Original Article

Habitat alteration influences male signalling effort in the Australian desert goby

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Male sexual signals provide vital information about the quality of the signaller and can have important consequences for male reproductive success. Habitat changes, however, are expected to affect male sexual displays. An important question, therefore, is to determine if and how such sexual displays are adjusted to changes in the signalling environment, especially in highly dynamic systems or those affected by human-induced environmental change. Desert, rivers, and springs are among the world's most threatened habitats. Many of these fragile water bodies are being overwhelmed by invasive weeds and excess primary productivity as an indirect result of human agricultural demand for freshwater. Here, we investigated the effects of altered habitat on the courtship effort of male desert gobies, *Chlamydogobius eremius*. Male courtship effort was observed in an environment that was either dominated by bulrush (*Typha sp.*) or modified by increased algal turbidity (*Scendesmus sp.*). We found that males that were exposed to an environment dominated by bulrush spent more time courting in these environments compared with environments that were unaltered. In contrast, males that were exposed to environments modified by increased algal turbidity not only took longer to initiate courtship but also spent less time courting females. These results suggest that different habitat alterations can have important consequences for the reproductive behavior of affected organisms and, ultimately, the direction of sexual selection.

Key words: **anthropogenic change, courtship, mate choice, sexual selection.**

INTRODUCTION

Sexual signals used by males to attract females can have a direct bearing on male reproductive success. Despite the potential reproductive benefits, such displays can also be costly for males to produce and maintain (e.g., heightened predation risk: Woods et al. 2007; high energy demand: Hoefler et al. 2008). As a result, males are expected to adjust their signalling effort to maximize their reproductive payoffs while, at the same time, minimize associated costs (Head et al. 2010). Typically, sexual signals are finely attuned to the local environmental conditions in which they have evolved. This can have important consequences when conditions change—both for the efficacy of sexual signals and the behavior of the signaller (Wilgers and Hebets 2011).

Most animals have experienced natural environmental change during their evolutionary history, but the higher speed of anthropogenic change can prove to be challenging for many species (Tuomainen and Candolin 2011). Human actions can have immediate impacts on the signalling environment and, in so doing, the effectiveness of sexual traits and/or signalling behavior (Wong et al. 2007). In this respect, different species appear to vary in their ability to adjust their signals in response to altered conditions (Wong and Candolin, 2014). Urban great tits, *Parus major*, for example, are able to increase the frequency of their acoustic signals so that they can be heard in noisy urban environments (Slabbekoorn and Peet 2003). Male tree frogs, *Hyla arborea*, by contrast, cannot (Lengagne 2008). Some animals may even respond in ways that are maladaptive, resulting in so called "evolutionary traps" (Rodewald et al. 2011).

For animals living in an increasingly human-dominated world, the capacity to adjust can have important consequences, not only for individual fitness but the viability of populations and, ultimately, the persistence of species (Candolin and Wong 2012; Wong and Candolin, 2014). In aquatic systems, for example, human-induced water turbidity can affect the signalling environment by reducing visibility—with negative reproductive repercussions, including altered mate choice (Sundin et al. 2010), mating system breakdown (Järvenpää and Lindström 2004), and even hybridization between closely related species (Seehausen et al. 1997). On the other hand, aquatic environments heavily impacted by agriculture and land degradation, can also create a more structurally complex habitat through the rampant growth of vegetation, which may allow more individuals to settle into territories (Candolin 2004) or provide them with greater cover against would-be predators (Candolin and Voigt 1998).

