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Evidence for incipient alarm signalling in fish

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Abstract

In Focus: Bairos-Novak, K.R., Ferrari, M.C.O., & Chivers, D.P. (2019). A novel alarm signal in aquatic prey: Familiar minnows coordinate group defences against predators through chemical disturbance cues. *Journal of Animal Ecology*, *88*, 1281–1290, https://doi.org/10.1111/1365-2656.12986. Chemicals released during predation have long been studied as cues to nearby prey that predators are active in the vicinity. Until now, these chemicals have been labelled as cues because there was no compelling evidence for the necessary components of a communication system, namely (a) voluntary control of release of information, (b) capacity for graded responses and (c) the presence of specialized structures for the production and release of the signal. New findings by Bairos-Novak, Ferrari, and Chivers (2019) show that fathead minnows alter the potency of disturbance "cues" when in the presence of other fathead minnows compared to when they are alone and produce either more or different disturbance "cues" when in the presence of familiar conspecifics compared to when they are in the presence of unfamiliar conspecifics. The behavioural response to these cues is shoaling, which would confer fitness benefits to the sender, thereby qualifying as a signal rather than a cue. This is a significant advancement in the field of chemical ecology of aquatic organisms because disturbance "cues" by fathead minnows bear two of the three hallmarks of an incipient disturbance "signal".

KEYWORDS
anti-predator behaviour, audience effect, disturbance cue, fathead minnow, signal evolution

Predation exerts unforgiving selection on prey populations. This is especially the case for fecund organisms, such as fishes, for which a very small percentage of offspring survive long enough to reproduce. Lima and Dill (1990) parsed predation into component steps of detection, attack, capture and ingestion. Each step in this predation sequence is associated with release of chemical information that provides receivers with information about the presence and nature of predation risk (Smith, 1992; Wisenden, 2000). Compounds released from mechanically damaged epidermal tissue, called alarm cues, reliably indicate the presence of an actively foraging predator (Ferrari, Wisenden, & Chivers, 2010; Von Frisch, 1941). In addition to their direct effects on prey behaviour, alarm cues serve as the unconditioned stimulus for forming associations between risk and predator odour (conditioned stimulus) and other correlates of alarm cue release (Suboski, 1990). Taken together, the ways in which fish use chemical information to assess risk have spawned a rich literature (for recent reviews see Ferrari et al., 2010; Wisenden, 2015a).

Literature about chemically mediated anti-predator behaviour has long wrestled with the distinction between gathering of public information by receivers (i.e. chemical cues) and deliberate release of information by senders (alarm pheromones or alarm signals) (Wisenden, 2015b). Alarm cue systems are driven solely by receiver-side selection, whereas alarm pheromones/alarm signals also involve sender-side selection to promote production and release of chemical signals in the correct context (Wisenden, 2015b, Figure 1). Until Bairos-Novak et al. (2019) highlighted here, all previous studies of chemically mediated predator–prey interactions have been descriptions of alarm cue systems, despite incorrect usage of terms such as

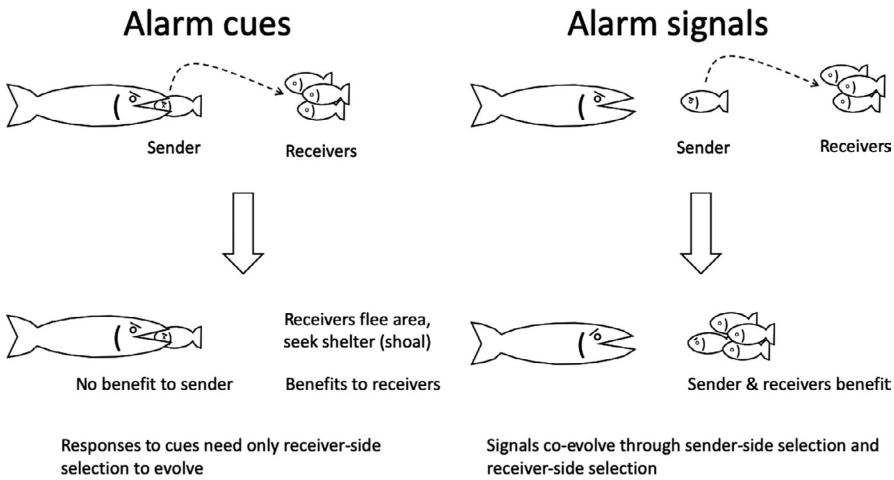

FIGURE 1 Responses to alarm cues (left panel) evolve because receivers that detect and respond to chemicals associated with predation decrease their probability of predation, and ultimately have a higher probability of reproduction. No benefits need to accrue to the sender for alarm cues to evolve. Damage-release alarm cues, dietary cues and kairomones (predator odours) can all be explained by receiver-side selection acting alone. Alarm signals (right panel) require the involvement of sender-side selection, shaped by fitness benefits that accrue to the sender from responses of receivers. Bairos-Novak et al. (2019) are the first to demonstrate incipient signalling (sender-side selection) in the context of chemically mediated predator–prey interactions in aquatic habitats

