order of females was used in both rounds.

After the 3 females had been presented to the males, the left lateral side of the males was quickly photographed under standardized conditions (Candolin 1999). Males were individually secured in a small glass box (6 × 6 × 3 cm) containing a moistened black sponge that fixed the male in place and served as a nonreflective background. The glass box was placed at a fixed distance (56 cm) from a Minolta RD 175 digital camera mounted on a stand in a dark room. A 40 W incandescent light bulb positioned to one side of the box and camera provided the only source of illumination. A strip of white paper and 3 plastic strings of red, blue, and green were secured on the side of the box to act as a color reference to which each photograph was standardized before color analysis. The entire photographing procedure took less than 1 min, and the males did not have time to fade. The extent of the red coloration was determined from the digital images using image analysis software, Image J 1.34s (http://rsb.info.nih.gov/ij/), and the YUV color model, which decomposes color into 3 components: Y = luminance, U = blue color component, and V = red color component. Areas that ranged in color from yellow to red to purple were selected (Y = 32–255, U = 0–143, V = 141–255), and their size in relation to the total size of the photographed male was recorded. Color vision of sticklebacks differs from that of humans in that they are sensitive to ultraviolet light (Rowe et al. 2004; Boulcott and Braithwaite 2005). However, because we concentrated on red coloration, which does not have a UV component, and as recent research suggests that human and stickleback judgments of male "redness" can be considered similar (Rowe et al. 2006), our measurements do reflect a relative increase or decrease in the intensity of the red patch. The length and wet weight of the fish were measured at the end of the experiment.

The lateral half of the fluviarum that was used for the clear and turbid water treatments was alternated between sessions. The experiment was conducted in 2 separate fluviaria on 2 different tables, so that 2 replicates could be conducted each day. Between each experimental session, the fluviarum was emptied, rinsed, and filled with new aerated seawater. Altogether, we used 63 females and 21 male pairs in the experiment (3 females presented/male pair).

Analyses

Paired *t*-test was used to test for differences in courtship behavior between the paired males and for differences in the time that the females spent with each of the 2 males. Because 3 females were shown to each male pair, the mean values of the behaviors recorded during these 3 trials were used in the analyses to avoid pseudoreplication. A multiple regression was used to determine whether differences between the males in courtship and in coloration determined the time that a female spent with each male. The time that a female spent with each male was calculated as the percentage of the total time that she spent with the 2 males. The difference between the males in courtship activity and coloration was calculated as (male A − male B)/(male A + male B), where male a is the male in turbid water. To visualize and extrapolate the difference in courtship activity required for females to express mating preferences, we regressed the relative time spent with each male on the difference in courtship activity between the 2 males.

When analyzing the spawning decision of the females, only the first female to spawn were included in the analysis because the mate choice of subsequent females may be influenced by the presence of eggs in the nests (Goldschmidt et al. 1993). The first nest inspected was recorded for all 3 females because we assumed that the presence of eggs would not influence which nest a female first approached. One sample *t*-test and binomial test were used to determine if females preferred one male to the other. Logistic regression was used to determine if spawning decision depended on the difference between the 2 males in courtship activity and red coloration. All data were checked for normality and homogeneity of variance before analyses.

Table 1

The correlation and difference in courtship activity and red coloration between paired males in turbid and clear water

	Correlation between males		Difference between males	
	R	*P*	*t*	*P*
Zigzags	0.60	0.004	0.67	0.512
Leads	0.63	0.002	0.87	0.394
Fanning frequency	0.42	0.057	1.14	0.267
Fanning time	0.33	0.149	1.06	0.301
Red area	0.45	0.042	2.37	0.028

Paired *t*-test was used. $N = 21$.

RESULTS

The paired males did not differ in any of the courtship activities recorded, but the male in turbid water expressed more red coloration than the male in clear water (Table 1). Thus, males adjusted red coloration but not courtship activity to water turbidity. Overall, the measured traits were correlated between the 2 males, except for fanning behavior (Table 1), which indicates that both males were reacting to the behavior of the females.