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Desert, rivers, and springs are among the world's most threatened habitats (Kodric-Brown et al. 2007). The scarcity of freshwater imposes considerable demand on these highly dynamic but fragile aquatic systems and their inhabitants (Davis et al. 2013). One species that is facing increasing pressure from anthropogenic sources is the desert goby, *Chlamydogobius eremius*, a small freshwater fish endemic to Central Australia. The biology, habits, and ecology of this species make it an excellent system for studying the impacts of environmental change and altered habitat complexity on sexual selection. During the breeding season, male gobies establish territories under crevices and attempt to attract passing females to their nest by performing short bouts of courtship displays that involve flaring of the male's colourful fins accompanied by jerky body movements (Symons et al. 2011). Many of the rivers and springs inhabited by desert gobies, however, are also relied on by livestock (i.e., cattle), which trample and graze the margins, and contribute nutrients into the water causing increased primary productivity and extensive growth of aquatic weeds (Lucas and Jones 2009). Such activities are likely to influence the signalling environment and, in so doing, affect male reproductive behaviors. Accordingly, the aim of this study was to investigate how habitat changes caused by eutrophication and livestock grazing affect male courtship behavior in desert gobies. Specifically, we experimentally exposed male gobies to 2 kinds of disturbance to the visual environment associated with anthropogenic degradation of aquatic habitat: 1) changes in habitat complexity caused by rampant growth of riparian vegetation and 2) altered visibility caused by algal-induced water turbidity. On the one hand, we might expect that increased vegetation/algae might impact negatively on visual displays by reducing visibility (Candolin et al. 2007). On the other hand, the safety afforded by increased vegetation and/or reduced conspicuousness to would-be predators from elevated turbidity levels (Michelangeli and Wong 2014), may actually facilitate male courtship behavior (Candolin and Voigt 1998).

METHODOLOGY

Housing & experimental set-up

Desert gobies were collected from the Lake Eyre Basin of Central Australia using dip and seine nets. Fish were transported back to the laboratory at Monash University in 50 L coolers filled with water to a depth of 30 cm (density ~100 fish/cooler). Each tub was aerated using air pumps, and received a 50% change of dechlorinated tap water once during the 2 days it took to transport the fish by car from the desert. This method of transportation resulted in zero mortality.

Back in the laboratory, gobies were housed in separate-sex 300-L aquaria at a temperature of 24–26 °C on a 12 h light:dark cycle. Water within the tanks was maintained at a salinity of 5% (using Coralife Scientific Marine Grade Salt, ESU Inc., Franklin, WI). Salinity levels were monitored using a Hanna H198130 conductivity meter and, if necessary, adjusted to the desired concentration by the addition of either salt or filtered tap water. All fish were fed daily on a diet of commercially prepared pellets and brine shrimp, *Artemia* spp.

We conducted 2 experiments to investigate the effects of modified habitat complexity caused by human disturbance on the courtship behavior of male desert gobies. The first experiment considered the effects of increased riparian vegetation growth and the second examined the effects of algae-induced turbidity. All experimental trials were carried out in aquaria measuring 65-cm long × 20-cm wide, which were filled to a depth of 20 cm with water

maintained at the same salinity and temperature levels as the stock tanks, and aerated using air stones. Experimental aquaria were divided into 2 sections: a large male compartment (55 × 20 cm) that was manipulated depending on treatment (see below), and a smaller female compartment (10 × 20 cm). We used a perforated clear plastic divider to separate the 2 sections so that the fish could see and interact with one another during experimental trials. The males were each provided with an artificial nest in the form of a 9-cmlong piece of plastic tube made of polyvinyl chloride (PVC) (3-cm diameter; sensu Wong and Svensson 2009), which sat flush on the gravel substrate surface with the opening facing the female compartment. Males used in our study were all sexually mature individuals, as determined by the presence of nuptial colouration (Wong and Svensson 2009). Females used as stimulus fish were all gravid, as determined by their distended bellies. Different sets of fish were used for each experiment. The research detailed in this paper was approved by the Biological Sciences Animal Ethics Committee of Monash University.

Experiment 1: effect of dense vegetation

To determine the effects of increased riparian vegetation growth on courtship behavior, males gobies were sequentially exposed to 2 treatments in a randomized order: open habitat ($n = 21$) versus dense vegetation ($n = 21$). In the dense vegetation treatment, we added 12 bunches of bulrush (*Typha*) into the male compartment of the experimental aquaria, whereas in the open habitat treatment, the male compartment of the aquaria was left bare. Both treatments are reflective of conditions that desert gobies would encounter in the field (Allen et al. 2002, Kodric-Brown et al. 2007)

