SOCIAL LEARNING OF PREDATION RISK AND SAFETY: FISH BEHAVIOUR AS A MODEL FOR FEAR RECOVERY

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Abstract

As animal behaviour theory has developed over the past 70 years, much attention has gone toward social information use. Social cues in a variety of forms can be critically important in finding food and mates, in defending territories, and in avoiding predators. A wide variety of prey species are capable of learning from social information regarding predation threats, but little attention has gone toward factors that influence the acquisition of such information, how it compares to other learning mechanisms, or how prey learn socially about the absence of risk. Herein, I present research with fathead minnows, *Pimephales promelas*, where I first showed that learned fear responses were similar between social learning and individual learning, but socially-acquired information was more persuasive and had an overriding effect on previously learned safety. Using repeated exposures to general predation cues that lacked specific information about the predator's identity, I induced uncertainty in naïve individuals (observers) or in knowledgeable individuals (models) within a social pairing. Repeated exposure to risk, regardless of uncertainty, promoted a high-risk phenotype that was characterized by propensity to freeze, stereotypic route-tracing, and neophobia – a phenomenon where animals show generalized fear responses toward novel stimuli. Attempting to weaken this phenotype, I paired high-risk individuals with models that were experienced with an odour as safe, but a single conditioning with one 'safety model' had little effect. Instead, interacting with high-risk individuals caused models to indirectly acquire the high-risk phenotype. Hence, this social transfer of information caused models to behave fearfully, making them poor demonstrators of safety. To counteract this, I used groups of calm models, or multiple, individual calm models in succession. Both strategies weakened fear in observers, as well as socially-transferred fear in models, but surprisingly this effect was much stronger among individuals exposed to risk in isolation, despite their tendency for stronger neophobia initially. While our basic knowledge of social systems has grown substantially in recent years, rarely has it been applied to human issues. My work bridges animal behaviour theory and human psychology, arguing that our understanding of predation-related fear and the information transfer in social animals can prove fruitful in understanding post-traumatic stress and behavioural therapy for its recovery.

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Chapter 1: Introduction to predation risk and social learning[1]

1.1. The threat of predation and the defences of prey

The threat of predation is one of the strongest selective forces shaping the ecology of animal life (Lima & Dill 1990; Sih 1987). Antipredator defences in all forms evolve because they provide prey species with survival and reproductive benefits (Edmunds 1974). In particular, the ability of prey to respond to predation risk at the individual level (phenotypic plasticity) is critically important for fitness (DeWitt, Sih & Wilson 1998; Miner et al. 2005). In response to risk, some individuals modify their morphology (e.g., body size or depth, armour thickness, tail depth) to decrease the likelihood of a predator attack or to increase their chances of survival during attacks (e.g., Relyea 2001; Trussell 1996). Some species alter life-history traits such as their age or size at sexual maturation (e.g., Abrams & Rowe 1996; Crowl & Covich 1990), and the onset of habitat shifts (e.g., during metamorphosis) in a way that decreases predation risk at a particular life stage (Chivers et al. 2001a; Sih & Moore 1993). However, behavioural responses appear to be the most plastic and widespread antipredator strategies among animals, whether being aggression, fleeing, or hiding (Fordyce 2006; Lima 1998). Such behavioural modifications are generally faster to enact than alternatives, and thus the first line of antipredator defence.

A prerequisite for implementing behavioural defences is the ability to distinguish between what is actually a predation threat and what is not (Blumstein & Bouskila 1996; Brown, Poirier & Adrian 2004). Although prey can often avert predation by avoiding risky habitats or activity at risky times, they often cannot be confined to those safe niches that typically are associated with no or little food gain (Lima & Bednekoff 1999b). Thus, while the energetic cost

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[1] Some of the content of this chapter is published in the following book chapter, with sections removed or rephrased for brevity. Several other sections have also been added and have not been published.

Crane AL, Ferrari MCO. (2013) Social learning of predator recognition: advances and future directions. In: Social Learning Theory: Phylogenetic Considerations Across Animal, Plant and Microbial Taxa (Clark ed.). Nova Science Publisher NY, USA. Pp. 53-82.

of antipredator behaviour may be lower than other types of defences (e.g. morphological defences), the time devoted to antipredator behaviour decreases the time available for other fitness-enhancing activities, such as foraging, mate courting, and territory defence (Blumstein, Daniel & Springett 2004a; Koch, Lynch & Rochette 2007; Orrock et al. 2008). Therefore, it is critical for prey to collect information about their environment and correctly distinguish between situations of risk and safety, adjusting their behaviours to maximize resource gain while minimizing their risk of being attacked (Ferrari, Sih & Chivers 2009; Lima & Dill 1990). Helfman (1989) demonstrated that prey adjust the intensity of their antipredator responses to match the level of threat posed by the predator. Damselfish, *Stegastes planifrons*, displayed increased avoidance behaviour when a predator was closer. Since Helfman's (1989) study, the optimization (i.e., cost-benefit trade-off) of predator avoidance vs. normal activity has been consistently demonstrated across taxa, and is now dogma in predation ecology, generally being referred to as 'threat sensitivity' (e.g., Bishop & Brown 1992; Chivers et al. 2001b; Ferrari et al. 2005).

1.2. Fear effects

An underlying link among all animals, at least during early life periods, is a persistent threat of an immediate and potentially violent death, which causes *fear* (Zanette & Clinchy 2017). The scientific literature often uses the term 'fright' (Pfeiffer 1962) in place of fear, or instead uses more specific statements to avoid anthropomorphizing. However, the use of these terms is now widely accepted due to the universality of the behavioural, physiological, and neurobiological effects of fear among animal species, including humans (Clinchy et al. 2011; Clinchy, Sheriff & Zanette 2013). Hereafter, I will use these terms interchangeably.

Research demonstrates that fear can have severe and long-lasting effects on animal ecology, especially when risk levels are high (Zanette & Clinchy 2017). For example, one behavioural outcome of living in a high-risk environment is neophobia – a phenomenon where prey show generalized fear toward novel stimuli. Neophobia can also be viewed as a lack of learning that risk is absent (Chivers et al. 2014; Greenberg & Mettke-Hofmann 2001). The concept of neophobia was initially developed in a foraging context, whereby populations of birds and mammals from different environments differed in their willingness to sample novel food (reviewed in Gentsch, Lichtsteiner & Feer 1981; Greenberg & Mettke-Hofmann 2001; Voelkl, Schrauf & Huber 2006).

The Dangerous Niche Hypothesis posits that neophobia is an adaptive trait because extra caution protects prey from potential risk (Greenberg & Mettke-Hofmann 2001). According to this hypothesis, prey should exhibit greater caution in riskier habitats. Thus, when the likelihood of facing novel predators is high, neophobia can help prey survive encounters with predators, even when they have no prior experience (Benard & Fordyce 2003; Ferrari et al. 2015b; Ferrari et al. 2015c). Neophobia should be especially beneficial under highly variable predation risk if it can be suppressed during low-risk periods (Brown et al. 2013). This plasticity is important because neophobia must also incur costs, or else it would be a universal trait. Ferrari et al. (unpublished data) documented costs of neophobia in a predator-free environment where neophobic damselfish, *Pomacanthus chrysurus*, were poorer competitors than non-neophobic individuals. Similarly, in a study on laboratory rats, *Rattus norvegicus*, neophobic individuals experienced a 20% increase in stress-related mortality (Cavigelli & McClintock 2003). Clearly, a high level of vigilance has an energetic cost and reduces time doing other fitness-related activities. While this is preferable to being consumed, neophobia can become maladaptive when the chances of being consumed are low, as in safe environments. Hence, it is not surprising that neophobia appears plastic in its expression, where riskier environments lead to both stronger and longer avoidance responses toward novel cues (Brown et al. 2014; Brown et al. 2013).

1.3. Uncertainty

Prey face a pervasive challenge of making appropriate decisions based on their current environment, the probable actions of others (e.g., predators and conspecifics), and the consequences of their available options (Dall 2010; Dall & Johnstone 2002). However, a fundamental aspect of the risk landscape is high spatial and temporal variability, with predators coming and going on a moment-to-moment, daily, lunar, or seasonal basis (Ferrari et al. 2010a; Sih 1992). Hence, the past knowledge of prey may not be valid at a new point in time, at new locations, or after using a less reliable mode of risk detection (e.g., indirect vs. direct, or olfactory vs. visual in some systems) (Giraldeau, Valone & Templeton 2002; Hickman, Stone & Mathis 2004; Laland & Williams 1998). This unpredictability leads to ‘uncertainty’, defined by Dall (2010) as “the moment-by-moment degree to which events are determined by factors that are out of an animal’s control or immediate experience”. Uncertainty poses a major problem for prey because they may under- or over-respond to a stimulus (i.e., at an incorrect intensity), switch to another type of response, or even completely fail to respond, all of which potentially harming fitness (Ferrari, Crane & Chivers 2016). This uncertainty drives prey to adopt a ‘play it safe’ strategy and usually over-respond to predation threats in the absence of perfect information (Bouskila & Blumstein 1992), as predicted by Error Management Theory (Johnson et al. 2013). However, a model put forth by McNamara et al. (2012) predicts that prey should under-estimate risk when faced with uncertainty. I suspect that this is indeed the case in low risk environments, but not in situations where prey have learned that their environment is highly dangerous.

1.4. Learning about predation risk

Prey encounter a variety of stimuli (tactile, auditory, visual, or chemical) that can indicate predation risk, either before, during, or after an attack (Chivers & Smith 1998; Endler 1986). Some species innately recognize visual stimuli from predators, such as eye-like circles (Janzen, Hallwachs & Burns 2010). Other predation-related cues include chemical stimuli that are directly released by the predator such as their odour (a ‘kairomone’), diet cues, or cues from injured prey (Mathis & Crane 2017), in addition to cues that indirectly indicate the presence of a predator (e.g., predator habitat cues or the time of day when predators are active). Some aquatic species avoid predator odour without having prior experience with the predator, while also being capable of learning new predation-related information (e.g., Berejikian, Tezak & LaRae 2003; Epp & Gabor 2008; Gall & Mathis 2010; Vilhunen & Hirvonen 2003). Many other species lack innate recognition of predator odour and must rely more heavily on learning to recognize these cues as dangerous (Berejikian et al. 2003; Brown & Chivers 2005; Ferrari, Wisenden & Chivers 2010b). Typically, only a one-time experience is sufficient for predator-related information to be learned. This contrasts with the multiple training sessions that are often required in other contexts like foraging (e.g., Crane & Mathis 2011; Reader, Kendal & Laland 2003). It is not surprising to find such efficient learning when individuals deal with predators, due to the unforgiving nature of predation. Most studies have focused on learning to recognize novel predators based on either their odour or visual appearance, and Wisenden (2008) demonstrated that fish can learn to recognize an auditory cue as threatening.

Like any other communication system, learning has benefits and costs. In the context of predator-related information, prey must learn about predators to respond appropriately upon encounter, and then to survive and reproduce. However, collecting this information incurs costs such as travelling, sampling, sensory alertness (vigilance), and cognitive-processing costs. For instance, collecting direct, first hand, information can also be time consuming, and fatal, but it may also reduce uncertainty about predation risk (Arai et al. 2007; Griffin & Boyce 2009; Griffin & Haythorpe 2011; Rieucau & Giraldeau 2011). Many prey species are known to learn about predators via the risky behaviour of inspection (Brown & Godin 1999; FitzGibbon 1994; Godin & Crossman 1994; Magurran 1986) or when making behavioural displays toward predators to deter them (e.g., mobbing in birds) (Lorenz 1931; Ostreiher 2003). A few studies have demonstrated learning from witnessing a predator attack (Arai et al. 2007; Griffin 2009; Griffin & Haythorpe 2011). Berger et al. (2001) reported that moose, *Alces alces*, increased vigilance and responded to auditory cues from wolves, *Canis lupus*, after witnessing the predator kill their offspring, although the degree of individual learning is unknown in these studies when social cues were also available.

1.5. Social learning

Much attention has gone to the way that prey animals can learn from second-hand information. Through direct teaching by more experienced individuals, or via ‘eavesdropping’ on publicly-available information, naïve animals, including young, can quickly learn to find and capture food, how to choose mates, and how to successfully identify predator threats (Galef & Giraldeau 2001; Shier & Owings 2007; White 2004). Learning indirectly from social information allows prey to collect potentially life-saving information with minimal exposure and costs. However, one potential drawback is that the acquired information may sometimes be inaccurate, irrelevant, or in the worst case, erroneous (Danchin et al. 2004; Giraldeau et al. 2002; Laland & Williams 1998; Mineka & Cook 1986; Rendell et al. 2010).

Group-living animals, and those living in close aggregations, have ample opportunity to acquire knowledge or skills from observing others (Hoppitt & Laland 2013), even across species when living in sympatry (Conover 1987; Ferrari & Chivers 2008; Mathis, Chivers & Smith 1996). In the context of predation risk, social learning is frequently observed in mammals, birds, fishes, as well as in gregarious amphibians (e.g., Ferrari, Messier & Chivers 2007). While this mode of learning was initially thought to be limited to highly social species, there is now evidence that social learning of predation risk can occur in non-social species (Coolen, Dangles & Casas 2005; Crane, Mathis & McGrane 2012; Wilkinson et al. 2010; Wong et al. 2005), revealing that they, too, pay attention to the fearful behaviour of surrounding conspecifics.

In predation ecology, a social learning event involves an observer learning to recognize a specific habitat or species as a threat, or learning to display specific behaviours, from a model (Dugatkin 2009). These models are often referred to as 'tutors' or 'demonstrators', but I generally prefer to use the term 'model' to remove any innuendo that the individual is purposefully signalling the observer. Although fear reactions provide social information to nearby individuals, the purpose of such reactions is often to escape threats, rather than notifying others. The cues emitted by the model can be visual, auditory, chemical, or tactile. However, the vast majority of studies have allowed the observer and model to fully interact, thus allowing for multi-modal cue use and preventing the identification of the specific cue that triggered social learning (Ward & Mehner 2010).

For the successful transmission of predator-related information to occur, the model obviously must convey the dangerous nature of the situation (Kelley et al. 2003; Krause 1993; Mineka & Cook 1986). Moreover, the intensity of the observer's learned response positively correlates with that of the model (Ferrari et al. 2005; Griffin & Evans 2003; Mineka & Cook 1993; Vieth, Curio & Ernst 1980), representing threat-sensitivity in a social learning context. This allows observers not only to label novel predators as risky, but also to distinguish whether they represent a high vs. low threat. While the intensity of the responses from the observer and their model are correlated, the observer's learned response may be slightly weaker than that of the model, perhaps due to the perception of lesser risk by observers that are not directly exposed to the predator, or due to information degradation (Curio 1988).

Defining social cues

Griffin (2008) defined social learning broadly as "instances in which the behaviour of a demonstrator, or its by-products, modifies the subsequent behaviour of an observer". Thus, learning from public information constitutes as social learning even when the model plays no active role in the teaching process (Danchin et al. 2004). Moreover, cues that are released by an injured model during a predation event, such as damage-released chemical cues, fit this definition. Prey that detect these cues often learn to associate predation risk with the sight or odour of a predator, which will elicit antipredator responses in future encounters (Brown & Chivers 2005; Ferrari et al. 2010b). Some experts view this mode of learning as a form of social learning because the cues are technically social cues, being released by companion individuals (Brown & Laland 2003; Griffin 2004). We might even ask, does the model need to be alive for social learning to occur? Kruuk (1976) showed that gulls, *Larus argentatus* and *Larus fuscus*, can learn to display increased vigilance towards a mounted owl when a dead gull was put in close proximity. Damaged-released chemical cues differ from other social cues in that they are not controlled and modified by the model according to its interpretation of risk, and hence, these cues cannot be transmitted dishonestly (Brown & Chivers 2005; Ferrari et al. 2010b). For these reasons, I tend to consider damage-released chemical cues to be non-social cues. Going forward, herein, I will use the term ‘social learning’ to refer only to learning via observing the behaviour of models, as their behavioural cues can be voluntarily modulated.

Voluntarily-released social cues

Many species use alarm vocalizations to warn others of eminent danger (e.g., Blumstein 1999; Templeton, Greene & Davis 2005), whereas numerous others learn about risk by visually observing fear reactions in models. In a classic study by Curio (1978), blackbirds, *Turdus merula*, learned to mob a novel predator by observing a conspecific model mobbing it. Similarly, Mineka et al. (1984) showed that rhesus monkeys, *Macaca mulatta*, watching a conspecific display ‘alarm’ behaviour in the presence of a snake learned to subsequently respond to the predator with an alarm response. It was not until the 1990s that researchers began investigating social learning of predation risk in ‘lower’ vertebrates. That decade was rich in literature on social learning in fishes (e.g., Brown & Laland 2003; Mathis et al. 1996; Suboski et al. 1990). To date, all studies on social learning of risk in fishes have involved species that are considered social, forming tight shoals or schools, and possessing group evasion behaviours.

The experimental demonstration of social learning of predation risk involves a standard methodological approach (Fig. 1.1) (Mathis et al. 1996). First, during what is generally referred to as the ‘conditioning phase’, a predator-naïve individual (the observer) is paired with a predator-experienced individual (the model). Together the pair is exposed to a predator stimulus where the experienced model reacts, giving the naïve observer an opportunity to learn. However, to demonstrate that the observer did in fact learn a new response after observing the model, the observer must display the response to the conditioned stimulus in the absence of the model. This takes place in the ‘testing phase’ (Mathis et al. 1996). Because one advantage of social learning is its potential to spread quickly throughout a population (Hoppitt & Laland 2013), a few researchers have explored how a predation-related piece of information can spread through a chain of transmission where naïve observers become experienced models for new, naïve observers. Cook et al. (1985) showed that in macaques, *M. mulatta*, information could propagate through a chain of two individuals, but the intensity of the response was not maintained through the learning chain. Suboski et al. (1990) showed that zebrafish, *Danio rerio*, could maintain learning through a chain of three individuals, and Curio et al. (1978) showed that information could be socially transmitted through a chain of seven blackbirds, *T. merula*.

