## Original Article

# A recent predatory encounter influences male courtship in a desert-dwelling fish

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Increased predation risk is one of the greatest costs associated with sexual signaling. Studies have shown that individuals often adjust their signaling behavior in the presence of predators with consequences for current reproductive opportunities. Predation risk, however, can vary over time and is rarely (if ever) constant. Despite this, surprisingly little is known about how recent exposure to a predator might influence an individual's subsequent signaling behavior. Here, we set out to determine how a previous encounter with a piscivorous predator affected courtship behavior in a freshwater fish, the desert goby, *Chlamydogobius eremius*. We tested male courtship before and after manipulating their perception of risk. We found that male gobies previously exposed to a predatory fish, the spangled perch, *Leiopotherapon unicolor,* took longer to initiate courtship and subsequently spent less time courting females. Such males, instead, spent more time taking refuge in their nests. In contrast, unexposed control male gobies and males that were exposed to a nonpredatory fish, the Lake Eyre Hardyhead, *Craterocephalus eyresii,* did not alter their courtship behavior. Our results suggest that male courtship behavior is not only sensitive to the immediate presence of a predator but can persist even after the predatory threat has abated.

*Key words*: **courtship, mate choice, predation risk, sexual selection.**

## INTRODUCTION

Attractive courtship displays can benefit the signaler by enticing potential mates, but such displays can also be costly. Not only are these displays time consuming and energetically demanding to perform (Kotiaho et al. 1998; Woods et al. 2007), but they can also leave the signaler vulnerable to predation (Zuk and Kolluru 1998; Jennions et al. 2001). In this regard, courting individuals are often found to be preferentially attacked and more likely captured by predators (Magnhagen 1991; Godin and McDonough 2003; Lindstrom et al. 2006; Hoefler et al. 2008). For example, male wolf spiders, *Pardosa milvina*, performing leg raising displays suffer a higher predation cost compared with non-courting males (Hoefler et al. 2008). In light of such costs, it is well established that males will often adjust their courtship behaviors when a predator is present to mitigate the risk of being eaten (Candolin and Voigt 1998; Hedrick 2000; Lohrey et al. 2009).

Behavioral adjustments in response to the immediate threat of predation can involve changing reproductive tactics or ceasing courtship altogether (Hedrick 2000; Taylor et al. 2005; Bernal et al. 2007). For example, in the presence of predators, male guppies, *Poecilia reticulata*, are more likely to engage in sneak copulations rather than courtship (Godin 1995). Such behavioral adjustments,

however, can result in missed mating opportunities (e.g., Godin 1995) and, in the case of species that respond to predators by taking refuge, limit the ability of individuals to acquire further information regarding the predatory threat (Sih 1997; Hugie 2003, 2004; Wong et al. 2005). Thus, the signaler is often confronted with a trade-off between maximizing their current mating opportunities and minimizing their risk of predation (Magnhagen 1991).

While several studies have shown that males will readily reduce their courtship in the presence of predators (Forsgren and Magnhagen 1993; Godin 1995; Fuller and Berglund 1996; Candolin 1997; Koga et al. 1998; Figueira and Lyman 2007), far fewer (if any) have investigated how a recent encounter with a predator may affect subsequent male signaling effort. This is surprising, as the threat of predation is rarely constant, but varies across time (Lima and Dill 1990). Indeed, evidence from studies of female mate choice show that the effects of predation on female behaviors can often persist even after the predatory threat has abated (Hedrick and Dill 1993; Jennions and Petrie 1997; Johnson and Basolo 2003). Given that males are often more susceptible to predation because of their bright colors, elaborate ornaments, and/or conspicuous displays (Magnhagen 1991; Koga et al. 2001; Stuart-Fox et al. 2003; Woods et al. 2007), one might expect males to also respond in a risk-sensitive manner and to adjust their courtship behavior accordingly (Lima and Dill 1990; Sih 1997).

The desert goby, *Chlamydogobius eremius*, is a small freshwater fish endemic to the Lake Eyre Basin of Central Australia. The species

is locally abundant throughout its range where it inhabits both permanent and temporary bodies of water, from ephemeral rivers to artesian-fed springs (Allen et al. 2002). Within these habitats, desert gobies often co-occur with other species of fish, including the spangled perch, *Leiopotherapon unicolor*, an aggressive opportunistic carnivore (Wager and Unmack 2000) that is known to feed on gobies (Michelangeli M, Wong BBM, unpublished data). The desert goby is sexually dimorphic, with males being larger and more brightly colored than females (van Lieshout et al. 2013). Male desert gobies shelter and establish nests under rock crevices in shallow water and attract passing females using elaborate courtship displays, which involve the blackening and raising of the male's dorsal and anal fins (Svensson et al. 2010; Lehtonen et al. 2011; Svensson et al. 2012). Owing to the conspicuousness of their displays, courting males may be exposing themselves to greater predation risk. Accordingly, using the desert goby, we set out to investigate how a recent encounter with a predator, the spangled perch, influences subsequent male signaling behavior. If males respond in a risk-sensitive manner, we predict that males should take longer to initiate courtship and subsequently spend less time courting after predatory exposure.

