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*Biol. Lett.* 2009 **5**, 600-602 first published online 17 June 2009  
doi: 10.1098/rsbl.2009.0350

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# Risk-sensitive mating decisions in a visually compromised environment

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**Reproductive activities are often conspicuous and can increase the risk of predation. Evidence suggests that individuals are capable of responding to predators in a risk-sensitive manner. However, most studies tend to consider only the predator-mediated responses of males and females in isolation and with little regard to differences in local environmental conditions. Here, we experimentally investigate the effects of environmental visibility (turbidity) and predation risk on reproductive decisions in the sand goby, *Pomatoschistus minutus*, when exposed to a visually oriented predator, the European perch, *Perca fluviatilis*. We found that gobies were more reluctant to spawn in the predator's presence, although larger males spawned sooner than smaller males. Interestingly, latency to spawning was unaffected by the visual environment, suggesting that gobies may be relying on non-visual cues under turbid conditions.**

**Keywords:** predation risk; eutrophication; mate choice; sexual selection; Gobiidae

## 1. INTRODUCTION

Reproduction can be a costly pursuit. For species that are vulnerable to predators, conspicuous courtship and mating behaviours can increase the likelihood of detection (Hoefler *et al.* 2008) and are often in direct conflict with activities needed to mitigate the risk of being eaten (Dunn *et al.* 2008). Although individuals can adjust their reproductive behaviours to the level of threat (e.g. Evans *et al.* 2002), predator-mediated responses of males and females are often considered in isolation, with studies typically manipulating perceptions of risk in only one of the sexes (but seldom both at the same time) (Forsgren 1992; Candolin & Voight 1998). Since the activities of one sex may imperil the other (Pocklington & Dill 1995), reproductive decisions by both sexes need to be considered concurrently in order to gain a more meaningful understanding of how the risk of predation can influence mating outcomes (Fuller & Berglund 1996; Dunn *et al.* 2008).

Often overlooked, local environmental conditions may be important for reproductive decisions under predation risk. For example, in a mate choice study, Simcox *et al.* (2005) found that male Panamanian

bishops (*Brachyraphis episcopi*) from high-predation localities were only choosy when light levels were dim, presumably to lessen the likelihood of detection by would-be predators. It is worth bearing in mind, however, that the same environmental conditions responsible for reducing the risk of detection can also make it more difficult for prey to notice the presence of would-be predators (Rand *et al.* 1997). Hence, if the levels of detection by both predator and prey shift concomitantly under different environmental conditions, there may be no net change in predation risk (Rand *et al.* 1997).

The visual environment in many shallow, aquatic habitats can often exhibit remarkable temporal and spatial variation owing to changes in water clarity caused by phytoplankton blooms (Raateoja *et al.* 2005). The input of nutrients from anthropogenic activities has exacerbated the severity of this phenomenon by contributing to eutrophication (Larsson *et al.* 1985). The effects (if any) of altered visibility on the spawning decisions of fishes that breed in shallow-water habitats remain largely unknown (Wong *et al.* 2007).

The sand goby (*Pomatoschistus minutus*) is a small European inhabitant of shallow coastal waters afflicted by eutrophication (Järvenpää & Lindström 2004). Male gobies build nests under empty mussel shells or rocks, attract females using courtship displays and take exclusive care of the eggs after spawning (Lindström 1988). Here, we set out to compare the latency to spawning in sand gobies in both the presence and absence of a visually oriented piscivorous predator, the European perch (*Perca fluviatilis*), under both clear and turbid water conditions. Algal turbidity greatly diminishes the predation success of perch by reducing visibility in the water column (Radke & Gaupisch 2005), but is also likely to compromise the efficacy of visual cues available to sand gobies (Järvenpää & Lindström 2004). Sand gobies are therefore an excellent model for investigating the effects of algal turbidity and predation risk on reproductive decisions.

## 2. MATERIAL AND METHODS

### (a) Collecting and housing

Fishes were collected from the Baltic Sea and kept under natural light and temperature conditions in an outdoor facility at the Tvärminne Zoological Station in southern Finland. Sand gobies were housed in separate-sex aquaria and maintained on a diet of *Neomysis integer* shrimp and chironomid larvae. Perch were kept in large, plant-filled tubs and fed live *Crangon crangon* shrimp.

### (b) Experimental set-up

We employed a 2 × 2 factorial design to investigate the effects of predation risk (presence versus absence of perch) and visual environment (clear versus turbid water) on the time taken for sand gobies to spawn.

