




Association of predation risk with a heterospecific vocalization by an anabantoid fish

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Abstract

Honey gouramis (*Trichogaster chuna*) received chemical alarm cues derived from conspecific epidermal tissue and, simultaneously, the vocalization produced by a heterospecific gourami species, the sparkling pygmy gourami (*Trichopsis pumila*). Control trials paired water with the vocalization. In trials that received alarm cues, honey gouramis significantly increased activity relative to control trials that received water, suggesting an attempt to flee and search for refuge. When the recording of the vocalization was later replayed to test fish without any additional chemical cue, fish that had previously experienced the alarm cue froze while those that had received water with the vocalization did not change their behaviour. These data indicate that honey gouramis recognize and respond to chemical alarm cues, making this report the second anabantoid species to be recorded with this response. Second, these data indicate that honey gouramis can associate risk of predation with a novel auditory stimulus, including vocalizations from other species. These data suggest the potential for vocalizations to evolve into alarm signals in this group of fishes.

KEYWORDS

anabantoidei, chemical alarm cues, predator-prey, risk assessment, vocalization

1 | INTRODUCTION

Predation, and avoidance of risk of predation, shape the behavioural decision-making of most animals (Lima & Dill, 1990). In aquatic habitats, public information in the form of chemical compounds passively released as a by-product of predator-prey interactions constitute a rich source of information about predation risk. The presence of these chemicals cue the best timing and context for executing antipredator behavioural strategies that minimize predation risk (Ferrari *et al.*, 2010; Wisenden, 2000, 2015a; Wisenden & Chivers, 2006). Damage-released chemical alarm cues innately invoke antipredator behaviours such as area avoidance, reduction in activity, increased shoal cohesion and movement out of the water column (Ferrari *et al.*, 2010; Lawrence & Smith, 1989; Mathis & Smith, 1992; von Frisch, 1942) and responses to a broader range of stimuli are often acquired by associative learning (Brown, 2003; Göz, 1941; Hall & Suboski, 1995; Mathis & Smith, 1993; Suboski, 1990). Recognition

and response to a novel stimulus is acquired when the novel stimulus (conditioned stimulus) is presented simultaneously with a chemical alarm cue (unconditioned stimulus). This so-called releaser-induced recognition learning (Hall & Suboski, 1995) requires only a single pairing of unconditioned and conditioned stimulus for near-permanent association to occur because natural selection selects strongly against slow learners.

The use of auditory stimuli to detect risk of predation is relatively understudied even though many fish species have an excellent sense of hearing (Ladich, 2019, 2021). Fishes in the Otophysi possess specialized vertebrae, Weberian ossicles, that link the gas bladder to the inner ear, giving them an excellent sense of hearing (Kasumyan, 2008; Ladich, 2019; Popper & Fay, 1993; Yan, 1998). The Otophysi is a speciose group representing approximately 67% of all freshwater fish species (Nakatani *et al.*, 2011), suggesting that the enhanced ability to detect auditory stimuli contributed to their evolutionary success. Fathead minnows *Pimephales promelas* Rafinesque 1820, glowlight tetras

Hemigrammus erythrozonus Durbin 1909 and zebrafish *Danio rerio* Hamilton 1822 can associate novel auditory stimuli with risk of predation when a tone is played at the same time that test fish are simultaneously exposed to chemical alarm cues released from the damaged skin of conspecifics (Seigel *et al.*, 2021; Wisenden *et al.*, 2008).

Some non-otophysan fishes have independently become hearing specialists. The Anabantoidei (gouramis, bettas) of equatorial Asia and Africa occur in warm-water bodies with low levels of dissolved oxygen (Adamek-Urbańska *et al.*, 2021). These fishes possess a labyrinth organ of vascularized canals in their head (the suprabranchial chamber) that hold atmospheric air for the purpose of gas exchange. Thus, analogous to the otophysi, anabantoids possess an internal pocket of air that serves secondarily as a resonating chamber for detecting sound (Ladich & Popper, 2001; Ladich & Yan, 1998; Yan, 1998). Sensitivity to the acoustic landscape offers an evolutionary opportunity to use sound for the detection of predation risk.

