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Changed environmental conditions weaken sexual selection in sticklebacks

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Abstract

Environmental heterogeneity can cause the intensity and direction of selection to vary in time and space. Yet, the effects of human-induced environmental changes on sexual selection and the expression of mating traits of native species are poorly known. Currently, the breeding habitats of the three-spined stickleback *Gasterosteus aculeatus* are changing in the Baltic Sea because of eutrophication and increased growth of algae. Here we show that enhanced growth of filamentous algae increases the costs of mating by inducing an increase in the time and energy spent on courtship and mate choice. This is not followed by a concomitant increase in mate attraction, but instead the strength of selection on male red nuptial coloration and courtship activity is relaxed. Thus, the high investment into the costly sexually selected traits is maladaptive under the new conditions, and the mating system mediates a negative effect of the environmental change on the population. We attribute these environmentally induced changes in the benefit of the mating traits and in the strength of sexual selection to reduced visibility in dense vegetation. Anthropogenic disturbances hence affect the selection pressures that mould the species, which could have long-term effects on the viability and evolution of the populations.

Introduction

The environment has a profound effect on the evolution of reproductive traits. Characters such as courtship activity, mate choice, mating behaviour and parental effort are, over evolutionary time, adjusted to factors like predation risk, resource availability, and population demography (Lima & Dill, 1990; Resetarits & Wilbur, 1991; CluttonBrock *et al.*, 1997). Local differences in environmental conditions can therefore result in population differences in reproductive traits (Arnqvist, 1992; Endler & Houde, 1995; Simmons *et al.*, 2001; Kwiatkowski & Sullivan, 2002). These differences may be genetic, or result from phenotypic plasticity, in which case genetic changes may arise with time (West-Eberhard, 2003).

Because of human activities, many habitats are rapidly changing. The consequences this may have for sexual selection of the species that naturally inhabit these areas are poorly known. Sudden changes in the environment could affect who reproduces and influence sexual selection (Seehausen *et al.*, 1997; Järvenpää & Lindström, 2004). The lack of studies on the effects of anthropogenic disturbances on sexual selection is surprising, given the importance of sexual selection as a major force of evolution (Andersson, 1994; Hoekstra *et al.*, 2001). Sexual selection incurs a cost due to fitness costs of sexually selected displays that displace individuals from their survival optimum (Fisher, 1958; Lande, 1980). This implies that sexual selection and viability selection can oppose each other (Jennions *et al.*, 2001). However, changes in conditions could change the relative intensity of the two forces, which could decrease the viability of the population if a new equilibrium between sexual and viability selection is not quickly reached (Tanaka, 1996; McLain *et al.*, 1999;

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Houle & Kondrashov, 2002; Kokko & Brooks, 2003). On the other hand, strong sexual selection could be beneficial for the population under new environmental conditions if it accelerates adaptive evolutionary change (Proulx, 1999; Lorch *et al.*, 2003). Hence, whether strong sexual selection is advantageous or not under environmental change is unclear.

Eutrophication is a serious environmental problem along the coasts of Europe, with notorious effects in the Baltic Sea (Bonsdorff *et al.*, 2002). It arises from increased input of nutrients which, in turn, enhances the growth of filamentous algae and phytoplankton. This changes the animal communities, but the long-term effects are unknown (Bokn *et al.*, 2002; Bonsdorff *et al.*, 2002). A species that is likely to be affected by the environmental changes currently affecting the Baltic Sea is the three-spined stickleback *Gasterosteus aculeatus*. Sticklebacks breed in shallow coastal waters and could benefit from increased algal growth through concealment from predators (Candolin & Voigt, 1998), but may suffer costs due to reduced visibility and lower mate encounter rate (Candolin & Voigt, 2001a).

