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Habitat deterioration relaxes resource competition and sexual selection in the threespine stickleback

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1 Research paper

2 **Habitat deterioration relaxes resource competition and sexual selection in the threespine**
3 **stickleback**

4

5 **Abstract**

6 The operation of sexual selection depends on ecological conditions. Thus, changes in
7 environmental conditions because of human activities can alter the strength and direction of
8 sexual selection, with implications for evolutionary trajectories and the viability of populations.
9 We show that aquatic algal blooms can relax the operation of sexual selection by influencing
10 which males are available to attract females. This is by influencing the ability of males to maintain
11 a resource needed in mate attraction. When we exposed two competing threespine stickleback
12 males (*Gasterosteus aculeatus*), whose attractiveness to females was known, to either clear or
13 algal-turbid water, nest abandonment was more common in clear water, and it was usually the
14 unattractive male that abandoned his nest. In turbid water, on the other hand, nest
15 abandonments were less common and when they occurred, the probability increased that the
16 attractive male abandoned his nest, and that the unattractive male subsequently occupied it. This
17 change in the composition of nesting males increased the mating success of unattractive males.
18 Thus, our results reveal a new mechanism through which habitat deterioration can influence
19 sexual selection, by altering success in the competition for a resource critical in mate attraction, a
20 territory with a nest in this case. This could be a common mechanism, considering the prevalence
21 of resource competition in mate choice systems. On a broader level, our results emphasise the
22 importance of considering the impact of environmental changes on the outcome of resource
23 competition when investigating the influence that environmental disturbances have on the
24 operation of sexual selection and thereby on evolutionary processes and population dynamics.

25

26 Keywords: environmental change, female choice, male-male competition, nest, stressor, territory

27

28 **Introduction**

29 Human activities are altering habitats at an alarming rate. This is influencing evolutionary
30 processes, including sexual selection (Candolin and Wong 2019, Martinossi-Allibert et al. 2019,
31 Rosenthal and Stuart-Fox 2012, Swaddle et al. 2015). Several studies find habitat alteration to
32 influence the ability of females to find males (e.g. Gurule-Small and Tinghitella 2018, Heuschele et
33 al. 2012, Myhre et al. 2013, Schmidt et al. 2014) or make informed mate choices (Coomes et al.
34 2019, des Aunay et al. 2014, Iglesias-Carrasco et al. 2017), and thereby to alter the operation of
35 sexual selection (Candolin 2019). However, habitat alteration can also influence which mates are
36 available to choose among, which similarly could influence mate choice and sexual selection. Yet,
37 this possibility has received little attention.

38 The possibility that habitat alteration influences the composition of available mates is especially
39 likely in species where resources have to be competed for and monopolised for individuals to be
40 able to attract mates. Environmental factors are known to influence the outcome of competition
41 for resources in general, and the effect can even be larger than the effect of intrinsic properties of
42 individuals (Lane and Briffa 2018). In support of an effect of environmental conditions on the
43 competition for resources needed in mate attraction, a few studies find changes in the
44 environment to alter the number of individual monopolising resources and, thus, being available
45 as mates (e.g. Candolin et al. 2014, Candolin and Vlieger 2013, Ryder and Sillett 2016). However,
46 whether such changes also influence the composition of the available mates is unknown. This is
47 surprising as males of many species compete for territories, nest sites and resources essential in
48 mate attraction, and changes in the environment could influence which males are successful in the
49 competition (Andersson 1994). If large changes occur, female mate choice could be altered and
50 influence the operation of sexual selection. Changes in sexual selection could, in turn, influence
51 the ability of the species to adapt to the altered conditions, as sexual selection is a potent
52 evolutionary force (Cally et al. 2019, Candolin and Heuschele 2008, Kingsolver et al. 2001, Parrett
53 et al. 2019).