The females spent more time with the male in clear water (paired $t_{20} = 3.11$, $P = 0.006$) (Figure 2) and visited this male more often than the male in turbid water (paired $t_{20} = 2.25$, $P = 0.036$). To determine whether female preferences depended on differences in courtship activity or red coloration between the 2 males, principal components were first calculated for the differences in courtship that were strongly correlated, that is, the differences in the frequency of zigzags and in the frequencies of leads to the nest ($r = 0.94$, called zigzag leads) and the differences in the frequency of fanning bouts and in the time spent fanning ($r = 0.99$, called fanning behavior). A multiple regression using these principal components showed that the proportion of time that females spent

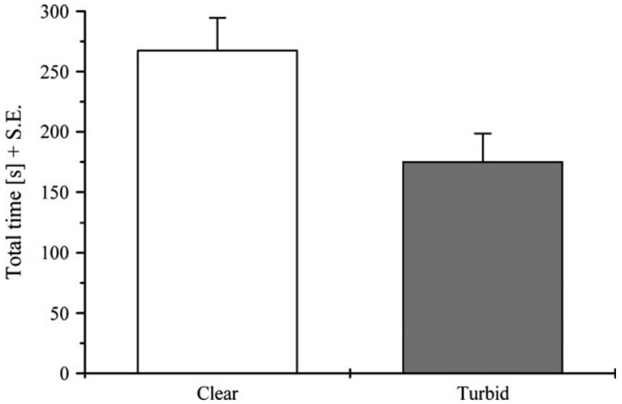

Figure 2
The mean time (s) that the 3 females spent with the paired males in clear and turbid water. Total session time was 900 s (15 min). $N = 21$.

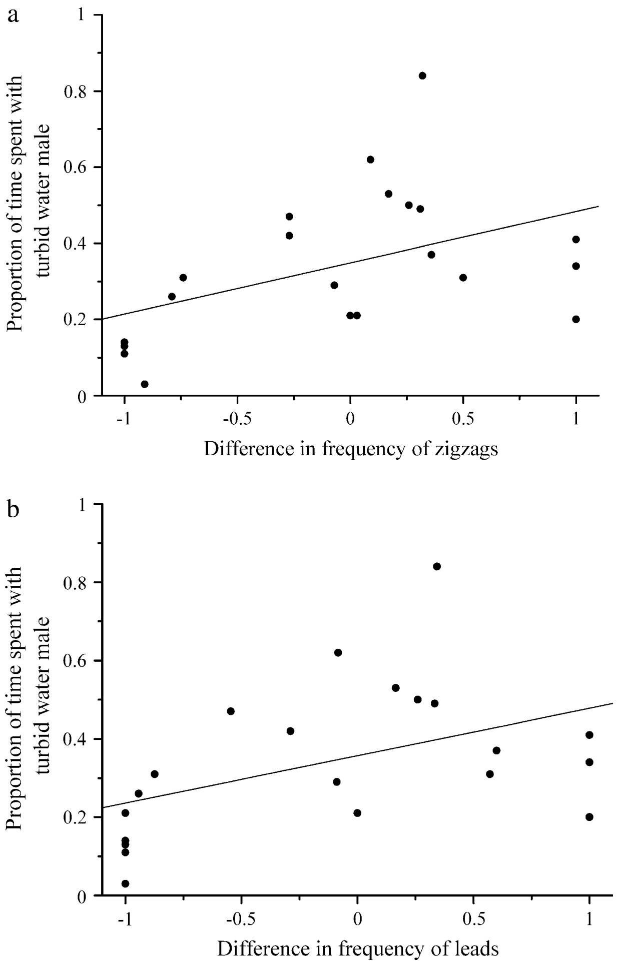

Figure 3
The dependence of the time spent with the male in turbid water on the difference in courtship activity between the paired males. Higher values on the *x* axis indicate that the male in turbid water courted more. The difference between the males in (a) the frequency of zigzags movements and (b) the frequency of leads to the nest.

