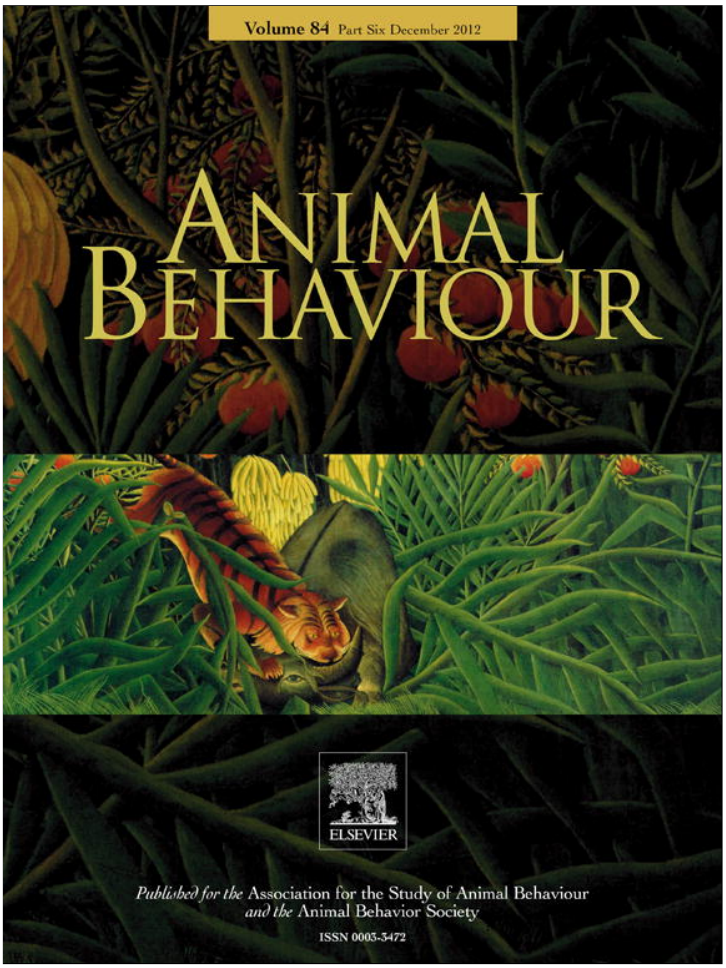
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Animal Behaviour 84 (2012) 1541–1545

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Algal blooms impact the quality of nest construction in three-spined sticklebacks

Bob B. M. Wong [a,*], Ulla Tuomainen [b], Ulrika Candolin [b]

[a] School of Biological Sciences, Monash University, Melbourne, Australia
[b] Department of Biosciences, University of Helsinki, Helsinki, Finland

ARTICLE INFO

Article history:
Received 16 July 2012
Initial acceptance 17 August 2012
Final acceptance 14 September 2012
Available online 22 October 2012
MS. number: 12-00540

Keywords:
eutrophication
extended phenotype
Gasterosteus aculeatus
parental care
sexual selection
signal
three-spined stickleback
turbidity

Purpose-built nests for rearing offspring have important fitness consequences. Nests not only provide a protective environment for developing young but also in some species can serve as important signalling devices that reveal crucial information about the quality of the builder. Nesting behaviour and nest structure are often adjusted to suit local environmental conditions. An important question is what happens when conditions are altered as a result of anthropogenic activities. Human-induced eutrophication is an insidious, global problem. Here, we investigated experimentally the impact of algal blooms on nest construction in a fish: the three-spined stickleback, *Gasterosteus aculeatus*. We found that males took longer to complete their nests under algal conditions. Completed nests were also smaller and possessed wider nest entrances. Together, our results suggest that human-induced algal blooms can have profound effects on nesting behaviour and nest construction, with implications for both offspring survival and the utility of nests as extended phenotypic signals.
© 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Many animals lay their eggs or raise their young in purpose-built nests. By influencing the development and survival of offspring, both the location and quality of the nest can have important fitness consequences (Eggers et al. 2006; Byrne & Keogh 2009). In some species, nests also reveal crucial information about the quality of the builder and, in so doing, perform a vital signalling function ('extended phenotype signal' sensu Schaedelin & Taborsky 2009). Nest decorations in black kites, *Milvus migrans*, for example, serve as a reliable indicator of the builder's physical prowess (Sergio et al. 2011), whereas in barn swallows, *Hirundo rustica*, the amount of nesting material collected by males is correlated positively with immune response (Soler et al. 2007). Thus, in species in which males alone are responsible for nest building, nest characteristics can play a pivotal role in both mate attraction and female choice (e.g. Östlund-Nilsson 2000; Kleindorfer 2007; but see Lehtonen & Wong 2009).