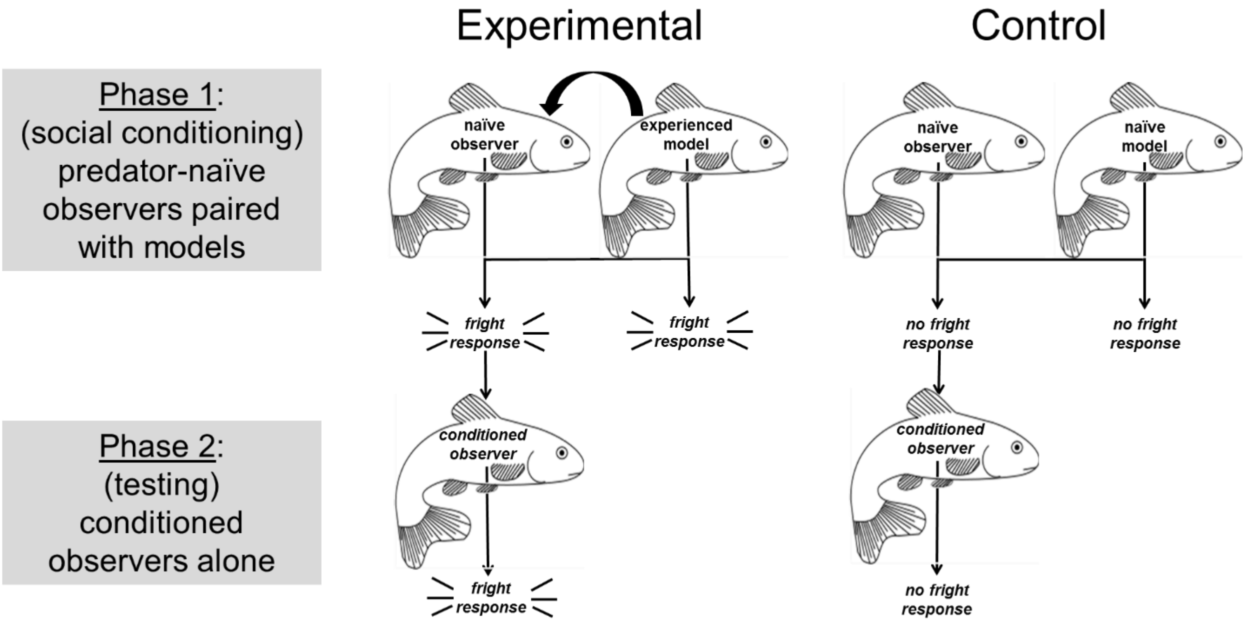

Figure 1.1. Experimental demonstration of social learning of predator-recognition [modified from Mathis et al. (1996)]. This standard methodology involves a conditioning phase where naïve individuals are paired with experienced individuals, where social information about risk can be transferred (bold arrow). Subsequently, observers are tested in the absence of the model to confirm whether they learned the information.

1.6. Learning safety

Learning about predators is not limited to risk, also extending to safety where a stimulus is learned as nonthreatening instead of dangerous or neutral. The learning of safety can occur via repeated exposures to a stimulus (e.g., the odour or sight of a novel individual) in the absence of negative consequences (Ferrari & Chivers 2011). When such experience prevents a subsequent association between the stimulus and risk, psychologists refer to this as 'latent inhibition' (Acquistapace, Hazlett & Gherardi 2003; Lubow 1973). For example, when damselfish, *Pomacentrus moluccensis*, were repeatedly exposed (six times) to a novel odour, they failed to learn it as risky during a subsequent pairing with damage-released conspecific cues (Mitchell et al. 2011). Latent inhibition has been demonstrated in several aquatic species (e.g., Acquistapace et al. 2003; Ferrari & Chivers 2006b, 2011). While the research on social learning is ripe with examples of learning of risk, little is known about the ability of animals to socially acquire information about the safety of novel species or habitats (see details in Chapter 2).

1.7. Study species and 'Schreckstoff'

The fathead minnow (*Pimephales promelas*; family Cyprinidae) is a fish species of small size (<10 cm) and one of the most common fishes in North America, being widely distributed from Mexico to Canada's Northwest Territories, occupying ponds, lakes, and rivers (Page & Burr 1997). Fathead minnows are prey to many predator species, including other fish, birds, and aquatic invertebrates (Warren, Burr & Tomelleri 2014). Although many fish species are social, the fathead minnow has been one of the most studied, along with zebrafish, *D. rerio*, and guppies, *Poecilia reticulata*. Fathead minnows (hereafter, minnows) spend the majority of their time engaged in social interactions, living in large social groups referred to as 'shoals' in fishes (Pitcher 1986). They also can make synchronized movements when avoiding danger (Chivers, Brown & Smith 1995; personal observations). During the reproductive season, males display social competition for mates by defending territories, and then the males defend the fertilized eggs from predators, including conspecifics (Martinovic-Weigelt et al. 2012; McMillan & Smith 1974).

For decades, minnows have been a classic model for understanding fear reactions. Like numerous fish species, they have cells in their skin that contain a substance that was originally described by von Frisch (1938, 1941) as 'Schreckstoff', meaning 'fright stuff' (Stensmyr & Maderspacher 2012). Unexpectedly, von Frisch discovered the substance when studying whether fish could hear. Later research would show that indeed they can (e.g., Popper & Fay 1973). In von Frisch's research, he began to label individual fish by severing a tail nerve which discoloured the tail fin. However, he noticed that releasing one of these individuals into their original social group caused the entire group to be reluctant to approach it. He supposed that fear had spread quickly throughout the entire population.

We now know much more about the mechanisms underlying von Frisch's observations almost a century ago. When minnow skin is physically damaged by a predator, the Schreckstoff is released and reliably indicates that a predator has attacked (Ferrari et al. 2010b; Mathis & Smith 1992). Nearby conspecifics (and in some cases sympatric heterospecifics) that detect the substance via olfaction will innately recognize risk in their environment (Ferrari et al. 2010b; Pollock & Chivers 2003) and respond rapidly with overt antipredator behaviours such as dashing, freezing, increased shelter use, increased shoaling, and overall reductions in activity (Smith 1992). Moreover, predators that consume minnows will release the substance as diet cues (Mathis & Smith 1993), eliciting the same responses. Many other aquatic species, including invertebrates, respond to such cues in similar fashion (i.e., alarm reactions) (Ferrari et al. 2010b). Hereafter, I refer to these cues generally as 'alarm cues' (sensu: Chivers, Brown & Ferrari 2012).

There is evidence that alarm cues evolved either for the benefit of warning kin (e.g., Gerlach et al. 2001), disrupting predation events via the attraction of predators (e.g., Mathis, Chivers & Smith 1995), or for protection against pathogens, parasites, or ultraviolet radiation (Chivers et al. 2007), where the alarm response evolved secondarily. At the same time, there has been much curiosity surrounding the chemistry of alarm cues. In minnows and zebrafish, *D. rerio*, purine-N-oxides elicit the alarm response (Brown et al. 2000; Parra, Adrian & Gerlai 2009), whereas compounds lacking the nitrogen functional group do not. In catfish, *Ictalurus punctatus*, synthetic hypoxanthine-3-N-oxide elicits responses that match the intensity of those toward conspecific skin extract (Brown et al. 2003), whereas another compound (pyridine-N-oxide) possessing a N-oxide functional group elicits a weaker response. More recent work on skin extracts from zebrafish has revealed that their alarm substance is a chemical mixture that includes glycosaminoglycan chondroitin (Mathuru et al. 2012). Ecological evidence demonstrates that the chemistry of the alarm substance must be highly variable across species, as animals typically do not respond to the alarm cues of other species unless being congeneric, and then responding with a decreasing intensity as the phylogenetic distance with the donor increases (Commens-Carson & Mathis 2007; Mirza & Chivers 2001; Mitchell, Cowman & McCormick

2012). This variation across species likely allows prey to avoid costly responses toward alarm cues from other species that are irrelevant.

Like other species, when minnows detect alarm cues in conjunction with the sight or odour of a novel predator, they learn the predator cues as a threat (Ferrari et al. 2010b). Indeed, across species, this ‘alarm-cue learning paradigm’ has been most studied in minnows, being substantially moved forward by the work of R.J.F. Smith and colleagues (e.g., Chivers & Smith 1995; Mathis, Chivers & Smith 1993; Smith 1992). In addition to alarm-cue learning, minnows demonstrate social learning via observing fearful conspecifics (Ferrari et al. 2005; Mathis et al. 1996). Both forms of learning can occur after only a single conditioning and can increase survival in a predation context (Manassa & McCormick 2013; Mirza & Chivers 2000).

1.8. Research objectives

A few studies have looked into factors that affect the efficacy of social learning, such as specific traits of the model, or group composition (e.g., size and observer-to-model ratio) (Ferrari & Chivers 2008; Kavaliers, Colwell & Choleris 2005; Mathiron, Crane & Ferrari 2015). However, little is known about the effect of uncertainty on social learning, or how extrinsic factors (e.g., environmental conditions such as high- vs. low-risk environments) affect learning outcomes. My overall objective, herein, was to assess factors that potentially play a role in the transfer of social information about risk and safety. More specifically, I explored three over-arching questions:

How do individual and social-learning mechanisms compare when current information is new vs. when current information conflicts with prior information? In Chapter 2, I compare the intensity of learned antipredator responses between alarm-cue and social-learning mechanisms in different contexts. Some minnows were conditioned to recognize an odour as safe before testing whether the two risk-learning mechanisms would override the previous information, thus exploring what minnows learn in a conflicting situation. Other minnows had no prior experience with the odour as safe, and thus did not experience conflicting information. These minnows were naïve to the odour when given the opportunity to learn it as a threat via the two mechanisms, allowing me to compare their learning outcomes. In an experiment presented in Chapter 4, I reversed the information about risk and safety by testing whether social information about safety could override the previous learning of risk. Chapters 5 and 6 also assess how minnows manage conflicting situations about risk and safety in the context of social learning.

Are social models less reliable when they exhibit uncertainty about risk, and likewise, does uncertainty for observers make social models more influential? In the experiment presented in Chapter 3, I attempted to manipulate the reliability of models by making them uncertain about what cues were threatening. I then explored how observers reacted to these unreliable responses, and whether they could learn from these models about specific threats. In reversed fashion, Chapter 4 explores how uncertainty about risk in observers affects social-learning outcomes when their models are knowledgeable about a cue. The experiments in Chapters 5 and 6 also assess learning by observers that are uncertain about risk, with Chapter 5 involving observers and models that were both uncertain about risk.

Does a group of social models influence the acquisition of fear and a subsequent learning of safety? In Chapters 5 and 6, I sought to determine whether interacting with more than one model would facilitate social learning. Specifically, I wanted to know if fearful observers could learn safety from groups of models, either together in time or in succession. I also tested whether social isolation vs. social companionship plays a role in fear acquisition and safety learning. These experiments involved a few variations in models: whether they were experienced with safety or risk, how many were present, and for how long. In Chapter 6, I assess how these pairings affected both the observers and models within each pairing.

1.9. Anticipated significance

Animal behaviour theory has developed substantially since Tinbergen published his book on social behaviour (1953), with a tremendous amount of research exploring the social lives of animals – from acoustic communication in marmots (Blumstein 2007) to chemical communication in insects (Wilson 1965), interference competition in birds (Minot & Perrins 1986), and social learning in fishes (Mathis et al. 1996). While most early work focused on understanding which species are capable of social learning and how such information is transferred among group members, much of the present research, including social network theory, aims to understand factors that affect the origin, quantity, content, and reliability of information transfer. Herein, I present a case where the field of animal behaviour, and specifically social learning theory, can inform and provide insights into factors affecting fear severity in humans and the potential for overcoming such fear, with specific attention on post-traumatic stress (see Chapter 7). In my view, the field of animal behaviour is a crucial source of information to anyone interested in understanding factors that modulate the social transfer of risk or safety-related information. Yet, applications of social learning theory outside of animal ecology, and specifically to human psychology, are relatively rare, as animal models informing human psychology are often viewed as unconvincing.

1.10. Ethical statement

The following studies were approved by the University of Saskatchewan's University Committee on Animal Care and Supply (protocol # 20130079). I collected all fish under a Saskatchewan Ministry of Environment Special Collection Permit. Fish currently either remain in laboratory stock colonies (protocol # 20160074) or have been humanely euthanized with an overdose of tricaine methanesulfonate (MS-222).

Chapter 2: Social learning of conflicting information[2]

2.1. Introduction

There are a few basic ways for prey to learn about predation risk, and we might expect prey to learn better (and/or have less uncertainty) from some learning modalities or types of cues compared to others. For instance, visual cues from models can be highly accurate in space and time and usually provide information about the target of the response (e.g., the model mobbing a predator) (Jacobs 2002), but they also require the observer to recognize that a model has changed its normal behaviour, which may be difficult in complex habitats or at night. Auditory cues do not allow this directionality; hearing a mobbing call does not provide information on the target of the call. In contrast, chemical cues are available all the time and can travel long distances if moved by air or water, but they may be less reliable in space and time if they persist long after predation occurs and if currents render their origin inaccurate, creating situations where the pairing of cues might even be completely fortuitous (Ferrari et al. 2010b; Mathis & Crane 2017).

A number of theoretical models have investigated the occurrence of individual vs. social learning in the context of foraging or mate choice (Beauchamp 2000; Galef & Laland 2005; Laland 2004; Rendell et al. 2010). These producer/scrounger type games have led to insights into factors driving the dynamics of social learning and the limitations associated with each context. Observers should not copy the behaviour of others indiscriminately, and the direction of learning

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[2] Most of the content of this chapter comes from the following publication. Changes have been made to avoid redundancy with other chapters and for consistency among chapters.

Crane AL, Ferrari MCO. (2015) Minnows trust conspecifics more than themselves when faced with conflicting information about predation risk. Animal Behaviour 100: 184-190.

Portions of the introduction have been modified from:

Crane AL, Ferrari MCO. (2013) Social learning of predator recognition: advances and future directions. In: Social Learning Theory: Phylogenetic Considerations Across Animal, Plant and Microbial Taxa (Clark ed.). Nova Science Publisher NY, USA. Pp. 53-82.

should allow for the most accurate and beneficial information to be transmitted to the observers. For instance, in guppies, *P. reticulata*, young females copy the mate choice of older females, while older females are not affected by the choice of younger females (Dugatkin & Godin 1992; Dugatkin & Godin 1993). Deciding who to copy or which copying strategy (e.g., random, frequency-dependent, maximize pay-off) to employ has received some attention. However, the outcome of these models may differ for the transmission of predation-related information because responding to non-threatening cues is much less costly than failing to respond to risky ones.

In the context of predation, only a few comparisons have been made among different learning modalities. Studies by Curio et al. (1978) and Vieth et al. (1980) showed that blackbirds, *T. merula*, can learn to become wary of a mounted predator either by hearing the mobbing calls of conspecifics (auditory cues only) or by hearing the mobbing calls while also seeing a conspecific near the predator (auditory and visual cues). The addition of the visual cues did not seem to increase wariness, indicating that the two cues were likely redundant and non-additive. The authors then attempted to condition the observers to become wary of mounted predators that were previously learned as safe (see Chapter 1). When these non-responsive individuals observed the mounted predator paired with mobbing calls (auditory cues only), they failed to subsequently increase their wariness towards the mount. However, they learned to increase wariness after receiving both auditory and visual cues of conspecifics.

In another example, macaques, *M. mulatta*, were pre-exposed to a novel snake, either alone vs. paired with a non-fearful conspecific (Mineka & Cook 1986). In both cases, the observers learned not to behave fearfully towards the snake. When both groups were then exposed to a conspecific model displaying a fear response toward the snake, the monkeys that were pre-exposed to the snake alone immediately learned to fear the snakes, whereas the monkeys that were previously paired with non-fearful conspecifics did not. Thus, it appears that social cues are persuasive enough to override individual learning, but prior social learning is more difficult to reverse.

2.2. Objectives

In this study, I sought to compare social learning via a live conspecific model vs. individual learning from alarm cues, and in a situation where information about risk conflicted with past information about safety. I first gave minnows the opportunity to learn a novel odour as safe from repeated exposure to the odour without negative consequences (Fig. 2.1). I then gave minnows a conflicting situation, providing them with new information that indicated the odour was risky via either the alarm-cue or social-learning mechanism. This dilemma forced minnows to make a decision based on the value of their previously learned information (the cue was safe) and that of the new information (the cue is risky). After this conflicting phase, minnows were individually exposed to the odour alone, and their antipredator behaviour was measured (2×2×2 design; Fig. 2.1). A control group received background exposures to water, rather than to the predator odour, allowing me to compare the intensity of the learned response via the two mechanisms in the absence of conflicting information. I expected that social learning and alarm-cue learning would result in similar intensities of learned responses because the predator experience of social models occurred via alarm-cue learning. However, the intensity of responses could also be slightly less via social-learning than alarm-cue learning since the intensity of the response weakens over a transmission chain (Curio 1988; Suboski et al. 1990).

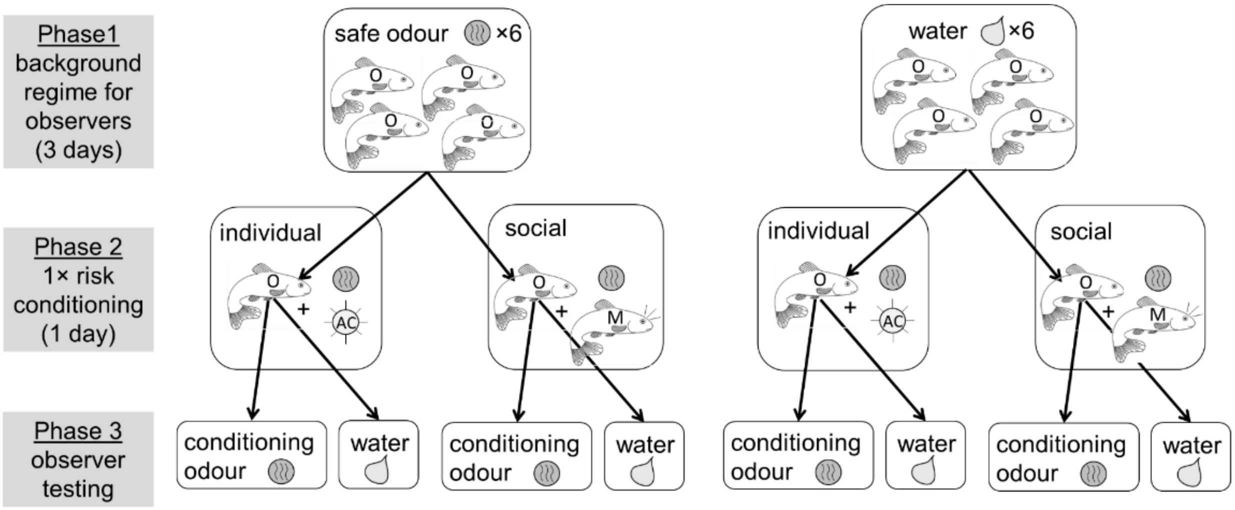

Figure 2.1. Experimental design testing whether individual and social information about risk overrides prior individual knowledge of safety. First, observer (O) minnows had the opportunity to learn an odour as safe before being conditioned to fear the odour, either individually with alarm cues (AC) or socially with an experienced conspecific model (M). Observers were tested alone 1 d later to determine whether their fear persisted.