## METHODS

### Desert goby collection and housing

Desert gobies were collected from Warriner Creek (29°15′11.12″S, 136°42′15.64″E) in the Lake Eyre Basin of Central Australia, November 2010. Fish were transported back to the laboratory in 50 L coolers filled with water to a depth of 30 cm (density: ~100 fish per 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 from the desert back to the laboratory. There was zero mortality during transportation.

Back in the laboratory, gobies were housed in separate-sex aquaria (300 L) and kept at a temperature of 24–26 °C on 12 h light:dark cycle. Water within tanks was maintained at a salinity of 5% to mimic field conditions (using Coralife Scientific Marine Grade Salt; ESU Inc.; Wong and Svensson 2009). 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 live brine shrimp (*Artemia* spp.).

## Experimental procedure

Sexually mature males, distinguishable by their nuptial coloration (Symons et al. 2011), were randomly chosen (mean total length ± standard error [SE] = 5.4±0.6 cm; weight ± SE = 3.1±0.74 g, *n* = 36) and introduced into individual aquaria (65 cm long × 25 cm wide, water depth = 20 cm) 3 days prior to experimentation. Experimental aquaria contained a fine gravel substrate (~3 cm layer) and were maintained at the same salinity and temperature levels as the stock tanks (Wong and Svensson 2009). Aquaria were separated into 2 compartments using a clear divider: one for the focal male and the other for the stimulus (see below). The clear divider was firmly secured into position with inserts that prevented the movement of water (and any associated olfactory cues) between compartments. A PVC pipe (9 cm long; 3 cm diameter) was placed inside the male's compartment as a nesting resource (Wong and Svensson 2009). Each pipe was capped at one end with the opening facing the stimulus compartment and was anchored in place by securing it onto a piece of ceramic tile that was buried into the substrate.

Each experimental trial consisted of 3 stages (see Figure 1). Stage 1 involved observing a male's behavior over a 10-min period when presented with a female (mean length ± SE = 5.1±0.4 cm; mean weight ± SE = 2.2±0.6 g, *n* = 36). A female was randomly selected from a stock tank and placed inside a smaller tank (measuring 18 cm long × 6 cm wide), which was then positioned lengthwise within the stimulus compartment (Figure 1). The female remained within this smaller tank for the duration of the experiment. Female size did not differ between treatments (analysis of variance: $F_{2,33} = 0.46$, $P = 0.95$; see treatment details below). The female was given 5 min to acclimate, during which, the use of an opaque screen between the male and stimulus compartments prevented visual contact between the fish. After acclimation, the opaque screen was removed. We then carried out spot samples of male behavior every 10 s for 10 min. Specifically, during each spot sample, we recorded whether the male was courting (i.e., performing a fin display: flared fins and jerky body movements), whether the male was in his nest or whether he was outside his nest but not courting (sensu Wong
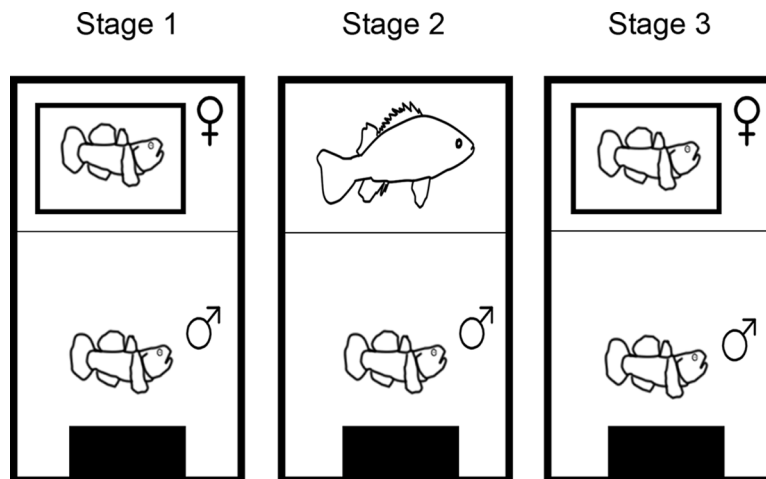


