

## Field verification of the use of chemical alarm cues in a coral reef fish

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**Abstract** Chemical alarm cues function as early indicators of a predation threat and influence the outcome of predator–prey interactions in the favour of the prey animal. The tropical goby, *Asterropteryx semipunctatus*, responded with a stereotypical alarm response, including reduced movement and feeding, following exposure to water that contained chemical cues from injured conspecifics under natural field conditions. Gobies did not exhibit an alarm response when challenged with extracts from damaged fish from a different taxonomic family. The behavioural response in the field was similar to that observed in laboratory experiments. This study verifies the use of chemical alarm cues in a marine fish in their natural environment.

**Keywords** Behaviour · Chemical alarm cue · Coral reef fish · Goby · Olfaction · Predation risk

### Introduction

A wide diversity of fishes have been found to release chemical alarm cues upon capture by predators (Smith 1992; Chivers and Smith 1998; Brown 2003; Brown and Chivers 2005). These alarm cues function to warn conspecifics of the presence of an active predator (Mathis and Smith 1993). The alarm cue is only released upon damage of the epidermis of a prey fish and therefore acts as an honest indicator of predation threat.

Until recently the majority of studies on chemical alarm cues were conducted in the laboratory. Magurran et al. (1996) examined the behavioural response of European minnows (*Phoxinus phoxinus*) in the wild and found no significant anti-predator behavioural response to conspecific alarm cues. They argued that laboratory studies are ecologically unrealistic and yield false-positive results, and called for field tests to verify the use of chemical alarm cues by fishes under natural conditions. In recent years a number of field studies have been conducted to provide field verification of the existence of chemical alarm cues. Field-based trapping studies have demonstrated that Trinidadian guppies (*Poecilia reticulata*) (Brown and Godin 1999), brook stickleback (*Culaea inconstans*) (Wisenden et al. 1995), fathead minnows (*Pimephales promelas*), and finescale dace (*Chrosomus neogaeus*) (Brown et al. 2000) avoid areas labelled with alarm cues. Avoidance of areas labelled with skin extracts from conspecifics has also been demonstrated in wild populations of blacknose shiners (*Notropis volucellus*) (Wisenden et al. 2004), redbelly dace (*Phoxinus eos*), finescale dace (*C. neogaeus*) (Friesen and Chivers 2006), minnows (*P. promelas*) (Wisenden and Barbour 2005), brook charr (*Salvelinus fontinalis*) (Leduc et al. 2004), and brook stickleback (*Culaea inconstans*) (Friesen and Chivers 2006) by direct observation using underwater cameras. Mirza and Chivers (2000) demonstrated that brook charr (*S. fontinalis*) trained to recognise predator odour by pairing alarm cues with chemical stimuli from the predator, gained a survival benefit during staged encounters with a predator in the field. It appears that chemical alarm signalling is common in freshwater fishes and of ecological importance under natural conditions.

The majority of fishes shown to utilise chemical alarm cues inhabit freshwater systems. Of the few marine fish species that have been examined, alarm systems have been

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described in sculpins (Cottidae) (Hugie et al. 1991; Chivers et al. 2000), catfish (Ariidae) (Smith 2000) and gobies (Smith 1989). To date, no field studies have been conducted to verify the response to conspecific alarm cues in marine fishes. The tropical marine goby *Asterropteryx semipunctatus* (family Gobiidae) has been shown to respond with an alarm response to conspecific skin extract in the laboratory (Smith 1989). The present study investigated the existence of a chemical alarm response in *A. semipunctatus* under natural field conditions. The results were compared to similar laboratory trials to determine the utility of laboratory tests of alarm cues.

## Materials and methods

### Field experiment

In order to test if *A. semipunctatus* respond to chemical cues from conspecifics in their natural environments, underwater experiments were conducted in Pioneer Bay, Orpheus Island, Great Barrier Reef, Australia. The coral rubble on the reef flat and reef crest is the preferred habitat of *A. semipunctatus*, which forms large aggregations in these areas. All experimental trials were conducted using SCUBA on the reef flat at depths between 3 and 5 m.