Focal males (mean length ± SE = 56.28 ± 1.14 mm; mean weight ± SE = 4.13 ± 0.24 g) were acclimated to the test aquarium before the start of the trial for a minimum of 3 days. One day before the start of the trial, a gravid female (mean length ± SE = 47.12 ± 0.50 mm; mean weight ± SE = 2.38 ± 0.07 g), was placed into the smaller compartment of the experimental aquaria for acclimatization. During this time, a black opaque divider was inserted over the clear partition between the male and female compartments to prevent visual contact. The opaque divider was firmly secured into position with inserts that prevented the movement of water (and any associated olfactory cues) between compartments. A day later, the opaque divider was removed and we recorded the time it took for the focal male to begin courting the female. The male was given a maximum 150 min to begin courting the female. Once the male had initiated courtship, we recorded the total time the male was courting over the 10-min sampling period, as well as the amount of time the male subsequently spent inside its nest (sensu Wong and Svensson 2009, Svensson et al. 2010, Michelangeli and Wong 2014). Behaviors were recorded by direct observation, with the observer sitting 2 m away from the brightly lit tanks in an otherwise darkened room so that the fish could not see the observer.

After completion of the first treatment, the female was removed and returned to her stock tank. We then either removed or added bulrush to the male's compartment (depending on the treatment that was applied first) to prepare the aquarium for the second treatment. The whole process was then repeated with the same male using a second, randomly chosen female as a stimulus.

Experiment 2: effect of algal turbidity

To determine the effects of increased algal turbidity on courtship behavior, male gobies were sequentially exposed to 2 treatments in a

randomized order: clear water (n = 20) versus turbid water (n = 20). Focal males (mean length ± SE = 54.43±1.45 mm; mean weight ± SE = 2.15±0.19 g) were introduced into experimental aquaria a minimum 3 days prior to the commencement of trials. An hour before each trial, an extra 4 cm of water was added to each aquarium so that the total depth was increased to 24 cm. For turbid treatments, this extra water was mixed with a unicellular alga, *Scenedesmus sp.*, so that tanks simulated turbid conditions associated with algal blooms. *Scenedesmus* is an abundant genus of unicellular green algae that is commonly found in turbid freshwater systems worldwide (Pentecost 1984). In the clear water treatment, the 4 cm of clean water was added to ensure that males, irrespective of treatment, were subjected to the same level of disturbance. Turbidity was measured using a HACH 2100Q Portable Turbidimeter (Hach Company, Notting Hill, VIC, Australia) and was significantly higher in tanks supplemented with algae (mean NTU ± SE: 9.43±1.2) than in the control (i.e., clear water) tanks (mean NTU ± SE: 0.80±0.30; paired t-test: t_{22} = 31.22, P = <0.001). These values fall within the range of turbidity levels encountered in the field (Wong BBM, unpublished data). In addition, all tanks were aerated throughout experiments so that dissolved oxygen did not differ between treatments (dissolved oxygen levels in turbid water trials = 79.1±0.85%; clear water trials = 79.6±0.67%; paired t-test t_{38} = 0.49 P = 0.63).

Immediately after water was added, we used a similar experimental procedure as outlined in experiment 1. A gravid female (mean length ± SE = 54.95±4.6 mm; mean weight ± SE = 2.34±0.5 g) was introduced into the smaller compartment within the experimental aquarium of each male and given a 1-h acclimatization period. During this time, a black opaque divider was inserted over the clear partition between the male and female compartments to prevent visual contact. An hour later, the opaque divider was removed and we recorded the time it took for the focal male to begin courting the female. For this experiment, we only gave the male a maximum of 60 min to begin courting. This was done because we found that, in experiment 1, the majority of males (approx. 70%) courted females within 1 h. Once the male had initiated courtship, we again quantified the courtship behaviors he was directing toward the female (fin flaring displays and jerky body movements) using the same method as in experiment 1.

At the conclusion of the first treatment, the female was removed and returned to her stock tank. The focal male was then moved to another experimental aquarium where the whole process was then repeated with the alternate treatment, using a second, randomly chosen female as a stimulus.