Here, we tested if an anabantoid species, the honey gourami *Trichogaster chuna* (Hamilton 1822), can learn to associate auditory stimuli with predation risk. Rather than using an artificial tone stimulus as the unconditioned stimulus, we used a recording of the territorial call of a heterospecific gourami species, the sparkling pygmy gourami *Trichopsis pumila* Arnold 1936. These species do not overlap geographically. *T. chuna* occur in India and Bangladesh, whereas *T. pumila* occurs in Thailand, Laos and Indonesia (Froese & Pauly, 2021). Thus, this experiment tested three questions. First, we tested if honey gouramis recognize and respond to chemical alarm cues from conspecifics. Second, we asked if honey gouramis use releaser-induced recognition learning to associate predation risk with an auditory stimulus. Third, we asked if honey gouramis can associate risk of predation with a vocalization from another species of gourami, implying the present and/or future potential for vocal alarm calls in the anabantoidei.

2 | MATERIALS AND METHODS

Adult honey gouramis (*Trichogaster chuna*) were purchased through a local pet store and held in 185 l stock tanks filled with heated dechlorinated tap water. Fish were fed commercial flake food. Laboratory lights were set in a 12 h light:12 h dark cycle.

2.1 | Stimulus preparation

An alarm cue was made by killing five adult honey gouramis [total length (mean \pm s.d.) = 41.2 \pm 1.8 mm] with an overdose of MS222 (methane tricaine sulfonate) in accordance with MSUM IACUC protocol 19-R/T-BIO-018-N-Y-C. Skin fillets on both sides of each fish were carefully removed and placed in 150 ml of distilled water. A total of 18.98 cm² of skin was homogenized with a hand blender (Cuisinart Smart Stick 2 Speed Hand Blender, Cuisinart, Stamford, CT, USA) for 30 s to release alarm cues. The resulting solution was filtered through a loose wad of polyester fibre, diluted to 170 ml, aliquoted into 17 10 ml doses (1.11 cm² of skin per dose) and frozen at -20°C until needed.

The auditory stimulus was a 3-s long video recording of a sparkling pygmy gourami (*Trichopsis pumila*) (<https://www.youtube.com/watch?v=BWDsDkUMRMc>, mp3 file in Supporting Information Appendix S1), clicks and grunts repeated 10 times for a total duration of 30 s. The call was played through a pair of waterproof earbud earphones (PyleHome marine grade IP-7 model PWPE10B, Sound Around Inc., Brooklyn, NY, USA) placed inside the tank on the bottom in the centre of the panel facing the observers. The earbud earphones were connected to an iPhone8, played with the phone's volume set to maximum. This format produced a standardized, repeatable auditory stimulus (Figure 1).

2.2 | Experimental protocol

Individual honey gouramis were placed in 37 l aquaria ($W \times L \times H = 25 \times 50 \times 30$ cm) with a bare glass bottom and a small shelter object made from a ceramic tile (10.8 \times 10.8 cm) on four cylindrical legs 4.8 cm in length. Tanks were visually isolated by placing rigid black plastic Coroplast panels between adjacent tanks. Each tank was equipped with an air-powered sponge filter. A second piece of airline tubing was wedged into the filter's lift tube for surreptitious injection of test stimuli. The injection tube was about 2 m long and extended out into the aisle of the aquarium room where observers could inject test cues without disturbing test fish. A grid measuring 5 \times 5 cm was drawn on the face of the pane facing observers to facilitate scoring of activity (number of lines crossed in 5 min) and vertical distribution (horizontal row within the grid occupied by the fish), recorded every 10 s for 5 min. We also recorded the time (s) spent in the shelter. We recorded activity, vertical distribution and shelter use for 5 min before and after cue injection. In addition, we noticed that during playback of the croak call during test trials, honey gouramis engaged in freezing behaviour, defined as remaining motionless for at least 10 consecutive seconds. We recorded the seconds engaged in freezing behaviour during the 30 s long period while the croak vocalization was being played.

Each fish was tested twice: once in a conditioning trial and again in a test trial. For conditioning trials, test fish were presented with the

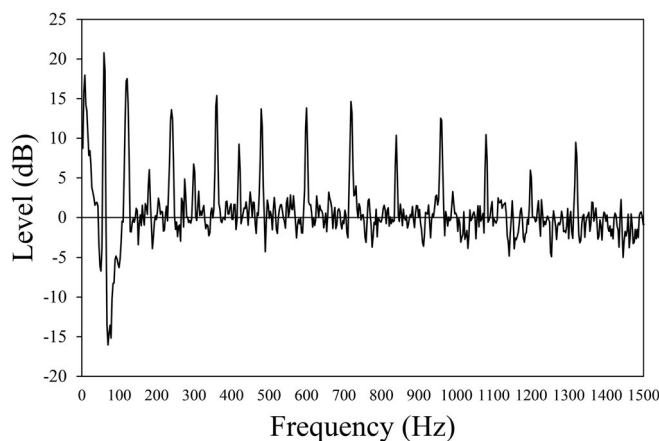


FIGURE 1 Spectrograph of the call of a sparkling gourami (*Trichopsis pumila*) used as the novel auditory stimulus in conditioning training. Here the ambient background noise level is set to 0 dB