*Asterropteryx semipunctatus* were exposed to chemical cues from: (1) damaged skin of conspecifics; or (2) damaged skin from a phylogenetically distant species, *Pomacentrus moluccensis* (family Pomacentridae). *P. moluccensis* also lives in a different habitat from *A. semipunctatus* so we would not predict cross-species recognition of heterospecific alarm cues (Mathis and Smith 1993). The conspecific skin extract contains an alarm cue (Smith 1989) and was therefore predicted to trigger an alarm response in conspecifics. To control for a general alarm response to the chemical stimuli from any injured fish, *A. semipunctatus* was exposed to skin extract from *P. moluccensis* in control trials. Thirteen control and treatment trials were conducted.

Skin extracts were prepared from 13 *A. semipunctatus* (mean standard length (SL)  $32.46 \pm 3.86$  mm SD) and 13 *P. moluccensis* (mean SL  $47.33 \pm 4.11$  SD). To prepare skin extracts underwater, a fish (either *A. semipunctatus* or *P. moluccensis*) was caught using anaesthetic clove oil (Munday and Wilson 1997), put in a  $70 \times 50$  mm<sup>2</sup> click-seal bag containing approximately 30 ml of sea water and killed by a quick squeeze of the brain case. The skin of the fish was then rubbed lightly against a sharp object placed in the bag 25 times on each flank, causing superficial damage to the skin, but only a minor damage to the muscle tissue. A disposable syringe equipped with a needle was used to puncture the bag and withdraw 15 ml of the water contained

in the bag. The capture of the “donor” fish and the preparation of the skin extract were performed at least 10 m down current from the focal prey fish to be tested for an alarm response.

A 1.5 m plastic stimulus injection tube was attached to the substratum using metal skewers. The tubing terminated approximately 1 m up-current from the focal *A. semipunctatus*, and thus created a distance of approximately 2.5 m between the fish and the observer. The focal fish were adults (estimated to be 30 to 35 mm SL), that lived in groups of moderate density (visually estimated as 15–20 m<sup>-2</sup>) within a rubble bed. The stimulus tube was set up so that the focal goby was the first goby directly down current of the tube. During trials the current speed was estimated from the movement of neutral density particles moving over at 0.5 m distance and did not exceed 0.04 m s<sup>-1</sup> (range 0.01 to 0.04 m s<sup>-1</sup>). Behaviour of the fish was quantified 6 min before and after the injection of a stimulus. At the end of the pre-stimulus period the test stimulus, consisting of conspecific skin extracts (containing the alarm cue) in treatment trials, and skin extracts from *P. moluccensis* (alarm cue extract control) in control trials, were injected into the tubing immediately followed by 60 ml of seawater to slowly flush the stimulus through the tubing. Both stimulus and control substances had no colour and were not visually detectable by the observer when released.

*Asterropteryx semipunctatus* is a cryptic negatively buoyant benthic fish that moves episodically with movements separated by periods when they remain stationary on the substratum. *A. semipunctatus* responds to chemical stimuli from injured conspecifics and visual cues of live predators by remaining motionless, freezing and by bobbing (Smith 1989). Behaviours in four categories were recorded: moves, feeding strikes, bobs and retreats into shelter, the latter two being rare. Each time a goby changed position it was recorded as a move. A bob consisted of slowly raising the anterior of the body by extension of the pelvic fins, followed by a slow ascent and gulping of water. A fish could bob without changing position, change position without bobbing or do a combination of the two. All feeding strikes made by fish were counted regardless whether the prey item was caught or not.

### Laboratory trials

To compare the behavioural responses to conspecific skin extract of *A. semipunctatus* in the laboratory and under natural field conditions, experiments were conducted to investigate the response of *A. semipunctatus* to skin extracts from conspecifics and from a phylogenetically distant species (swordtails, *Xiphophorus helleri*) in the laboratory. Swordtails were obtained commercially and were maintained in

dechlorinated fresh water at approximately 27°C. All gobies were collected in Pioneer Bay, Orpheus Island using clove oil and a hand net. The gobies were brought back to James Cook University where they were maintained in flowing seawater under approximately 12L:12D photoperiod at 27°C. The gobies were fed daily with live brine shrimp (*Artemia franciscana*) and commercial flake food during a 2-week acclimation period.