We investigated whether increased growth of filamentous algae influences (i) the cost of mating in terms of time and energy spent on courtship and mate inspection, and (ii) the strength of selection on red nuptial coloration and courtship activity. Changes in the cost of mating could influence the cost–benefit balance of sexual selection and, hence, the strength and direction of sexual selection on mating traits. This, in turn, could have further consequences for the future evolution and the viability of the populations. To investigate the effects on increased algal growth on mating costs and on sexual selection, we performed both field observations and a laboratory experiment. In the field study, we recorded male courtship activity and female inspection behaviour under different algal cover. In the laboratory study, we experimentally determined whether the effort spent on mate choice and courtship depends on algal cover, and whether this influences the strength and direction of sexual selection on red nuptial coloration and courtship behaviour.

Materials and methods

Sticklebacks in the northern Baltic Sea migrate from deep water to shallow coastal waters at the beginning of May. Males establish territories, build nests out of algae and sand, and attract females for spawnings (Wootton, 1976). Breeding males develop a bright red belly and blue eyes and court females though 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 behaviour. Females leave immediately after spawning and the male alone cares for the eggs and newly hatched fry for 2–3 weeks.

Field observations

We observed males nesting in sparse and dense algal vegetation in a shallow bay of the Baltic Sea, Långskär Bay, in Southern Finland (60°N, 23°E) during the height of the breeding season, 7–20 June 2004. The nests had either 25% or 75% of the area surrounding the nest covered by filamentous algae. The density of algae was scored by visually estimating the percentage of a 1 × 1 m area around the nest that was covered by filamentous algae, mainly *Cladophora glomerata*. Patches with different densities of algae were interspersed along the shore. The water depth of the nests varied from 20 to 80 cm. Each male was observed for 30 min. The observations were carried out from the shore or from rock outcrops situated in the bay. Observations involved noting the amount of time that passing females spent inspecting the male before following him to the nest or leaving the territory, and the time that the male spent courting the female and the frequency of zigzag movements towards each female. Whether the females spawned in the nests could not be determined. The times and frequencies were square-root transformed before analyses.

Aquarium experiment

Sticklebacks were caught with Plexiglas traps (Candolin & Voigt, 2001b) before the breeding season in early May 2004, from the same area where the field observations had been carried out. They were housed in flow through aquaria under natural light and water temperature conditions and fed on frozen chironomid larvae. Fish that turned out to be males, as determined by the development of blue eye colour, were transferred to separate holding aquaria. A lack of suitable nesting materials discouraged breeding behaviour.

Randomly selected males were transferred to individual aquaria (60 × 30 × 30 cm) with either high or low algal density to experimentally determine whether the effort spent on mate choice and courtship increases with algal cover, and whether this influences the strength of sexual selection on mating traits. The aquaria with low algal density contained only a nesting dish at one end of the aquarium. The dish was filled with sand, filamentous algae (*C. glomerata*) for nest construction, and an artificial plant for hiding (see Candolin, 1997). The aquaria with high algal density contained, in addition to the nesting dish, bunches of 15-cm long, thin, green polypropylene strings that mimicked filamentous algae. They were distributed over the bottom so that about 75% of the bottom, up to a height of 15 cm, was covered by artificial algae. The density represented the density of algae found in nature, with the treatment with dense vegetation corresponding to a very high density of algae in the field. The males were measured for standard length to the nearest millimetre and weighed to the nearest 0.01 g before being placed in the aquaria.

One day after a male had built a complete nest and performed the creeping through behaviour (van Iersel, 1953), a gravid female enclosed in a Plexiglas cylinder was introduced into the aquarium, 40 cm from the nesting dish. After 5 min, the female was released and allowed to spawn with the male. The fish were video filmed for 15 min. If a female did not spawn within 15 min, the aquarium was checked once an hour to determine the spawning time. Spawning time corresponds to both female inspection time and male courtship time since the fish were constantly interacting. The following male behaviours were recorded: number of (i) zigzag bouts towards the female, (ii) leads to the nest, (iii) bites towards the female, and (iv) fanning bouts at the nest (Wootton, 1976). As the behaviours were strongly correlated, principal components were calculated. Only the behaviours recorded when the female was enclosed in the cylinder, when male behaviour was less affected by female behaviour compared with freely interacting fish, were included in the analyses (Table 1). However, qualitatively similar results are gained in the subsequent analyses if the behaviours of freely interacting fish are used.