Environmental conditions can profoundly influence building behaviour and nest architecture. Evidence suggests that nest builders are capable of adjusting both the location and structure of their nests to improve their functional capacity under a range of environmental conditions (Burton 2006; Eggers et al. 2006; Rushbrook et al. 2010). Less well understood is the impact that anthropogenic disturbance might have on nest-building behaviour. Recent work in northern cardinals, *Cardinalis cardinalis*, showed that male preference for nesting in an exotic shrub, the Amur honeysuckle, *Lonicera maackii*, reduced the reproductive performance of otherwise high-quality individuals because of increased nest predation (Rodewald et al. 2011). In that study, it was suggested that human-induced changes to the environment, by influencing nesting behaviour, can create ecological or evolutionary traps, whereby once-adaptive behaviours become maladaptive in the new selective environment. Whether this is true for other nest-building species remains to be tested.

Eutrophication is having an alarming effect on aquatic ecosystems the world over. This is particularly true in the Baltic Sea, where an increase in nutrient input is promoting the rampant growth of filamentous algae and phytoplankton, resulting in dramatic changes to habitat structure and water clarity (Larsson et al. 1985; Raateoja et al. 2005). These changes have had a direct impact on the mating systems of several Baltic fish species that breed in shallow coastal waters (Järvenpää & Lindström 2004; Candolin et al. 2006). One such species, the three-spined stickleback, *Gasterosteus aculeatus*, is a model candidate for investigating the effects of environmental deterioration on male nest-building behaviour and nest structure.

* Correspondence: B. B. M. Wong, School of Biological Sciences, Monash University, Victoria 3800, Australia.
E-mail address: bob.wong@monash.edu (B. B. M. Wong).

0003-3472/$38.00 © 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2012.09.031

Author's personal copy

Male sticklebacks establish territories close to the shore, where they build and defend nests constructed from plant material. When completed, the nest serves as a focal point for the male's elaborate courtship displays, which if successful will result in the female depositing her eggs inside the nest. Males, alone, are responsible for taking care of the developing embryos and defending the brood against would-be predators. The design, structure and location of the nest are known to affect offspring survival (Sargent & Gebler 1980; Sargent 1982). In some stickleback populations, the quality of nest construction also acts as an extended phenotypic signal, providing females with crucial information about the builder's physiology and parenting skills (Barber et al. 2001; Rushbrook & Barber 2008). In the Baltic Sea, environmental changes are currently having a profound impact on reproductive behaviours in sticklebacks. For example, altered conditions are affecting nest-building motivation (Candolin & Salesto 2006) and parental care (Candolin et al. 2008), while reduced visibility is undermining the efficacy of visual signals (Wong et al. 2007; Heuschele et al. 2009). Here, we aimed to test how environmental changes brought about by phytoplankton blooms might affect the quality of nest construction.

METHODS

Collecting and Housing

Sticklebacks were collected with seine nets from Kotka in the Gulf of Finland at the start of the breeding season. In total, 400 fish were collected, of which 30 males and 174 'stimulus' females were used in the current study (see below); the rest were kept for use in unrelated experiments. Fish were transported in coolers back to an outdoor facility at the Tvärminne Zoological Station, where they were housed in separate-sex 500-litre aquaria ($\sim$100 fish per tank) under natural light and temperature conditions, and fed on a diet of frozen chironomid larvae ad libitum. At the completion of the study, all fish were returned to the sea.

Experimental Procedure

Male nesting behaviours were investigated both in clear sea water and in water containing a nontoxic flagellate algae (*Isochrysis* sp.). The latter is a naturally occurring member of the local phytoplankton community (Heuschele et al. 2009), and was used to simulate the frequently occurring algal blooms now affecting sticklebacks in the Baltic Sea. We employed a paired design so that each male ($N = 30$) was subjected to both clear and algal conditions, with the order of exposure randomized for each male.