2.3. Methods

Fish collection and maintenance

Using Gee's inverted traps, minnows (unsexed with total length ranging 30–65 mm) were collected in August 2013 from Feedlot Pond, located on the University of Saskatchewan campus, in central Saskatchewan. Minnows from Feedlot Pond are exposed to a variety of predators, including birds and beetles, but they are naïve to fish predators (e.g., Chivers & Smith 1994; Mathis et al. 1993). Extensive trapping over the past 25 years has revealed no fish predators at this site, and no studies on minnows from this population have found innate recognition of fish odours as a threat.

After collection, minnows were transported to the R.J.F. Smith Centre for Aquatic Ecology and the Aquatic Predation and Environmental Change Laboratory at the University of Saskatchewan. These facilities have flow-through water delivered from incoming municipal water that passes through laboratory filtration systems (particulate and carbon filters). This 'system' water is delivered to tanks (either 76-l aquaria with gravel substrate or 950–2460-l pools) that are equipped with outflow pipes, aeration, and lighting (15:9 h light:dark cycle). Minnows were fed flake food (Nutrafin Max) every morning and received a 30% water change daily.

Obtaining minnow alarm cues and novel odour

I used standard procedures for making alarm cues (Crane et al. 2011; Ferrari & Chivers 2006a), sacrificing five individuals with a blow to the head, in accordance with the Canadian Council on Animal Care. I then removed skin from each side of the body and used a homogenizer (Polytron PT-2500E) to mix the skin into solution, which I diluted in system water to reach a standard and ecologically relevant concentration (1 cm^2 / 40 l) that is known to represent a high level of threat and elicit a fear response when 5 ml is injected into a 37-l tank (Ferrari, Capitania-Kwok & Chivers 2006a; Wisenden 2008). The injected solution would initially be concentrated at the location of the injection, and over time would become diluted in the tank's water, eventually reaching a concentration of 1 mm^2 of skin in 2800 L. After being homogenized and diluted, the alarm-cue solution was frozen at -20°C in 100-ml aliquots until being thawed before use.

To obtain a novel odour for this experiment, I collected northern pike, *Esox lucius*, from Pike Lake, SK, using a seine. Although pike are not innately recognized as predators by minnows from Feedlot Pond, northern pike (hereafter, pike) are one of the primary native predators of minnows in the region such as at Pike Lake (Page & Burr 1997). The collected pike (*n*=2) were housed in 76-l aquaria that were wrapped in opaque polyethylene sheeting to ensure visual isolation from surrounding tanks. Prior to stimulus collection, each pike was fed two swordtail, *Xiphophorus hellerii* (30–40 mm total length) to facilitate the evacuation of any minnow diet cues (Ferrari, Messier & Chivers 2006b; Mathis & Smith 1993). After 4 d, pike were placed individually into 37-l tanks with clean water, but filled with a volume of water that was proportional to the size of the pike (50 ml/g of fish). After 24 h without water filtration, pike were removed and the water was frozen at -20°C in 600-ml aliquots.

Phase 1: Prior exposure to safety

All minnows had acclimated to the laboratory for >2 months and were behaving calmly before being used in the experiment. First, they were moved into 37-l testing aquaria with gravel substrate and a shelter object (a 10×10 cm ceramic tile with 2-cm plastic legs). The front surface of each tank was covered with a plastic film (5% visual light transmission) that, coupled with overhead tank lighting, provided a clear view of each fish while minimizing visual cues from my presence. The side and rear surfaces of experimental tanks were covered with opaque polyethylene sheeting to block visual stimuli from surrounding tanks. Each tank was equipped with an injection hose (a 150-cm piece of tubing attached parallel to the air stone), through which stimuli could be gently injected into the tank with a syringe and then flushed with tank water that had been withdrawn just prior to the injection (Ferrari et al. 2006a; Ferrari et al. 2006b).

Minnows were given 24 h to acclimate to experimental tanks before their first exposure. Over the next 3 d, minnows were exposed to 20 ml of either pike odour or system water (water, hereafter) twice a day (six exposures total; Fig. 2.1). In previous studies with fishes, six prior exposures were enough to ensure the learning of safety (Ferrari & Chivers 2006b; Mitchell et al. 2011). In this experiment, these exposures occurred in the morning (0800–1000 h) and afternoon (1300–1600 h), with a full water flush being conducted 1 h following each injection.

Phase 2: Fear conditioning with different cues

After the sixth prior exposure (and the subsequent water change), the shelters were removed from the tanks in preparation for the social conditioning phase. The absence of shelters is thought to facilitate shoaling rather than agonistic behaviours among fish. In half of the tanks, a model was added. As a procedural control, I dipped a net in the tanks not receiving a model. Models were always slightly larger than observers (size difference <10 mm total length), so that I could distinguish between them. Models had been conditioned 5 h earlier, with an exposure to 20 ml of pike odour paired with 5 ml of alarm cues. Over the next 18–24 h, observers had the opportunity to fully interact with these conditioned models before I injected 20 ml of pike odour, giving observers the opportunity to learn from the models that pike odour was dangerous. I reasoned that a full interaction with models would be the most influential to observers, and I did not intend to assess the relative importance of specific cue types (e.g., visual vs. chemical vs. tactile) or a specific behaviour (e.g., freezing vs. dashing). For the alarm-cue learning group, I injected 20 ml of pike odour paired with 5 ml of alarm cues. All tanks received a water change and had shelters returned 1–4 h following conditioning, at which point I removed the models with a net. To control for procedural disturbance, I once again moved a net in the other tanks for 10 s.

Phase 3: Testing the intensity of fear

Testing took place 1 d following risk conditioning. I chose to feed minnows 1 h before testing, because hunger can weaken responses to predation risk (Brown & Smith 1996; Whitham & Mathis 2000). First, I waited to begin a trial until fish were moving, and then assessed their reductions in activity (i.e., their typical antipredator response) (Smith 1992). Holding a tally denominator and a multiple digital timer, I measured the behaviour of each individual during an 8-min baseline pre-stimulus period. The number of lines crossed on a grid (6.3×6.3 cm) by the midpoint of the minnow’s body was quantified as a measure of distance moved, along with the time spent under shelter (centre of the body) and the time spent foraging, where minnows angled (~45°) their heads downward to search the gravel. Following this pre-stimulus period, either 20 ml of pike odour or water was added via the injection hose, and the response variables were recorded again during an 8-min post-stimulus period to assess the change in behaviour due to the odour. Observations were conducted blind to the background and conditioning treatments, and the order of testing was randomized across treatments. Each day, following the end of the trials, minnows were moved into a new housing tank, while experimental tanks were cleaned for another round of trials. No fish was tested more than once. Sample sizes were 20–32 per group.

Statistical Analyses

Data on baseline behaviour were analyzed together (lines crossed, time under shelter, and time spent foraging) using a 2-way MANOVA with the prior exposure treatment (safety or no safety) and the conditioning type (alarm cue or social cue) as factors. To assess behavioural responses to the testing cue (pike odour or water), data from pre- and post-stimulus behaviours were computed as changes in behaviour (post – pre) for time under shelter and time spent foraging, whereas data for lines crossed varied greatly among individuals, so I used a proportional change [(post – pre)/pre] to better standardize the response among individuals. Again, I analyzed the three response variables (proportional change in lines crossed, change in time under shelter and change in time spent foraging). The full-factorial 3-way MANOVA design included the prior exposure treatment (safety or no safety), the conditioning type (alarm cue or social cue) and the testing treatment (pike odour or water). Because MANOVA assumptions were not fully met, I used Pillai's Trace for its robustness to non-normality and covariance heterogeneity (Olson 1976), which occurred for some treatment groups for some response variables. I used post-hoc 2-way MANOVAs to interpret significant interactions by splitting the data, first by conditioning type and again by the prior exposure treatment. Because data were tested twice in post-hoc analyses, I used Bonferroni corrections dividing alpha by the number of comparisons ($\alpha/2$ where $\alpha=0.05$). All analyses were conducted in SPSS 23.

2.4. Results

Social learning of risk overrides individually learned safety

Baseline activity during the pre-stimulus period did not differ among treatments (all main effects and interactions: $p>0.3$). When analyzing behavioural changes, I found a significant 3-way interaction where responses to testing cues depended on a combination of the prior exposure treatment and the conditioning type (prior exposure × conditioning type × testing cue: $p=0.009$; Table 2.1a, Fig. 2.2). Post-hoc analyses revealed that alarm-cue learning was inhibited by prior exposure to pike odour (prior exposure × testing cue: $\alpha=0.025$, $p<0.001$; Table 2.1b), and thus minnows had learned safety via latent inhibition. However, the individually-learned safety was overridden by social learning of risk (prior exposure × testing cue: α=0.025, *p*=0.79; Table 2.1c, Fig. 2.2).

Table 2.1. Results of alarm-cue vs. social learning: statistical test output for behaviour in response to prior exposure (odour vs. water), conditioning type (alarm-cue or social learning mechanism), and the testing cue (the odour or water). Significant terms of interest are in bold type.

	F	***df***	***p***
a) overall 3-way MANOVA			
prior exposure	4.84	3, 190	0.003
conditioning type	0.92	3, 190	0.43
testing cue	35.28	3, 190	<0.001
prior exposure × conditioning type	5.07	3, 190	0.002
prior exposure × testing cue	6.47	3, 190	<0.001
conditioning × testing cue	2.04	3, 190	0.11
prior exposure × conditioning type × testing cue	3.95	3, 190	**0.009**
b) post-hoc 2-way MANOVA for alarm-cue conditioned observers			
prior exposure	11.30	3, 94	<0.001
testing cue	16.86	3, 94	<0.001
prior exposure × testing cue	11.54	3, 94	**<0.001**
c) post-hoc 2-way MANOVA socially-conditioned observers			
prior exposure	0.20	3, 94	0.90
testing cue	19.35	3, 94	**<0.001**
prior exposure × testing cue	0.36	3, 94	0.79
d) post-hoc 2-way MANOVA for no conflicting information			
conditioning type	1.29	3, 95	0.28
testing cue	33.79	3, 95	**<0.001**
conditioning type × testing cue	2.10	3, 95	0.11
e) post-hoc 2-way MANOVA for conflicting information			
conditioning type	4.85	3, 93	0.004
testing cue	6.10	3, 93	0.001
conditioning type × testing cue	4.52	3, 93	**0.005**

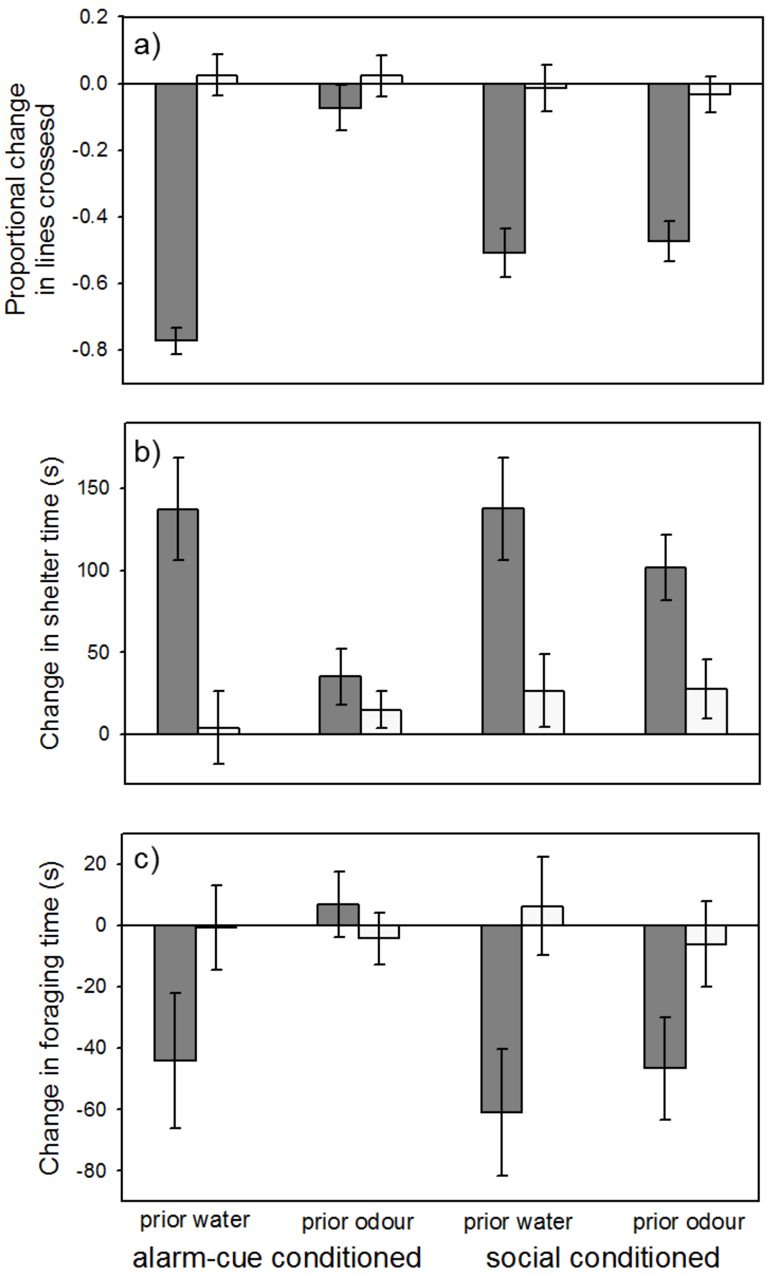

Figure 2.2. Mean (±SE) proportional change in (a) the number of lines crossed, (b) time spent under shelter, and (c) time spent foraging by minnows with prior exposure (6×) to predator odour or water that were subsequently conditioned with alarm cues or social cues and tested with predator odour (dark bars) or water (white bars).

Social and alarm-cue learning are similar in intensity

In the absence of conflicting information, alarm-cue learning tended to have a stronger influence in terms of lines crossed (Fig. 2a). However, the overall intensity of fear did not differ significantly between the alarm-cue and social-learning mechanisms (conditioning type: α=0.025, p=0.28; conditioning type × testing cue: α=0.025, p=0.11; Table 2.1d).

2.5. Discussion

Here, I considered alarm-cue learning to be a form of individual learning in the sense that it occurred without the presence of social companions. In the absence of conflicting information, learned fear responses were fairly similar in intensity between the social and individual mechanisms, with a nonsignificant tendency for social learning to be slightly weaker, as has been observed in studies on transmission chains (Curio 1988; Suboski et al. 1990). However, individual learning via other mechanisms could lead to different outcomes. For instance, learning about predation risk by directly escaping a predator attack should provide prey with multiple cues, and presumably more certainty about risk (Brown & Smith 1998; Suboski & Templeton 1989). However, Vilhunen et al. (2005) found that Arctic charr, *Salvelinus alpinus*, that were chased by a predator and had witnessed attacks learned to respond to the predator's odour at the same intensity as those that learned socially without the predator's presence. Overall, there have been few tests of learning from direct exposure to predators, and I am not aware of any studies on learning after injury from a predator attack. This form of individual learning would presumably be more persuasive and would override prior expectations about safety. Such tests have ethical challenges but could increase our understanding of learning mechanisms and their role in conflicting situations.

As documented in other fish species, minnows in this study learned safety from repeated exposure to an unknown odour in the absence of negative consequences. This learned safety was demonstrated via latent inhibition (see Chapter 1), affirming that information about risk does not universally override learned safety. However, minnows that interacted with fearful models ignored their prior assessment of safety, showing a learned fear response to the odour. Thus, social cues appear more persuasive than individual information when conflicting with past information about safety, similar to previous studies (Mineka & Cook 1993; Vieth et al. 1980).

In this study, minnows serving as models were always larger than observer minnows, indicating that models were older and had more experience with predators. Whether learned responses from smaller models differ from those of larger models would be interesting to test. Because adult minnows are unlikely to 'outgrow' the gape of many predators, both sizes should be vulnerable to the same predators, so smaller models should be as reliable as larger individuals. However, in other species, growth and life-stage development presumably play important roles, and perhaps more so in situations where the cost of being wrong is relatively small (e.g., learning locations of food: Duffy, Pike & Laland 2009). In contrast, the high cost of being wrong about predation could dictate that the reliability of social information is less important, and thus learned responses about risk are conservative in a broad sense.

My comparison of social and alarm-cue learning involved two inherent confounding factors. By definition, social learning requires the presence of another individual, while individual learning does not. However, the isolated nature of the individual-learning treatment likely promoted fear (see Chapter 5) rather than the retention of learned safety, as occurred here. Another inherent confound was the availability of different types of information. Interacting with fearful models should provide multi-modal information (Seyfarth et al. 2010) such as visual and tactile cues, as well as non-injury chemical cues that are generally referred to as ‘disturbance cues’ (Johnston & Johnson 2000; Vavrek et al. 2008) which are released in the urine or diffused across the gills in some aquatic species (Wisenden 2000). Disturbance cues alone, however, do not appear to mediate predator-recognition learning (Ferrari et al. 2008; Vilhunen et al. 2005). In contrast to fully interacting with multiple cues from a fearful model, alarm-cue learning involves the availability of only chemical cues. This difference could well be the driving factor that made social learning more persuasive in this study. Whether the opportunity for social learning of safety can override individually learned risk is explored in Chapter 4.

Chapter 3: Unreliable models and socially-transferred neophobia[3]

3.1. Introduction

Social information varies in reliability (i.e., the probability of being correct) (Traub 1994). Indiscriminate social learning may be prevalent when reliability cannot be externally assessed, but in other cases, social learning outcomes may depend on the reliability of the information (Dugatkin & Godin 1993). For instance, in marmots, *Marmota flaviventris*, observers discriminate between reliable and unreliable models that display alarm calls when predators are present (reliable cues) but also when predators are absent (unreliable cues) (Blumstein, Verneyre & Daniel 2004b). When exposed to unreliable cues, observers became uncertain about predation risk, and reacted by assessing threats independently, thus decreasing their time spent foraging. Reliability of models likely varies according to several factors. For instance, related individuals might perform antipredator responses that are more appropriate than those of genetically distinct individuals. Moreover, if observers pay more attention to closely related models, they should have greater potential to learn from them, as was found in deer mice, *Peromyscus maniculatus*, that learn from relatives about biting flies, *Stomoxys calcitrans* (Kavaliers et al. 2005). Phenotypic traits (e.g., size or dominance status) may also promote

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[3] Most of the content of this chapter comes from the following publication. Changes have been made to avoid redundancy with other chapters and for consistency among chapters.