croak call of a sparkling gourami and either 10 ml of alarm cue ($n = 15$) or 10 ml of blank control water ($n = 15$). Tanks were drained and refilled with fresh dechlorinated water and all injection lines were replaced between conditioning trials and test trials. For test trials, all fish ($n = 30$) were presented with the croak call of a sparkling gourami.

2.3 | Data analysis

Few of the variables were normally distributed (Kilmogorov–Smirnov test, $P < 0.05$), therefore we used Mann–Whitney U tests to compare the change in behaviour of fish in water (control) trials to change in behaviour to fish conditioned with an alarm cue. Separate tests were conducted for conditioning trials and test trials. We used Wilcoxon matched-pairs signed-ranks tests to compare change in behaviour in conditioning trials versus change in behaviour in test trials. The statistical software used was SPSS (version 26, <https://www.ibm.com/products/spss-statistics>).

2.4 | Ethical statement

The care and use of experimental animals complied with the Office of Laboratory Animal Welfare (OLAW) animal welfare laws, guidelines and policies as approved by the Minnesota State University Moorhead Institutional Animal Care and Use Committee, permit reference number 19-R/T-BIO-018-N-Y-C.

3 | RESULTS

3.1 | Conditioning trials

There was no statistically significant change in vertical distribution ($Z = -0.748$, $P = 0.455$) but the alarm cue caused a significant

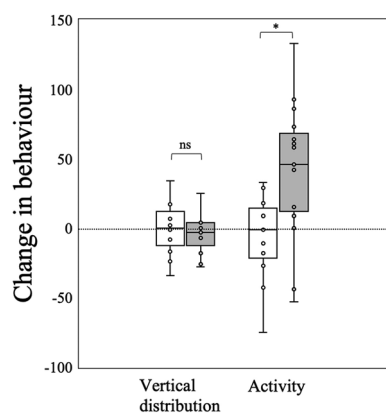


FIGURE 2 Median \pm quartiles change in activity and vertical distribution for conditioning trials (croak call of sparkling pygmy gourami *Trichopsis pumila* + either water or alarm cue) by honey gouramis (*Trichogaster chuna*). Open bars, trials that used water as the cue; shaded bars, trials that used alarm cue. ns, not significant ($P > 0.05$), *Significant difference ($P < 0.05$)

increase in activity ($Z = -2.469$, $P = 0.014$; Figure 2). Shelter objects were used in only two of the 15 trials during conditioning and never in any of the test trials, therefore those data are not shown. During conditioning trials freezing behaviour occurred in two of the 15 trials that used alarm cues but none that used water. There was no difference in frequency of freezing behaviour between water trials and alarm cue trials ($Z = -1.439$, $P = 0.150$; Figure 3).

3.2 | Test trials

Freezing behaviour occurred only during the 30 s window while the croak call was played in test trials. Fish conditioned with alarm cue + croak froze significantly longer and more frequently than fish

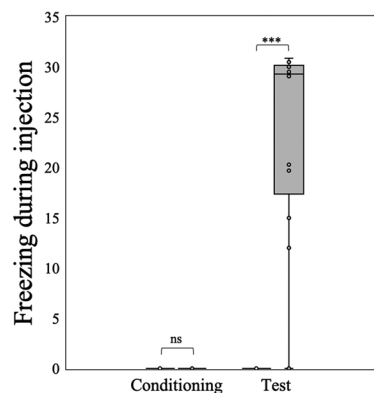


FIGURE 3 Median \pm quartiles duration (s) of freezing behaviour by honey gouramis (*Trichogaster chuna*) during cue injection during conditioning trials (croak call of sparkling pygmy gourami *Trichopsis pumila* + either water or alarm cue) and during subsequent test trials (croak call only). Open bars, trials that used water as the cue; shaded bars, trials that used alarm cue. ns, not significant ($P > 0.05$), ***Significant difference ($P < 0.001$)