alarm "pheromone" or alarm "signal" in the alarm cue literature. The distinction between cue and signal is not a pedantic one. It is important to recognize the evolutionary processes that gave rise to responses to passively released cues (through receiver-side selection for adaptive responses to public information that reduce probability of detection, capture and ingestion) versus those that have evolved to include sender-side selection for the production and voluntary release of pheromone signals (Wisenden, 2015b, Figure 1).

A significant distractor in the study of chemically mediated predator–prey interactions has been the presence of specialized club cells in the skin of Ostariophysan fishes. The Ostariophysi is a superorder of fishes that comprise 64% of all freshwater species, including minnows, characins, catfishes and sundry others, that all possess club cells and behavioural alarm reactions to skin extract (Pfeiffer, 1977). These club cells are ideally positioned to serve as the source of an alarm substance (often called "*Shreckstoff*", which is the original term that Von Frisch (1941) used in his description of the phenomenon), leading many in the field to refer to these cells as alarm substance cells. Evolutionary ecologists were quick to recognize the paradox of cells that produce a signal that does not seem to benefit the sender (e.g. Smith, 1992). This problem was resolved when these cells were found to function as part of the immune system; that is, they perform a function that accrues fitness benefits to the individual that possesses them (Chivers et al., 2007). Epidermal club cells are best understood as being primarily maintained by their immune function in response to epidermal damage, but because they are located in the skin they became secondarily incorporated into an alarm cue system through receiver-side selection for detection and response to components of skin released by predator attack (Hintz, Courtney, Rachel, David, & Winnifred, 2017). Thus, until Bairos-Novak et al. (2019), detection of predation risk through olfaction seemed squarely in the realm of cues, that is the gathering of public information, and not through an evolved system of communication where senders accrue fitness benefits through control of the timing and context of signal release (Wisenden, 2015b).

Bairos-Novak et al. (2019) focussed their attention on another form of chemical information: disturbance cues released by startled, but uninjured, prey (Hazlett, 1985; Mirza & Chivers, 2002; Wisenden, Chivers, & Smith, 1995). Receivers respond to disturbance cues with increased predator vigilance, and anti-predator behaviours such as cohesive shoaling, which confers anti-predator benefits (Mathis & Smith, 1993; Mirza & Chivers, 2001). Compounds released by startled prey are linked to release of urine in crayfish (Hazlett, 1990; Zulandt Schneider & Moore, 2000), amphibians (Kiesecker et al., 1999) and fish (Percidae: *Etheostoma nigrum*, Wisenden unpublished data) and therefore hold the potential to evolve from a spontaneous, involuntary by-product of predator–prey encounters (cues) to become shaped by natural selection to be released under voluntary control in ways that accrue fitness benefits to the sender. Through clever experimental design, Bairos-Novak et al. (2019) demonstrated variation in potency of disturbance cue as predicted signalling theory. Sender fathead minnows (*Pimephales promelas*), when chased by a model predator, released cue of greater potency when in the presence of other minnows than when no audience was present. This suggests that senders voluntarily increased cue potency to influence or manipulate nearby receivers to initiate a shoaling response that would include, and benefit, the sender. Moreover, Bairos-Novak et al. (2019) took the additional step to test the effect of audience familiarity. Individuals familiar with one another mount more effective shoaling responses than do individuals that are not familiar with each other (Chivers, Brown, & Smith, 1995). When Bairos-Novak et al. (2019) experimentally manipulated familiarity of the audience with the sender, senders increased signal potency when in the presence of familiar individuals relative to disturbance cues released in the presence of unfamiliar individuals. This indicates that release of disturbance cues is graded in proportion to the potential fitness benefit to the sender, analogous to how a courtship display may vary in intensity depending on the reproductive value of a prospective mate.

The final component of a full signalling system would be the presence of specialized tissue to produce, store and release unique substances, that is an alarm pheromone, for communicating presence of predation risk. Voluntary release of the bladder partially meets this definition, but only partially. For example, it would be important to know whether variation in disturbance cue effectiveness is due to adjustment in volume of urine release (quantitative) or by changing the chemical components released into the urine (qualitative). Nevertheless, as it stands, Bairos-Novak et al. (2019) are a significant advance in the study of chemically mediated predator–prey interactions in aquatic organisms because it is the first evidence of an incipient alarm signal shaped by sender-side selection.

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