Crane AL, Mathiron AGE, Ferrari MCO. (2015) Social learning in a high-risk environment: incomplete disregard for the 'minnow that cried pike' results in culturally-transmitted neophobia. Proceedings of the Royal Society: Biological Sciences 282: 20150934.

A small portion of the introduction was modified from:

Crane AL, Ferrari MCO. (2013) Social learning of predator recognition: advances and future directions. In: Social Learning Theory: Phylogenetic Considerations Across Animal, Plant and Microbial Taxa (Clark ed.). Nova Science Publisher NY, USA. Pp. 53-82.

directional social learning. The study by Kavaliers et al. (2005) also provided evidence that subordinate observers learned better than dominant individuals. In damselfish, *Acanthochromis polyacanthus*, juvenile observers learn better from adult individuals than from other juveniles (Karplus, Katzenstein & Goren 2006). Perhaps, when prey undergo extensive changes in predators throughout their life history, similar-sized individuals would best facilitate social learning of predation risk because these individuals would share the same predators, but to my knowledge this has not been reported.

The reliability of information should also be affected by its timing. For instance, in grackles, *Quiscalus lugubris,* the order of social and predator cues did not affect the learning outcome, as long as the cues had some temporal overlap (Griffin & Galef 2005), and in mynahs, *Acridotheres tristis*, a lack of overlap led to a complete failure in learning (Griffin 2009). Korpi and Wisenden (2001) showed that when predator cues and alarm cues were presented 5 min apart, successful learning of the predator still occurred. The latent nature of the chemicals in the water may explain why learning still occurred after 5 min. However, this latency may potentially lead to fortuitous pairings, which could render the learned information unreliable. In addition to the timing of the cues, the specific type of cue may also contribute to its reliability. Perhaps a cue that lacks specificity will lead to failed learning. For instance, the disturbance cues released upon encountering perturbation without any physical damage elicit fright behaviour in nearby conspecifics but do not convey any information regarding the cause of the disturbance, a predator or otherwise (Bryer, Mirza & Chivers 2001; Vavrek et al. 2008; Wisenden 2000). This may explain why studies have documented failure to learn from disturbance cues (Ferrari et al. 2008; Vilhunen et al. 2005). In contrast, alarm cues reliably indicate that a predator has either injured or killed a conspecific, and thus should be more reliable than disturbance cues at expressing a predation threat. However, alarm cues alone (i.e., in the absence of predator cues) still provide no information about the identity of the predator. As such, I consider alarm cues alone as being ‘general predation cues’ (sensu: Sih et al. 2010). When prey are exposed to alarm cues repeatedly, they know that attacks have occurred but they remain uncertain about the causes, often becoming neophobic, responding to all perturbations rather than only dangerous ones (e.g., Brown et al. 2013). Thus, these uncertain, neophobic individuals may be viewed by observers as being less reliable in a way that is colliqualiy known as ‘crying wolf’.

3.2. Objectives

I predicted that, like other species, minnows exposed repeatedly to alarm cues would become neophobic. My main objective, however, was to explore whether naïve observers would distinguish between an informed response of models (a ‘reliable’ response) towards known risky cues vs. an uninformed, neophobic response (an ‘unreliable’ response). If there are subtle differences between informed and uninformed responses, observers might recognize unreliable models and either (1) spend more time assessing the potential threat, like marmots, *M. flaviventris* (Blumstein et al. 2004b), (2) respond as they would to an informed response if unable to judge reliability, or (3) they might tend to ignore unreliable responses. To test this, I paired predator-naïve observers with individuals that could potentially model either an informed or uninformed fear response depending on whether they were exposed to a known odour or a novel odour. Hence, these models (hereafter, ‘high-risk models’) were experienced with a specific predator odour, while also being repeatedly exposed to alarm cues alone to induce neophobia (Fig 3.1). Then, during a conditioning phase, I paired observers with these models and exposed the pair to either the predator odour known by the model or to a novel odour, giving the naïve observer an opportunity to learn from either the model’s experienced or neophobic response. The third phase of the experiment consisted of testing the observers on their own to determine whether they had acquired fear from either of the two types of responses. To confirm that my social-learning methodology was sound, I also tested social learning of risk under normal, low-risk conditions (2×2×2 design; Fig 3.1).

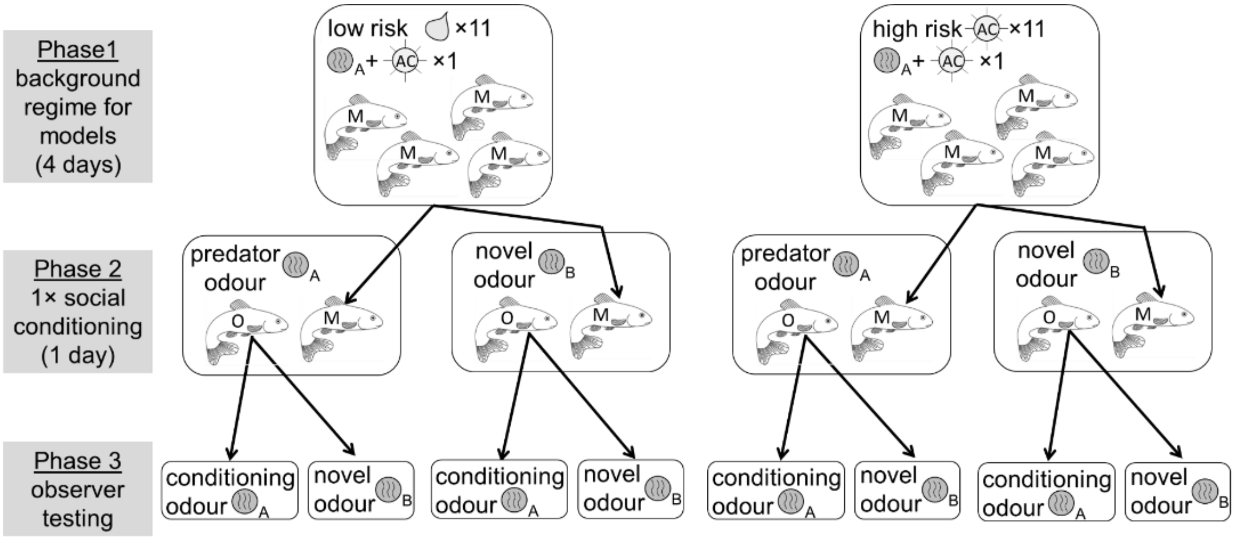

Figure 3.1. Experimental design where naïve observers were conditioned with experienced models from either a high- or low-risk background. All models (M) were experienced with the predator odour as a threat via an alarm cue (AC) pairing, but high-risk models were exposed repeatedly to alarm cues, instead of water, to elicit uncertain responses toward a novel odour. Models were then paired with observers (O) during a conditioning phase where observers had the opportunity to learn from the responses of models to a known odour or a novel odour. Observers were tested 1 d later to determine whether they had learned.

3.3. Methods

Experimental cues

These experiments involved the use of two novel odours for which I used pike and lake sturgeon, *Acipenser fulvescens* (hereafter, sturgeon). For this experiment, these fishes (*n*=2 per species) were loaned to me from other research laboratories at the University of Saskatchewan. Each individual was temporarily starved (4 d) prior to their odour being collected to prevent the odour from containing diet information (Diana 1979). Collection of odours occurred as in Chapter 2 except a weaker concentration was used (100 ml of water per g of fish). After odour collection, all individuals were returned to their holding tanks and immediately fed. Alarm cues were prepared as in Chapter 2.

Phase 1: Background experience for observers and models

All observers were maintained in a low-risk environment during the background phase (76-l housing tanks, ~50 fish per tank). They were not given any predator experience and thus remained naïve to each of the collected odours. Minnows that would serve as models, however, were moved into experimental tanks (see Chapter 2 for tank details) in groups of four. After 1 d of acclimation, 5 ml of alarm cues were injected repeatedly into tanks to elicit a neophobic response that could be interpreted by observers as unreliable, whereas the low-risk control models were repeatedly exposed to water (Fig. 3.1). The cues were injected three times per day for 4 d, once in the morning (0800–1100 h), at midday (1100–1400 h), and in the afternoon (1400–1700 h) with a minimum of 2 h between each exposure. There was one exception to this treatment routine; on the morning of day 4, all models were exposed to 5 ml of alarm cues paired with an additional 20 ml of a novel odour, giving them the opportunity to learn the odour as a predator odour. Hence, models from both risk regimes would display experienced responses toward a known odour that could be interpreted by observers as a reliable response (Fig. 3.1). A full water flush was performed 1 h following the last exposure each day. Because I was concerned about the potential for innate differences in responses toward the pike and sturgeon odours due to differences in evolutionary history or some other intrinsic factor, I randomized which odour served as the predator odour during the background phase. Half of the exposures involved pike as the predator and half involved sturgeon.

Phase 2: Social conditioning trials

Each observer was randomly assigned to a single model from either the high- or low-risk backgrounds (Fig. 3.1). To distinguish between models and observes, I again employed a small size difference (<10 mm total length). However, in this chapter and subsequent chapters, models were larger than observers in approximately half of the trials and reversed in the others. In this study, the members of each observer-model pair were moved individually into experimental tanks and allowed to acclimate together for 24 h. No shelter object was provided during this period to prevent shelter competition and facilitate shoaling between the pair. After the 24-h period, I injected 20 ml of either the predator odour (the same odour used in phase 1) or a novel odour (the other odour).

I conducted behavioural observations on both the observers and the models during the social conditionings, as described in Chapter 2. One deviation, however, was that the presence of more than one fish allowed me to quantify shoaling behaviour. Every 15 s, a score of 1 (no shoaling) was given when the fish were more than a body length apart or a score of 2 (shoaling) when within a body length of each other. Increases in shoaling are a well-documented antipredator response of minnows (Pfeiffer 1962; Smith 1992). The model was removed 1 h after the end of each trial, a shelter was added to the tank, and a full water flush was conducted. Observations did not occur for all conditionings, as sample sizes were large (n=46–50 per treatment group, where k=8 for lines crossed with observers and models measured individually vs. k=4 for their paired shoaling values). Each minnow was only used once, as either a model or an observer.

Phase 3: Testing fear in observers

Observers acclimated alone for ≥16 h before testing. During this phase, observers were tested for their responses to 20 ml of either the conditioning odour (i.e., the odour they experienced in the presence of the model) or to the novel odour (the other odour, to which they were still naïve). I measured response variables as in Chapter 2, but foraging time was highly variable and not included in the analyses. Sample sizes were 22–27 per experimental group (k=8).

Statistical analyses

I assessed differences in pre-stimulus lines crossed using a 4-way repeated-measures ANOVA, testing for the effects of the models' risk treatment (low vs. high), conditioning odour (predator vs. novel) and fish role (model vs. observer, as repeated-measures in the same tank replicate), while also introducing odour species (pike vs. sturgeon) as a blocked factor to test for potential bias. For pre-stimulus shoaling index, only one value was obtained from each pair of fish (observer + model). Hence, a 3-way ANOVA was performed, testing the effects of the risk treatment, conditioning odour, and odour species. Because the treatments had no effects on pre-stimulus behaviour (p>0.1 for all terms and interactions for both response variables), I computed a change in response for each variable, as in Chapter 2. I then performed a 4-way repeated measures ANOVA on the change in lines crossed, and a 3-way ANOVA on the change in shoaling index. For data collected during the testing phase, the response variables (activity and shelter use) could be analyzed together with a multivariate approach. Again, I assessed differences in pre-stimulus behaviour (4-way MANOVA), testing the effect of risk (low vs. high), conditioning odour (predator vs. novel), testing odour (conditioning vs. novel), and odour species as factors. Again, pre-stimulus values did not differ significantly among treatments

(p>0.1 for all terms), and I analyzed the change in behaviour (4-way MANOVA). When overall tests revealed significant interactions, data were split for post-hoc analyses, with specific tests varying as presented below. Again, I used α=0.05 and conducted analyses in SPSS 23, as well as hereafter.

3.4. Results

Information from high-risk models is partially ignored

During the conditioning period, significant interactions occurred between the risk treatment and the conditioning odour (p<0.001), and the risk treatment and fish role (p=0.034; Table 3.1a; Fig. 3.2). There also was no effect of odour species (p=0.62; not depicted), indicating that minnows had no bias toward the pike or sturgeon odours. High-risk models responded more strongly than their observers when exposed to both odours (p<0.001; Fig.3.2). However, there was no effect of cue (p=0.26) and no interaction between the two factors (p=0.38; Table 3.1b; Fig. 3.2), revealing that models did not discriminate between the predator odour and the novel odour, and observers did not discriminate between the responses of models. In contrast, with the low-risk treatment, I found a significant effect of the conditioning odour (p<0.001), no effect of fish role (p=0.07) and no interaction between the two factors (p=0.14; Table 3.1c; Fig. 3.2). Hence, both observers and models responded strongly to the predator odour while not responding to the novel odour under the low-risk conditions. Similarly, shoaling index was affected by a significant interaction between the risk treatment and the conditioning odour (p<0.001; Table 3.2; Fig. 3.3). When models came from the low-risk background, the model and observer shoaled more in response to the predator odour compared to the novel odour (t_{93}=4.4, p<0.001), whereas shoaling did not differ in response to the predator and novel odours when models were from the high-risk background (t_{97}=1.4, p=0.16; Fig. 3.3). Again, species did not affect responses (p=0.17; Table 3.2; not depicted), indicating no bias.

Table 3.1. Results for the number of lines crossed for observers and models during conditioning: statistical test output, testing for the effects of the risk treatment (low vs. high risk for models), the conditioning odour (predator vs. novel), the fish role (model vs. observer, as repeated measures), and the species used for the odour (pike vs. sturgeon). Significant terms of interest are in bold type.

	F	***df***	***p***
a) overall RM-ANOVA			
Within subjects			
role	22.38	1, 187	**<0.001**
role × risk	4.58	1, 187	**0.034**
role × conditioning odour	0.28	1, 187	0.60
role × odour species	0.01	1, 187	0.93
role × risk × conditioning odour	2.85	1, 187	0.09
Between subjects			
risk	<0.01	1, 187	0.96
conditioning odour	12.62	1, 187	**<0.001**
odour species	0.24	1, 187	0.62
risk × conditioning odour	26.67	1, 187	**<0.001**
b) post-hoc RM-ANOVA for pairings with high-risk models			
Within subjects			
role	25.92	1, 96	**<0.001**
role × conditioning odour	0.78	1, 96	0.38
role × odour species	0.46	1, 96	0.50
Between subjects			
conditioning odour	1.29	1, 96	0.26
odour species	0.01	1, 96	0.92
c) post-hoc RM-ANOVA for pairings with low-risk models			
Within subjects			
role	3.40	1, 90	0.07
role × conditioning odour	2.23	1, 90	0.14
role × odour species	0.59	1, 90	0.44
Between subjects			
conditioning odour	37.78	1, 90	**<0.001**
odour species	0.69	1, 90	0.41

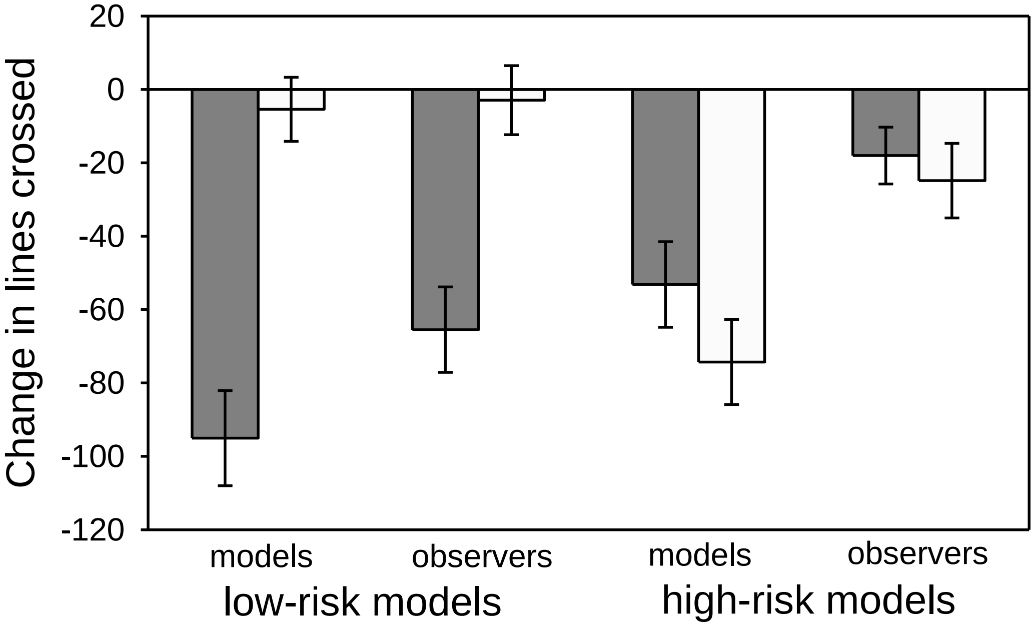

Figure 3.2. Mean (±SE) change in the number of lines crossed by low- and high-risk models and their naïve observers during conditioning when exposed to either predator odour (dark bars) or novel odour (light bars).

Table 3.2. Results for shoaling of observer-model pairs during conditioning: statistical test output, testing the effects of the risk treatment (low vs. high risk for models), the conditioning odour (predator vs. novel), and the species used for the odour (pike vs. sturgeon). Significant terms of interest are in bold type.