For each trial, a sexually mature male (identified by the presence of nuptial coloration) was introduced into a 10-litre experimental aquarium. Tanks were visually isolated using sheets of cardboard to prevent neighbouring males from seeing one another. Each tank contained a shallow sand-filled nesting dish (11 cm diameter), as well as an excess of *Cladophora glomerata* (6 g wet mass) and 20 red threads (each 70 mm long) as nesting material. Male sticklebacks have been observed to use decorations in their nests, and males have previously been shown to prefer red in their decorative material (Östlund-Nilsson & Holmlund 2003). Depending on the order of the treatment, the experimental tank was filled with either clear sea water or an algae–sea water mixture prepared according to previously published methods (e.g. Wong et al. 2007). Turbidity levels, measured with a Hach 2100P portable nephelometer, were significantly higher in trials containing algae (mean turbidity $\pm$ SE $= 8.47 \pm 0.43$ nephelometric turbidity units (NTU); range 6.08–15.6 NTU) compared with those without algae (1.44 ± 0.11 NTU; range 0.66–3.26 NTU; paired t test: $t_{29} = 15.32$, $P < 0.001$). These values are well within the range observed in the Baltic Sea (Granqvist & Mattila 2004).

To encourage nest construction, each male was presented with a gravid female in a glass jar twice a day (morning and afternoon) for 10 min as a stimulus (total number of stimulus females used during the study = 174). A nest was completed when it had a clear nest entrance, and when the male was observed either creeping through or over the nest (Barber et al. 2001). After completing his nest, the male was removed from the aquarium and his lateral sides photographed under standardized conditions using methods described in Heuschele et al. (2009). The male was then placed into a holding tank while we measured, photographed and removed the nest for drying (see below). The experimental aquarium was then emptied, cleaned and refilled with either clear sea water or the algae–sea water mixture (depending on which treatment was applied first). The next day, the male was introduced back into the experimental tank and the process repeated with the second treatment. The wet mass ($\pm$0.01 g) and standard length ($\pm$1 mm) of each male was measured at the completion of both treatments (Wong et al. 2007).

Nest Characteristics

For each nest, we measured the width of its entrance with a ruler ($\pm$0.5 mm) and photographed the entire nest from above (using the same ruler for scale). After photography, the nest was gently lifted out of the experimental aquarium, placed onto a flat surface for drying and photographed again from above against a white background together with a ruler for calibration. Dried nests were individually weighed ($\pm$0.01 g). The total area, A_{Tot} (area covered by minimum area polygon enclosing all visible nest material), and bulk area, A_{Bulk} (area through which no basal substratum was visible), of each nest was measured from the photographs using the image analysis program ImageJ version 1.44 (http://rsb.info.nih.gov/ij/). In addition, we counted the red threads that had been incorporated into each nest and recorded how the males had used the threads from the photographs. Specifically, a male was deemed to have used the threads as decorations if threads were concentrated around the nest entrance and were clearly visible. By contrast, threads were deemed to have been used as building material if they were much more evenly distributed over the nest and incorporated into the matrix of the actual nest structure (Fig. 1). Lastly, we calculated a neatness index ($I_n = A_{Bulk}/A_{Tot}$) for each nest based on the proportion of visible thread ends and bits of algae not glued to the nest (Barber et al. 2001).

Male Coloration

The extent of red nuptial coloration was calculated from the mean values obtained from the left and right sides of each fish using ImageJ. We first cropped each image so that the fish was presented against a white background. Using the plug-in 'Threshold Color' (http://www.dentistry.bham.ac.uk/landinig/software/software.html) and the HSB colour mode, we then selected the area of red in each image based on the following values: hue = 0–21 and 238–255, saturation = 83–255 and brightness = 0–255 after Heuschele et al. (2009). Following this, the image was converted into 8-bit greyscale and the total red area determined using the 'Image/Adjust/Threshold' and 'Analyze/Measure' commands. We also measured the male's total body area to calculate the percentage of red area for each fish.