54 An emerging human-induced environmental problem in many aquatic ecosystems, which can
55 influence the operation of sexual selection, is the occurrence of algal blooms. Enrichment with
56 nutrients through human activities, i.e. cultural eutrophication, promotes the growth of algae,
57 which can result in the sudden development of massive algal blooms, particularly when rising

58 water temperatures make conditions favourable for algal blooms (Carstensen et al. 2015, Gobler
59 et al. 2017, O'Neil et al. 2012, Thomas et al. 2012). Blooms vary in extent in time and space, and
60 may fade away after a few days when nutrients have been used up or grazing has reduced their
61 abundance, or, alternatively, when the conditions become less favourable because of decreasing
62 temperature or currents bringing in cold or nutrient poor water (Carstensen, et al. 2015, Sliwinska-
63 Wilczewska et al. 2019). Such rapid shifts in algae concentration and turbidity can influence the
64 operation of sexual selection by reducing visibility and hampering the efficient use of visual signals
65 and cues in mate choice, such as courtship activity and nuptial coloration (Candolin 2009,
66 Seehausen et al. 1997, Sundin et al. 2017, van der Sluijs et al. 2011, Wong et al. 2007). However,
67 changes in algal turbidity could also influence the composition of available mates and thereby
68 alter mate choice. Reduced visibility during algal blooms could influence the willingness of
69 individuals to invest in the competition for resources needed in mate attraction, particularly if
70 reduced visibility decreases encounter rates with potential mates (Heuschele, et al. 2012) or the
71 ability of individuals to gain or maintain resources needed for reproduction (Candolin, et al. 2014).
72 The impact could vary depending on the phenotypic and genetic characteristics of the individuals
73 and thereby alter the composition of the available mates. Such changes in mate composition
74 could, in turn, influence the reproductive success of the individuals and thereby population
75 dynamics. The changes could also alter the distribution of reproductive success among individuals
76 and, thus, the evolutionary trajectory of the species.

77 An area that has been severely affected by eutrophication during the last decades is the Baltic Sea
78 (Andersen et al. 2017, Korpinen et al. 2012). Excessive input of nutrients by humans has promoted
79 primary production, which has increased the frequency and extent of algal blooms (Finni et al.
80 2001, Fleming-Lehtinen and Laamanen 2012). The blooms reduce visibility, which influences the
81 mate choice system of species relying on visual cues for mate choice (Candolin 2009, Järvenpää
82 and Lindström 2004). In particular, the nest brooding threespine stickleback (*Gasterosteus*
83 *aculeatus*) has been affected by the blooms, as it reproduces in shallow water where intense algal
84 blooms are common. Males build a nest to which they attract females to spawn, and then care
85 alone for the eggs spawned into the nest until hatching (Wootton 1984). Reduced visibility
86 hampers the ability of stickleback females to find nesting males (Heuschele, et al. 2012) and to
87 evaluate their qualities, which can alter their mate choices (Engström-Öst and Candolin 2007,
88 Heuschele et al. 2009). Whether algal blooms also influence which males are available to choose

89 among is unknown. Yet, this is likely, as threespine stickleback males compete intensively for
90 territories and nesting sites, and the ability of males to establish and defend territories, or their
91 motivation to do so, could vary depending on environmental conditions.

92 We investigated if algal blooms influence the composition of threespine stickleback males
93 available for females to choose among. We expected blooms to alter the composition of nesting
94 males by increasing the probability that subdominant males are able to defend and maintain a
95 territory with a nest in the presence of more dominant males. This is because deteriorating
96 visibility reduces aggressive interactions among males (Candolin, et al. 2014, Candolin and Vlieger
97 2013), and this could increase the ability of subdominant males to establish and maintain a nest
98 site under male-male competition. In addition, the willingness of attractive males to defend a nest
99 site could decrease when visibility deteriorates, as poor visibility reduces the ability of females to
100 detect males and evaluate their quality (Candolin et al. 2016), which decreases the quality of the
101 nest site to attractive males. Correspondingly, the willingness of less attractive males to defend a
102 nest site under algal blooms could increase, as their probability of mating could improve when the
103 ability of females to judge male quality decreases.