Statistical analysis

Statistical analyses were carried out using the statistical program R 2.11.1 (R Development Core Team 2010). In both experiments, the time taken to begin courting was examined using survival analysis, which takes into account any males that did not court during the sampling period. The relationship between courtship latency time and treatment was analysed using a Cox-proportional hazards regression. This semiparametric model deals effectively with time-to-event data characterized by right censoring (in this case, if a male had failed to initiate courtship) and an unknown distribution, which in this analysis was a cluster distribution (Hougaard 2000). A cluster distribution was used to accommodate the paired data design, which eliminates variability between subject, giving a greater statistical precision to a given sample size. Paired t-tests were used to compare male courtship behavior between the 2 treatments in both experiments. For each experiment, focal fish that failed to court in both treatments were excluded from the analysis.

RESULTS

### Experiment 1: effect of dense vegetation

We found no effect of treatment on the time taken for males to commence courting females (z = 0.47, P = 0.63; Figure 1a. Of the 21 males used in this experiment, 17 initiated courtship in the open treatment and 20 in the vegetated treatment.

We found that male desert gobies spent less time inside their nest (t_{20} = −2.31, P = 0.03; Figure 2a) and more time courting the female (t_{20} = 2.36, P = 0.03; Figure 2b) in the dense vegetation treatment. Males thus increased their courtship effort in dense vegetation.

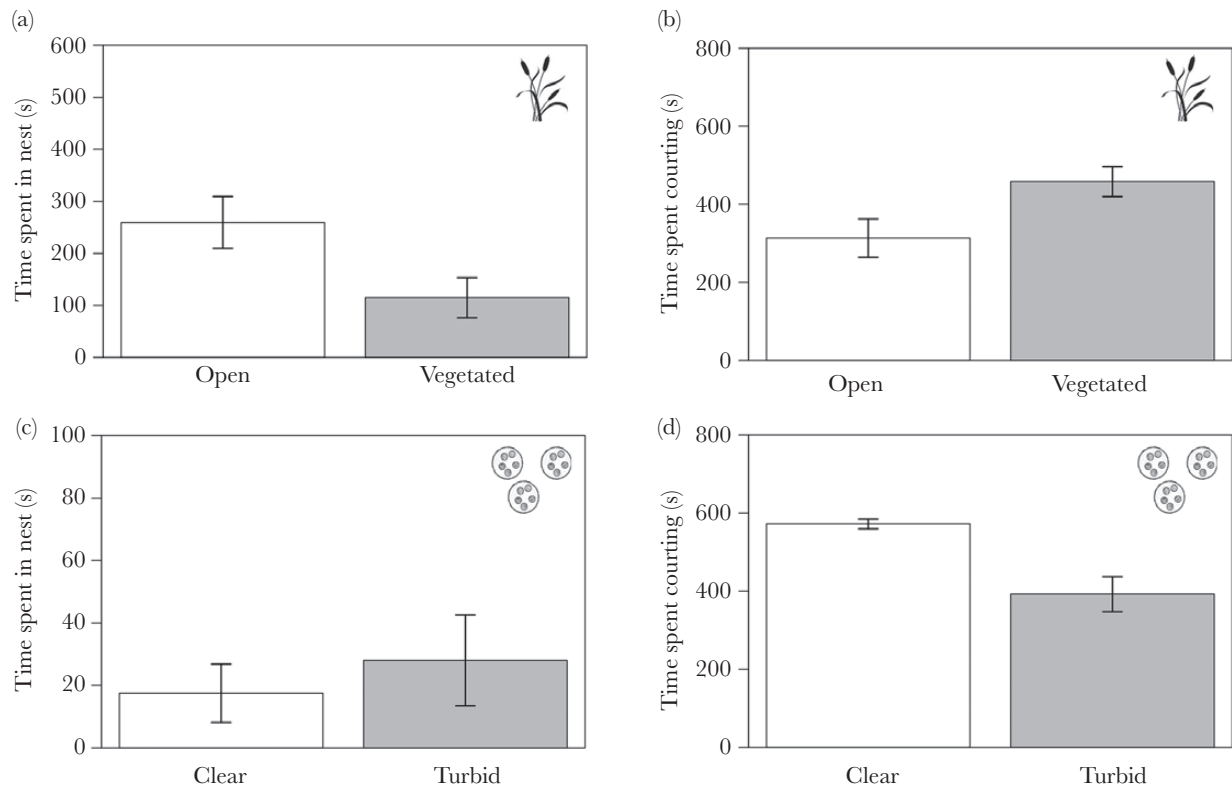### Experiment 2: effect of algal turbidity