Statistical Analysis

We used linear and generalized linear mixed models (LMM and GLMM) with male identity as a random factor and treatment (clear

Author's personal copy

Figure 1. Examples of nests with (a) visible decorations at the nest entrance and (b) with the threads incorporated into the nest as building material.

or turbid) as a fixed factor, and additional factors, such as male size and redness, when appropriate. Only male weight was used as a covariate for size to avoid problems of collinearity. We used statistical software R v 2.11.1 (R Development Core Team 2010) and the 'lme' function from the nlme-package for normally distributed data and the 'lmer' function from the lme4-package, using the logit link function for binary response variables. Nest entrance, nest weight and red area were right skewed and were therefore log10 transformed before analysis. Building time was divided into two categories: $<$24 h and $>$24 h and analysed using GLMM with a logit link function. In addition, use of threads (ornamentation versus building material) was analysed using a binomial GLMM. Where appropriate, we checked the homogeneity and normality of the residuals using qq-plots and histograms to confirm the reliability of our analyses.

Ethical Note

Experiments complied with all relevant state laws, and was approved by the Biological Sciences Animal Ethics Committee of Monash University and the Animal Experimental Board in Finland (STH421A).

RESULTS

Males completed their nests more slowly in the algal treatment. Specifically, although 21 of 30 males built their nests in fewer than 24 h in clear water, only 14 of the 30 males did so in the algal treatment (GLMM with binomial errors: $Z = 2.03$, $N = 30$, $P = 0.042$). We found no effect of order on nest-building time (GLMM with binomial errors: $Z = 1.42$, $N = 30$, $P = 0.16$). There was a positive linear relationship between male size and nest size (total area: LMM: $F_{1,28} = 6.76$, $P = 0.015$; bulk area: LMM: $F_{1,28} = 10.80$, $P = 0.003$). Males also built nests with a larger nest entrance in the presence of algae (LMM: $F_{1,29} = 42.12$, $P < 0.001$), although the nests themselves were smaller, both in terms of weight (LMM: $F_{1,29} = 8.53$, $P = 0.007$) and area (total area: LMM: $F_{1,29} = 11.42$, $P = 0.002$; bulk area: LMM: $F_{1,29} = 12.87$, $P = 0.001$; Fig. 2).

Treatment had no effect on the number of threads (decorations) used (LMM: $F_{1,28} = 1.02$, $P = 0.32$; mean clear $\pm$ SE $= 12.1 \pm 1.35$; mean turbid $\pm$ SE $= 8.7 \pm 1.49$), but larger nests incorporated more red threads (LMM: $F_{1,29} = 15.97$, $P < 0.001$). There was no difference between treatments in whether males used their threads as nest decorations or as construction material (43% of males used the threads as ornaments in the algal treatment versus 57% in the clear water control; GLMM with binomial errors: $Z = 0.30$, $N = 30$, $P = 0.76$). Treatment did not affect nest neatness (LMM: $F_{1,29} = 2.34$, $P = 0.14$). However, when male size was incorporated into the model, we found that larger males built neater nests (LMM: $F_{1,28} = 13.10$, $P = 0.001$).

Males did not differ between treatments in the expression of nuptial coloration (total red area: $F_{1,29} = 1.54$, $P = 0.23$; relative red area: $F_{1,29} = 1.04$, $P = 0.31$).

DISCUSSION

The results of our study suggest that algal blooms affect nest-building behaviour and nest architecture in sticklebacks. We found that males took longer to complete their nests in the presence of algae. This result is comparable to that reported in an earlier study, in which increased vegetation cover was found to have a similar effect on nesting activity (Candolin & Salesto 2006). In the field, algal growth and turbidity, and hence the suitability of locations for nest building, can vary both spatially and temporally. It would seem that males are less motivated to build nests in conditions of poor visibility, probably because reduced visibility diminishes mate encounter rates (Candolin & Voigt 2001) and increases the cost of mate attraction to courting males (Engström-Öst & Candolin 2007).

Nests completed in the presence of algae were also smaller and possessed wider nest entrances. Why? It is well established that nest architecture can have a direct bearing on offspring survival by protecting them from the vagaries of the surrounding environment. Several studies suggest that male sticklebacks may be capable of influencing the functional capacity of their nests by adjusting both nest site selection (Candolin & Voigt 2001) and the structure of their nests (Kraak et al. 2000; Rushbrook et al. 2010) to suit local environmental conditions. Flow regime, for instance, affects nest architecture in sticklebacks, with males building smaller, more streamlined nests in faster flowing water (Rushbrook et al. 2010). However, in a study testing the effects of macroalgae, Candolin & Salesto (2006) found that male sticklebacks did not adjust nest construction under different macroalgal densities. Hence, differences in nest architecture could potentially be an adaptive plastic response to variable environments but may depend on the exact nature of the environmental change (Bruton & Gophen 1992).

