Animal Behaviour 119 (2016) 49–57

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Uncertainty in risky environments: a high-risk phenotype interferes with social learning about risk and safety

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ARTICLE INFO

Article history:
Received 15 January 2016
Initial acceptance 4 April 2016
Final acceptance 2 May 2016
Available online 25 July 2016
MS. number: A16-00049

Keywords:
cultural transmission
decision making
neophobia
secondary traumatization
stereotypy

Uncertainty about risk is a pervasive problem for prey that must continuously manage risk in an ever-changing world. Prey can, however, minimize this uncertainty by learning from the information they sample in their environment. How uncertainty affects learning about risk has been the subject of recent attention, but no studies have examined how uncertainty affects learning about risk (or safety) via social information. Here, we sought to assess whether uncertainty would make social information about risk and safety more persuasive. We induced uncertainty in minnows, *Pimephales promelas*, by exposing them to a background regime of incomplete information about predation risk in the form of conspecific alarm cues without any information about a specific predator. For other fish, we paired the alarm cues with a novel odour to give minnows the opportunity to be certain about the predator's chemical signature. Then, uncertain and certain minnows were given an opportunity to use social information from live conspecifics (models) that were experienced with the odour as being either risky or safe. Compared to control fish (no background risk), minnows that were both certain and uncertain developed a high-risk phenotype. These individuals spent less time moving and foraging, were more likely to develop a behavioural stereotypy (rapid-loop swimming) and displayed neophobic responses, regardless of their social conditioning. Control fish also developed neophobic responses after interacting with risk-experienced models, presumably because the models' high level of background risk triggered high-risk behaviour that indicated the environment was risky. Thus, whether these observers learned specific information from risk-experienced models or only learned generalized fright remains unknown. In contrast, we found weak evidence that interacting with safe-experienced models can reduce fright in observers to a previously known threat. Alternative approaches to safety conditioning may be more influential.

Animals face a pervasive challenge of making appropriate decisions according to their current environment, the probable actions of others and the consequences of their available options (Dall, 2010; Dall & Johnstone, 2002). This is critically important in balancing cost–benefit trade-offs in fitness-related activities such as foraging, mating and predator avoidance (Ferrari, Sih, & Chivers, 2009). However, an animal's environment perpetually changes. For instance, predators and prey alter their activity patterns and habitat use over both short- and long-term scales, giving rise to a spatiotemporal landscape of fluctuating risk (Ferrari, Brown, Bortolotti, & Chivers, 2010; Lima & Bednekoff, 1999; Sih, 1992). Growth and life-history changes potentially add more novelty in risk for prey, such as facing risk at a new time of day, in a new microhabitat, or from an entirely new predator species (Brown et al., 2011; Ferrari, Brown, Bortolotti, & Chivers, 2011). Hence, the past knowledge of prey may not be valid at a new point in time, at new locations, or after using a relatively less reliable mode of risk detection (e.g. social versus direct, or olfactory versus visual in some systems: Giraldeau, Valone, & Templeton, 2002; Hickman, Stone, & Mathis, 2004; Laland & Williams, 1998). All of this unpredictability in local risk leads to uncertainty, defined by Dall (2010, page 195) as 'the moment-by-moment degree to which events are determined by factors that are out of an animal's control or immediate experience'. Normally, prey optimize their antipredator decisions (Lima & Dill, 1990) by correctly modulating the intensity of their behaviour to match the perceived level of threat, where more extreme antipredator responses are displayed when risk is greater, a phenomenon known as threat sensitivity (Edelaar & Wright, 2006;

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http://dx.doi.org/10.1016/j.anbehav.2016.06.005
0003-3472/

Helfman, 1989; Helfman & Winkelman, 1997; Kesavaraju, Damal, & Juliano, 2007). However, uncertainty poses a major problem for prey because they may under- or over-respond to the stimulus (i.e. at an incorrect intensity), switch to another type of response, or even completely fail to respond, all of which potentially harms their fitness (Ferrari, Crane, & Chivers, 2016).

Learning is a critical mechanism for reducing uncertainty about predators. Collecting direct, first-hand information about predation should greatly lower uncertainty, but it could also be fatal. In contrast, learning indirectly via publically available information allows prey to minimize uncertainty without severe risk (Crane & Ferrari, 2013). A good model for addressing questions about predator recognition learning has long been the fathead minnow, *Pimephales promelas* (Ferrari, Trowell, Brown, & Chivers, 2005; Mathis, Chivers, & Smith, 1996). As in numerous fish species, their skin contains a substance that, when released by mechanical damage, indicates a predator attack (Ferrari, Wisenden, & Chivers, 2010). When this alarm cue is detected in conjunction with other stimuli (e.g. sight or smell of a predator), minnows learn the stimuli as a threat via a Pavlonian-like process (Suboski, 1990). Minnows also learn from observing frightened conspecifics, and this type of learning can in some cases be more persuasive than individual learning (Crane & Ferrari, 2015). Experimentally demonstrating social learning involves a standard paradigm where a naïve observer is exposed to a novel stimulus in the presence of an experienced conspecific (the model, or often the tutor or demonstrator). The pairing of the stimulus with a fright response from the model (the conditioning phase) leads to a learned association, where the observer learns to respond to the stimulus with an antipredator response in the absence of the model (the testing phase) (Crane & Ferrari, 2013). Only a single pairing is sufficient for both social learning of risk and alarm cue learning.