**Figure 1**

Male courtship behavior in the presence of a female measured before (stage 1) and after (stage 3) manipulating male perception of predation risk (stage 2). Stage 2 involved exposing a male either to a predator (Spangled Perch), a nonpredatory species (Lake Eyre Hardyhead), or an empty compartment (control).

and Svensson 2009; Svensson et al. 2010; Lehtonen et al. 2011; Symons et al. 2011). We also recorded the time taken for males to first begin courting the female. Any trials involving males that did not initiate courtship during this first 10-min observational period were terminated.

Stage 2 involved manipulating the male's perception of predation risk. At the conclusion of stage 1, the opaque divider was immediately reinstated and the female was removed. In the control treatment ($n$ =12), the stimulus compartment previously occupied by the female was left empty. In the predator treatment ($n$ = 12), the female was replaced by a spangled perch (mean length ± SE = 11.7 ± 1.4 cm; $n$ = 4), which was randomly selected from a separate stock tank. In the nonpredatory treatment ($n$ = 12), we replaced the female with a randomly selected Lake Eyre Hardyhead, *Craterocephalus eyresii* (mean length ± SE = 6.1 ± 0.4 cm; $n$ = 3). Hardyheads are an omnivorous species commonly found in sympatry with desert gobies, but, in contrast to the spangled perch, is a relatively innocuous species that feeds on plant material and invertebrates (Wager and Unmack 2000). This third treatment was included in our study to ensure that any behavioral changes in the predation treatment were, in fact, due to a higher perceived risk of predation rather than male gobies merely responding to the presence of another species. Perch used in this study were bought from a commercial supplier (Subscape Aquarium, Melbourne). Lake Eyre Hardyheads were collected from the wild (Warriner Creek, Lake Eyre Basin). The transition between stages (i.e., removing the female and replacing her with the treatment) took <2 min. After a 5-min acclimation period, the opaque divider was removed and the male goby was exposed to the treatment for 30 min. To avoid possible differences in the level of disturbance, all aquaria were subjected to the same level of manipulation with the opaque dividers (i.e., including the control).

In stage 3, the opaque divider was reinserted. Any fish present in the stimulus compartment (i.e., perch, hardyhead) were removed and the same female goby that was used in stage 1 of each trial was reintroduced. Again, the female was housed within a small tank to ensure that she was not responding to any chemical cues that could have been left by the presence of any fish (i.e., perch or hardyhead) used during stage 2, and thereby influencing the male's behavior (Evans et al. 2002). After a 5-min acclimation period, the divider was removed and the same process of behavioral observation as in stage 1 was repeated. At the conclusion of each treatment, we tallied male courtship effort (i.e., the number of 10 s spot samples the male was observed courting; sensu Wong and Svensson 2009) and the number of times the male was observed to be inside his nest during the 10-min sampling period in both stage 1 and stage 3.

## Statistical analysis

Statistical analyses were carried out using the statistical package R 2.10.1 (R Development Core Team 2010). All data were checked to ensure appropriate statistical assumptions were met and if necessary, transformed accordingly. Time taken for males to court in stages 1 and 3 were compared using semiparametric survival analysis to take into account censored data (i.e., those males that failed to court within the 10-min trial). Specifically, the relationship between the time taken for males to court and treatment was analyzed using Cox-proportional hazards regression. Any males that failed to court within stage 3 were "right-censored" for analysis. A linear mixed effects model was used to compare the time males spent courting between stage 1 and stage 3 in each treatment. This model incorporated the random effect of each individual male, with treatment and stage as fixed factors. The model was fitted using maximum likelihood.