Males took significantly longer to begin courting females in turbid than in clear water (z = 4.36, P = <0.001; Figure 1b). Of the 20 males used in this experiment, 17 initiated courtship in both treatments. The remaining 3 males courted in the clear treatment but not in the turbid treatment.

Males did not differ in the amount of time they spent inside their nest (t_{16} = 0.91, P = 0.38; Figure 2c). However, when males were outside of their nest, we found that they spent significantly more of their time courting females in clear water than in turbid water (t_{16} = 3.79, P = <0.001; Figure 2d). In other words, males reduced their courtship effort in turbid conditions.
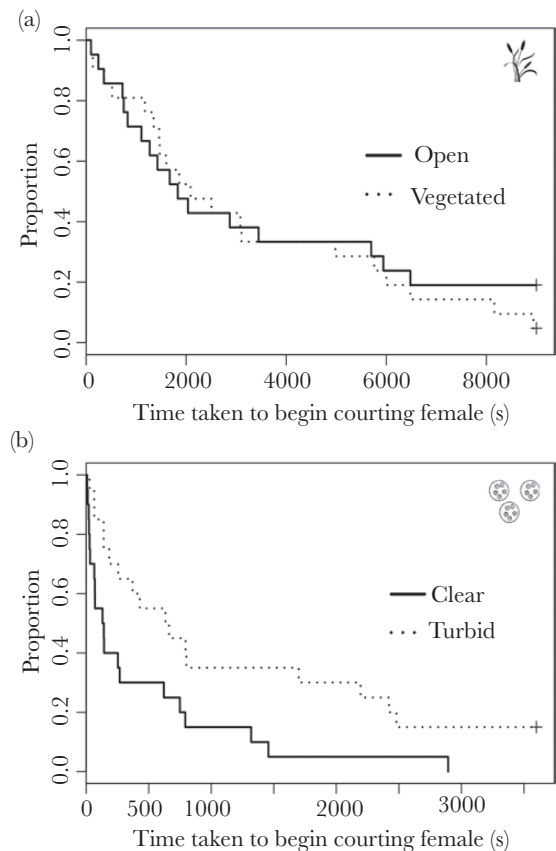
Figure 1
Kaplan Meier curve showing the time taken for male desert gobies to begin courting in the (a) vegetation and (b) algal experiments. In both cases, the "+" indicates right-censored data.

(a)

(b)

(c)

(d)

Figure 2
The mean (± SE) amount of time (s) male desert gobies spent inside their nest and courting females in the (a and b) vegetation and (c and d) algal experiments.

DISCUSSION

Two impacts of human disturbance on freshwater systems, algal turbidity and increased growth of riparian vegetation, appear to affect the courtship behavior of male desert gobies. Interestingly, however, these habitat alterations caused opposite responses from courting males. Male gobies exposed to environments dominated by invasive bulrush, increased their courtship effort when compared with unaltered environments. Conversely, male gobies subject to environments modified by algal turbidity not only took longer to initiate courtship but also spent less time courting females. The differential courtship effort observed between the 2 vegetation types suggests that both habitat alterations affect signaling dynamics in contrasting ways. It would seem that the greater vegetated cover created by the bulrush likely offered males a more protective courting environment, whereas the poorer visual environment caused by increased algal turbidity reduced the efficacy of colorful courtship displays and therefore male motivation to perform them.