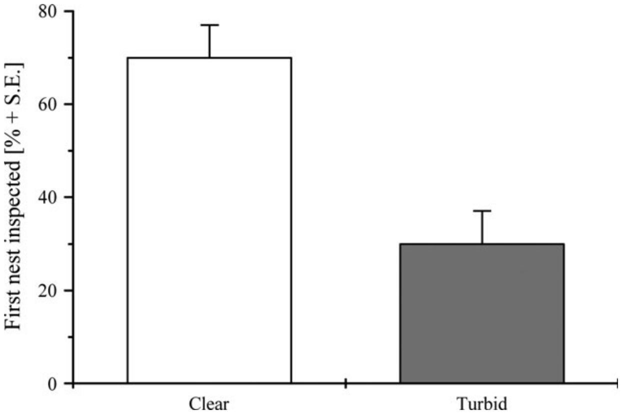

Figure 4
The first nest that was inspected by the 3 females, given as percentages.

with the male in turbid water in relation to the time spent with both males depended on the difference between the males in the frequency of zigzag leads ($r^2 = 0.22$, $t_{1,19} = 2.32$, $P = 0.032$) (Figure 3) but not on the difference in fanning behavior ($t = 0.67$, $P = 0.51$) or red coloration ($t = 1.13$, $P = 0.27$), which were excluded from the regression model.

The male in turbid water needed to court more than the male in clear water to receive the same amount of attention from the female because the females spent less than 50% of their active time with the male in turbid water when the 2 males courted equally much (linear regression; Figure 3a, zigzags: *y* intercept = 35 ± 4% (SE), $t = 3.95$, $P = 0.001$, slope: $r^2 = 0.22$, $F = 5.26$, $P = 0.033$; Figure 3b, leads: *y* intercept = 36 ± 4% (SE), $t = 3.69$, $P = 0.002$, slope: $r^2 = 0.21$, $F = 5.12$, $P = 0.036$). Extrapolating from the figure, it is apparent that on average a male in turbid water needs to be the only male to court before he receives the same amount of attention from a female, 50%, as the male in clear water (Figure 3).

The females inspected the nest of the male in clear water before that of the male in turbid water in 70 ± 7% (SE) of replicates (1 sample *t*-test, $t_{20} = 2.890$, $P = 0.009$) (Figure 4). However, the spawning decisions of the females did not depend on water turbidity: in 8 out of 17 replicates where at least one of the females spawned, the first female to spawn chose the male in clear water (binomial test; not significant). The spawning decisions depended neither on the difference in courtship activity nor on the red coloration between the males (logistic regression: chi-square = 2.26, degrees of freedom = 3, $P = 0.52$; zigzag leads: Wald = 0.35, $P = 0.56$; fanning behavior: Wald = 1.84, $P = 0.18$; red coloration: Wald = 0.43, $P = 0.51$). Spawning decisions did not depend on male size because the inclusion of the difference in size between the 2 males had no significant effect on the model (Wald = 0.44, $P = 0.51$).

DISCUSSION

Increased water turbidity due to the growth of phytoplankton algae reduced the attractiveness of the males to females. For males in turbid water to receive the same amount of attention from females as males in clear water, the males needed to court much more than the males in clear water. The males in turbid water expressed more red coloration than males in clear water, but this was not found to influence female preferences. These results suggest that increased water turbidity enhances selection for intense courtship displays in sticklebacks because females paid attention to the male in turbid water only when he was displaying at a very high level.

Increased courtship activity should, however, increase the costs of mating in terms of time and energy spent on attracting females, and perhaps also enhances predation risk. These increases in the costs of mating might outweigh the benefits of increased attraction and result in an optimum level of courtship, above which further increases do not pay off. It is therefore possible that at very high turbidity levels, the costs of enhanced courtship display becomes higher than the benefits and that further increases in courtship activity will no longer be favorable. Instead, selection for other mating strategies, or the use of cues other than courtship in mate choice, could be enhanced (cf., Luyten and Liley 1991).

The reason for the lower interest of the females in the male in turbid water is probably reduced visibility. A male in turbid water is visible only at short distances and needs to be colorful and court vigorously to both receive and maintain the attention of females. Similarly, females of a goodeid fish, *X. variatus*, pay fewer visits to males in turbid water than to males in clear water, and only in clear water do the females prefer more ornamented males (Moyaho et al. 2004). Another potential reason for females spending less time with the turbid water males is that the phytoplankton produced odors, which affected the smell of the males. However, we used a fresh, exponentially growing culture of *B. submarina*, and the amount of off-flavors was probably negligible. Negative effects of turbidity on mate choice are also found in *P. latipinna*, where males spend less time associating with females under turbid conditions (Heubel and Schlupp 2006) Similarly, in sand gobies *P. minutus*, increased turbidity reduces the variation among males in mating success (Järvenpää and Lindström 2004), and in Lake Victoria cichlids, males are known to express less color in turbid water (Seehausen et al. 1997; Seehausen and van Alphen 1998).