## RESULTS

During stage 1, the time taken for males to initiate courtship did not differ between treatments (survival analysis: $z = 0.72$, $P = 0.88$; Figure 2a). However, we found a significant difference in courtship latency time in stage 3 (survival analysis: $z = 2.31$, $P = 0.02$), with males taking a significantly longer time to begin courting females after exposure to a predator compared with those males exposed to nothing (Tukey post hoc comparison: $t_{11} = -3.19$, $P = <0.01$) or to the nonpredatory hardyhead ($t_{11} = -2.97$, $P = 0.01$; Figure 2b). Indeed, half of the males exposed to the predator ($n = 6$) never courted during the observational period in stage 3.
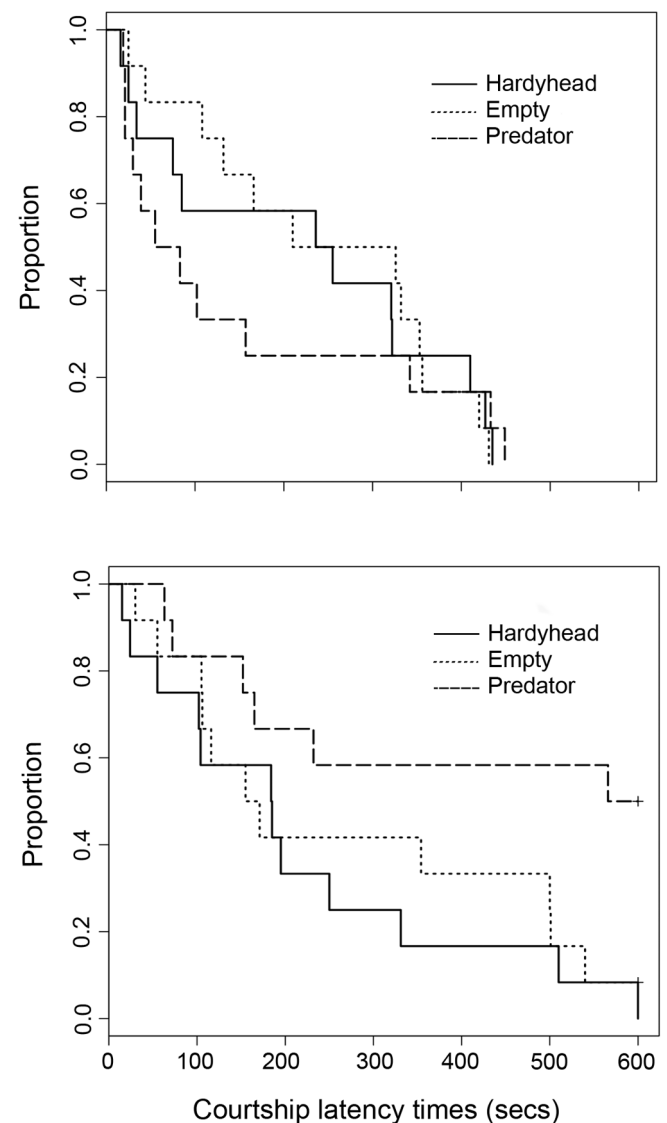


**Figure 2**
Kaplan–Meier survival curves showing latency times to courtship in male desert gobies, (a) before (stage 1) and (b) after (stage 3) treatment ($n = 12$); (+) indicates right-censored data. Confidence bands have been removed for clarity.

The mixed effects model found a significant interaction between stage and treatment on male courtship effort ($F_{2, 33}$ = 7.34, $P = 0.02$). Main effects test (Quinn and Keough 2002) revealed that this was due to a significant reduction in the time males spent courting between stages 1 and 3 in the predator treatment ($F_{1, 22}$ = 17.2, $P \leq 0.01$; Figure 3). By contrast, male courtship did not change between stages in either the control (i.e., no predator treatment; $F_{1, 22}$ = 0.82, $P = 0.37$) or the hardyhead treatment ($F_{1, 22}$ = 0.01, $P = 0.92$; Figure 3). Instead of courting, males in the predation treatment spent significantly more time in their nests after exposure to the spangled perch (stage 1: $255.8 \pm 50.4$ s, stage 3: $415.8 \pm 65.9$ s; paired $t$-test: $t_{11}$ = 2.38, $P = 0.03$).