	F	***df***	***p***
risk	0.04	1, 187	0.84
conditioning odour	4.66	1, 187	0.034
odour species	1.89	1, 187	0.17
risk × conditioning odour	16.77	1, 187	**<0.001**

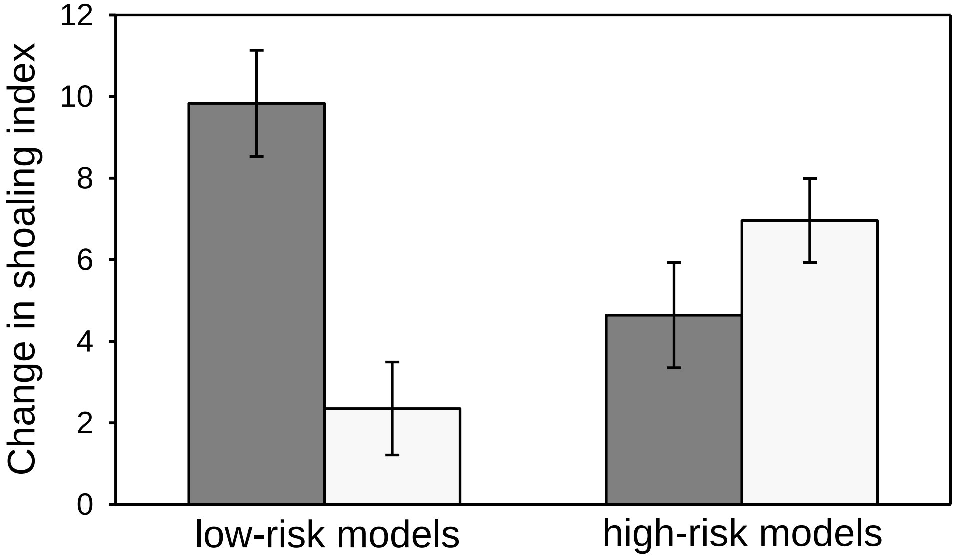

Figure 3.3. Mean (±SE) change in shoaling index for pairs of minnows (experienced model + naïve observer) exposed to either the predator odour (dark bars) or a novel odour (light bars) during conditioning. Models were from low or high-risk background.

Socially-transferred fear

During testing, a significant interaction between the risk treatment, the conditioning odour, and the testing odour occurred (*p*=0.047; Table 3.3a; Fig. 3.4), and again, species had no effect (*p*=0.77; not depicted). For observers conditioned with low-risk models, a significant interaction between the conditioning and testing odours (*p*<0.001; Table 3.3b) revealed that observers conditioned with knowledgeable models showed a strong antipredator response only to the predator odour, whereas the others did not acquire learned fright responses. Thus, social learning of risk from low-risk models was confirmed, as in Chapter 2 and other previous studies (e.g., Mathis et al. 1996; Mineka & Cook 1993). However, the response pattern was quite different for observers paired with high-risk models. I found no effect of the conditioning odour (*p*=0.60), testing odour (*p*=0.34), or an interaction between the two factors (*p*=0.88; Table 3.3c; Fig. 3.4), indicating that observers responded similarly to the conditioning and novel odours regardless of whether their model reacted to a known predator or a novel odour.

Table 3.3. Results of learning from high- and low-risk models: statistical test output for behavioural responses during the testing phase, assessing the effects of risk (low vs. high risk models), the conditioning odour (predator vs. novel), the testing odour (conditioning vs. novel), and the species used for the conditioning odour (pike vs. sturgeon). Significant terms of interest are in bold type.

	F	***df***	***p***
a) overall MANOVA			
risk	1.37	2, 189	0.26
conditioning odour	1.63	2, 189	0.20
testing odour	2.36	2, 189	0.10
species	0.26	2, 189	0.77
risk × conditioning odour	5.56	2, 189	0.005
risk × testing odour	3.01	2, 189	0.052
conditioning odour × testing odour	3.87	2, 189	0.023
risk × conditioning odour × testing odour	3.11	2, 189	**0.047**
b) post-hoc MANOVA for pairings with low-risk models			
conditioning odour	7.60	2, 93	0.001
testing odour	6.11	2, 93	0.003
species	0.85	2, 93	0.43
conditioning odour × testing odour	8.70	2, 93	**<0.001**
c) post-hoc MANOVA for pairings with high-risk models			
conditioning odour	0.51	2, 94	0.60
testing odour	1.10	2, 94	0.34
species	0.06	2, 94	0.94
conditioning odour × testing odour	0.13	2, 94	0.88

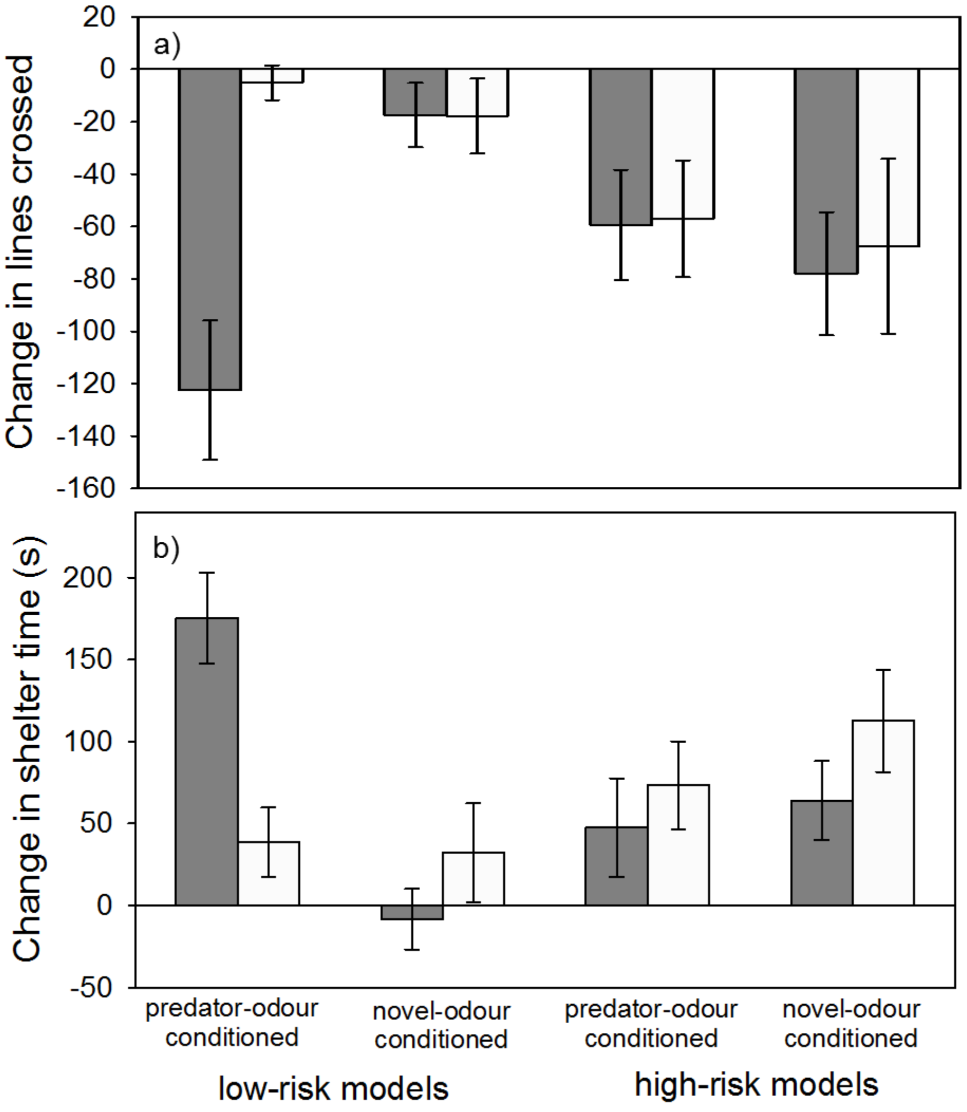

Figure 3.4. Mean (±SE) change in the number of lines crossed (a) and time under shelter (b) for observers during testing when exposed to their conditioning odour (dark bars), or to a novel odour (light bars) that was opposite of that experienced during conditioning. A prior social conditioning consisted of interacting with a model from either low or high background risk while being exposed to either the odour known as a predator by the model (predator-odour conditioned) or a novel odour (novel-odour conditioned).

3.5. Discussion

Fundamental to my results was the finding that repeated exposure to alarm cues induced neophobia in minnows, as had been reported in other species. When exposed to a novel odour, high-risk minnows exhibited decreased activity and increased shoaling behaviour, matching the levels of their experienced risk responses. Individuals that were paired with these models responded similarly after observing experienced vs. neophobic responses, indicating that observers did not view neophobic responses as being less reliable, at least in the short term. A more striking and unpredicted outcome, however, was that observers displayed fear responses toward a novel odour during testing, matching their conditioned responses (seen most clearly in Fig. 3.4a). How could this happen? Observers were not exposed to any stimuli known to cause the emergence of neophobic responses. One explanation could be that simply observing a model's fright response toward an odour caused neophobia in observers. Previous studies on social learning in fishes (e.g., Ferrari et al. 2005; Manassa et al. 2013; Mathis et al. 1996) used alternative controls (typically testing with water instead) and did not test for such an outcome. However, in this study, my results for observers paired with low-risk models demonstrate that simply observing a one-time fright response does not induce neophobia (Fig. 3.4). A more plausible explanation is that high-risk models consistently displayed fearful behaviours (i.e., not only in response to the novel odour), and this state of generalized fear was socially transferred to observers. This hypothesis is supported by the fact that some symptoms of stress in other species are socially transmitted (e.g., Dietz et al. 2011; McAdie & Keeling 2002). Regardless of the specific mechanism, neophobia was unequivocally acquired by observers via social interaction. While numerous studies have demonstrated the social transfer of specific information about predation risk, this was the first study to document the social transfer of generalized fear.

The acquisition of socially-transferred neophobia suggests that the responses of observers to the conditioning odour may have simply been a neophobic response, rather than a specific learned response. However, I cannot disregard the possibility that minnows learned to recognize the specific threat while also becoming neophobic. Whether minnows can learn from high-risk models should receive further attention. A study by Mitchell et al. (2016) addressed this question in tadpoles, *L. sylvaticus*. Individuals from a high-risk background initially showed similar intensities of fear in response to a conditioned predator odour vs. a novel odour. However, several days later, the neophobia had waned, but the learned response to the conditioning odour persisted (see Brown et al. 2015a for work on the waning of neophobia).

During the conditioning phase, observers tended to respond more weakly than models, as described in previous studies on social transmission (Cook et al. 1985; Curio 1988; Suboski et al. 1990). The weaker responses may reflect a short lag-time between the model's response and the observer's assimilation of that information, or it may reflect uncertainty about socially information. However, this ‘dilution’ pattern was roughly twice as pronounced among observers paired with high-risk models, perhaps suggesting that observers viewed all responses from high-risk models as being unreliable, and thus devalued their responses. However, the nature of the experimental design prevented determining whether observers detected unreliability in models or simply their higher level of background risk (i.e., high-risk models had both more uncertainty and higher risk than low-risk models). Thus, an alternative explanation for the more pronounced difference between high-risk models and their observers is the habituation of observers to consistent, fearful behaviour of models. This potential mechanism is consistent with the Risk Allocation Hypothesis (Ferrari et al. 2009; Lima & Bednekoff 1999b). In this hypothesis, the levels of vigilance and foraging behaviour depend on the level of risk and the proportion of time that predators are present. One key prediction is that prey faced with high-frequency risk will decrease their threat responses to fulfill other necessary activities such as foraging. More support for risk allocation as the underlying mechanism here comes from qualitatively comparing the behaviour of low- vs. high-risk models. The weaker response (~50% less) of high-risk models to the predator odour may be due to a cost-benefit trade-off between antipredator responses and foraging, whereas low-risk models had no such trade-off. Until this study, all work on social learning had occurred in a relatively risk-free environment. However, with the emergence of neophobia and socially-transferred neophobia, further study should explore the benefits and costs of learning specific information vs. being neophobic under different levels of environmental risk.

Chapter 4: Uncertainty in social learning of risk and safety[4]

4.1. Introduction

Theoretical models have explored how optimal behaviour is affected by an individual's uncertainty, primarily in the context of foraging (Stephens & Krebs 1986). One fundamental prediction is that uncertainty can be minimized by sampling the environment (e.g., foraging patches) and gathering information (e.g., prey availability and type). Sih (1992) was the first to explore uncertainty in the context of predation risk, manipulating levels of uncertainty with the experimental addition and removal of predators over time. More recently, several studies have induced uncertainty by exposing prey to general predation cues in the absence of specific information (e.g., Brown et al. 2014; Meuthen et al. 2016). One such example was a study by Ferrari et al. (2015a) where uncertainty about a predator's identity was induced in tadpoles, *Lithobates sylvaticus*, but with consistent information about the timing of the uncertain threat (morning or evening). Individuals that experienced risk during the morning displayed neophobic responses only during the morning, and vice versa, suggesting their uncertainty was confined to the time frame of the background risk.

Only a few studies have explored how background risk affects learning outcomes. In one example, Chivers et al. (2014) explored individual learning in damselfish, *Pomacentrus chrysurus*, maintained under different levels of risk. In low-risk conditions, fish learned an odour as nonthreatening, which blocked the subsequent learning that the odour was dangerous during a one-time alarm-cue conditioning (i.e., latent inhibition occurred). However, individuals maintained under high-risk conditions became neophobic and failed to learn the odour as non-

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[4] The content of this chapter is published in the following publication. Changes have been made to avoid redundancy with other chapters and for consistency among chapters.

Crane AL, Ferrari MCO. (2016) Uncertainty in risky environments: a high-risk phenotype interferes with social learning about risk and safety. Animal Behaviour 119: 49-57.

threatening, presumably because the cost of incorrectly learning an odour as safe in a high-risk environment is higher. In the context of my research, this study raised some interesting questions. Would the opportunity to learn safety be more persuasive if background risk had already ceased? Would it be more persuasive if socially mediated? And, in light of Chapter 3, is neophobia caused simply by exposure to high risk, or is uncertainty about risk a prerequisite? This latter question has been explored in an experiment with tadpoles, *L. sylvaticus*. When individuals were repeatedly exposed only to alarm cues, they became neophobic, but those that were repeatedly given specific information about the identity of the predator species did not, despite the overall risk level being the same (Ferrari et al. unpublished data).

4.2. Objectives

The objective of this experiment was to test how uncertainty in observers affects their ability to learn socially about risk or safety. Again, I reasoned that a background environment lacking specific information about risk would cause uncertainty manifested as neophobia, and here, I manipulated uncertainty while keeping the risk level constant. Observer minnows were first maintained under one of three background regimes: (1) certain risk about a specific odour (hereafter, odour$_A$), (2) uncertain risk, or (3) a no-risk control treatment (Fig. 4.1). At the same time, individuals that would serve as models were given experience with odour$_A$ as being either risky or safe. Then, during conditioning, observers and models were paired and exposed to odour$_A$, giving the observer an opportunity to learn from the model about risk or safety. The next day, in the absence of models, I assessed the baseline behaviour of observers to test for the acquisition of persistent fear behaviours, as hypothesised for high-risk individuals in Chapter 3. I then exposed observers to either the conditioning odour$_A$ or a novel odour$_B$ to determine whether they learned from the experienced model and whether they were neophobic (3×2×2 design; Fig. 4.1).

I predicted that uncertainty would promote neophobic responses that would be absent when observers were certain about the odour as a treat. I also expected that uncertain observers would be influenced by ‘safe models’ and learn the odour as a lesser threat, whereas safe models would have little-to-no effect on observers that were certain about risk (i.e., a one-time social assessment of safety would not override prior individual learning of risk). Likewise, I predicted that the behaviour of observers that were certain about risk 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 models might facilitate the correct identification of risk in uncertain observers, thus reducing their neophobia.

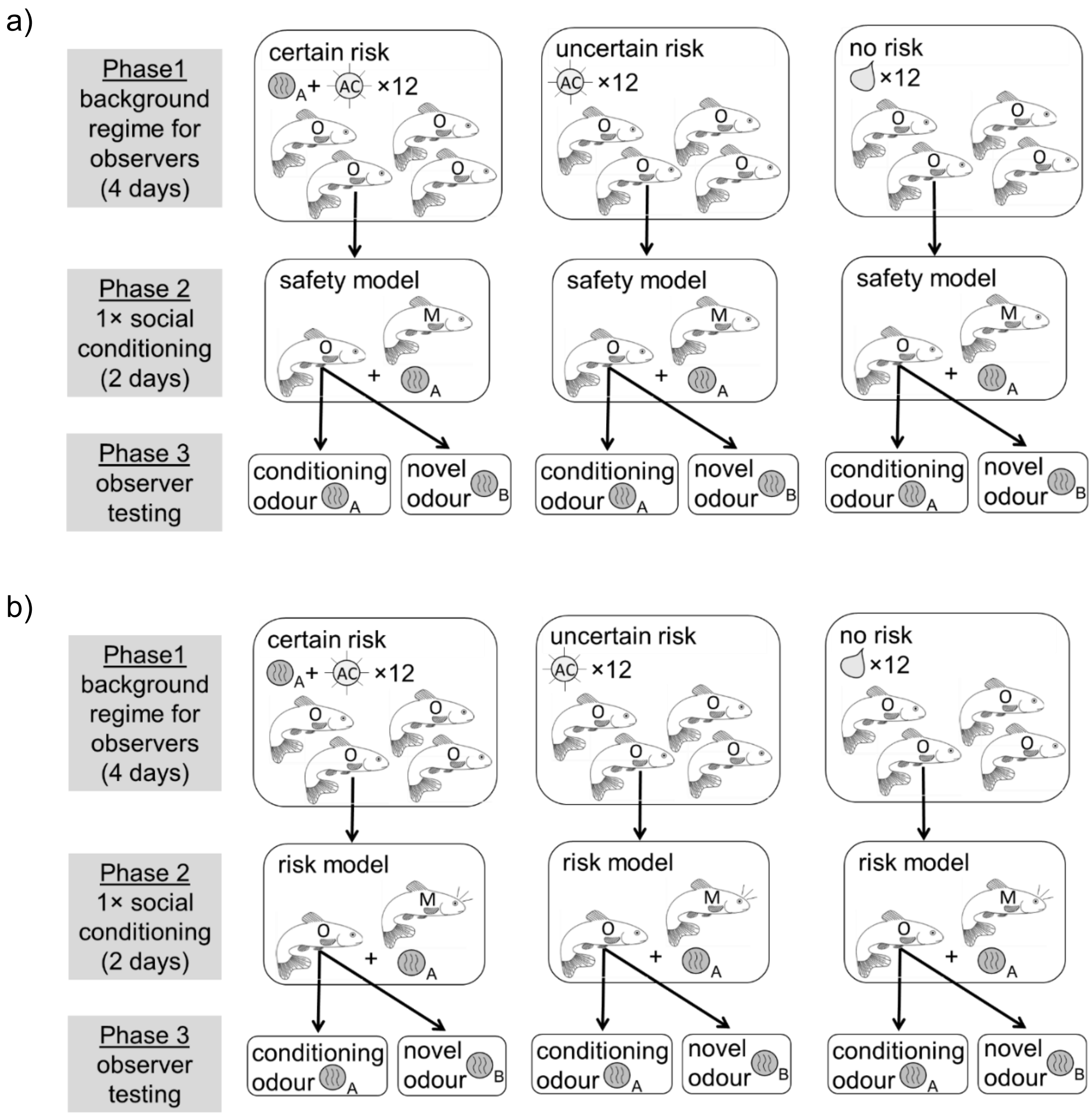

Figure 4.1. Experimental design where high risk observers were conditioned with models to recognize an odour as dangerous. Observers (O) had background experience with a high-risk environment in the form of repeated exposure to alarm cues (AC), paired either with (certain) or without (uncertain) the predator’s odour, or they had neither (no-risk control). Then, observers were exposed to the predator’s odour while being paired with models (M) that were experienced with the predator odour as being (a) safe via previous exposure to the odour without negative consequences, or as (b) risky via previous exposure to the odour with alarm cues. Finally, observers were tested for fear toward the predator odour vs. a novel odour.