Experimental trials were carried out in aquaria measuring (length × width) = 75 × 25 cm. Each aquarium had a 4 cm layer of fine sand on the bottom and was filled to a depth of 25 cm with sea water. Individual tanks were separated into two compartments using a clear plastic divider with holes drilled through the plastic to allow transfer of any chemical cues. The back compartment contained a clump of artificial vegetation and, depending on treatment, was potentially used for housing a perch during trials (discussed subsequently). The front compartment eventually housed a pair of gobies and contained a halved clay flowerpot (diameter 6 cm) as a potential nesting resource. The ceiling of the flowerpot was lined with a piece of transparent acetate film onto which the female could attach her eggs. The use of the transparency allowed us to remove and photograph the egg mass to determine the clutch size at the end of each trial.

Table 1. Spawning latency in the absence and presence of a predator in turbid and clear water treatments with male length as a covariate. Loglik(model) = -232,  $\chi^2 = 16.94$ , d.f. = 7,  $p = 0.018$ .  $p$ -values < 0.05 are highlighted in bold.

effect	value	s.d.	z-value	p-value
(intercept)	1.499	22.327	0.067	0.946
predation	78.191	34.121	2.292	<b>0.022</b>
turbidity	-11.619	32.922	-0.353	0.724
length	0.039	0.426	0.091	0.928
predation × turbidity	11.330	53.149	0.213	0.831
predation × length	-1.404	0.652	-2.153	<b>0.031</b>
turbidity × length	0.252	0.623	0.405	0.685
three-way interaction	-0.143	0.998	-0.143	0.886

All fishes used were weighed and measured before the experiment. For each trial, a male goby was introduced into the front compartment and given 24 h to construct a nest. After nest construction, we randomly assigned males to their respective treatments and adjusted visibility levels and predation risk. Reduced visibility was achieved by adding a mixture of unicellular algae (*Brachiononas submarina*) and water into the aquarium to achieve the desired turbidity. To ensure that all males were subjected to the same level of disturbance, an equivalent amount of clean sea water was added to the remaining tanks. Turbidity levels were significantly higher in tanks supplemented with algae (mean turbidity ± s.d. in algal tanks =  $3.495 \pm 1.511$  nephelometric turbidity units (NTU),  $n = 35$ ; clear water tanks =  $0.718 \pm 0.229$  NTU,  $n = 36$ ; Mann-Whitney  $U$ -test:  $U = 8.5$ ,  $p < 0.001$ ) and are well within the range recorded in the Baltic Sea during the sand goby breeding season (Granqvist & Mattila 2004). For trials requiring the presence of a predator, we introduced a perch into the back compartment (standard length ± s.d. =  $18.89 \pm 3.10$  cm). There was no difference in the size of the perch between clear and turbid treatments (independent  $t$ -test:  $t = 0.026$ , d.f. = 34,  $p = 0.97$ ).

Next, a gravid female was placed in the male compartment and given 24 h to spawn. We recorded the time taken to spawn by inspecting tanks every hour for the first 12 h and every 6 h thereafter. Inspections were carried out using an LED to minimize disturbance to fish.

### (c) Statistical analyses

The effect of treatment on time to spawning was tested using a parametric survival analysis with a logistic error distribution (Moya-Laraño & Wise 2000). Survival analysis uses maximum-likelihood estimates of the hazard function (the probability that a female will spawn during a given time period or event) of a lifetime variable (spawning latency). Trials in which spawning did not occur were recorded as 'right-censored'. All tests were two-tailed.

## 3. RESULTS

Latency to spawning was affected by predation risk, but not by the visibility level of the water. Specifically, gobies took significantly longer to spawn in the presence of a perch, and this was true under both clear and turbid water conditions (table 1; figure 1). In the presence of the predator, latency to spawning was also negatively correlated with male size (table 1; figure 2).

As large females are known to lay larger clutches, we included female size as a covariate in the analysis of egg number. Treatment had no effect on the number of eggs laid (two-way ANCOVA: all  $F_{1,55} < 1.270$ ,  $p = 0.265$ ), but female size had a positive effect (covariate effect,  $F_{1,55} = 20.84$ ,  $p < 0.001$ ). Latency to spawning had no effect on egg number (linear regression:  $b = -0.213$ , d.f. = 62,  $t = 0.030$ ,  $p = 0.976$ ).

## 4. DISCUSSION

We found that sand gobies were more reluctant to spawn in the presence of a predator. These results

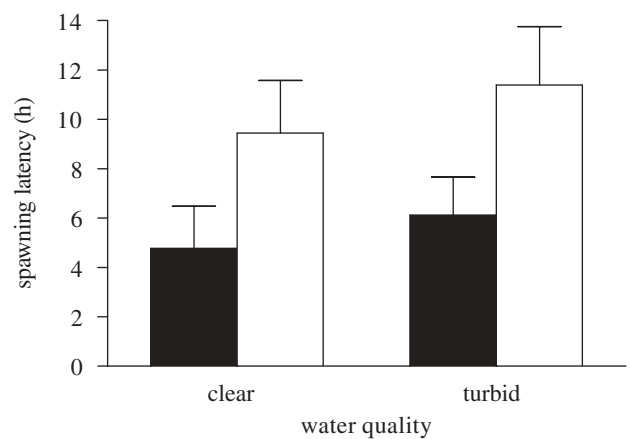


Figure 1. Effect of water clarity on latency to spawning (mean ± s.e.) in the absence (black bars) and presence (white bars) of a predator.