## DISCUSSION

We found altering a male's perception of predation risk affected his subsequent courtship behavior. Previously, studies have shown that males are at greater risk of being detected by predators when performing sexual displays (reviewed by Zuk and Kolluru 1998). The bioluminescent courtship signals of male *Photinus* fireflies, for instance, increase their vulnerability to visually oriented predators (Woods et al. 2007). Not surprisingly, males of many species often only perform elaborate displays when predation risk is low, as seen, for example, in the guppy (Endler 1987). In the present study, it would appear that the effect of previous encounters, at least in the short term, can persist even after the predatory threat had abated. Consistent with our prediction, we found that males spent more time inside their nest and, consequently, took longer to begin courting females in the predator treatments. In fact, half of the focal males did not court at all after exposure to the predatory spangled perch. In this regard, it is important to point out that, in the current study, males were tested 5 min after they were exposed to the perch as we were interested in male responses immediately after predator exposure. This time frame is comparable with previous work looking at the effect of predator exposure on female behaviors (e.g., swordtail fish: Johnson and Basolo 2003). However, we do not discount the possibility that predator exposure can also have longer term effects, which can be investigated in future studies by exploring, for example, the time taken for males to return to pre-exposure courtship levels.
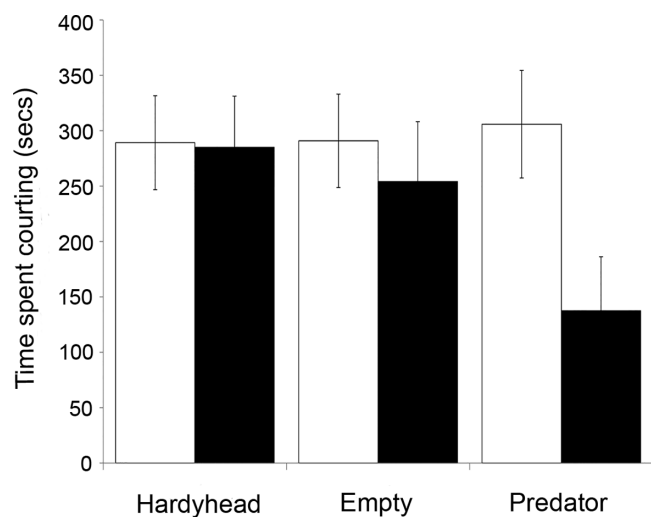


**Figure 3**
The mean (± SE) time males spent courting before (stage 1, white bars) and after (stage 3, black bars) exposure to treatment ($n = 12$).

Nevertheless, the response of male gobies are consistent with the antipredator behavior of other refuge-seeking species (Hedrick 2000), with males reducing courtship and increasing the use of refuge.

In some species, male reproductive strategies under high predation risk are often adjusted according to female behavior (Dill et al. 1999; Evans et al. 2002; Su and Li 2006). As a result, it can often be difficult to disentangle whether males are responding to the risk of predation per se, or to changes in female activity. For instance, male fiddler crabs, *Uca beebei*, reduced their surface activity and consequently their courtship behavior in the presence of predatory birds, however, as highlighted by the authors of that study, such a response may have been caused by reduced female activity (see discussion in Koga et al. 1998). Similarly, in guppies, when only females were exposed to increased predation risk, males performed fewer courtship displays (Dill et al. 1999). However, in contrast to these earlier studies, we controlled for any potential effect of female behaviors by only exposing male gobies to the predator. As a result, the behavioral adjustments reported in our study appear to be a direct result of the prior encounter with the predatory perch. Interestingly, the presence of the nonexposed female was not enough to alter the male's perception of predation risk. One explanation is that male desert gobies are more vulnerable to predator attacks during reproductive interactions due to their colorful displays and larger body sizes (i.e., have higher prey profitability; cf. Pocklington and Dill 1995). Consequently, if predators are differentially attracted to males, the presence of females may not be a reliable sign of a predator-safe environment (Forsgren and Magnhagen 1993).

Given the role of courtship in mate attraction, reduced courtship could have implications for male reproductive success (Wong and Svensson 2009; Svensson et al. 2010; Lehtonen et al. 2011; Symons et al. 2011; Svensson et al. 2012). Indeed, several studies have demonstrated that a reduction in male courtship effort under high predation risk decreases male attractiveness to females (Fuller and Berglund 1996; Candolin 1997; Kelly and Godin 2001). Choice of nest sites, however, could potentially moderate the effect of predators on courtship behavior. In desert gobies, the abundance of retreat sites can be highly variable, with shallow, rocky habitats affording greater protection from deep-bodied fish predators (Michelangeli M, Wong BBM, personal communication). Although we controlled for nest selection by offering males same-sized nests located in the centre of the aquarium, studies in other species have shown that individuals may choose nest location in response to predation risk. For example, male 3-spined sticklebacks, *Gasterosteus aculeatus*, prefer to nest in structurally complex habitat in the presence of predatory perch, *Perca fluviatilis*, and, by so doing, are able to court under the safety of cover (Candolin and Voigt 1998).

As far as we are aware, this is the first study to show that male courtship behavior is not only sensitive to the immediate presence of a predator but can also persist even after the predatory threat has abated. Males that were previously exposed to a predator preferred to take refuge in their nests than engage in courtship of a female. Importantly, these results suggest that prey sensitivity to predators can extend beyond direct contact and that studies only considering prey responses in the presence of predators may be missing an important aspect of prey behavior.

## FUNDING

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