4.3. Methods

Phase 1: Background regimes for observers and models

Minnows that would serve as naïve observers were moved into experimental tanks for background exposures, as in previous chapters. The certain-risk treatment consisted of exposures to 5 ml of alarm cues paired with 20 ml of odour$_A$, which was either pike or sturgeon odour (half of the replicates with each). For the uncertain-risk treatment, 5 ml of alarm cues were paired with 20 ml of water, and a no-risk control treatment consisted of 25-ml injections of water (Fig. 4.1). The background regimes were conducted as in Chapter 3. Other experimental tanks contained minnows that would serve as models, receiving background exposures on the same schedule as observers. Half of the models were experienced with odour$_A$ as a predator via exposure to 5 ml of alarm cues paired with 20 ml of odour$_A$ (i.e., risk models), whereas the other half learned odour$_A$ as being safe (i.e., safety models) from repeated exposure to 20 ml of odour$_A$ paired with 5 ml of water rather than alarm cues, thus inducing learned safety as in Chapter 2. I used an equal number of exposures (12 times) to that of observers, so that models would have the same amount of experience.

Phase 2: Social conditioning of risk and safety

Observers were paired with either safety models or risk models (Fig. 4.1) and together each pair was moved into a new experimental tank as in the previous chapters. Each pair had 40 h to acclimate before being exposed to a 20-ml injection of the conditioning odour$_A$, which always matched the species (pike or sturgeon) used during the background phase. Following the conditioning period (2–4 h later), the model was removed, a shelter was added to the tank, and a full water flush occurred. Behavioural observations were not conducted during this phase, and each individual was used only once.

Phase 3: Testing fear in observers

Observers acclimated alone for 16–20 h before being tested for their responses to either 20 ml of conditioning odour$_A$ (i.e., the odour they experienced in the presence of the model) or to novel odour$_B$ (the novel odour) (Fig. 4.1). In addition to lines crossed, time spent under shelter, and time spent foraging, I measured the time spent freezing (centre of body not changing position for >2s). Other details were as in previous chapters. Sample sizes were 29–35 per experimental group (k=12).

Statistical analysis

I analyzed the four response variables for the baseline data using a 2-way MANOVA, testing for the effects of the background-risk treatment (certain risk, uncertain risk, or no risk) and the social treatment (conditioning with risk models or safety models). Due to differences in pre-stimulus data (see below), I analyzed behavioural changes using a 4-way repeated-measures MANOVA. Thus, I was interested in time × factor interactions, depicted graphically by differences in slopes between the pre- and post-stimulus data. In a full-factorial model, I included the background risk treatment, the social treatment, the testing odour (conditioning odour or novel odour) and the odour species (pike vs. sturgeon) as fixed factors. As in Chapter 3, the odour species did not significantly affect the responses (time × species: $F_{4,351}$=1.94, p=0.10), and I decided to remove this factor from the model to yield a simpler 3-way repeated-measures MANOVA. The data were split for post-hoc tests, which were 2-way repeated-measures MANOVAs.

4.4. Results

Background risk affects baseline behaviour

Pre-stimulus baseline behaviour was significantly affected by the background-risk treatment (p<0.001; Table 4.1a; Fig. 4.2), but there was no effect of the social treatment (p=0.85; Table 4.1a) nor an interaction between the two factors (p=0.11; Table 4.1a). Univariate output revealed significant differences among background treatments in time spent foraging (p<0.001; Table 4.1b; Fig. 4.2a), with both uncertain and certain individuals spending less time foraging than control individuals (Tukey HSD: uncertain vs. control: p<0.001; certain vs. control: p=0.004; uncertain vs. certain: p=0.28). There were also non-significant tendencies for both high-risk treatments to spend more time freezing (p=0.055; Fig. 4.2c) and oddly to cross more lines (p=0.069), compared to the no-risk control. In addition to these responses, I noticed several instances of rapid swimming in circular loops near the walls of the tank. I quantified this behaviour as repeatedly crossing more than four lines in a clockwise or counter clockwise pattern in less than 1 s. Although frequencies were low (only 16 of 378 observations total), no instances of this behaviour occurred in the control treatment, and an overall χ^2 test revealed this behaviour varied significantly among the treatments (χ^2_2=9.21, *p*=0.01; not depicted). Group comparisons to control showed that looping was more common in both the certain (χ^2_1=9.61, α=0.017, *p*=0.002) and uncertain (χ^2_1=5.76, α=0.017, *p*=0.016) treatments, which were statistically similar (χ^2_1=1.00, α=0.017, *p*=0.32).

Table 4.1. Results for the influence of uncertainty and risk on baseline behaviour: statistical test output for behavioural responses, the risk treatment (no risk, certain risk, uncertain risk) and the social treatment (risk models vs. safe models). Significant terms of interest are in bold type.

	F	***df***	***p***
a) overall MANOVA for baseline behaviour			
risk treatment	5.02	8, 740	**<0.001**
social treatment	0.34	4, 369	0.85
risk treatment × social treatment	1.65	8, 740	0.11
b) univariate ANOVA on baseline foraging			
risk treatment	11.10	2, 372	**<0.001**
social treatment	1.13	1, 372	0.29
risk treatment × social treatment	1.03	2, 372	0.36
c) univariate ANOVA on time spent freezing			
risk treatment	2.93	2, 372	0.055
social treatment	0.02	1, 372	0.88
risk treatment × social treatment	0.56	2, 372	0.57
d) univariate ANOVA on lines crossed			
risk treatment	2.67	2, 372	0.069
social treatment	0.61	1, 372	0.81
risk treatment × social treatment	4.99	2, 372	0.007
e) univariate ANOVA on time under shelter			
risk treatment	1.95	2, 372	0.15
social treatment	0.23	1, 372	0.63
risk treatment × social treatment	4.17	2, 372	0.016

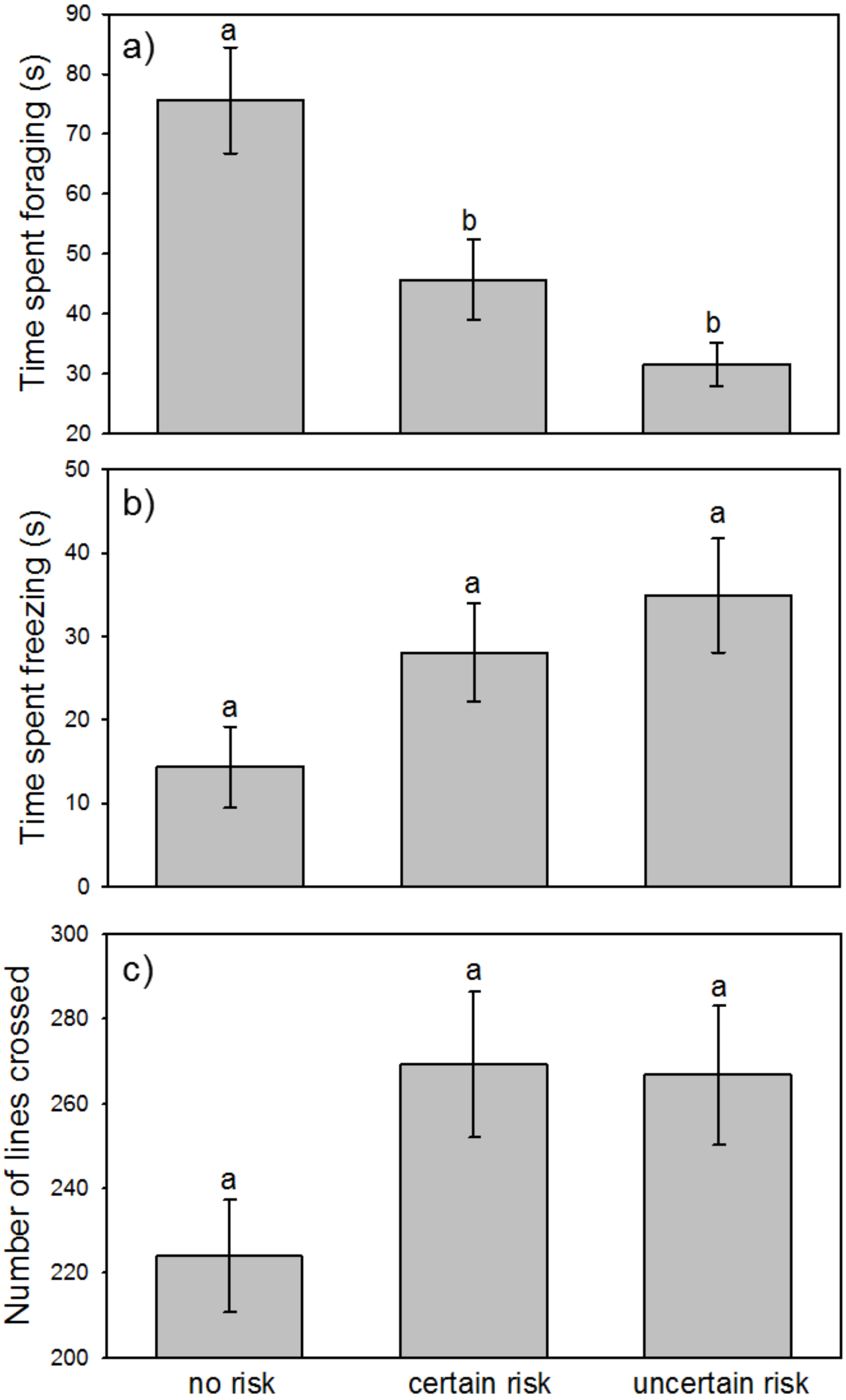

Figure 4.2. Mean (±SE) pre-stimulus (a) time spent foraging, (b) time spent freezing, and (c) number of lines crossed for minnows with prior background experience consisting of either no risk, certain risk (repeated exposure to alarm cues paired with an odour), or uncertain risk (repeated exposure to alarm cues alone). Minnows also received a social conditioning of risk or safety, which was nonsignificant and not depicted here for ease of main-effect interpretation. Letters above bars represent significant univariate differences.

Observers' learned responses and socially-transferred fear

The analysis on behavioural changes revealed that responses depended on a combination of the background-risk treatment and the social conditioning treatment (time × risk treatment × social treatment: $p<0.001$; Figs. 4.3 and Table 4.2a). Post-hoc testing revealed that minnows conditioned with risk-experienced models exhibited a fright response to both odours across all background treatments (time: $p<0.001$; Figs. 4.3, panels $a_{4–6}$ and $b_{4–6}$; Table 4.2b). However, individuals conditioned with safe models differed according to the background-risk treatment (time × risk: $p<0.001$; Figs. 4.3, panels $a_{1–3}$ and $b_{1–3}$; Table 4.2c), with minnows from the certain and uncertain risk treatments exhibiting similar fright responses to both the conditioning and novel odours, whereas the no-risk group responded to neither.

Table 4.2. Results for the influence of uncertainty on social learning of risk and safety: statistical test output for behavioural responses, testing the effects of time (pre vs. post as repeated-measures), the background risk treatment (no risk, certain risk, uncertain risk), the social treatment (risk models vs. safety models), and the testing odour (conditioning odour vs. novel odour). Significant time × factor interactions of interest are in bold type. Note: degrees of freedom differ from those of baseline responses due to the addition of the testing odour as a factor.

	F	***df***	***p***
a) overall 3-way RM MANOVA			
Within subjects			
time	136.45	4, 363	<0.001
time × risk treatment	6.27	8, 728	<0.001
time × social treatment	1.23	4, 363	0.30
time × testing odour	3.48	4, 363	0.008
time × risk treatment × social treatment	3.22	8, 728	**<0.001**
time × risk treatment × testing odour	1.11	8, 728	0.35
time × social treatment × testing odour	1.01	4, 363	0.40
time × risk treatment × social treatment × testing odour	0.43	8, 728	0.90
Between subjects			
risk treatment	8.04	8, 728	<0.001
social treatment	0.07	4, 363	0.99
testing odour	4.40	4, 363	0.002
risk treatment × social treatment	1.39	8, 728	0.20
risk treatment × social treatment	1.04	8, 728	0.40
social treatment × testing odour	0.81	4, 363	0.52
risk treatment × social treatment × testing odour	0.34	8, 728	0.92
b) post-hoc 2-way RM MANOVA for observers with risk models			
Within subjects			
time	72.24	4, 187	<0.001
time × risk treatment	1.60	8, 376	0.12
time × testing odour	1.14	4, 187	0.34
time × risk treatment × testing odour	0.71	8, 376	0.69
Between subjects			
risk treatment	4.69	8, 376	<0.001
testing odour	1.84	4, 187	0.12
risk treatment × testing odour	0.52	8, 376	0.84
c) post-hoc 2-way RM MANOVA for observers with safety models			
Within subjects			
time	65.31	4, 173	<0.001
time × risk treatment	7.57	8, 348	**<0.001**
time × testing odour	3.36	4, 173	**<0.001**
time × risk treatment × testing odour	0.77	8, 348	0.63
Between subjects			
risk treatment	5.19	8, 348	<0.001
testing odour	3.59	4, 173	0.008
risk treatment × testing odour	1.03	8, 348	0.42

Additionally, post-hoc testing on data from minnows conditioned with social safety revealed an interaction between time and the testing odour (*p*<0.001; Table 4.1c). This interaction indicated that individuals from the certain-risk treatment showed significantly stronger fright toward the novel odour vs. the odour their model knew as safe. However, univariate output indicated this effect was statistically significant for only one response variable (time spent freezing: $F_{1,176}$=11.7, *p*=0.001; Fig. 4.3a).

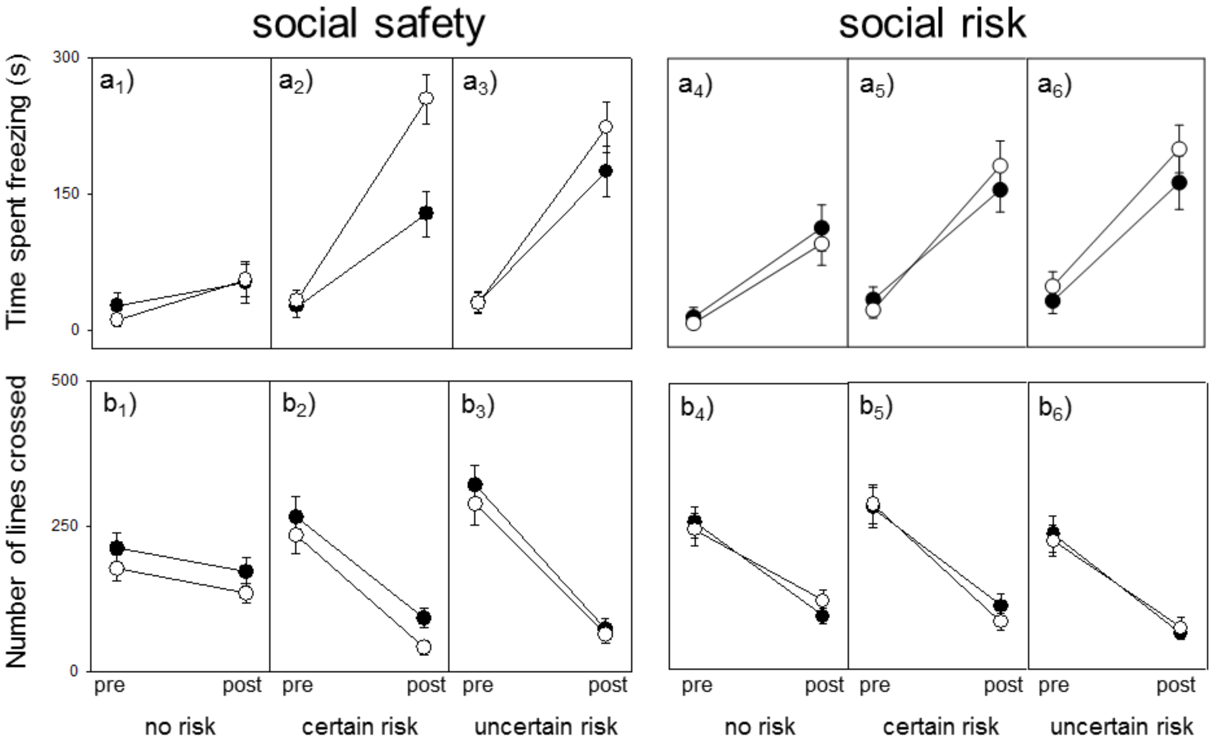

Figure 4.3. Mean (±SE) (a) time spent freezing and (b) number of lines crossed for minnows before (pre) and after (post) exposure to either the odour used in their prior social conditioning (black circles) or a novel odour (white circles). Social conditionings consisted of the opportunity to interact with a conspecific model that was experienced with an odour as being either safe or risky. Background experience for minnows was either no risk, certain risk via repeated exposure to alarm cues paired with an odour, or uncertain risk via repeated exposure to alarm cues alone. Note: not depicted here are time spent foraging with a pattern similar to lines crossed, and time spent under shelter with the reversed pattern.