In the present study, males in turbid water were more colorful than males in clear water. One possible explanation for this result is that males in turbid water were increasing their signaling output during courtship to counter the effects of algae. However, it is also conceivable that males may have increased their coloration after spawning because the males were photographed after they had received some eggs, in which case the measured coloration may actually reflect the color of males during the parental phase (rather than courtship).

Interestingly, the spawning decisions of the females were not affected by either water turbidity or male courtship activity. The decision was not associated with male size either, although stickleback females are known to prefer large males (Rowland 1989). Therefore, the females appeared to base their mate choice decision on traits other than those studied. These could be, for instance, odor cues. Recent research shows that female mate choice in sticklebacks is based on MHC-related odor cues, which make it possible for the female to achieve the optimal level of MHC diversity in their offspring (Reusch et al. 2001; Milinski et al. 2005). Male courtship and red color expression are, however, also important in attracting and maintaining the attention of females (Rowland 1989; Milinski and Bakker 1990). Females usually prefer more intensively colored males (Milinski and Bakker 1990; Braithwaite and Barber 2000) because high contrast might indicate stronger disease resistance (Barber et al. 2001). Courtship activity, on the other hand, is important in drawing the attention of the female and in exposing the red coloration (Candolin 1997; Candolin and Voigt 1998). A male in turbid water who does not court actively may not be noticed by the female and may, under normal field conditions, not receive any spawnings, irrespective of his other qualities. In the present small experimental aquaria, with short distances between the males, females were most likely able to detect both males when the partitioning sheet was removed, independent of courtship activity and red coloration. The females could hence base their final mate choice on traits other than courtship activity or red coloration. Thus, it is possible that, in future populations, selection for color-based mate choice may decrease and odor-based mate choice may increase due to increased turbidity of the water.

Intriguingly, males did not adjust their courtship activity to water turbidity, although the results suggest that this would have been beneficial. This may be due to the fish not being fully adapted to turbid water conditions and therefore not behaving optimally under the new conditions. In male guppies, for example, bright coloration and active courtship display are associated with clear water, and nondisplay tactics are an adaptation to turbid water (Luyten and Liley 1991). Decreased water transparency of the Baltic Sea (Sandén and Håkansson 1996), due to increased growth of phytoplankton algae, may, however, with time, cause an evolutionary change in the population. The stickleback population could evolve to generally court more or, alternatively, evolve stronger phenotypic flexibility in sexual displays in relation to environmental conditions. Sticklebacks are evolutionary adaptive and have adjusted to a range of different conditions (Schluter and McPhail 1992; Boughman 2001; McKinnon and Rundle 2002; Bell et al. 2004; McKinnon et al. 2004). Whether a genetic change will occur will depend on the heritability of the traits and on the consistency of selection.

A related study on the effect of increased growth of filamentous algae on sexual selection in sticklebacks showed that increased algae cover leads to an increase in courtship activity (Candolin et al. forthcoming). However, whereas an increase in courtship activity would be beneficial in increasing the interest of the females under increased water turbidity, as shown in the present study, the increased activity under increased algae cover had no favorable effect on female preferences. This suggests that the effect of eutrophication through increased growth of both phytoplankton and filamentous algae may be complex and that different factors may have different effects. Most likely, increased algae cover reduces visibility more than increased water turbidity at short distances, and an increase in courtship activity in dense vegetation cannot compensate for the negative effect of reduced visibility. More studies are needed to determine the ultimate effects of eutrophication on the opportunity of sexual selection and the strength of selection on different traits.

To conclude, this study shows that increased water turbidity favors an increase in courtship activity due to decreased visibility and impaired possibilities for visually based mate choice. However, males did not increase their activity under turbid conditions, which suggests that they have either not yet adapted to the new conditions or that increased cost of courtship opposes the benefit of increased activity. The ultimate spawning decision of the females was not affected by turbidity or courtship activity, which suggests that selection for odor-based mate choice could increase in future populations if the use of visual cues gets too costly. Because different components of eutrophication appear to have different, and sometimes opposing, effects on sexual selection in sticklebacks, a challenge of future studies will be to predict the combined effect of increased turbidity and growth of filamentous algae on sexual selection.

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