In the current study, a larger nest opening, together with a smaller, more open nest, is expected to facilitate the flow of water through the nest. Previous research on sticklebacks has suggested that eutrophic conditions may actually enhance egg hatching success through its positive effects on oxygen conditions and a reduction in nest intrusions (Candolin et al. 2008). Specifically, the quality of care provided by male sticklebacks is of crucial

Author's personal copy

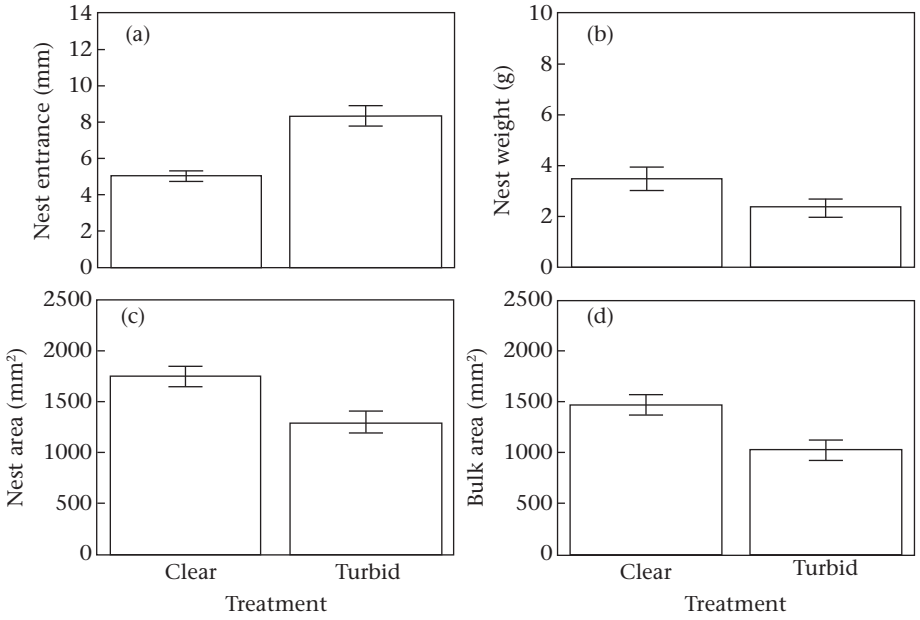


Figure 2. The effect of treatment (mean ± SE) on (a) nest entrance size, (b) nest weight, (c) total nest area and (d) bulk area. Linear mixed model with treatment (clear or turbid) as a fixed factor and male identity as a random factor. $N = 30$ for each treatment.

importance to offspring fitness, as males take care of the eggs exclusively. They do so by protecting the brood from would-be predators and by actively fanning the eggs with their pectoral fins to facilitate oxygen flow over the developing young (Sargent & Gebler 1980; Sargent 1982). Phytoplankton blooms have previously been shown to improve oxygen conditions during the day through heightened photosynthetic activity, thereby reducing the need for vigorous egg fanning behaviour (Candolin et al. 2008). Although nights in the study area are relatively short during the breeding season, nest structure could nevertheless be important if respiration exceeds photosynthesis and results in a drop in oxygen levels (Engström-Öst & Isaksson 2006). Larger nest entrances may therefore enhance water flow under low oxygen conditions, as demonstrated for instance in the sand goby, *Pomatoschistus minutus* (Lissåker et al. 2003). An increase in water flow, independent of oxygen levels, would also help prevent algae from settling on, and smothering, the eggs. Thus, having a larger nest entrance is likely to facilitate offspring development and survival under eutrophic conditions. Here, the lowered visibility associated with algal blooms is also expected to reduce the likelihood of visual detection by predators (Wong et al. 2009) and conspecific intruders (Candolin et al. 2008) and, in so doing, ameliorate some of the costs that may otherwise be associated with building smaller, more open, nests.