4.5. Discussion

The central finding of my results was that minnows exposed to high risk exhibited an overall pattern of significantly altered baseline behaviours. These minnows reduced foraging and had a tendency to spend more time freezing, while also tending to cross more lines, sometimes in a rapid route-tracing pattern, which is a known stereotypy in fishes (Casamitjana 2004; Kristiansen et al. 2004), as well as in other species in captivity under stressful conditions. In addition to fearful baseline behaviours, exposure to high risk induced neophobia. Collectively, I refer to these altered behaviours as the 'high-risk phenotype'. Counter to my expectations, however, minnows from both the uncertain- and certain-risk treatments displayed this phenotype. I predicted that repeated exposure to risk from a specific odour would cause only that odour to be interpreted as threatening, and thus minnows that were certain about the predator's identity would not become neophobic. However, guppies, *P. reticulata*, from a high-risk population have consistently demonstrated neophobia (Brown et al. 2013) despite being knowledgeable about their natural predators (Magurran & Seghers 1990). My study provides more evidence that uncertainty may not necessarily be prerequisite for the development of neophobia. One explanation for neophobia among knowledgeable minnows is that the level of risk interacts with certainty, where individuals that are certain will only display neophobia after a threshold of risk has been reached. However, another possibility is that while minnows were knowledgeable about the identity of the predator, they remained uncertain about when or from where attacks occur.

The observations of route-tracing (hereafter, pacing) during the pre-stimulus period were also unexpected, and in hindsight, I think I defined this behaviour far too conservatively. High-risk individuals spent much of their time pacing, although rarely in the circular pattern that I was quantifying. This behaviour was mixed with bouts of time freezing, which resulted in a tendency to cross more lines in a shorter amount of active time. Why did I not find this pattern in Chapter 3 though? One difference is that in that chapter I tested observers that were never exposed to risk directly. Although they acquired socially-transmitted neophobia, they apparently did not acquire the broader range of high-risk behaviours. In Chapter 3, I also recorded data on high-risk models that were exposed directly to risk, but again, I did not observe such pacing behaviour during conditioning trials. I hypothesize that because the models were being tested alongside their observers, they engaged in shoaling behaviour rather than pacing.

The fact that repeated conditionings in the certain-risk treatment (odour + alarm cue) elicited a high-risk phenotype revealed that my social-conditioning treatment was confounded. Because risk-experienced models were conditioned in the same way (repeatedly), they too would have displayed the high-risk phenotype. Hence, risk models presumably differed from safety models in two ways: (1) reacting with fright toward the known odour at the time of the injection and (2) exhibiting the high-risk phenotype throughout the 40-h period of pairing with observers. Thus, the subsequent behaviour of observers paired with risk models can only be attributed to interacting with the models and not to the specific conditioning event. This is a somewhat irrelevant point, however, because I found no evidence that fear demonstration had any effect on observers. A one-time observation of an experienced fright response did not decrease uncertainty in observers. Instead, to induce such an outcome, multiple conditionings with experienced models from low-risk backgrounds would likely be required.

As expected, control minnows paired with risk models learned to exhibit fright responses to the conditioning odour, whereas those paired with safety models did not. This would indicate that control minnows learned the predator odour from experienced models if not for the fact that they also exhibited socially-transferred neophobia. Hence, as in Chapter 3, observers that interacted with risk models may have simply been neophobic rather than learning the specific odour as a predator, and again I cannot discount the possibility of both specific learning and neophobia. However, qualitatively comparing these studies revealed an intriguing discrepancy, where socially-transferred neophobia appeared more intense in this study (~50% stronger in this study; see Fig. 3.4 for comparison). Unfortunately, I can only speculate on the reason for different intensities between the studies. Models were conditioned differently, but in both studies models received the same total number of risk exposures over the same duration of time. A more obvious difference is the longer length of time that observers interacted with models (24 h more in this study). This suggests that spending more time with neophobic companions increases socially-transferred neophobia, at least initially, until neophobia begins to wane.

A primary goal of this experiment was to assess the effect of safety demonstration on observers following individually-learned fear. My work presented in Chapter 2 showed that a one-time opportunity to learn risk socially can override multiple individual experiences with safety. Here, however, I found a small influence for a reversed pattern, with one of four response variables (time spent freezing) significantly affected by safety demonstration, and surprisingly only for individuals in the certain treatment, perhaps indicating that known fear is easier to override than fear of the unknown. In hindsight, the absence of a strong overall effect of safety demonstration is not surprising given that information was being transferred in a contradirectional fashion, not just from model to observer. Hence, the potential transfer of safety to the observer was overridden by the transfer of risk from observer to model, making them poor demonstrators of safety. Like before, perhaps safety demonstration would be more influential after multiple conditionings. These studies, taken together, provide evidence that when conflicting information about risk comes from social vs. individual modalities, social information about risk, whether new or prior, will be the prevailing influence (see Chapter 7 for applications to human fear-psychology).

Chapter 5: Calm social groups and socially-reinforced fear[5]

5.1. Introduction

Within social groups, a higher number of knowledgeable models would presumably increase the chances for observers to acquire their knowledge. We see this pattern in the context of task performance, where an increased number of models correlates with more accurate and efficient responses (e.g., Sugita 1980). Likewise, the social transfer of foraging information is enhanced by the presence of more knowledgeable individuals (Giraldeau, Caraco & Valone 1994). For example, Reebs (2000) found that the 'following' behaviour of observers undertaking a risky foraging task was stronger when the model-to-observer ratio was higher (5:7 vs. 1:11). Only, a few studies, however, have investigated the role of group size on social learning of predation risk, and with diverging conclusions. Consistent with predictions (see: Brown & Laland 2002; Giraldeau, Krebs & Davies 1997), Ferrari and Chivers (2008) reported that tadpoles, *L. sylvaticus*, conditioned with a higher model-to-observer ratio (5:2) responded to a predator with a greater fright intensity than tadpoles conditioned with a lower model-to-observer ratio (2:5). In a study by Mathiron et al. (2015), the intensity of socially-learned risk was similar between groups of two or four individuals. The authors hypothesized that the potential for enhanced learning from more individuals was counter-balanced by the dilution of risk in a larger group (i.e., safety in groups: Roberts 1996), and thus the social cue would have been weaker. However, Vilhunen et al. (2005) showed that charr, *S. alpinus*, learned to recognize a predator only when the model-to-observer ratio was low (4:16 vs. 10:10 and 16:4). The authors speculated that groups with a higher proportion of experienced individuals shoaled more tightly, and fish in

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[5] The content of this chapter comes from the following manuscript in press. Changes have been made to avoid redundancy with other chapters and for consistency among chapters.

Crane AL, Ferrari MCO. (in press). Learning of safety by a social fish: applications for studying post-traumatic stress in humans. Animal Behaviour.

tighter shoals would show weaker fright responses, whereas loose shoals would force models to display more conspicuous antipredator behaviours. While counter-intuitive, this potential mechanism deserves to be tested in other systems.

5.2 Objectives

In contrast to the role of group size in learning about risk, I am not aware of any studies that have explored such in the context of learning about safety. My goal in this experiment was to use calm conspecific models to weaken the high-risk phenotype that minnows acquire in high-risk environments. I sought to prioritize information transfer from the calm model to the neophobic observer, while minimizing the information transfer from the observer to the model. First, I induced the high-risk phenotype in observers via repeated exposures to alarm cues, while manipulating the social context (alone vs. in group) to determine whether group size alters the intensity of the acquired, high-risk phenotype and its potential weakening via the learning of safety (Fig. 5.1). Subsequently, I manipulated the number of safe models (zero, one or five) that were paired with the observer. My work in the previous chapters led me to hypothesize that the presence of more calm models would limit fear transfer from observers to models, which would thus promote a weakening of fear in observers. I also reasoned that, as in some other species, risk in isolation would lead to higher levels of the high-risk phenotype (e.g., Seetharaman et al. 2016), which I expected would be more difficult to override with calm models. Finally, I used control treatments involving ‘un-calm’ models to assess whether the mere pairing with conspecifics (companionship) facilitated safety transfer, or if *calm* models were necessary for this to occur (2×3×2 design; see Fig. 5.1 for the calm-model treatments).

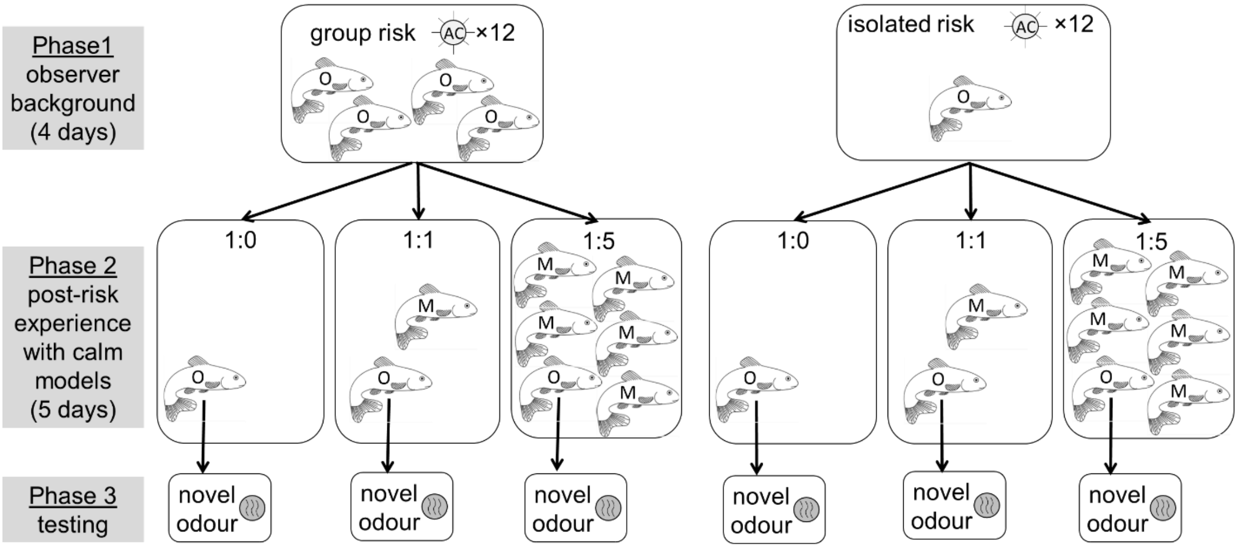

Figure 5.1. Experimental phases for risk-exposed individuals. Observer (O) minnows first experienced risk from repeated exposure to alarm cues (AC), either in isolation or in a group of 4 fish. Then, observers had a 5-day conditioning period with the opportunity to interact with calm models (M), either zero, one, or five models. Observers were tested alone, being exposed to a novel odour to determine whether models weakened the high-risk traits of observers. Control treatments involving un-calm models (identical 2×3 design) were conducted but are not depicted here.

5.3. Methods

Phase 1: Background regimes for high-risk individuals

In the initial phase of the experiment, minnows that would serve as high-risk individuals were repeatedly exposed to alarm cues as in previous chapters, except that minnows were either isolated or in a group of four individuals (Fig. 5.1). After the 4-d risk exposure, individual minnows were transferred to new tanks for their conditioning phase with models. My work in previous chapters showed that minnows do not acquire a high-risk phenotype in the absence of risk.

Phase 2: Post-risk conditioning with models

During this phase, the high-risk individuals shared experimental tanks with zero, one or five conspecific models. I chose these numbers based on previous work by Reebs (2000) and Ferrari and Chivers (2008), both revealing that five experienced models were significantly more convincing for observers. For half of the conditionings, the models were calm individuals, having acclimatized to the laboratory for several weeks without risk exposure (Fig. 5.1). The other half involved ‘un-calm’ models (i.e., individuals that had been exposed to the same high-risk background regime). For both groups, models and observers were allowed to fully interact for 5 d, giving observers the opportunity to learn from models about their new tank environment. I chose a time frame of 5 d because some preliminary observations indicated that neophobic responses could start to naturally wane in a safe environment after two weeks. I hypothesized that a 5-d period might allow me to detect a socially-weakened high-risk phenotype without the waning of the phenotype in the other treatments. After the conditioning period, all models were removed with a net. Fish in the 0-model treatment were also equally disturbed with a net to control for this procedural confound.

Phase 3: Testing for a weakened high-risk phenotype

To determine whether the high-risk phenotype had been weakened, I tested observers alone 1 d later, as in previous chapters. While moderate swimming is typically found in this species in the absence of risk (Chivers & Smith 1993; Ferrari et al. 2005; Mathis et al. 1993), my work in Chapter 4 demonstrated that minnows from high-risk backgrounds display pacing behaviour. Thus, I expected that highly anxious fish would cross more lines during the baseline period. I did not feed minnows the day of testing because I did not want to interfere with route-tracing, and thus, I did not measure foraging activity. Following the pre-stimulus period, I injected 20 ml of a novel odour, allowing me to assess the neophobic responses of minnows. Sturgeon odour was used as the novel odour, as in previous chapters where minnows raised in low-risk environments did not show a fright response to sturgeon odour. Sample sizes were 22–24 per group (*k*=10 rather than 12 because the 0-model treatment did not include a calm or uncalm model).

Statistical analysis

I conducted separate analyses for the calm and un-calm model treatments because the factors were not fully crossed due to the 0-model treatment having neither calm nor un-calm models. For each group, I analyzed response variables together using 2-way MANOVAs, where the number of models (0, 1, or 5) and the observers’ risk-acquisition context (group or isolated) were fixed factors. I first analyzed the pre-stimulus data alone to gauge baseline behaviour, with post-hoc MANOVAs comparing specific groups (0 vs. 1 and 0 vs. 5 models). I then assessed neophobia using a repeated-measures approach, assessing a change between the pre- and post-stimulus injection periods. Again, I concluded on neophobic responses using time (pre- vs. post-stimulus period) by factor interactions, depicted graphically by differences in slopes. Significant interactions between factors were interpreted by splitting the data by the background treatment and conducting post-hoc 1-way repeated-measures MANOVAs, comparing 0 vs. 1 and 0 vs. 5 models. For multiple comparisons, I used Bonferroni corrections to adjust alpha by the number of comparisons ($\alpha/2$ in this case).

5.4. Results

Risk acquisition context affects safety information transfer

Regardless of risk acquisition context, the baseline behaviour of observers was significantly affected overall by the number of calm models (number: $p<0.001$; Table 5.1a), with both one and five models having a calming effect (zero vs. one: $\alpha=0.025$, $p<0.001$, Table 5.1b; zero vs. five: $\alpha=0.025$, $p=0.001$, Table 5.1c; Fig. 5.2a and 5.2b). However, neophobic responses were context-dependent (time × background × number: $p=0.002$; Table S1d; Fig. 5.2a and 5.2b); observers that had experienced risk in a group showed a nonsignificant tendency for weakened neophobia after interacting with five calm models (zero vs. five: $\alpha=0.025$, $p=0.034$; Table 5.1e; Fig. 5.2a), whereas the presence of only one calm model had no influence (zero vs. one: $\alpha=0.025$, $p=0.72$; Table 5.1f; Fig. 5.2a). In contrast, minnows responded differently after experiencing risk in isolation. Their neophobic responses were substantially reduced by interacting with five calm models (zero vs. five: $\alpha=0.025$, $p<0.001$; Table 5.1g; Fig. 5.2b), and even with only one calm model (zero vs. one: $\alpha=0.025$, both $p<0.001$; Table 5.1h; Fig. 5.2b$_{1,2}$), despite their tendency for increased neophobia (Fig. 5.2a$_{1,2}$ vs. Fig. 5.2b$_{1,2}$).

Table 5.1. Results of interacting with calm models: statistical test output for baseline responses and neophobia (pre vs. post as repeated-measures) across background-risk treatments (group or isolation) and the number of calm models (zero, one, or five) during conditioning. Significant terms of interest are in bold type.

	F	***df***	***p***
a) overall 2-way MANOVA for baseline behaviour			
background	1.63	2, 129	0.20
number	8.26	4, 260	**<0.001**
background × number	1.49	4, 260	0.21
b) post-hoc 2-way MANOVA for baseline behaviour: 0 vs. 5 calm models			
background	2.59	2, 85	0.081
number	15.11	2, 85	**<0.001**
background × number	0.75	2, 85	0.48
c) post-hoc 2-way MANOVA for baseline behaviour: 0 vs. 1 clam model			
background	1.43	2, 87	0.24
number	7.05	2, 87	**0.001**
background × number	1.95	2, 87	0.15
d) overall 2-way RM MANOVA for neophobia			
Within subjects			
time	93.09	2, 129	<0.001
time × background	0.43	2, 129	0.96
time × number	6.68	4, 260	<0.001
time × background × number	4.32	4, 260	**0.002**
Between subjects			
background	2.90	2, 129	0.059
number	9.83	4, 260	<0.001
background × number	3.09	4, 260	0.016
e) post-hoc 1-way RM MANOVA for neophobia: group background, 0 vs. 5 calm models			
Within subjects			
time	32.91	2, 41	<0.001
time × number	3.68	2, 41	0.034
Between subjects			
number	8.30	2, 41	0.001
f) post-hoc 1-way RM MANOVA for neophobia: group background: 0 vs. 1 calm models			
Within subjects			
time	42.82	2, 43	<0.001
time × number	0.34	2, 43	0.72
Between subjects			
number	0.17	2, 43	0.84
g) post-hoc 1-way RM MANOVA for neophobia: isolated background, 0 vs. 5 models			
Within subjects			
time	42.48	2, 43	<0.001
time × number	12.33	2, 43	**<0.001**
Between subjects			
number	12.24	2, 43	<0.001
h) post-hoc 1-way RM MANOVA for neophobia: isolated background, 0 vs. 1 models			
Within subjects			
time	30.63	2, 43	<0.001
time × number	9.41	2, 43	**<0.001**
Between subjects			
number	11.64	2, 43	<0.001

