Animal Behaviour 83 (2012) 1505–1510

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

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

Habitat change influences mate search behaviour in three-spined sticklebacks

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ARTICLE INFO

Article history:
Received 8 November 2011
Initial acceptance 7 December 2011
Final acceptance 13 March 2012
Available online 27 April 2012
MS. number: 11-00899R

Keywords:
eutrophication
Gasterosteus aculeatus
habitat complexity
mate choice
multiple cues
sexual selection
three-spined stickleback

Mate choice is one of the main mechanisms of sexual selection, with profound implications for individual fitness. Changes in environmental conditions can cause individuals to alter their mate search behaviour, with consequences for mate choice. Human-induced eutrophication of water bodies is a global problem that alters habitat structure and visibility in aquatic ecosystems. We investigated whether changes in habitat complexity and male cue modality, visual or olfactory, influence mate search behaviour of female three-spined sticklebacks, *Gasterosteus aculeatus*. We allowed gravid females to search for mates in experimental pools that contained two nesting males and one social female, under low and high structural complexity (created from green Plexiglas sheets), with access to either visual or olfactory cues of the individuals. We found increased habitat complexity reduced the number of visits to nesting males, while a switch from visual to olfactory cues reduced the time spent searching for males, the number of visits to nesting males, the time spent evaluating males, and the relative time spent associating with males rather than females. Thus, females decreased mate searching and mate evaluation in the absence of visual stimulation. This reduced the rate of mate encounters and probably also the opportunity for choice. Our results show that changes in habitat structure and visibility can alter female mate searching, with potential consequences for the opportunity for sexual selection.

Studies on the impact of anthropogenic activities on ecosystems focus mainly on ecological processes and how changes in these influence the abundance and distribution of species. Less attention has been given to human-induced changes in evolutionary processes and how alterations in the strength and direction of selection influence population dynamics, despite growing evidence for contemporary evolution (e.g. Hairston et al. 2005; Candolin & Heuschele 2008; Hendry et al. 2008; Pelletier et al. 2009).

Sexual selection is one of the mechanisms of evolution, and one of its main components is mate choice. Mate choice depends on mate encounter rate, which is influenced by environmental conditions (Real 1990, 1991; Crowley et al. 1991). Changes in the environment, such as degraded visibility or reduced population density, can alter the costs and benefits of mate searching and cause individuals to change their search behaviour (Candolin & Wong 2012). Female fiddler crabs, *Uca mjoebergi*, for instance, reduce their investment in mate searching when the distance to more attractive males is large (Booksmythe et al. 2008), while tree swallows, *Tachycineta bicolor,* choose extrapair mates closer to their own nest when the cost of mate searching is increased experimentally (Dunn & Whittingham 2007). In general, the effects of altered search costs on mate choosiness are well documented.

Surprisingly little attention has, however, been paid to the effect of anthropogenic activities on mate search behaviour and its consequences for adaptive mate choice. Considering the profound impact that humans are having on the environment, and the crucial importance of mate encounter rate in mate choice (Kokko & Mappes 2005), more research is clearly needed. Mate searching precedes mate choice and determines the number and quality of mates encountered. Changes in mate searching because of environmental change could thus have profound implications for mate choice, irrespective of the direct effect of the environment on mate choice. Moreover, human-induced environmental changes are usually more rapid than natural changes and can preclude genetic adaptation, which forces individuals to rely on earlier evolved behavioural reaction norms to survive the changes (Kinnison & Hairston 2007; Tuomainen & Candolin 2010). These behavioural responses are not necessarily adaptive and can drive populations into decline (Ghalambor et al. 2007; Candolin & Wong 2012). Thus, changes in mate search behaviour can influence both the probability of mating and the quality of the mates acquired, and can impinge on population persistence.

A growing human-induced problem in aquatic ecosystems is eutrophication. Increased input of nutrients into the water triggers

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0003-3472/$38.00
doi:10.1016/j.anbehav.2012.03.027

primary production, which alters habitat structure and reduces visibility (Cloern 2001). This has been found to influence mate choice in a range of aquatic species (Heuschele et al. 2009; Sundin et al. 2010; Maan et al. 2010; van der Sluijs et al. 2010), but effects on mate search behaviour have received little attention. In the Baltic Sea, the three-spined stickleback, *Gasterosteus aculeatus,* breeds in habitats that currently are changing because of increased growth of micro- and macroalgae. Shallow bays that previously were sparsely vegetated have become densely vegetated with filamentous algae, particularly with *Cladophora glomerat*a, while the water has become more turbid because of the growth of phytoplankton. These changes have been found to reduce mate encounter rate of males in the field (Candolin & Voigt 2001), impede the ability of females to discriminate among males and prolong mate evaluation time (Engström-Öst & Candolin 2007; Wong et al. 2007; Candolin et al. 2007). In addition, female sticklebacks switch from a predominant use of visual cues to an increased use of olfactory cues when visibility is poor (Heuschele et al. 2009). The switch could influence mate choice, as olfactory signals provide information mainly on genetic compatibility (e.g. Aeschlimann et al. 2003), while visual signals convey information about both direct and indirect benefits (McLennan 2006).