All observations were conducted in 33 l tanks with flowing seawater (mean 0.40 l per min  $\pm$  0.08 SD). The substratum consisted of a 3 cm thick layer of aquarium gravel, and an airstone was placed at the back of the tank. Plastic tubing was attached to the airline to enable the injection of extracts into the tank. The end of the tubing was attached approximately 1 cm from the airstone, which facilitated the rapid dispersal of the extracts in the test tank. Broken terracotta tiles were placed in the middle of the tanks forming a low, structurally complex 5  $\times$  5  $\times$  5 cm<sup>3</sup> shelter in order to mimic the coral rubble shelters gobies inhabit naturally. Groups of three, randomly selected gobies were placed in 13 aquaria (21 males, mean SL 33.67 mm  $\pm$  5.18 SD; 18 females, mean SL 31.36 mm  $\pm$  5.18 SD). Pilot tests indicated that individuals in groups of less than three gobies per test tank displayed abnormal behaviour spending most of their time under shelter. By putting gobies in groups of three their activity levels and group densities were similar to that observed in the wild.

Skin extracts were prepared from five male (mean SL 32.24 mm  $\pm$  4.74 SD), and eight female (mean SL 29.64 mm  $\pm$  7.16 SD) *A. semipunctatus*. The donor fish were killed by a quick squeeze of the brain case. The skin extract was then prepared by putting the fish in a clean disposable plastic petri dish, making 25 superficial vertical cuts on each flank with a razorblade, and then rinsing it in 15 ml of seawater. The cuts damaged the skin but caused only minor flesh damage. The stimulus water was then filtered through filter paper (125 mm  $\varnothing$ , qualitative 1) to remove any solid particles such as scales and drawn up into a disposable syringe for injection into the tank. The skin extracts were used within 20 min of preparation as extracts may lose potency if frozen or stored for long periods at room temperature (Smith 1989).

As a standard testing protocol the behaviour of three *A. semipunctatus* was quantified for 10 min within each tank prior to the injection of the extract into the tank. Immediately prior to experimental observation 60 ml of tank water was drawn out through the stimulus injection tube and discarded to remove any stagnant water that may have collected in the tubing. Another 60 ml of tank water was drawn through the tubing and kept for later use. The chemical stimuli were then injected through the tubing followed by 60 ml of tank water in order to flush the test substance into the tank. The fish were then observed for

another 10 min. Both stimulus and control substances had no colour and were not humanly detectable when released. Trials with vegetable dye demonstrated that it took 39  $\pm$  4.47 s (mean  $\pm$  SD,  $n = 5$ ) following the injection for the dye to disperse throughout the tank. Thirteen control and treatment trials were successfully undertaken.

A single observer stood behind a blind, observing the tank through small eye slits and recorded the behaviour with mechanical counters. Behaviours in two categories were recorded: moves and feeding strikes. These behaviours were defined as per the field experiment above.