In some populations, the nests of sticklebacks not only affect offspring survival, but are also known to play an important signalling function in mate attraction and female choice (Östlund-Nilsson & Holmlund 2003). Nest construction in sticklebacks is energetically demanding (Rushbrook et al. 2010), and can provide choosy females with vital information about the quality of the builder (Barber et al. 2001). Previous work has shown that male sticklebacks incorporate contrasting pieces of red algae to decorate their nest entrances, and that females prefer males with more ornamented nests (Östlund-Nilsson & Holmlund 2003). Intriguingly, in the current study, we found no difference in the propensity for males to use red threads as ornaments under clear versus algal conditions. Indeed, from our results, it appears that there is considerable variation among males in the use of nest decorations even under clear water conditions, suggesting that the use of nest decorations may not be as common in the Baltic as in some other populations (Östlund-Nilsson & Holmlund 2003). Here, the utility of nest decorations could depend on nesting habitat; in the Baltic, sticklebacks often breed in rocky habitats, which would make nests (and any associated decorations) potentially less visible to females from a distance.

More generally, as far as we are aware, very little is known about how human-induced changes to the signalling environment might affect the efficacy of extended phenotypic traits. Evidence from studies of other visual traits, however, suggests that the strength of sexual selection can potentially be relaxed under algal conditions (Candolin et al. 2006; Wong et al. 2007; Engström-Öst & Candolin 2007). For instance, changes to visibility may compromise the efficacy of visual signals by making them less reliable (Wong et al. 2007; Lehtonen & Wong 2009). Females, in turn, may have to attend to alternative or additional cues in mate assessment (Heuschele et al. 2009). Altered conditions, in this regard, are likely to impact certain traits more so than others. For example, while a number of nest characteristics were found to differ in the presence of algae, the expression of male nuptial coloration remained unchanged. Also, independent of treatment, we found that larger males built larger nests. Future investigators may wish to examine how environmental changes might affect the relative importance of different traits across a wider range of sensory modalities.

Acknowledgments

We thank Nathan Geary for assistance with the experiment, and acknowledge the financial support of The Australian Research Council (to B.B.M.W.), the Academy of Finland (to U.C.) and Wihuri Foundation (to U.T.). The authors declare they have no conflicts of interest.

References

Barber, I., Nairn, D. & Huntingford, F. A. 2001. Nests as ornaments: revealing construction by male sticklebacks. *Behavioral Ecology*, **4**, 390–396.

Bruton, M. N. & Gophen, M. 1992. The effect of environmental factors on the nesting and courtship behaviour of *Tilapia zillii* in Lake Kinneret (Israel). *Hydrobiologia*, **239**, 171–178.

Author's personal copy

Burton, N. H. K. 2006. Nest orientation and hatching success in the tree pipit *Anthus trivialis*. *Journal of Avian Biology*, **37**, 312–317.

Byrne, P. G. & Keogh, J. S. 2009. Extreme sequential polyandry insures against nest failure in a frog. *Proceedings of the Royal Society B*, **276**, 115–120.

Candolin, U. & Salesto, T. 2006. Effects of increased vegetation cover on nesting behaviour of sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, **59**, 689–693.

Candolin, U. & Voigt, H. R. 2001. Correlation between male size and territory quality: consequences of male competition or predation risk? *Oikos*, **95**, 225–230.

Candolin, U., Salesto, T. & Evers, M. 2006. Changed environmental conditions weaken sexual selection in sticklebacks. *Journal of Evolutionary Biology*, **20**, 233–239.

Candolin, U., Engström-Öst, J. & Salesto, T. 2008. Human-induced eutrophication enhances reproductive success through effects on parenting ability in sticklebacks. *Oikos*, **117**, 459–465.

Eggers, S., Griesser, M., Nystrand, M. & Ekman, J. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proceedings of the Royal Society B*, **273**, 701–706.

Engström-Öst, J. & Isaksson, I. 2006. Effects of macroalgal exudates and oxygen deficiency on survival and behaviour of fish larvae. *Journal of Experimental Marine Biology and Ecology*, **335**, 227–234.

Engström-Öst, J. & Candolin, U. 2007. Human-induced water turbidity alters selection on sexual displays in sticklebacks. *Behavioral Ecology*, **18**, 393–398.