The use of multiple cues in different sensory modalities can facilitate the detection and recognition of potential mates, provide additional information on mate quality and improve the evaluation of cues (Møller & Pomiankowski 1993; Johnstone 1996; Candolin 2003; Hebets & Papaj 2004; Bro-Jørgensen 2010). Changes in environmental conditions that reduce the number of cues that can be used, or the efficiency and information content of these cues, could require an increased mate search effort to maintain a high mate encounter rate. We investigated whether female sticklebacks adjust their mate search behaviour to changes in habitat complexity and availability of male cues, visual or olfactory, to maintain a high mate encounter rate. Dense vegetation has been found to reduce mate encounter rate in the field (Candolin & Voigt 2001), but the mechanism underpinning the reduction is unknown. A reduction in mate encounter rate could result in reduced mate choice, which in turn could influence offspring production and the genetic constitution of the population (Neff & Pitcher 2004; Candolin & Wong 2012).

METHODS

Fish Collection and Maintenance

Adult three-spined sticklebacks were caught with minnow traps from a shallow bay on Långskär Island in the Baltic Sea, close to Tvärminne Zoological Station in southern Finland (60° N, 23° E). The fish were caught in May and June 2008. They were transported to the station within 30 min, in buckets (ca. 1 fish/litre) filled with water from the site. All fish were healthy and active on arrival. The fish were housed in an outdoor facility under natural light conditions. Females were housed in large flow-through holding tanks (150 litres) at a density of 0.25 fish/litre. Males were placed in individual flow-through aquaria (10 litres) that contained a nesting dish (11 cm in diameter), which was filled with sand and filamentous algae, *C. glomerata,* as nesting material (Candolin 1997). A gravid female, enclosed in a transparent perforated Plexiglas cylinder, was presented to each male for 30 min daily to stimulate nest building. All fish were fed frozen bloodworms (chironomid larvae) ad libitum. After the experiment, the fish were released at the site of origin. The experiment was conducted in June and early July and all trials were performed between 0900 and 1700 hours. The experimental procedures were approved by the Animal Care Committee of the University of Helsinki (86-06 and STH421A).

Mate Search Experiment

To investigate whether habitat structural complexity and male cue modality influence female mate search behaviour, we allowed females to search for males under two artificial habitat complexities, low and high, created from Plexiglas sheets, and with access to either visual or olfactory cues of males. We transferred two randomly selected males, which had completed nest building and had entered the courtship stage, together with their nesting dishes, to a pool with a diameter of 1.5 m and a water depth of 20 cm. The males were enclosed in separate Plexiglas cylinders (diameter 30 cm; Fig. 1). A nongravid female was added, enclosed in her own cylinder, to control for the interest of the female in shoaling with conspecifics rather than searching for nesting males. The three cylinders were evenly distributed within the pool (Fig. 1). To manipulate cue availability, the cylinders were either opaque with small holes, allowing the transmission of olfactory cues but not of visual cues, or transparent and sealed, allowing the transmission of visual cues but not of olfactory cues. All individuals were transferred to the pools in the evening before the experimental trial took place to give them time to acclimatize.

During the day of the experimental trial, we presented a gravid female in a water-filled glass jar to each male for 5 min to stimulate courtship (Rowland 2004). After the stimulus females had been removed, we placed a clear Plexiglas cylinder with a gravid female (diameter 12 cm, open at both ends) next to the social female. After 5 min of acclimatization, we gently removed the cylinder and

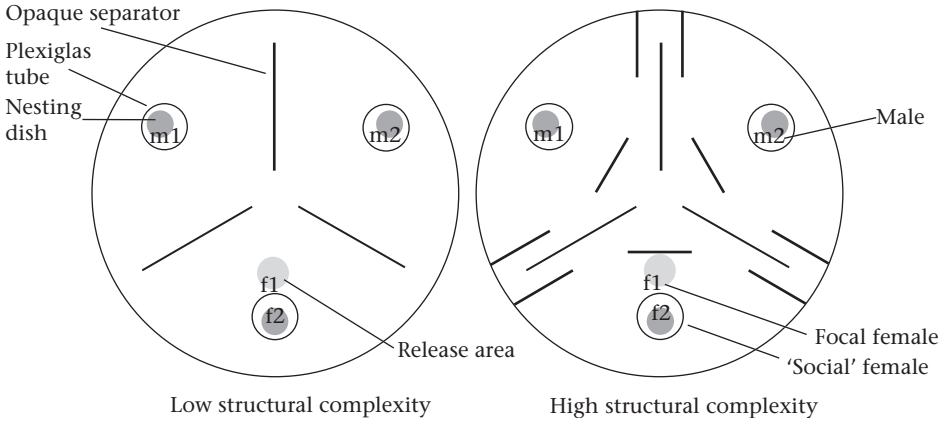

Figure 1. Experimental pools with low and high structural complexity.