Effect of dense vegetation

It is well established that conspicuous reproductive behaviors often increase an individual's susceptibility to would-be predators. This is particularly true of males due to their bright nuptial coloration and intense courtship displays (Endler 1987; Godin and McDonough 2003; Stuart-Fox et al. 2003; Husak et al. 2006). In many species, males are also larger and, thus, represent more profitable prey. It is likely that the perceived risk of predation is lower in densely vegetated habitats, as increased vegetation often restricts predator movement and vision making prey less vulnerable (e.g., Anderson 1984). For example, male three-spined sticklebacks, *Gasterostus*

aculeatus, enjoy higher breeding success when nesting in concealed sites compared with males with exposed nests (Kraak et al. 1999). Hence, under the increased safety of cover, it is likely that males can behave more boldly (Candolin et al. 2007). Such cover may be particularly important for male desert gobies, which have been observed to reduce their courtship effort when they perceive predation risk to be high (Michelangeli and Wong 2014). However, the benefits of increased cover (compared with a more open habitat) can be diminished if dense vegetation restricts vision and reduces mate encounter rates (Candolin 2004), thus decreasing the probability of mate detection and increasing the costs of mate assessment (Järvenpää and Lindström 2004).

In our study, there was no effect of bulrush presence on male latency to begin courting. However, once the male had approached the female, we found that they invested greater effort into courting her in the dense vegetation treatment. In densely vegetated habitats, intense courtship may be required to attract females and maintain their interest (Engström-Öst and Candolin 2007). Thus, the cost of courtship is increased as males have to invest more time and energy into mate attraction. At the same time, the reduced risk of predation means that males can also afford to invest more effort into courtship. This could affect the male's mating probability as intense courtship under predation risk (Candolin 1997) and in habitats with poor visibility has been observed to influence the attractiveness of males to females (Candolin et al. 2007; Engström-Öst and Candolin 2007).

Effect of algal turbidity

Male desert gobies took longer to detect and begin courting females in turbid water. It is suggested that in low light conditions,

perception of patterns and coloration changes much more rapidly with viewing distance (Endler 1992). Turbidity causes reduced penetration of light into the water column, deteriorating the visual spectrum and thus reducing the ability to detect and perceive conspecifics (Utne-Palm 2002). For example, male sailfin mollies, *Poecilia latipinna*, were found to spend less time associating with females in turbid environments (Heubel and Schlupp 2006), whereas male broad-nosed pipefish, *Syngnathus typhle*, were shown to be less efficient in evaluating potential mates (Sundin et al. 2010). Consequently, females may need to be in closer proximity to males in order for them to effectively detect each other. Such a possibility is supported by the findings of Long and Rosenqvist (1998) who observed male guppies courting females at closer, less variable distances under poor visual conditions.

The time in which it takes males to first begin courting females in turbid water may be particularly important for male mating prospects. In other fish species, females have been observed to become less discriminating in turbid water due to the higher cost imposed on mate searching (Järvenpää and Lindström 2004; Candolin et al. 2007). As courtship displays are often utilized to entice potential suitors, male desert gobies which detect and begin courting females quicker in turbid water might have a selective advantage as they are more likely to gain the attention of the female and thus more likely to mate. In contrast, those males who delay their courtship attempt due to an inability to detect the female may lose their opportunity to more vigilant males, irrespective of quality. This has the potential to change the direction of sexual selection and would be an interesting avenue for future research.

Apart from taking longer to initiate courtship, males also reduced the total time they spent courting in turbid water. Several studies have suggested that visual signals may become less conspicuous to females when visibility is reduced (Candolin et al. 2007, Engström-Öst and Candolin 2007, Chapman et al. 2009), and, as a result, may also alter female mate choice for these signals (Seehausen et al. 1997). For example, female goodied fish, *Xenoteca variatus*, prefer more speckled, ornamented males in clear—but not turbid—water (Moyaho et al. 2004). Similarly, in desert gobies, if the utlity of visual signals is undermined under turbid conditons, it is conceivable that males may decrease their courtship effort, especially if courtship is also energetically demanding (Olsson et al. 2009) and/or if turbidity also renders females less attractive to males (Sundin et al. 2010). Whether or not this decrease in courtship effort is an adaptive response is not certain, particularly as in other systems a compensatory increase in signaling effort in turbid conditions can be beneficial (Dugas and Franssen 2011, Eaton and Sloman 2011). Alternatively, males may benefit from using other mating strategies (Candolin 2009) or rely on other sensory cues (Heuschele et al. 2009) in order to overcome visually poor environments.

