



Minnows trust conspecifics more than themselves when faced with conflicting information about predation risk



Adam L. Crane ^{a, *}, Maud C. O. Ferrari ^{b, 1}

^a Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada

^b Department of Veterinary Biomedical Sciences, University of Saskatchewan, Saskatoon, SK, Canada

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Prey often face uncertainty when learning about predation risk because stimuli indicating risk can vary in reliability. However, the way this uncertainty is expressed at the individual level is often poorly understood. Here, we compared how prey fish (*Pimephales promelas*) responded to information conflicting with their previous experience when this information came from contrasting sources. First, fish had the opportunity to learn that a novel odour was safe from repeated exposure to the odour in the absence of negative consequences, or they received pseudo-exposures. Then, using one of two learning paradigms, we conditioned fish to recognize that the 'safe' odour was actually the odour of a predator. Fish were exposed to the odour paired with either (1) cues released from injured conspecifics (alarm cues), allowing for the fish to learn alone, or (2) cues from a knowledgeable (frightened) conspecific responding to the risky odour, allowing fish to acquire the information via social learning. Fish were tested individually following conditioning, and movement, foraging, shelter use and freezing were quantified. Learned antipredator responses were similar between the two mechanisms for individuals with no prior exposure to the odour. However, fish that knew the odour as safe did not acquire a fearful response to the odour following conditioning with alarm cues, whereas interaction with frightened conspecifics appeared to cause fish to ignore their prior learning of safety, suggesting that learning from a live conspecific was more persuasive than individual assessment via alarm cues. This study adds to the body of literature contrasting the reliability of information sources and their consequences on cognition, communication and group dynamics.

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Group-living animals, and those in close aggregations, have the potential to acquire knowledge or skills from observing others (Hoppitt & Laland, 2013). While acquiring information on one's own may sometimes be more relevant and more reliable, it can also be time consuming, dangerous and quickly outdated (Rieucou & Giraldeau, 2011). Social learning, however, can be a fast learning mechanism that helps animals adjust to complex and changing environments with limited exposure (Rendell et al., 2010). By eavesdropping on publicly available information, naïve animals can quickly learn to find and capture food, how to choose mates and how to successfully avoid predators (Crane & Ferrari, 2013; Galef & Giraldeau, 2001; White, 2004).

Predation is a major evolutionary force that shapes many characteristics of prey including their behavioural defences (Lima & Dill,

1990). However, the risk of predation can be unpredictable for prey because threats can fluctuate in time and space, and thus, prey often face uncertainty about predation risk (Ferrari, Brown, Bortolotti, & Chivers, 2010; Sih, 1992). Although prey can often avoid predation through avoidance of risky habitats, or risky times, they often cannot be confined to those safe niches because these are usually associated with no or low food gain (Ferrari, Sih, & Chivers, 2009; Lima & Bednekoff, 1999). Therefore, it is critical for prey to correctly distinguish between situations of risk and safety and adjust their behaviours accordingly to maximize gain while minimizing their risk of being attacked (Lima & Dill, 1990).

Prey encounter a variety of stimuli that potentially indicate predation threat, and while some species innately recognize cues from some predators, many others must learn to recognize these cues as risky (Berejikian, Tezak, & LaRae, 2003; Brown & Chivers, 2005; Ferrari, Wisenden, & Chivers, 2010). Learning from direct experience with predators should reduce uncertainty about risk but also poses great costs, including death (Arai, Tominaga, Seikai, & Masuda, 2007; Griffin & Boyce, 2009; Griffin & Haythorpe, 2011).

* Correspondence: A. L. Crane, Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2, Canada.

E-mail address: adam.crane@usask.ca (A. L. Crane).

¹ E-mail address: maud.ferrari@usask.ca (M. C. O. Ferrari).

In contrast, learning indirectly, and without being exposed to attack, should decrease the chance of mortality, but it potentially brings the cost of learning something inaccurate or irrelevant (Crane & Ferrari, 2013; Danchin, Giraldeau, Valone, & Wagner, 2004).

Learning from frightened conspecifics (i.e. models or demonstrators) is usually demonstrated with a standard methodological approach where a predator-naïve individual (the observer) is exposed to novel predator stimuli that are paired with a predator-experienced individual (the model) (Mathis, Chivers, & Smith, 1996). During this conditioning phase, the observer has the opportunity to learn from the model displaying a fright response, and subsequently, the observer is tested with exposure to the predator stimulus (or live predators) in the absence of the model to determine whether learning occurred (Crane & Ferrari, 2013; Mathis et al., 1996). This form of learning is commonly referred to as social learning. Once social learning has occurred, the observer may now serve as an experienced model for inexperienced individuals, thereby initiating a chain of transmission where the information can be passed multiple times (Crane & Ferrari, 2013). Previous work suggests the intensity of the learned response weakens as the chain becomes longer (Cook, Mineka, Wolkenstein, & Laitsch, 1985). However, the preservation of the fright response has been shown in a 3× chain of zebrafish (*Brachydanio rerio*) (Suboski et al., 1990) and a 7× chain of blackbirds (*Turdus merula*) (Curio, 1988).