104 Thus, we expected algal blooms to change the composition of nesting males towards an increased
105 representation of subdominant, less attractive males, through reduced aggressive interactions
106 among males and reduced willingness of attractive males to defend a poor nest site. Changes in
107 the composition of available males could, in turn, influence the distribution of mating success
108 among males. Females cannot postpone spawning after the eggs have been ovulated, but have to
109 spawn within 1-2 days (Wootton 1984). Males, on the other hand, can postpone courtship and the
110 attraction of females by waiting for conditions to improve. Postponing reproduction can be a
111 profitable strategy for males when the probability of attracting females is low, but could improve
112 in the future when the algal bloom have faded. This is because males have to enter the parental
113 stage 1-2 days after receiving the first clutch of eggs (when they no longer court females) to
114 ensure that all embryos in the nest are at the same developmental stage (Wootton 1984). The
115 parental stage is the most time-costly stage as it takes about 2 weeks, depending on water
116 temperature, until the hatched fry leave the nest. During the parental stage, the male fans fresh
117 water into the nest, alters the structure of the nest according to the developmental stage of the
118 embryos and hatched fry, and defends the offspring against predators, both con- and
119 heterospecifics. The parental stage is consequently also energetically costly (Wootton 1984).

120 Based on these predictions, we investigated (1) if a reduction in water visibility, equivalent to that
121 associated with an algal bloom, influences the probability of a subdominant threespine stickleback
122 male maintaining nest ownership under male competition, (2) if the probability of maintaining
123 nest ownership under poor visibility depends on the attractiveness of the male to females, and (3)
124 if changes in nest ownership under poor visibility influence the distribution of mating success
125 among males. We first determined the attractiveness of two nesting males, and then allowed
126 them to interact for one day in clear or algal turbid water to record dominance status and effects
127 of turbidity on nest ownership. We recorded both nest abandonments and whether the other
128 male took over the abandoned nest. Finally, we assessed the success of the two males in gaining
129 fertilisations.

130

131 **Materials and methods**

132 *Collection and Housing*

133 Adult threespine stickleback were collected using Plexiglas traps (Candolin and Voigt 2001) at the
134 start of the breeding season from the shores of the Baltic Sea in southern Finland (60°N, 23°E).
135 Fish were housed in large holding tanks with sea water (salinity 5.5 psu) at a density of 0.25 fish
136 per litre, a photoperiod of 18L:6D, and a temperature of 18°C. The fish were separated by sex
137 based on the development of eggs or nuptial coloration. Males were transferred to individual,
138 aerated aquaria (40 × 35 × 30 cm) and given a nesting dish (Ø 12.5 cm) filled with sand and some
139 filamentous algae, *Cladophora glomerata*, for nest construction (Candolin 1997). All aquaria were
140 visually isolated from neighbouring aquaria. To encourage nest building, a gravid female in a
141 perforated, transparent cup was presented to each male twice daily for 15 min. All fish were fed
142 twice daily ad libitum with frozen chironomid larvae. Only males that completed nest building
143 within two weeks were used in the experiment.

144 *Female preference*

145 Experimental aquaria (70 × 40 × 30 cm) were divided into three aerated compartments using
146 removable Plexiglas partitions: one transparent partition divided the aquarium into a front female
147 compartment (70 × 10 cm) and a back male compartment (70 × 30 cm), and an opaque partition
148 divided the back compartment into two adjoining male compartments (35 × 30 cm, Figure 1). Into

149 each male compartment, a male was placed together with his nesting dish containing a completed
150 nest. The males were randomly selected, but to ensure that the size difference between them
151 would not be too large, pairs where the size difference was larger than 5 mm were discarded. The
152 standard length and wet weight of the males were measured during transfer, and the males were
153 marked by clipping the tip of one of the three dorsal spines. Their body condition was calculated
154 as Fulton's Condition Factor K (Le Cren 1951). The distance between the nesting dishes, 50 cm,
155 corresponds to distances between nests in the field, where the density of territories can be high
156 at preferred spawning sites, with up to three nesting males per m² (Candolin 2004).

157 After the males had acclimatized for one day to the aquarium, a gravid female was placed into the
158 middle of the front compartment from where she could see both males and their nests (Figure 1).
159 She was first enclosed in a transparent Plexiglas cylinder (diameter 10 cm), and released after 5
160 min of acclimatization. Her mate preference was recorded during 15 min by noting the time she
161 spent within 5 cm of each male's compartment in a head-up posture, which indicates readiness to
162 spawn (Tinbergen 1951). A female was judged to prefer one of the males when she spent at least
163 75% of her inspection time by that male. The mate preference of three females was recorded,
164 with a 30 min break between female presentations. Each female was used only once. The
165 experiment was continued for trials where all three females preferred the same male.