CONCLUSIONS

In conclusion, habitat alterations, by the addition of either increased plant growth or excess algal turbidity, can influence male courtship behavior. Specifically, under turbid conditions male desert gobies took longer to initiate courtship and spent less time performing courtship displays, most likely a response to decreased visibility. However, in environments with increased vegetation density, males increased their courtship effort probably because they perceived the environment to be safer. Here, we did not consider the combined effects of both vegetative types on the reproductive behavior of male desert gobies, but this would likely be important

in systems suffering from human disturbance. Our results suggest that both habitat changes could have counteractive effects on each other. Although increased plant growth may provide more protective cover to perform colorful courtship displays, excess algal turbidity reduces the effectiveness of these displays and likely male preference to perform them. Consequently, the selection for other reproductive cues may become favored. Further exploration into strategies males might adopt when visual signals are deprived and its consequences on female mating decisions and predator–prey interactions will provide valuable insight into how aquatic species respond to environmental change. This may be particularly important considering that many aquatic systems are facing sustained long-term environmental alterations due to human disturbance.

REFERENCES

Allen GR, Midgley SH, Allen M. 2002. Field guide to freshwater fishes of Australia. Melbourne: CSIRO Publishing.

Anderson O. 1984. Optimal foraging by largemouth bass in structured environments. Ecology. 65:851–861.

Candolin U. 1997. Predation risk affects courtship and attractiveness of competing threespine stickleback males. Behav Ecol Sociobiol. 41:81–87.

Candolin U. 2004. Effects of algae cover on egg acquisition in male three-spined stickleback. Behaviour. 141:1389–1399.

Candolin U. 2009. Population responses to anthropogenic disturbance: lessons from three-spined sticklebacks, *Gasterosteus aculeatus*, in eutrophic habitats. J Fish Biol. 75:2108–2121.

Candolin U, Salesto T, Evers M. 2007. Changed environmental conditions weaken sexual selection in sticklebacks. J Evol Biol. 20:233–239.

Candolin U, Voigt HR. 1998. Predator-induced nest site preference: safe nests allow courtship in sticklebacks. Anim Behav. 56:1205–1211.

Candolin U, Wong BBM. 2012. Behavioural responses to a changing world: mechanisms and consequences. Oxford: Oxford University Press.

Chapman BB, Morrell L, Krause J. 2009. Plasticity in male courtship behaviour as a function of light intensity in guppies. Behav Ecol Sociol. 63:1757–1763.

Davis J, Pavlova A, Thompson R, Sunnucks P. 2013. Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. Glob Chang Biol. 19:1970–1984.

Dugas MB, Franssen NR. 2011. Nuptial coloration of red shiners (*Cyprinella lutrensis*) is more intense in turbid habitats. Naturwissenschaften. 98:247–251.

Eaton L, Sloman K. 2011. Subordinate brown trout exaggerate social signalling in turbid conditions. Anim Behav. 81:603–608.

Endler JA. 1987. Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). Anim Behav. 35:1376–1385.

Endler JA. 1992. Signals, signal conditions, and the direction of evolution. Am Nat. 139:S125–S153.

Engström-Öst J, Candolin U. 2007. Human-induced water turbidity alters selection on sexual displays in sticklebacks. Behav Ecol. 18:393–398.

Godin JGJ, McDonough HE. 2003. Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. Behav Ecol. 14:194–200.

Head ML, Wong BB, Brooks R. 2010. Sexual display and mate choice in an energetically costly environment. PLoS One. 5:e15279.

Heubel K, Schlupp I. 2006. Turbidity affects association behaviour in male *Poecilia latipinna*. J Fish Biol. 68:555–568.

Heuschele J, Mannerla M, Gienapp P, Candolin U. 2009. Environment-dependent use of mate choice cues in sticklebacks. Behav Ecol. 20:1223–1227.

Hoefler CD, Persons MH, Rypstra AL. 2008. Evolutionarily costly courtship displays in a wolf spider: a test of viability indicator theory. Behav Ecol. 19:974–979.