Granqvist, M. & Mattila, J. 2004. The effect of turbidity and light intensity on the consumption of mysids by juvenile perch (*Perca fluviatilis* L.). *Hydrobiologia*, **514**, 93–101.

Heuschele, J., Mannerla, M., Gienapp, P. & Candolin, U. 2009. Environment-dependent use of mate choice cues in sticklebacks. *Behavioral Ecology*, **20**, 1223–1227.

Järvenpää, M. & Lindström, K. 2004. Water turbidity by algal blooms causes mating system breakdown in a shallow-water fish, the sand goby *Pomatoschistus minutus*. *Proceedings of the Royal Society B*, **271**, 2361–2365.

Kleindorfer, S. 2007. Nesting success in Darwin's small tree finch, *Camarhynchus parvulus*: evidence of female preference for older males and more concealed nests. *Animal Behaviour*, **74**, 795–804.

Kraak, S. B. M., Bakker, T. C. M. & Hocevar, S. 2000. Stickleback males, especially large and red ones, are more likely to nest concealed in macrophytes. *Behaviour*, **137**, 907–919.

Larsson, U., Elmgren, R. & Wulff, F. 1985. Eutrophication and the Baltic Sea: causes and consequences. *Ambio*, **14**, 9–14.

Lehtonen, T. K. & Wong, B. B. M. 2009. Should females prefer males with elaborate nests? *Behavioral Ecology*, **20**, 1015–1019.

Lissåker, M., Kvarnemo, C. & Svensson, O. 2003. Effects of low oxygen environment on parental effort and filial cannibalism in the male sand goby, *Pomatoschistus minutus*. *Behavioral Ecology*, **14**, 374–381.

Östlund-Nilsson, S. 2000. Are nest characters of importance when choosing a male in the fifteen-spined stickleback (*Spinachia spinachia*)? *Behavioral Ecology and Sociobiology*, **48**, 229–235.

Östlund-Nilsson, S. & Holmlund, M. 2003. The artistic three-spined stickleback (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, **53**, 214–220.

R Development Core Team 2010. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Raateoja, M., Seppälä, J., Kuosa, H. & Myrberg, K. 2005. Recent changes in the trophic state of the Baltic Sea along SW coast of Finland. *Ambio*, **34**, 188–191.

Rodewald, A. D., Shustack, D. P. & Jones, T. M. 2011. Dynamic selective environments and evolutionary traps in human-dominated landscapes. *Ecology*, **92**, 1781–1788.

Rushbrook, B. J. & Barber, I. 2008. A comparison of nest building by three-spined sticklebacks *Gasterosteus aculeatus* from still and flowing waters. *Journal of Fish Biology*, **73**, 746–752.

Rushbrook, B. J., Head, M. L., Katsiadaki, I. & Barber, I. 2010. Flow regime affects building behaviour and nest structure in sticklebacks. *Behavioral Ecology and Sociobiology*, **64**, 1927–1935.

Sargent, R. C. 1982. Territory quality, male quality, courtship intrusions, and female nest-choice in the threespine stickleback, *Gasterosteus aculeatus*. *Animal Behaviour*, **30**, 364–374.

Sargent, R. C. & Gebler, J. B. 1980. Effects of nest site concealment on hatching success, reproductive success, and paternal behaviour of the threespine stickleback, *Gasterosteus aculeatus*. *Behavioral Ecology and Sociobiology*, **7**, 137–142.

Schaedelin, F. C. & Taborsky, M. 2009. Extended phenotypes as signals. *Biological Reviews*, **84**, 293–313.

Sergio, F., Blas, J., Blanco, G., Tanferna, A., López, L., Lemus, J. A. & Hiraldo, F. 2011. Raptor nest decorations are a reliable threat against conspecifics. *Science*, **331**, 327–330.

Soler, J. J., Martín-Vivaldi, M., Haussy, C. & Møller, A. P. 2007. Intra- and interspecific relationships between nest size and immunity. *Behavioral Ecology*, **18**, 781–791.

Wong, B. B. M., Candolin, U. & Lindström, K. 2007. Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. *American Naturalist*, **170**, 184–189.

Wong, B. B. M., Järvenpää, M. & Lindström, K. 2009. Risk-sensitive mating decisions in a visually compromised environment. *Biology Letters*, **5**, 600–602.