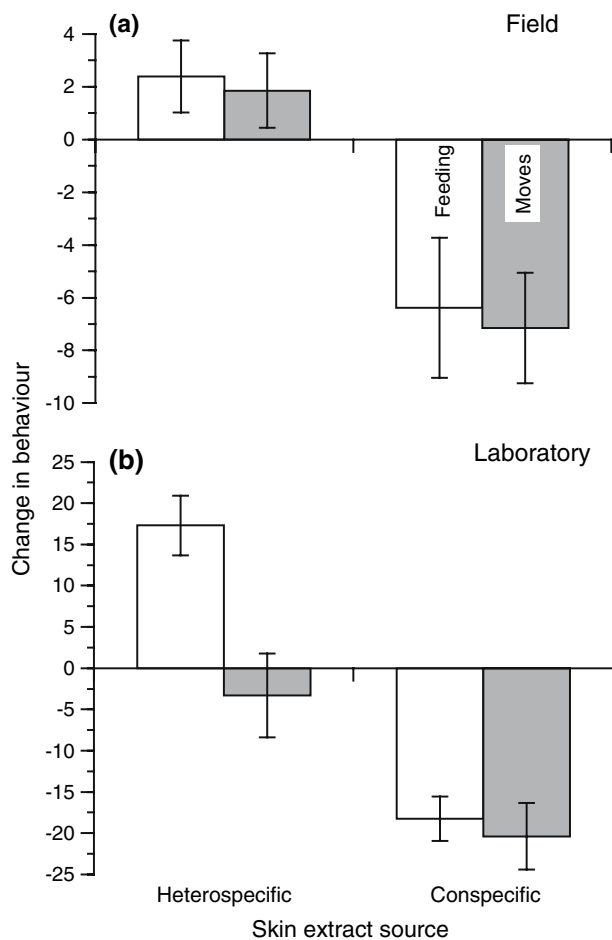
#### Statistical analyses

The influence on fish behaviour of the two skin extracts (Treatments: conspecific and heterospecific skin extracts) was tested with one-way MANOVA. Separate analyses were undertaken for the laboratory and field experiments due to differences in methodology employed preventing direct statistical comparison. The dependent variables were the difference between the pre and post-stimulus counts of the number of feeding strikes and moves for each trial. Only feeding strikes and moves were sufficiently common to allow statistical comparison. For the laboratory trials, data were converted to mean behaviour per fish (as total behaviours of three fishes were recorded during the trials). To further explore the nature of significant differences found by MANOVA, one-way ANOVAs were used to examine whether there were significant differences between treatments in one or both variables. A Bonferroni corrected  $\alpha$  of 0.025 was used for these tests to maintain an experiment-wise type I error rate of 0.05 (Quinn and Keough 2002). Assumptions of normality and homogeneity of variance were examined using residual analysis.

#### Results

The presence of SCUBA divers had no obvious effect on the behaviour of gobies in the field. Gobies spent the majority of their time feeding on the algal-coated coral rubble and occasionally on particles in the water column. Any potential effect that SCUBA divers had on the behaviour of the gobies would have been the same for treatment and control trials and would therefore not have influenced the overall results.

There were significant changes in the goby behaviour in response to the two skin extracts (i.e., control and conspecific) in both the field (Pillai's trace = 0.354,  $df$  2, 23,  $p = 0.006$ ) and laboratory (Pillai's trace = 0.723,  $df$  2, 23,  $p < 0.001$ ). In the field, gobies reduced their number of moves and number of feeding strikes in response to conspecific skin extracts (Fig. 1a, Table 1a). In contrast, gobies



**Fig. 1** Mean change ( $\pm$ SE) in number of feeding strikes, and moves of *Asterropteryx semipunctatus* between observation periods before and after exposure to skin extracts from a heterospecific (extract control: *Pomacentrus moluccensis* for field study and *Xiphophorus helleri* in the laboratory) or conspecific skin extract in the **a** field (6 min observation periods) or **b** laboratory (10 min observation periods);  $n = 13$  trials

displayed slight increases in feeding strikes and moves in response to heterospecific skin extracts (Fig. 1a, Table 1a).

A similar trend was shown in the laboratory, with a decrease in the number of moves and number of feeding strikes in response to conspecific skin extracts, and an increase in feeding strikes in response to heterospecific extracts (Fig. 1b, Table 1b). There was no detectable change in moves in response to heterospecific extracts (Fig. 1b). Overall, gobies showed similar behavioural trends in the field and laboratory trials between skin extract treatments (Fig. 1).

## Discussion

In the field experiment, clear differences were found in the behavioural responses of *A. semipunctatus* to conspecific skin extracts, and skin extracts from *P. moluccensis*. Indi-

**Table 1** Comparison of mean change in number of moves and feeding strikes of *Asterropteryx semipunctatus* between observation periods before and after exposure to skin extracts from a heterospecific or a conspecific skin extract (Treatment) in the field (a) and laboratory (b) experiments

	Source of variation	df	MS	F	p
a. Field					
Movement	Treatment	1	526.500	12.746	0.0015
	Error	24	41.30		
Feeding	Treatment	1	499.846	8.642	0.0072
	Error	24	57.839		
b. Laboratory					
Movement	Treatment	1	8209.385	62.054	<0.0001
	Error	24	132.295		
Feeding	Treatment	1	1895.538	6.868	0.0149
	Error	24	275.994		

$n = 13$  trials

viduals subjected to water that contained cues from an injured conspecific significantly reduced their movement and feeding strikes. This is a stereotypical alarm response similar to that seen in response to chemical or visual cues of their natural predators, such as lizardfish (Smith 1989; Smith and Smith 1989). *A. semipunctatus* did not exhibit increases in anti-predator behaviours in response to skin extracts from either of the two phylogenetically distant fish species, which suggests that the alarm response is not a general response to any injured fish, but rather the response is triggered by specialised alarm chemicals produced in the epidermis by conspecifics (Smith and Smith 1989).