The nuptial coloration of the males was determined immediately after spawning. The males were caught with a dip-net and their left side was photographed under standardized conditions in a large dark box containing a digital camera (see Candolin, 1999). The photography procedure took <1 min and the males did not have time to fade as a result of handling stress (Candolin, 1999). The extent and quality of the red coloration was determined from the digital images using image analysis software to exclude observer biases (MCID, Imaging Research Inc., Brock University, St. Catharine, ON, Canada). Areas that ranged in colour from yellow to red to purple were selected [hue: 1–50 and 340–359; saturation (chroma): 0–0.631; intensity (brightness): 0.157–0.663], and their size and mean hue, saturation and intensity recorded (Candolin, 1999). A tristimulus system constructed to fit the human eye was used, as colour vision of sticklebacks does not differ greatly from that of humans (reviewed by Frischknecht, 1993; McKinnon, 1995). Both absolute and relative sizes (percentage of total lateral area) of the red areas were used in the analyses. However, qualitatively similar results are gained with both measures and only relative sizes are presented.

Table 1 Principal component matrix for courtship towards a female.

	PC1
Zigzag bouts	0.90
Leads to the nest	0.91
Fanning bouts	0.54
Bites	–0.61
Variance explained	57.0%

Analyses

To determine whether selection on male courtship activity and red nuptial coloration is determined by algal cover, the dependence of time until mating on the traits and their interaction with vegetation was calculated using a GLM with a gamma distribution. Time until mating reflects the willingness of females to spawn with a male and corresponds to one selection episode (i.e. mate choice) (Shackleton *et al.*, 2005). Stickleback females finally spawn with a male if left together long enough, as ovulated eggs have to be shed. Time until spawning is therefore the best measure of female interest under aquarium conditions. The measured traits were standardized to a mean of zero and a standard deviation of one. The measure of breeding success, time until spawning, was converted to relative fitness with a mean of 1. To calculate selection coefficients for each habitat, relative fitness and standardized variables were calculated separately for each habitat.

To compare the strength and direction of selection arising from mate choice under the two environmental conditions, standardized selection gradients were calculated using multivariate regression methods (Lande & Arnold, 1983; Endler, 1986; Phillips & Arnold, 1989). Selection gradients describe the direct selection on a trait by holding effects of other trait constant. Although gradients estimated in the laboratory do not estimate the intensity of selection in nature, they give indications of the relative effects of the two habitats on selection. The linear gradients, β', were calculated from linear models: $w = a + \sum \beta_i z_i$, whereas quadratic and correlational selection gradients γ' were calculated from full models including quadratic terms and cross-product terms:

$$w = a + \sum \beta_i z_i + \frac{1}{2}\sum \gamma_{ii} z_i^2 + \sum\sum \gamma_{ij} z_i z_j + \epsilon.$$

Quadratic selection gradients estimate the curvature of the selection functions, i.e. whether stabilizing or disruptive selection occurs, although they cannot always detect it (Schluter, 1988), whereas correlational selection gradients estimate whether a trait's effect on fitness depends on its interactions with other traits. The residuals from the regression models were approximately normally distributed and estimates for standard errors and significance of selection gradients were therefore obtained from the regression models.

Results

Field observations showed that males spent more time courting a female ($t_{33} = 2.76$, $P < 0.01$) and courted more intensely in terms of zigzag movements ($t_{33} = 6.57$, $P < 0.001$) in denser algal growth (Fig. 1). Moreover, females that entered the territory of a male spent more time inspecting the male and its nest if the density of algae was high ($t_{33} = 2.87$, $P < 0.01$, Fig. 1). Overall, the