166

167 Figure 1. The experimental aquarium with the two male compartments visually isolated from each
168 other with a removable opaque divider (before male interaction), and the female compartment
169 isolated from the male compartments with a removable transparent divider. The location of the
170 nesting dishes of the two males is indicated, as is the location of the transparent cylinder in which
171 the female was held before being allowed to choose between the two males. The grey zones in the
172 female compartment indicate the zones for determining mate preference.

173

174 *Nest holding ability*

175 To investigate the influence of algal blooms on the ability of the males to maintain their nests
176 when faced with a competing male, the two nesting males were exposed to either clear or algal-
177 turbid sea water. Algal turbidity was manipulated by adding a solution of the nontoxic flagellate
178 algae *Isochrysis* sp. to the algal treatment to a level of 10 nephelometric turbidity units (NTU),
179 while the same amount of clear sea water (NTU 1) was added to the clear-water treatment. The
180 solution was added after the last female presentation over the course of 1 h to imitate the inflow
181 of algae. Turbidity levels were measured with a portable nephelometer (Hach 2100P). The chosen
182 algae is part of the phytoplankton community of the Baltic Sea, and was cultivated according to
183 previously published methods (Vlieger and Candolin 2009). Turbidity in the Baltic Sea varies
184 between 0.5 and 45 NTU, but rarely exceeds 30 NTU (Granqvist and Mattila 2004). The aquaria
185 were continuously aerated to ensure algae survival. Two bunches of artificial vegetation were
186 placed into the female compartment to serve as shelters for males that abandoned their nest
187 during the next stage of the experiment (male interaction).

188 The males were allowed to acclimatize for 1 h to the turbid (or clear) water, after which all
189 partitions were removed. After 24 h of direct interaction, the behaviour of the males and the size
190 of their territories were determined by observing the males for 15 min. The number of attacks on
191 the other male was recorded for each male, and territory size was recorded as how far from the
192 nest each male ventured, and where the boundary was set in replicates were both males
193 maintained his territory. The identity of the nest owner(s) was noted. A gravid female (different
194 from the ones that had been used to determine female mate preferences) was then released into
195 the middle of the aquarium and followed until spawning occurred, or until two hours had passed if
196 no spawning occurred. Her choice of nest and the identity of the male that fertilized her eggs were
197 noted. Males, including males dispelled from their nest site, could attempt to fertilise the eggs
198 spawned into the nest of the other male through sneak fertilisation (Vlieger and Candolin 2009).

199 To test whether water turbidity influenced the probability of nest abandonment and nest
200 takeover, and whether the attractiveness of the male that abandoned his nest (preferred or not by
201 females) differed between turbidity treatments, logistic regression was used. To test whether
202 water turbidity influences whether the preferred or the non-preferred male abandoned the nest

203 sites, Fisher's exact test was used. To test whether water turbidity and male attractiveness
204 influenced attack rate by each male on the other male, a generalised linear mixed model (GLMM)
205 with a Poisson probability distribution and a log link function was used (as the response variable
206 was a count variable), with turbidity and male attractiveness as fixed factors and male pair as a
207 random factor. To test for differences between the preferred and the non-preferred male in body
208 size and condition, a paired t-test was used. To test for an effect of turbidity on female mate
209 choice (after male interaction), logistic regression was used. All analyses were performed using the
210 software package IBM SPSS Statistics v. 25 (Armonk, NY: IBM Corp.).

211

212 **Results**

213 Abandonment of the two nest sites by one of the two males during male-male interaction
214 occurred more often in clear water (24 out of 26) than in algal turbid water (12 out of 26) (logistic
215 regression: $b = 2.64$, $SE = 0.84$, $Wald = 10.00$, $P = 0.002$). In no trials did both males abandon the
216 nest sites. The attractiveness of the male that abandoned the nest sites differed between
217 treatments ($b = 2.28$, $SE = 0.85$, $Wald = 7.20$, $P = 0.007$, Figure 2): in clear water the non-preferred
218 male more often abandoned the nest sites (21 out of 24 abandonments), while there was no
219 difference between the two males in nest abandonment in turbid water (non-preferred male
220 abandoned in 5 out of 12 abandonments). Thus, the non-preferred male abandoned the nest sites
221 less often in turbid water (21 out of 26 trials in clear water and 5 out of 26 trials in turbid water,
222 Fisher's exact test, $p < 0.001$), while the attractive male did not differ in nest abandonments
223 between clear and turbid water (3 out of 26 trials in clear water and 7 out of 26 trials in turbid
224 water, $P = 0.29$).