Another learning mechanism that is available in a wide variety of aquatic organisms is alarm cue learning (Ferrari, Wisenden, et al., 2010). This occurs when chemical cues (usually from conspecifics) are released by injury during a predation event. Prey then have the opportunity to detect these alarm cues, associate them with other stimuli (e.g. the sight, smell or sound of a predator), and then learn these as indicators of risk. In recent years, this form of learning has become viewed as a form of social learning because the alarm cues are social in that they are released by companion individuals (Griffin, 2004; Lindeyer & Reader, 2010; Zentall & Galef, 1988). However, contrary to true social cues, the information transmission (timing of release, quantity, quality) is not controlled by the sender, and the information content is not modifiable based on the interpretation of the sender, and hence, cannot be sent dishonestly. For these reasons, we tend to consider alarm cues to be nonsocial cues, in much the same way the odour of a predator is not considered a social cue. In the context of this study, we will refer to social learning when the learning results from interacting with live conspecifics, which have the ability to modulate the cues detected by the observer.

While there are a variety of cues available for prey to use in predator recognition learning, few comparisons have been made among different learning modalities. Some work has compared learning via visual cues from models and learning via auditory cues from models (alarm calls), finding learned responses from these types of cues were similar (Curio, Ernst, & Vieth, 1978; Vieth, Curio, & Ernst, 1980). However, we might expect prey to learn better (and/or have less uncertainty) with some types of cues compared to others (Crane & Ferrari, 2013). For instance, visual cues from models can be highly accurate in space and time and usually provide information about the target of the response, but they also require the observer to recognize that a model has changed its normal behaviour, which may be unlikely in complex habitats or at night. Chemical cues, however, are available all the time, and can travel long distances if moved by air or water, but may be less reliable in space and time, as they persist long after predation occurs, and are moved by currents that can create erroneous pairings (Ferrari, Wisenden, et al., 2010).

In contrast to learning about 'risk', prey can also learn 'safety' (i.e. recognizing stimuli as nonthreatening) via repeated

encounters with novel stimuli in the absence of negative consequences (Ferrari & Chivers, 2011). When this prior experience subsequently prevents a learned association between the stimuli and risk, latent inhibition has occurred (Acquistapace, Hazlett, & Gherardi, 2003; Lubow, 1973). For example, when damselfish (*Pomacentrus moluccensis*) were repeatedly exposed (6×) to a novel odour, they failed to learn it as risky during a subsequent pairing with alarm cues. However, repeated pairing with alarm cues (≥3×) reversed (i.e. released) the learned safety (Mitchell, McCormick, Ferrari, & Chivers, 2011). Latent inhibition of alarm cue learning has been shown in other aquatic species (e.g. Acquistapace et al., 2003; Ferrari & Chivers, 2006b, 2011) and for auditory learning via alarm calls in birds (Vieth et al., 1980). When blackbirds (*T. merula*) were previously exposed to mounted owls (predators) and then exposed to a mounted owl paired with conspecific alarm calls, they subsequently ignored the mock predator (Vieth et al., 1980). However, when the mounted owl was paired with the sight of a conspecific mobbing the owl, observers became wary of the predator, indicating that visual cues from models were more persuasive than auditory cues (Vieth et al., 1980). Similarly, rhesus monkeys, *Macaca mulata*, that had previously shown no fear towards a toy snake (predator) when alone, immediately learned that it was dangerous when interacting with conspecifics that were frightened of the snake (Mineka & Cook, 1986). Interaction with live conspecifics also appears particularly persuasive in other contexts such as communication (song) learning and the length of the sensitive learning period in birds (*Zonotrichia leucophrys*) (Baptista & Petrinovich, 1984, 1986; Nelson, 1998; Petrinovich & Baptista, 1987). However, socially learned food preferences in rats (*Rattus norvegicus*) waned after individually experiencing negative consequences and having more time with alternatives (Galef & Whiskin, 2001). These studies draw attention to the dilemmas animals face from encountering different types of information.

In this study, we sought to compare the value of information learned via a live conspecific to that learned via alarm cues, using fathead minnows, *Pimephales promelas*. Both forms of learning can occur after only a single conditioning and can also increase survival in a predation context (Manassa & McCormick, 2013; Mirza & Chivers, 2000). This comparison involves some inherent differences between these two forms of learning. For instance, social learning requires the presence of another individual whereas alarm cue learning does not. Moreover, interacting with frightened models should provide more information (Seyfarth et al., 2010) about risk, compared to alarm cue learning. The presence of frightened models can provide visual, mechanical and chemical cues for observers (Johnston & Johnson, 2000; Vavrek et al., 2008), although such chemical 'disturbance' cues alone do not mediate predator recognition learning (Ferrari et al., 2008). In contrast, during alarm cue learning, only chemical cues from injured conspecifics are provided and, unlike social cues, they are not modifiable by the model.

We first gave minnows the opportunity to learn a novel odour (pike, *Esox lucius*, odour) as safe, by repeatedly exposing them to the odour without negative reinforcement. We then used a conflicting context to force minnows to make a choice between the value of their previously learned information (the cue is safe) and new information (the cue is risky) acquired via the alarm cue or social learning mechanism. After this conflicting phase, minnows were individually exposed to the odour and their antipredator behaviour was measured. Our control group allowed us to compare the intensity of the learned response via the two mechanisms. We expected minnows that learned from models to respond either (1) as much as those learning from alarm cues because the models learned from the same alarm cue concentration, or (2) slightly less than those learning from alarm cues because the intensity of the

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