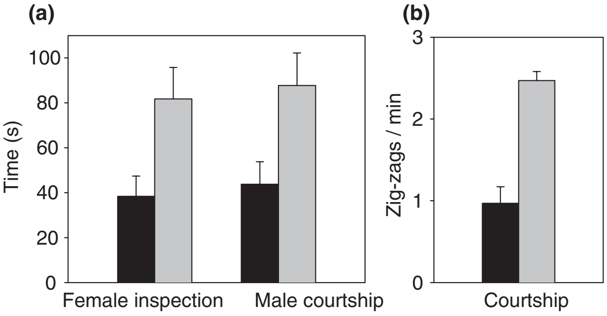

Fig. 1 Sticklebacks courting in the field in sparsely (black) and densely (grey) vegetated habitats. (a) The mean time (+SE) that a female inspected a male and the male courted the female during one female visit. (b) The frequency of zigzag movements of the male towards the female. Untransformed values are shown.

total number of zigzag movements within 30 min was higher in the more vegetated habitat ($t_{33} = 3.07$, $P < 0.01$). The total time spent courting did not significantly depend on habitat structure ($t_{33} = 1.25$, $P = 0.22$), as males detected and courted fewer females in dense vegetation, although the reduction was not statistically significant [sparse (mean ± SD): 1.52 ± 1.03, dense: 1.05 ± 0.67, Mann–Whitney *U*-test, $N = 42$, $U = 162$, $P = 0.117$].

The results from the laboratory study support those from the field; males spent more time courting and tended to perform more courtship under dense algal cover ($t_{46} = 1.94$, $P = 0.058$), whereas females spent more time inspecting a male ($t_{46} = 2.26$, $P < 0.05$, Fig. 2). The red coloration of the males did not depend on vegetation cover ($t_{46} = 0.04$, $P = 0.969$). Despite this increased investment into courtship and mate choice, the intensity of selection on male red nuptial coloration and courtship activity was relaxed in the vegetated habitat (Fig. 3). This is demonstrated by the significant interactions between vegetation and the male traits, which indicate that the slopes of selection and thus the intensity of selection differed between the two habitats (Table 2). Moreover,

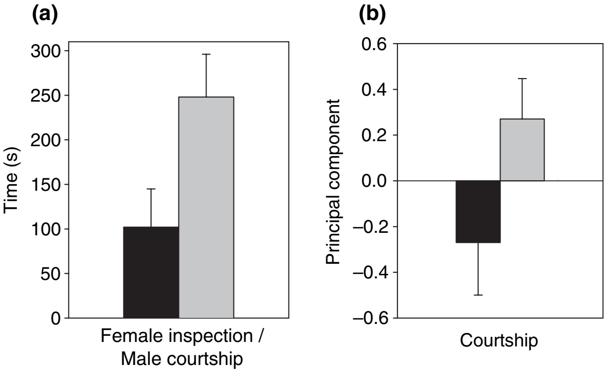

Fig. 2 Sticklebacks courting in aquaria in sparsely (black) and densely (grey) vegetated habitats. (a) The mean time (+SE) that a male courted a female and the female inspected the male before spawning, and (b) the courtship activity of the male calculated as principal components of four courtship behaviours.