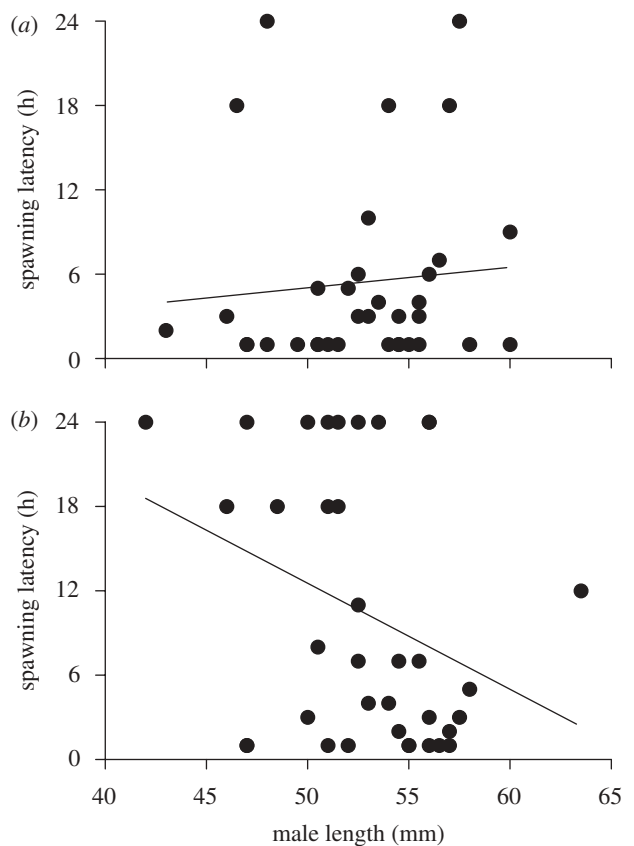


Figure 2. Effect of male size on latency to spawning in the (a) absence and (b) presence of a predator.

are consistent with individuals responding in a risk-sensitive manner (reviewed in Dunn *et al.* 2008). Both predator avoidance and mate acquisition can have important fitness consequences, but the two activities are usually incompatible and may often have to be traded against one another. In this regard, studies on taxa as diverse as arthropods (e.g. Koga *et al.* 1998), fishes (e.g. Fuller & Berglund 1996; Evans *et al.* 2002) and salamanders (Uzendoski *et al.* 1993) consistently report a decrease in reproductive activities under predation risk.

Our results, however, also suggest that the predatory threat can affect individuals differently. In the presence

of the perch, latency to spawning was influenced by male size, with larger males spawning sooner. Why? Owing to their conspicuous reproductive behaviours, males, in general, tend to be more vulnerable to predators than are females (reviewed in Kokko & Wong 2007). The actual risk of being eaten, however, can vary among males. For example, although larger males may represent more profitable prey, smaller males may be less adept at evading capture or may be preferentially targeted by gape-limited predators. In the context of life-history tradeoffs, different sized males may therefore invest differently in current reproductive effort owing to differences in residual reproductive value. In addition, even though female sand gobies do not necessarily prefer larger males (reviewed in Lehtonen & Lindström 2009), females may be less inclined to resist their mating attempts in the presence of predators, as demonstrated, for example, in guppies (Kelly & Godin 2001) and amphipods (Dunn *et al.* 2008).

In our study, latency to spawning was unaffected by the visual environment. The level of turbidity simulated in our experiment falls within the range reported in the Baltic during the sand goby breeding season (Granqvist & Mattila 2004) and is comparable to that used in other studies in which reproductive activities have been affected (Järvenpää & Lindström 2004). In particular, similar levels of turbidity have previously been shown to reduce the capture success of visually oriented predators such as perch (Radke & Gaupisch 2005). However, by reducing visibility in the water column, such conditions also compromise visual cues that are relied upon by sand gobies (Järvenpää & Lindström 2004). Our results, nevertheless, suggest that gobies may be able to assess risk using other, non-visual (e.g. chemical) cues, the relative importance of which may shift depending on local environmental conditions (Heuschele & Candolin 2007). Future studies should test reproductive responses in the presence of predators that differ in their reliance on visual detection and probe the generality of our findings by considering the role of other sensory modalities under a range of different signalling environments.

This experiment was approved by the animal care committee of the University of Helsinki.

We thank A. Svensson and T. Lehtonen for comments on the manuscript, and the Academy of Finland, the Australian Research Council and the Finnish Graduate School in Evolutionary Ecology for funding.

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