Hougaard P. 2000. Analysis of multivariate survival data. Heidelberg: Springer Verlag.

Husak JF, Macedonia JM, Fox SF, Sauceda RC. 2006. Predation cost of conspicuous male coloration in collared lizards (*Crotaphytus collaris*): an experimental test using clay-covered model lizards. Ethology. 112:572–580.

Järvenpää M, Lindström K. 2004. Water turbidity by algal blooms causes mating system breakdown in a shallow-water fish, the sand goby *Pomatoschistus minutus*. Proc Biol Sci. 271:2361–2365.

Kodric-Brown A, Wilcox C, Bragg JG, Brown JH. 2007. Dynamics of fish in Australian desert springs: Role of large-mammal disturbance. Divers Distrib. 13:789–798.

Kraak SB, Bakker, TC, Mundwiler B. 1999. Sexual selection in sticklebacks in the field: correlates of reproductive, mating, and paternal success. Behav Ecol. 10:696–706.

Lengagne T. 2008. Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. Biol Cons. 141:2023–2031.

Long K, Rosenqvist G. 1998. Changes in male guppy courting distance in response to a fluctuating light environment. Behav Ecol Sociobiol. 44:77–83.

Lucas SD, Jones DL. 2009. Urine enhances the leaching and persistence of estrogens in soils. Soil Biol Biochem. 41:236–242.

Michelangeli M, Wong BBM. 2014. A recent predatory encounter influences male courtship in a desert-dwelling fish. Behav Ecol. 25:928–932.

Moyaho A, Garcia C, Ávila-Luna E. 2004. Mate choice and visibility in the expression of a sexually dimorphic trait in a goodeid fish (*Xenotoca variatus*). Can J Zool. 82:1917–1922.

Olsson KH, Kvarnemo C, Svensson O. 2009. Relative costs of courtship behaviours in nest-building sand gobies. Anim Behav. 77:541–546.

Pentecost A. 1984. Introduction to freshwater algae. Surrey: Richmond Publishing.

R Development Core Team. 2010. R version 2.9.1. Vienna: Foundation of Statistical Computing.

Rodewald AD, Shustack DP, Jones TM. 2011. Dynamic selective environments and evolutionary traps in human-dominated landscapes. Ecology. 92:1781–1788.

Seehausen O, Alphen J, Witte F. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science. 277:1808–1811.

Slabbekoorn H, Peet M. 2003. Birds sing at a higher pitch in urban noise. Nature 424:267.

Stuart-Fox DM, Moussalli A, Marshall NJ, Owens IP. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. Anim Behav. 66:541–550.

Sundin J, Berglund A, Rosenqvist G. 2010. Turbidity hampers mate choice in a pipefish. Ethology. 116:713–721.

Svensson PA, Lehtonen, TK, Wong BBM. 2010. The interval between sexual encounters affects male courtship tactics in a desert-dwelling fish. Behav Ecol Sociobiol. 64:1967–1970.

Symons N, Svensson PA, Wong BB. 2011. Do male desert gobies compromise offspring care to attract additional mating opportunities? PLoS One. 6:e20576.

Tuomainen U, Candolin U. 2011. Behavioural responses to human-induced environmental change. Biol Rev. 86:640–657.

Utne-Palm A. 2002. Visual feeding of fish in a turbid environment: physical and behavioural aspects. Mar Freshwater Behav Physiol. 35:111–128.

Wilgers D, Hebets E. 2011. Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments. Curr Zool. 57:175–186.

Wong BBM, Candolin U. 2014. Behavioral responses to changing environments. Behav Ecol. Advance Access published October 15, 2014, doi:10.1093/beheco/aru183

Wong BB, Candolin U, Lindström K. 2007. Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. Am Nat. 170:184–189.

Wong BBM, Svensson PA. 2009. Strategic male signalling effort in a desert-dwelling fish. Behav Ecol Sociobiol. 63:543–549.

Woods WA Jr, Hendrickson H, Mason J, Lewis SM. 2007. Energy and predation costs of firefly courtship signals. Am Nat. 170:702–708.