225 The intensity of direct male aggressive interactions, measured as attack rate, was lower in turbid
226 water (GLMM: $F_{1,100} = 7.78$, $P = 0.006$) and differed between the preferred and the non-preferred
227 male depending on water turbidity (interaction between turbidity and attractiveness: $F_{1,100} = 10.60$
228 $P = 0.002$): in clear water the preferred male performed more attacks than the non-preferred
229 male, while there was no difference between the males in turbid water (Figure 3). When only one
230 male maintained his territory after male interaction, he occupied the whole aquarium in clear
231 water (territory size always 70 cm in width), with the other male hiding in the vegetation, while
232 the territory was smaller in turbid water (mean width = 54 cm, $SD = 10$ cm), with the non-nesting

233 male moving more freely around. The preferred and the non-preferred males did not differ in
 234 body length (paired t-test: $t_{51} = 1.58$, $P = 0.12$), wet weight ($t_{51} = 0.11$, $P = 0.92$), or body condition
 235 ($t_{51} = 0.94$, $P = 0.35$).

236 Nest takeover after a male had abandoned his nest was more common in turbid water (6 out of
 237 12) than in clear water (3 out of 24, logistic regression: $b = 1.94$, $SE = 0.84$, $Wald = 5.30$, $P = 0.021$,
 238 Figure 4). In all trials with nest takeover, it was the non-preferred male that took over the
 239 abandoned nest of the preferred male, independent of turbidity treatment, while abandoning his
 240 self-built nest.

241 Female spawning decision was not influenced by water turbidity (females spawned in 19 out of 26
 242 trials in both treatments), but she spawned more often with the non-preferred male in turbid
 243 water (10 out of 19) than in clear water (1 out of 19, $b = 3.00$, $SE = 1.12$, $Wald = 7.08$, $P = 0.008$,
 244 Figure 5). The eggs were always fertilized by the nest owner (also when the nest had a new owner)
 245 and no successful sneaking occurred.

246

247

248

249 Figure 2. Number of trials in clear and algal turbid water in which a threespine stickleback male
 250 abandoned the two nest sites after 24 h of interaction with another male. Bars show whether the
 251 abandoning male had been preferred by females prior to interaction, and number of trials in which
 252 none of the two males abandoned the nest sites. In no trials did both males abandon the nest sites.

Figure 3. Attack rate per 15 min by two interacting threespine stickleback males in clear and turbid water. The preferred male had been preferred by three females prior to 24 h of male interaction.

Figure 4. Number of trials in clear and turbid water in which a threespine stickleback male took over an abandoned nest of another male after 24 h of male interaction (in trials where nest abandonment had occurred). Bars show whether the male taking over the nest had been preferred by females before male interaction, and number of trials in which none of the two males took over the nest of the other male.

265

266 Figure 5. Number of trials in clear and algal turbid water in which a threespine stickleback female
 267 spawned, or did not spawn, with one of two interacting males. Bars show whether the chosen male
 268 had been preferred by females in clear water before 24 h of male interaction.

269

270 Discussion

271 Algal turbidity altered the composition of courting males available for females to spawn with.
 272 Unattractive males, which usually were subdominant males, more often hold on to their nest site
 273 in turbid water than in clear water when the attractive male maintained his nest site, and usually
 274 occupied the nest site of the attractive male when he abandoned his nest site. Thus, algal turbidity
 275 changed the composition of courting males towards unattractive ones, which, in turn, increased
 276 the probability that females would spawn with an unattractive male.