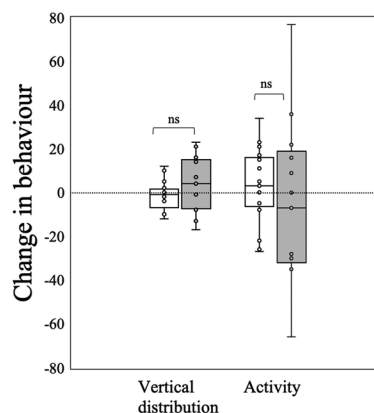


FIGURE 4 Median \pm quartiles change in activity and vertical distribution by honey gouramis (*Trichogaster chuna*) for test trials (croak call only). Open bars, fish that had been conditioned with water + croak call of sparkling pygmy gourami *Trichopsis pumila*; shaded bars, fish that had been conditioned with alarm cue + croak call. ns, not significant ($P > 0.05$)

conditioned with water (duration of freezing $Z = -4.546$, $P < 0.001$; Figure 3). Thirteen of the 15 trials for fish that had been conditioned previously with alarm cue exhibited freezing behaviour when the croak call was played (frequency of freezing, Fisher exact test $P < 0.001$). There were no other changes in behaviour (vertical distribution $Z = -1.245$, $P = 0.213$; activity $Z = -1.100$, $P = 0.271$; Figure 4).

4 | DISCUSSION

Initially, honey gouramis gave no response to playback of the croak call from a sparkling gourami unless the call was paired with honey gourami chemical alarm cues, indicating no pre-existing recognition of the call. Gouramis increased activity in response to conspecific alarm cues, clearly aroused and hypervigilant, but showed very little freezing behaviour. In contrast, freezing was the dominant response to the croak call in test trials by fish conditioned with alarm cue + croak call, but only while the call was being played. Taken together, these data indicate that (a) honey gouramis respond behaviourally to chemical alarm cues released from damaged skin of conspecifics, (b) honey gouramis are able to acquire recognition of a novel acoustic indicator of risk through releaser-induced associative learning and (c) they can form an association of risk with a vocalization of a heterospecific gourami.

Our data cannot distinguish whether or not conditioned responses to heterospecific vocalizations were specific to the auditory stimulus with which they were conditioned, or if the response is a generalized response to any sound stimulus. However, previous work using zebrafish showed that auditory stimuli are not generalized in the same way that visual and olfactory stimuli are (Seigel *et al.*, 2021). In that study, zebrafish conditioned to one tone frequency responded when that same tone frequency was replayed but did not respond when a different tone frequency was played (Seigel *et al.*, 2021). Behavioural responses to novel auditory stimuli observed here would be the same if honey gouramis interpreted vocalizations of sparkling gouramis as an alarm call, a sound issued by the predator or a sound from any source that is correlated with the release of chemical alarm cues.

Although most small-bodied fishes exhibit a suite of antipredator behavioural strategies, antipredator behavioural responses are not well characterized for anabantoid fishes. The behavioural responses observed in this study are similar to general responses to predation risk in small shoaling fishes, such as reduction in activity (including freezing), and skittering/dashing and flight (increase in activity), but not others such as movement out of the water column, shoal cohesion and seeking shelter (Ferrari *et al.*, 2010; Lawrence & Smith, 1989). Species-specific responses may reflect constraints of the natural habitat in which these species evolved. It is interesting that the fish increased lines crossed with little freezing in response to alarm cue and auditory cue, but then during retesting with the auditory cue conditioned fish froze without changing their lines crossed. It may be the case that the alarm cue indicated an imminent threat that causes a flight response, whereas freezing might be more effective toward the vocalization alone because an attack has not yet occurred. Anabantoids are generally solitary and often occur in dense

vegetation (Craig *et al.*, 2004; Gupta, 2015; Menon, 1999; Rahman, 2005; Wolf & Kramer, 1987) where there would be little opportunity or antipredator benefit from rapid flight and shoaling behaviour. Freezing behaviour is an effective strategy to avoid detection because predators detect motion visually and via mechanosensory receptors (e.g., Allouche & Gaudin, 2003; Modgan, 2019). Within anabantoid fishes, aggression directed at a mirror image by *Betta splendens* Regan 1910 is suppressed by chemical cues released from a torn fin, suggesting increased allocation to predator vigilance in response to chemical alarm cues (Ingersol *et al.*, 1976). Larval paradise fish (Anabantiformes: *Macropodus opercularis*, L. 1758) freeze ('hang') in the water column in response to visual and chemical stimuli from cichlid predators (Miklósi *et al.*, 1997). Croaking gouramis (*Trichopsis vittata*, Cuvier 1831) reduce escalated conflicts and frequency of vocalizations when a predator is nearby (Maidtisch & Ladich, 2021).