Previous studies have suggested that the response to chemical alarm cues is a result of laboratory artefact or biased field trapping studies (e.g., Magurran et al. 1996). In the present study, *A. semipunctatus* responded with a similar decrease in movement and feeding strikes in both the field and laboratory trials. The consistency of the results, recorded by the same observer, indicates that the fright response to conspecific skin extracts is not a laboratory artefact in *A. semipunctatus* but in fact is triggered by chemical alarm cues contained in the epidermis of conspecifics.

Cursory examination of the magnitude of the change in behaviours in response to skin extracts suggests that there was a greater response elicited by gobies in the laboratory trials than in the field. This enhanced response in the laboratory may be due to a reduction in the number of competing stimuli in the laboratory compared to the field (Mirza and Chivers 2003). However, it is difficult to determine whether the magnitude of difference is a methodological artefact or is representative of a real difference in the intensity of response between field and laboratory fish. The magnitude

of difference in behavioural response to skin extracts may be due to a number of differences between the field and laboratory experiments, which complicate the interpretation of the relative magnitude of the responses. Due to the logistics of recording behaviour in the field and the potentially short latency period of the chemical cue preparations, we devised a methodology to extract a chemical alarm cue and a control cue underwater. It is likely that the cue concentrations between field and laboratory trials were different, although attempts were made to make them as comparable as possible. A number of studies of freshwater species have shown that the intensity of anti-predator responses can be directly proportional to the concentration of alarm cues to which fish are exposed (e.g., Brown et al. 2001a). Differences in current regime, small-scale turbulence, topography of the substratum and behavioural confounding from other naturally released cues will always be a problem in such comparisons of field and laboratory results. Other factors that may have influenced the relative magnitude of the response in the field and laboratory trials in the present study include: the difference in the species from which control cues were extracted; the history of predation of the test subjects (Brown 2003); the duration of the observation periods (6 min in the field vs 10 min in the laboratory); the difference in substratum between field and aquarium trials (Houtman and Dill 1994); and differences in the ambient density of conspecifics (Brown et al. 2006). Despite these problems, it is still notable that similar patterns of response were observed in the field and laboratory studies, indicating a consistent influence of alarm cues on fish behaviour.

Evidence suggests that future results obtained from laboratory experiments on *A. semipunctatus* can be interpreted with respect to the ecology of this species in its natural environment. Several recent studies using similar direct observation techniques (Brown and Godin 1999; Brown et al. 2001b; Golub et al. 2005) or underwater cameras (Leduc et al. 2004; Wisenden et al. 2004; Wisenden and Barbour 2005) have verified the use of chemical alarm cues in natural settings for a number of freshwater prey animals.

*Asterropteryx semipunctatus* consistently responded to conspecific skin extracts with a reduction in activity. Reduced activity is a common alarm response in fishes and is an especially effective anti-predator behaviour in cryptic species (Edmund 1974). By reducing movement and feeding in response to conspecific skin extracts, gobies are likely to increase their probability of survival by reducing the risk of detection and capture by predators (Mathis and Smith 1993; Berejikian et al. 1999). In freshwater systems the detection of alarm cues (Mirza and Chivers 2000), predator diet cues (Mirza and Chivers 2003) and disturbance cues (Mirza and Chivers 2002) has been demonstrated to enhance the survival of brook charr (*S. fontinalis*) during staged encounters with a predator.

In conclusion, evidence suggests that chemical alarm cues emitted by a damaged *A. semipunctatus* during capture may trigger anti-predator behaviour in conspecifics that detect the cue, both in the field and in the laboratory. *A. semipunctatus* has also been shown to be capable of rapidly learning the identity of potential predators through the coupling of novel olfactory cues with alarm cues (Larson and McCormick 2005). Studies indicate that anti-predator behaviour elicited from alarm cue detection can be transmitted visually to other conspecifics, as well as to heterospecifics, that did not detect the chemical cue (Smith and Smith 1989; Mathis et al. 1996). This social learning can result in the rapid identification of predators within a local area (Brown and Laland 2003); a mechanism which will particularly benefit individuals when they first enter a local area as either naïve recruits or immigrants (McCormick and Holmes 2006). A mechanism that is as flexible as the olfactory learning of predators is likely to be particularly useful in fishes that inhabit species-diverse and spatially patchy coral reef environments. The present study is one of the first steps toward demonstrating the ecological importance of olfactory alarm cues in the ecology of coral reefs fishes.

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