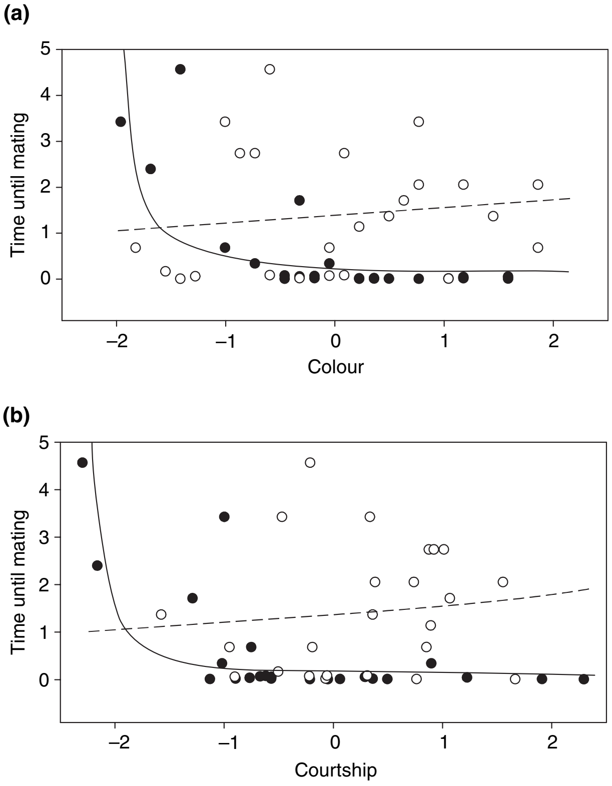

Fig. 3 Selection on (a) red coloration and (b) courtship activity in sparsely (filled dots) and densely (open dots) vegetated habitats. Lines are the results of a GLM with gamma distribution of the dependence of time until mating on male traits and their interaction with vegetation using standardized values.

Table 2 The dependence of time until spawning on male red coloration and courtship activity (PC) in sparsely and densely vegetated habitats. A GLM with a gamma distribution was used for analysis. $N = 48$.

	Time until spawning	
	Estimate (SE)	*t*
Colour	7.16 (2.05)	3.50**
Courtship	7.10 (2.73)	2.60*
Vegetation	−12.27 (3.28)	−3.74**
Colour × courtship	4.20 (2.01)	2.09*
Veg. × colour	−7.25 (2.05)	−3.53**
Veg. × courtship	−7.23 (2.74)	−2.64*
Veg. × colour × courtship	−4.17 (2.02)	−2.06*
Intercept	13.04 (3.28)	3.98**

$^{*}P < 0.05$, $^{**}P < 0.01$.

Table 3 Selection on male red coloration and courtship activity (PC) in sparsely and densely vegetated habitats. Linear selection gradients were calculated from linear multivariate regression models, whereas the quadratic and interaction terms were calculated from full models. $N = 24$.

			Colour		Courtship	
	β (SE)	t	γ (SE)	t	γ (SE)	t
Sparse vegetation						
Colour	1.91 (0.73)	2.60*	5.38 (2.76)	1.95		
Courtship	0.95 (0.46)	2.04*	3.56 (4.00)	0.89	−0.22 (1.92)	−0.12
Dense vegetation						
Colour	−0.12 (0.22)	−0.53	0.36 (0.56)	0.66		
Courtship	−0.11 (0.23)	−0.49	0.32 (0.64)	0.49	0.16 (0.46)	0.33

*$P < 0.05$.

the selection gradients show that significant selection on the two male traits is operating in the open habitat but not in dense vegetation (Table 3). In addition, the significant three-way interaction suggests that the interaction between colour and courtship in determining time until spawning might differ between the two habitats (Table 2), being lower in the vegetated habitat (Table 3). However the three-way interaction could be consistent with many different patterns. No significant correlational selection was detected (Table 3), which suggests that more research is needed to determine the effect of vegetation on possible interactions between the traits.

Discussion

Dense vegetation increased the effort sticklebacks spent on courtship and mate choice, but reduced the strength of selection on male red nuptial coloration and courtship activity. The increased courtship activity did not enhance the attractiveness of the males, but instead the time until mating increased and the correlation between courtship activity and time until mating disappeared. As courtship is costly in terms of time and energy, the increase in courtship activity appears maladaptive under the new conditions. It is, however, plausible that the cost of mate choice is reduced under increased vegetation cover if, for example, the risk of predation is reduced. This would allow males to court more than in open habitats. Nevertheless, the increased effort did not pay off when it came to attract females and was therefore maladaptive.