This study is one of the first reports of releaser-induced recognition learning (Suboski, 1990) in an anabantoid fish (see also Ingersol *et al.*, 1976). The learned association of predation risk with auditory stimuli demonstrated in this study corroborates earlier work on fathead minnows (Wisenden *et al.*, 2008) and zebrafish (Seigel *et al.*, 2021), both cyprinids in the otophysi (cyprinids, characins, silurids, catostomids) that possess Weberian ossicles that enhance detection of auditory stimuli (Amorim, 2006). The suprabranchial chamber used by anabantoids for gas exchange preadapted them to evolve into hearing specialists, including the ability to use auditory information for detecting, and learning to recognize, predation risk.

Labyrinth fishes have exploited the acoustic sensory modality for communication by innovating anatomical specializations to emit vocalizations during intrasexual contests over social hierarchies and intersexual communication during courtship (Amorim *et al.*, 2015; Ladich, 2015). Several genera of gouramis (*Betta*, *Colisa*, *Macropodus*, *Trichogaster*, *Trichopsis*) produce sounds, and of these, species in *Trichopsis* are the ones in which these anatomical specializations are most developed and they are also the genus that are most reliant on acoustic elements in behavioural displays (Ladich & Myrberg, 2006).

The evolution of sounds produced in response to predation is ripe for further study (Ladich, 2021). Vocalizations in response to danger or distress are well documented in at least 200 species in 37 families of marine fish and many ostariophysans such as characins and catfish (Fish & Mowbray, 1970; Myrberg Jr., 1981; see Ladich & Myrberg, 2006; Ladich, 2021 for reviews). It is important to distinguish between sounds released by prey that detect the presence of a predator ('disturbance vocalizations') from sounds released by prey that have been captured by a predator ('distress vocalizations'). There is no evidence that either type of sound reduces the probability of attack by a predator (Ladich, 2021), therefore fitness benefit to the senders of these sounds likely accrues from receivers other than the predator (e.g., McGregor, 2005). Sounds emitted by disturbed, but not-captured prey may serve as a means of alerting conspecifics and inducing shoaling defences that benefit the sender (Bairos-Novak *et al.*, 2019). Examples of 'disturbance vocalizations' are found in longspine squirrel fish *Holocentrus rufus* Walbaum 1792 and soldierfish

Myripristis berndti Jordan & Evermann 1903 that emit grunts and staccato sounds when moray eels enter their territory (Salmon, 1967; Winn *et al.*, 1964). Cod *Gadus morhua* L. 1758 produce grunts in response to conger eel and click sounds in response to seals or humans (Brawn, 1961; Ladich, 2021; Vester *et al.*, 2004). Serranids produce drumbeats when approached by sharks (Myrberg Jr., 1981). Alarm calls by the doradid *Platydoras costatus* L. 1758 and the pimelodid *Pimelodus blochii* Valenciennes 1840 are of high frequency, above the hearing ability of their predators and can only be perceived by hearing specialists (Ladich, 1997), suggesting a private communication channel to exclude illegitimate receivers (Dabelsteen, 2005).

The majority of vocalizations emitted in the context of predation are distress calls, emitted when in the jaws of a predator, or human-induced (Ladich, 2021). These calls are public information that provide useful information to nearby prey (Wisenden & Chivers, 2006; Wisenden & Stacey, 2005) and may ultimately attract kleptoparasites or secondary predators that prey on the primary predator, allowing the call sender to escape (Chivers *et al.*, 1996; Högstedt, 1983; Wisenden, 1998). Fitness benefits from distress calls have not yet been verified experimentally.

The ability to detect sounds, the ability to associate sounds with predation risk and the ability (in some) to produce sound would seem to provide all the of the components necessary for incipient evolution of alarm calling in this remarkable group of fishes (Wisenden, 2015b). However, evidence to date suggests that in at least one species, the croaking gourami, response to the visual presence of an oscar cichlid predator *Astronotus ocellatus* Agassiz 1831 is to reduce intrasexual interactions, including the croak call associated with these behaviours (Maiditch & Ladich, 2021). To our knowledge alarm calls are not known for any anabantoid species but perhaps future study will reveal one.

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AUTHOR CONTRIBUTIONS

Conception of research question and experimental design by B.D.W., A.R.S., I.G.D. and M.C.S. Data generation by A.R.S., I.G.D. and M.C.S. Spectrograph by A.S., A.R.S., I.G.D. and M.C.S. Data analysis and manuscript preparation by B.D.W.

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