277 The cause of the improved ability of unattractive males to maintain a nest site in algal turbid water
 278 was probably relaxed male-male competition and a correlation between attractiveness and
 279 dominance. The attractive male was more aggressive in clear water than in turbid water and
 280 dominated over the unattractive male, which caused the unattractive male to abandon his nest
 281 site in clear water. In turbid water, on the other hand, the territories were smaller and the attack
 282 rate between the males was lower, which allowed the unattractive male to maintain his nest site
 283 despite the presence of the attractive male. This agrees with earlier studies that find reduced
 284 visibility to reduce the size of territories and relax aggressive interactions among males (Candolin,

et al. 2014, Candolin and Vlieger 2013), as well as male attractiveness to correlate with male dominance (Candolin 1999). Our expectation of a decline in the willingness of attractive males to defend their nest site under turbid conditions was not upheld, as attractive males were not more likely to abandon their nest site when visibility deteriorated. However, when nest abandonments occurred in turbid water, the probability was higher that the attractive male was the male that abandoned his nest. The unattractive male often took over the abandoned nest of the attractive male, but the attractive male never changed nests by abandoning his self-built nest and taking over the nest of the unattractive male.

The higher probability that unattractive males would be nest owners in turbid water increased the probability that females would spawn with them. In clear water, male-male competition ensured that mostly attractive males were available for females to spawn with, which consequently facilitated female choice for these males. In turbid water, on the other hand, male-male competition was relaxed and unattractive males were more likely to hold on to their nest site. Combined with an earlier recorded reduction in the ability of females to carefully evaluate males under poor visibility (Candolin et al. 2007, Candolin, et al. 2016, Engström-Öst and Candolin 2007, Wong, et al. 2007), this increased the probability that females spawned with an unattractive male.

Such changes in the composition and spawning success of nesting males are likely to occur in the field under algal blooms. Territories are smaller and aggressive interactions are less frequent in habitats with poor visibility (Candolin 2004, Candolin, et al. 2014), which should favour subdominant males, as shown in the present study. The distribution of mating success among nesting males is also more equal in habitats with poor visibility (Candolin 2004), which suggests that unattractive males have a higher probability of attracting females when visibility deteriorates. Thus, algae blooms are likely to influence the mating success of males in the field and thereby the strength of sexual selection. This could, in turn, influence the evolutionary trajectory of the species, by influencing the evolution of both sexually selected traits, such as red nuptial coloration and courtship behaviour, and naturally selected traits, such as dominance and general viability.

Altered distribution of mating success among males could influence also population dynamics through effects on the number and viability of offspring produced. Unattractive males generally sire less viable offspring than attractive males (Candolin, et al. 2016) and have a lower hatching success (Candolin 2000), which suggests that an increased mating success of unattractive males

could influence offspring production and recruitment. Females usually prefer to spawn with dominant males that can defend the eggs in the nest against nest destroyers and egg predators, the main causes of failed reproductive success in the population (Candolin and Vlieger 2013). Unattractive, subdominant males could have a higher hatching success in turbid water than in clear water, because of fewer intrusions from competing males and possible predators, but their ability to defend the eggs and raise them to the hatching stage is likely to decrease when water conditions again improve, as algal turbidity can vary from day to day (Carstensen, et al. 2015, Sliwinska-Wilczewska, et al. 2019).

The impact that altered sexual selection in disturbed environments has on population viability is generally poorly known (Candolin and Heuschele 2008, Candolin and Wong 2019, Holman and Kokko 2013, Martinez-Ruiz and Knell 2017). Yet, considering the importance that sexual selection plays in both evolutionary processes and population dynamics (Cally, et al. 2019), more attention should be paid to the topic. Our results reveal a new mechanism through which environmental change can influence sexual selection, by altering the outcome of competition for resources needed in mate attraction and, thus, the composition of individuals available for mate choosers to select among. This could be a common mechanism, considering that males of many species compete fiercely for resources needed in mate attraction (Andersson 1994).

To summarise, our results show that algal blooms can increase the proportion of unattractive males available for females to mate with, which can increase the mating success of these males. This reveals an earlier unexplored pathway through which environmental disturbances can influence sexual selection: by altering the outcome of competition for resources critical in mate choice. Such effects could be common, considering the prevalence across organisms of male resource defence. Thus, more attention should be directed to the effects of environmental disturbances on resource competition, as well as to the consequences that these effects may have for the evolutionary trajectory and viability of populations.

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