As the investigated traits are costly in terms of the expenditure of energy and time, and perhaps in increasing the risk of predation, the results suggest that increased eutrophication could influence the evolution of the male mating traits and female preferences. Visual traits like red nuptial coloration and intense courtship may change or decrease in importance, while other traits, like olfactory cues, could increase in importance. In the current study, changes in the strength of sexual selection were the consequence of phenotypic flexibility in female mate preferences and male behaviour. Whether genetic changes will arise with time and result in an evolutionary response depends on the heritability of the traits, the genetic correlations and the consistency of selection. Sticklebacks are capable of rapid adaptive evolution and have adjusted to a range of new environments (Schluter & McPhail, 1992; Taylor & McPhail, 2000; Boughman, 2001; McKinnon & Rundle, 2002; Bell *et al.*, 2004; McKinnon *et al.*, 2004). An evolutionary response to the changed selection due to anthropogenic disturbance would therefore be expected, with visual cues decreasing in importance while other cues could increase in importance.

The fact that increased investment into the costly sexual displays was maladaptive when it comes to increasing mating probability further implies that increased vegetation cover could impose a fitness cost on the present population. Stickleback males care alone for the eggs for 2–3 weeks and good condition is required to complete several breeding cycles within one breeding season (Candolin, 1998, 2000). Increased energy loss could therefore have negative effects on the number of cycles completed and decrease the reproductive output of the individuals. On the other hand, increased algal cover might reduce predation risk and hence allow more courtship (Candolin & Voigt, 1998), which could compensate for at least the increased time susceptible to predators. The magnitude of the costs and benefits of increased courtship activity on individual male lifetime fitness needs to be determined, along with the costs and benefits of increased female inspection time, before any firm conclusions can be drawn on the fitness consequences of increased vegetation cover for the population.

The relaxation of sexual selection may have consequences for the adaptation to new conditions. Strong sexual selection is suggested to be favourable under new environmental conditions in terms of accelerating adaptive evolutionary change (Lorch *et al.*, 2003). However, in the present study, the strength of selection on a few traits was reduced under the new conditions, whereas the cost of mating increased, due to the increased investment into the costly sexually selected traits. This suggests that the mechanism of sexual selection could reduce the rate of adaptive change and decrease the viability of the population. This depends, however, on whether the overall strength of sexual selection was reduced. If males switch to use other cues than visual ones when visibility reduces, then the strength of sexual selection may be restored.

How does an increase in algal cover relax the strength of sexual selection on the mating traits investigated? We consider three possibilities. First, dense algal cover may impair the ability of females to properly assess male red coloration and courtship. As a consequence, females may need to devote more time to assess each cue or, indeed, reduce the number of cues that can actually be assessed. In this regard, an increase in mating effort could limit the number of males that a female is able to encounter, which, in turn, could further relax the strength of selection. Secondly, females may exhibit habitat-dependent changes in mate preferences or switch to the use of other cues in mate assessment. When visibility is impaired, females may, for instance, rely more on chemical cues or those associated with nest characteristics (Candolin, 2003). The assessment of these alternative cues could require more time if the population has not yet adapted to their use. Thirdly, females may have been reluctant to spawn in dense vegetation. This, however, appears unlikely in the light of earlier research (Candolin, 2004).

In any case, our results show that increased algal growth can reduce the strength of sexual selection on mating traits that have traditionally been under strong selection. In support of an effect of vegetation on the overall strength of sexual selection, an earlier field study found reduced variation among males in number of eggs received at high algal cover (Candolin, 2004). To restore the strength of selection, the fish might increase the time and energy spent on reproduction at the expense of other viability enhancing activities, such as foraging and predator avoidance. However, this could have negative effects on the viability of the population. Alternatively, the fish could, over time, evolve to use other cues than visual ones in mate choice, such as olfactory cues, which could reduce the time and energy spent on sexual displaying and mate choice.

These results imply that anthropogenic disturbances can affect sexual selection on mating traits, and that this could potentially mediate negative effects on population viability. Most research on environmental change has focused on how human-induced changes might impact population output and biodiversity. The effects on sexual selection have received less attention, despite the obvious importance of sexual selection in moulding species and communities (Hoekstra *et al.*, 2001). A challenge of future studies will be to determine if the target and intensity of sexual selection on mating traits in sticklebacks change along with eutrophication, or if the investment into reproduction increases at the expense of other fitness enhancing traits, with negative effects on population viability.

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