Like other species that have been tested, fathead minnows develop generalized fright responses towards novel stimuli (i.e. neophobia) following repeated exposure to general predation cues in the form of alarm cues (Crane, Mathiron, & Ferrari, 2015). These neophobic responses should be beneficial for prey facing evolutionarily variable predation risk, so long as this trait is plastic and suppressed under low-risk conditions (Brown, Ferrari, Elvidge, Ramnarine, & Chivers, 2013). Most previous studies documenting neophobic responses have been in the context of novel objects and foraging opportunities (Biondi, Bó, & Vassallo, 2010; Greenberg, 1990; Greenberg & Mettke-Hofmann, 2001), but there are a few examples in an antipredator context (Brown, Chivers, Elvidge, Jackson, & Ferrari, 2014; Brown, Demers, Joyce, Ferrari, & Chivers, 2015; Chivers, McCormick, Mitchell, Ramasamy, & Ferrari, 2014; Meuthen, Baldauf, Bakker, & Thünken, 2015). In general, repeated exposure to alarm cues has been used to simulate a high-risk environment. Without being paired with other stimuli, alarm cues provide incomplete (nonspecific) information about predation risk, and thus do not bias subsequent responses towards one type of predator. Here, we reasoned that a background environment lacking specific information would cause uncertainty, which would drive neophobic responses.

In addition to learning about risk, prey can learn to recognize stimuli as nonthreatening or 'safe'. Repeated experiences with an initially novel stimulus without any negative consequences can prevent a subsequent learned association between that stimulus and risk, a phenomenon referred to as latent inhibition (Acquistapace, Hazlett, & Gherardi, 2003; Lubow, 1973; Mitchell, McCormick, Ferrari, & Chivers, 2011). Chivers et al. (2014) explored latent inhibition under different levels of background risk. Damselfish, *Pomacentrus chrysurus*, under low-risk conditions continued to recognize an odour as nonthreatening following a one-time exposure to the odour paired with conspecific alarm cues. However, fish from high background risk immediately learned the odour as dangerous, as their past experience with the odour as safe had only a minimal biological effect. A few other studies have also presented prey with dilemmas about risk and safety, but the information came from different sources (individual versus social). For instance, rhesus monkeys, *Macaca mulata*, learned that a mock predator (snake) was safe after being presented by itself, but they immediately learned danger after interacting with conspecifics that showed fear towards the snake (Mineka & Cook, 1986). Similarly, in fathead minnows, individually learned safety was overridden by a one-time social experience with a conspecific that was frightened by the stimulus (Crane & Ferrari, 2015). This raised the question as to whether social experience overrides individual experience or whether risk overrides safety when information comes from different sources.

The objective of this experiment was to test how uncertainty in observers would affect their ability to learn socially about the risk or safety of a stimulus. First, observers received either several exposures to alarm cues alone (uncertain observers), the same number of exposures to alarm cues but paired with an odour of a predator (certain observers), or only water (neutral observers). Then, during a social conditioning period, we paired the three types of observers with models that had previously been trained to recognize the odour either as risky (risk model) or as safe (safety model). Together, observers and models were exposed to the odour, giving the observer an opportunity to learn about the odour from the model. Finally, observers were tested alone by exposing them to either the conditioning odour or a novel odour ($3 \times 2 \times 2$ design; Fig. 1). We predicted that uncertainty would elicit neophobic responses that would be absent for observers that were certain about the odour as a treat. We also expected that uncertain observers would be influenced by safe models and thus learn the odour as a lesser threat, whereas safe models would have little to no effect on observers that were certain (i.e. a one-time social assessment of safety would not override a prior individual experience of risk). Likewise, we predicted that the behaviour of the observers that were certain would be unaffected by interacting with a risk model because the social information would be consistent with their prior individual experience. However, the demonstration of an experienced fright response from risk models might help uncertain observers correctly identify risk, thereby reducing neophobia.

METHODS

Ethics Statement

This study was approved by our University Committee on Animal Care and Supply (protocol: 20130079). We collected minnows under a Saskatchewan Ministry of Environment Special Collection Permit. These minnows are currently being reused in other behaviour experiments and ultimately will be euthanized.

Minnow Collection and Maintenance

Fathead minnows are a group-living species that responds to predation risk with reduced activity and increased shelter use (Smith, 1992). We collected adult minnows from Feedlot Pond on the University of Saskatchewan campus using Gee's inverted minnow traps. Minnows from this site are exposed to a variety of predators, including birds, snakes and beetles, but are naïve to fish predators (Chivers & Smith, 1994; Mathis, Chivers, & Smith, 1993). Before the experiment began, minnows were housed in 76-litre flow-through tanks with gravel substrate, aeration, 15:9 h light:-dark cycle and a daily ~30% flush with filtered dechlorinated tap water via a flow-through system. All minnows were fed flake food every morning throughout the experiment.