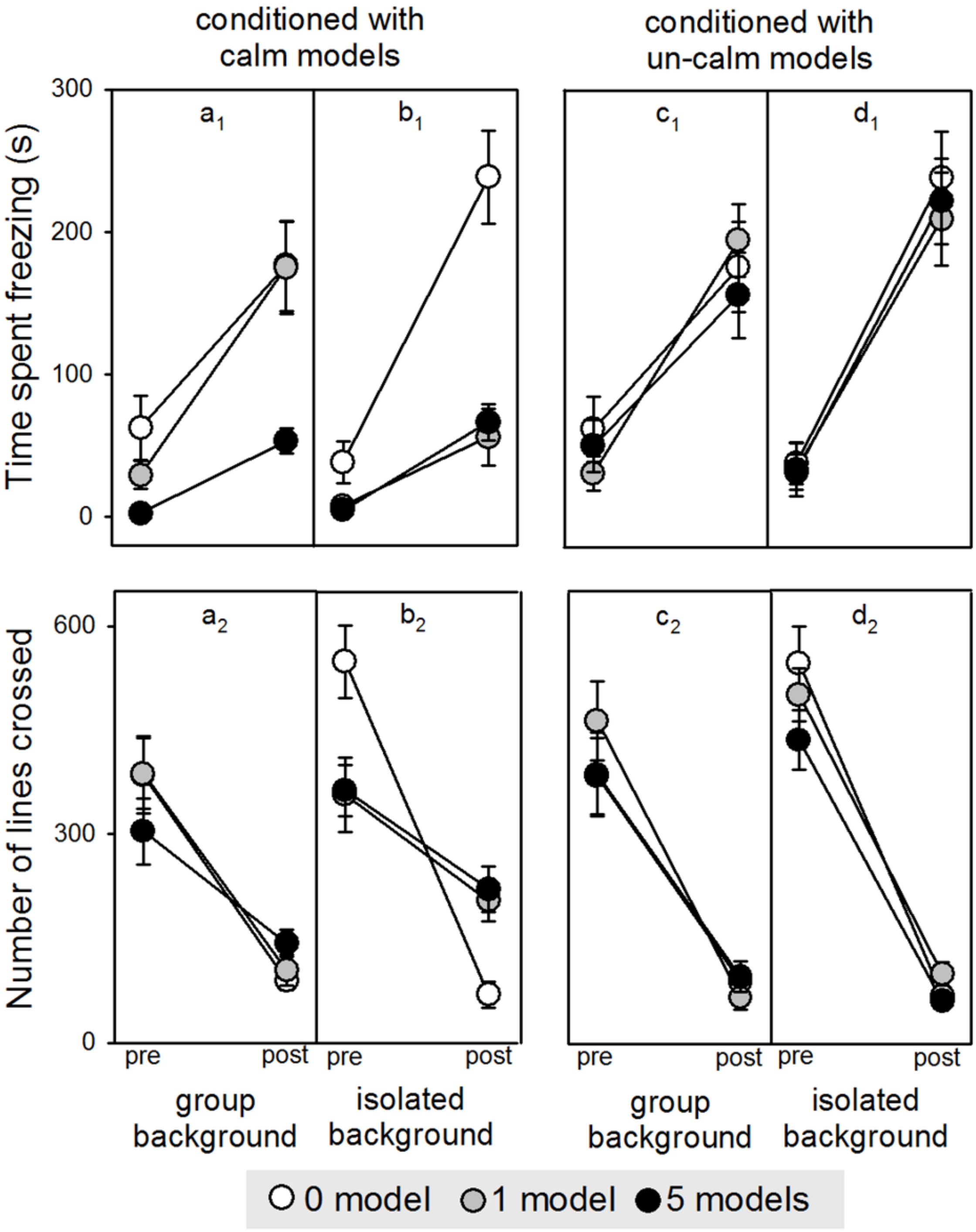

Figure 5.2. Mean (± SE) time spent freezing (upper panels) and number of lines crossed (lower panels) by observer minnows when tested alone, before (pre) and after (post) exposure to a novel odour. All observers had prior experience with a high-risk regime (repeated exposure to alarm cues) in either a group or in isolation. Then, for 5 d, observers interacted with zero, one, or five models. Models were initially either calm (via no risk exposures; panels a and b) or un-calm (via repeated exposures to risk; panels c and d). Steeper slopes (upwards for freezing, downwards for line crossed) represent stronger fearful responses to the novel odour.

Failed safety transfer via un-calm models

I found no influence of un-calm models on the observers' baseline behaviour or their neophobic responses (number and time × number: both p>0.40; Table 5.2; Fig. 5.2c and 5.2d). Hence, the simple pairing with other fish (companionship) did not alter the high-risk phenotype. Instead, calm models were necessary for the weakening from the high-risk phenotype. However, observers paired with un-calm models displayed less intense neophobia following risk exposure in a group compared to in isolation (time × background: p=0.029; Table 5.2c vs. 5.2d), again revealing that risk exposure in isolation led to more intense neophobia than risk exposure in a group.

Table 5.2. Results of interacting with un-calm models: statistical test output for baseline responses and neophobia (pre vs. post as repeated-measures) across background-risk treatments (group or isolation) and the number of un-calm models (zero, one, or five) during conditioning. Significant terms of interest are in bold type.

	F	***df***	***p***
a) overall 2-way MANOVA for baseline behaviour			
background	1.99	2, 132	0.14
number	0.99	4, 266	0.41
background × number	0.57	4, 266	0.68
b) overall 2-way RM MANOVA for neophobia			
Within subjects			
time	164.96	2, 132	<0.001
time × background	3.64	2, 132	**0.029**
time × number	0.49	4, 266	0.74
time × background × number	0.97	4, 266	0.43
Between subjects			
background	3.12	2, 132	0.048
number	0.82	4, 266	0.52
background × number	0.41	4, 266	0.80

5.5. Discussion

The study provides more evidence that social information is persuasive for minnows when assessing environmental risk. The presence of social models weakened the high-risk phenotype, but only under some circumstances. Foremost, the social models had to be calm to have any weakening effect (i.e., the mere presence of other individuals was not enough to weaken the high-risk phenotype). After interacting with five calm models, minnows that had previously experienced risk in a group showed only a modest weakening of the high-risk phenotype, whereas one calm model had no effect, presumably because the model indirectly acquired neophobia and stopped behaving calmly, as occurred in Chapters 3 and 4. What was striking, however, was that although minnows tended to display stronger neophobia after experiencing risk in isolation, the presence of even only one calm model significantly reduced those behaviours, as did the presence of five calm models. Thus, experiencing risk in a group appears to socially reinforce fear, making the learning of safety more difficult.

Socially-reinforced behaviours have been well studied in many contexts (Bandura & Walters 1977). For example, in competitive interactions, winning contests can cause dominant behaviour in future contests, and vice versa (e.g., in fish: Baenninger 1970). In monkeys, repeatedly observing rewards being given to conspecifics motivates observers to subsequently deliver or withhold rewards to others (Chang, Winecoff & Platt 2011). Social reinforcement has also received a fair bit of attention in work on social learning of predation risk. Research with mammals has involved as many as 20 social sessions (Huebner et al. 1979), with up to 15 sessions in work on fishes (Brown & Laland 2002), although much less attention has been given to other taxa. However, I am aware of only one study that attempted to override socially-reinforced behaviours. That was the aforementioned study by Mineka and Cook (1986) where socially-reinforced safety prevented monkeys, *M. mulata*, from learning fear. Another study in rats, *R. norvegicus,* assessed how social reinforcement of a threat (a shock) was affected by an isolated background environment (Angermeier 1960). Previously isolated individuals were not persuaded by the social information unless they could fully interact with models. Observer rats that received only visual cues did not learn the threat, suggesting that they were unfamiliar with the meaning of those social cues following their isolated rearing from birth. That study contrasts with my present findings, where previously isolated individuals were more persuaded by models, although I used wild-caught individuals with social experience in their natural environment. Overall, social reinforcement appears to infix behavioural antipredator decisions (see Chapter 7 for applications to human fear-psychology).

Chapter 6: Replacing models affects fear and its social transmission[6]

6.1. Introduction

In research on animal behaviour, much work has focused on the benefits of groups. Across taxa, examples abound in the contexts of foraging (Beauchamp 1998; Monaghan & Metcalfe 1985), competition (Maruhashi, Saito & Agetsuma 1998; Ryti & Case 1992), and predator vigilance and defence (Lima & Bednekoff 1999a; Magurran 1990). As mentioned in the previous chapter, a few studies have explored the influence of groups on learning about predation risk (Ferrari & Chivers 2008; Manassa et al. 2014; Mathiron et al. 2015; Vilhunen et al. 2005). Within the group, observers will often sample information from group members, one individual at a time, often based on neighbour distance (Couzin et al. 2005; Strandburg-Peshkin et al. 2013). However, in this context, all previous studies have assessed group information transfer in situations where all group members were together at one point in time, and thus not assessing how each piece of social information influenced an initially naïve observer. As seen in Chapters 4 and 5, attempting to override high-risk phenotypes in observers with safety-conditioned models in a one-on-one interaction poses a challenge due to the contradirectional transfer of risk information from the observer to the model. Whether separate encounters with individual models might weaken fear in observers over time, similar to encounters within a group, remains unclear. In such a scenario, the absence of information transfer among calm models could make them more susceptible to socially-transferred fear from observers.

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[6] The content of this chapter comes from the following manuscript that remains in preparation and has not yet been submitted for publication. Changes have been made to avoid redundancy with other chapters and for consistency among chapters.

Crane AL, Bairos-Novak KR, Sacco LH, Ferrari MCO. (in preparation). Replacement models experience less secondarily-acquired fear and promote fear recovery.

6.2 Objectives

My goal in this study was to assess the impact of the removal and subsequent replacement of a model on the weakening of the high-risk phenotype in observers. I also sought to closely monitor how models were affected by observers, and thus, I tested both the observers and the models, including those that were replaced (Fig. 6.1). I hypothesized that, as occurred in the previous chapters, models would acquire the high-risk phenotype from observers, hence becoming poorer models for demonstrating safety and for facilitating the weakening of the high-risk phenotype of observers. However, I expected that after model replacement, the new calm model would better demonstrate safety to high-risk observers, compared to previously affected models. Therefore, the periodic replacement of models should reduce fear in observers, and likewise, new replacement models should experience less socially-transferred fear compared to the models they replaced. Alternatively, the change from a familiar model to a new model could be so stressful that it prevents any weakening of the high-risk phenotype in observers.

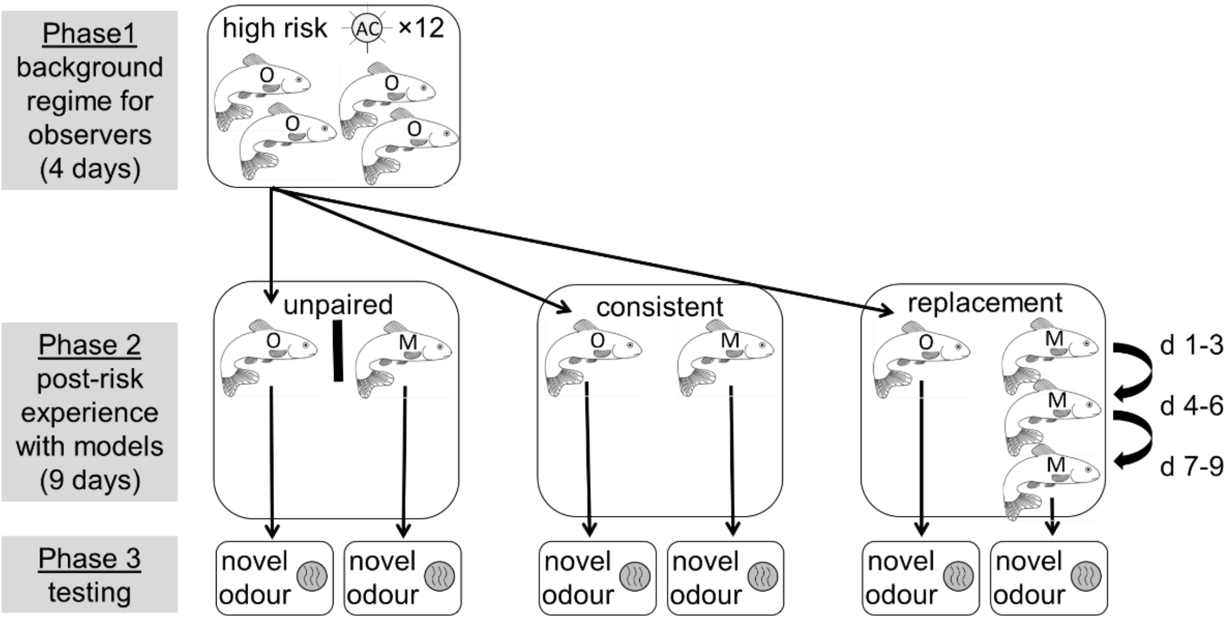

Figure 6.1. Experimental design testing whether replacement models alleviate fear in high-risk observers. Observers (O) experienced risk (AC = alarm cue) in a group, and then had 9 d to interact with calm models (M), except in the 'unpaired' control group where observers and models were separated. The replacement group differed from the consistent group by experiencing the removal and replacement of the model every 3 d. Testing with novel odour occurred 1 d later for observers, whereas all models were tested 1 d after their removal from the observer's tank.

6.3. Methods

Phase 1: Background regime for high-risk individuals

Minnows were housed in experimental tanks throughout the experiment, as in previous chapters. In the first phase of the experiment, minnows that would serve as high-risk observers were repeatedly exposed to alarm cues in groups of four (Fig. 6.1). I chose to expose fish in groups based on the results of Chapter 5 showing that the acquisition of fear in groups (i.e., socially-reinforced fear) was more difficult to override compared to fear in isolation. Other details were as in previous chapters.

Phase 2: Post-risk pairings with models

During a 9-d period, two groups of high-risk observers were individually paired with a single calm model (defined as in Chapter 5). As a control group, other high-risk observers were kept individually in tanks separate from their low-risk 'models' (the 'unpaired' group) (Fig. 6.1), allowing me to assess whether observers and models simply changed their responses over time, rather than due to the model-observer pairing. However, keeping these 'unpaired' observers isolated during 9-d period would have been an additional stressor on this treatment group (see Chapter 5), so I chose to add another high-risk individual (a non-focal fish) to interact with the 'unpaired' observers. Hence, I controlled for the presence of another fish, and thus, 'unpaired' observers were only unpaired in regard to the calm models. Likewise, in a separate tank, each model in the 'unpaired' treatment was paired with another calm individual, again to avoid a confounding stressor from isolation. In contrast, when observers were paired with calm models, the model either remained in the tank for the full 9 d (a consistent pairing), or the model was removed and replaced by a new low-risk model every 3 d (replacement pairings) (Fig. 6.1). Models were always removed gently with a net. To control for this disturbance across the treatment groups, I handled the other models (and the non-focal fish for unpaired observers) identical to the replacement models every 3 d, but instead of removing models as in the replacement pairings, they were immediately put back into the same tank. I chose a 3-d period because it allowed me to complete the testing phase within that 2-week time frame where I expected neophobia to persist in intensity. A 1–2 d pairing with replacement models was also considered, but I was concerned that a shorter period would be more stressful to models and prevent them from behaving calmly. At the end of the 9-d period, all models were moved individually into their own tanks, while observers remained in the same tank for testing.

Phase 3: Testing for a weakened high-risk phenotype

Observers and models were tested 1 d following the end of the social conditioning period, allowing me to assess their behaviour separately without the influence of one another. Behaviour was recorded as in previous chapters, except in this study, I focused more on pacing behaviour by measuring the time spent pacing (swimming >3 cm/s in a route-tracing pattern of any shape), defined more broadly than in Chapter 4. Again, I did not feed minnows prior to trials on the day of testing. After the pre-stimulus period, I injected 20 ml of a novel odour (sturgeon) and assessed any neophobic response. Sample sizes were 18–32 per group (a design involving three model treatments × two statuses plus the two groups of replaced models in the replacement-model treatment; Fig. 6.1).

Statistical analysis

I analyzed the behaviour of the observers and the final models on day 9 separately. I used 1-way MANOVAs with the treatment (unpaired, consistent, or replacement) as a fixed factor. First, I analyzed the pre-stimulus data alone to gauge baseline behaviour, with post-hoc MANOVAs comparing specific groups (consistent vs. unpaired and replacement vs. unpaired). I then assessed neophobic responses by using repeated-measures MANOVAs with treatment as a fixed factor and time (pre- vs. post-stimulus period) as the within-subjects factor. Finally, I used this same overall approach to assess the behaviour of replacement models from each conditioning period (days 1–3, days 4–6, days 7–9). Alpha was adjusted for multiple comparisons as in previous chapters.

6.4. Results

A weakened high-risk phenotype via replacement models

Baseline behaviour significantly differed among the treatments (*p*=0.003, Table 6.1a, Fig. 6.2a and 6.2c). Compared to the high-risk unpaired (control) fish, observers were calmer (i.e., more similar to controls) following replacement pairings (replacement vs. unpaired: α=0.025, *p*=0.003, Table 6.1c), but not following a consistent pairing with the same model (consistent vs.

unpaired: α=0.025, *p*=0.27, Table 6.1b). Neophobic responses also differed across treatments (*p*=0.004, Table 6.1d, Fig. 6.2a and 6.2c). Consistently-paired observers displayed neophobia at an even higher level than the unpaired (control) observers (α=0.025, *p*=0.017, Table 6.1e), although this outcome was influenced by many of the unpaired observers continuing to display pacing behaviour after the injection of the novel odour (Fig. 6.2c). In contrast, observers paired with replacement models, compared to unpaired observers, showed overall calmer behaviour during both stimulus periods (overall main effect: α=0.025, *p*=0.001, Table 6.1f; interaction: α=0.025, *p*=0.71, Table 6.1f).

Table 6.1. Results for high-risk observers interacting with models: statistical test output for baseline responses and neophobia (pre vs. post as repeated-measures) across modelling treatments (unpaired, consistent pairings, or replacement pairings). Significant terms of interest are in bold type.

	F	***df***	***p***
a) overall MANOVA for baseline behaviour			
treatment	4.13	4, 152	**0.003**
b) post-hoc MANOVA for baseline behaviour: unpaired vs. consistent			
treatment	1.35	2, 44	0.27
c) post-hoc MANOVA for baseline behaviour: unpaired vs. replacement			
treatment	6.59	2, 58	**0.003**
d) overall RM-MANOVA for neophobia			
Within subjects			
time	43.31	2, 75	<0.001
time × treatment	3.99	4, 152	**0.004**
Between subjects			
treatment	4.26	4, 152	0.003
e) post-hoc RM MANOVA for neophobia: unpaired vs. consistent			
Within subjects			
time	28.41	2, 44	<0.001
time × treatment	4.49	2, 44	**0.017**
Between subjects			
treatment	0.10	2, 44	0.91
f) post-hoc RM MANOVA for neophobia: unpaired vs. replacement			
Within subjects			
time	20.40	2, 58	<0.001
time × treatment	0.35	2, 58	0.71
Between subjects			
treatment	8.12	2, 58	**0.001**

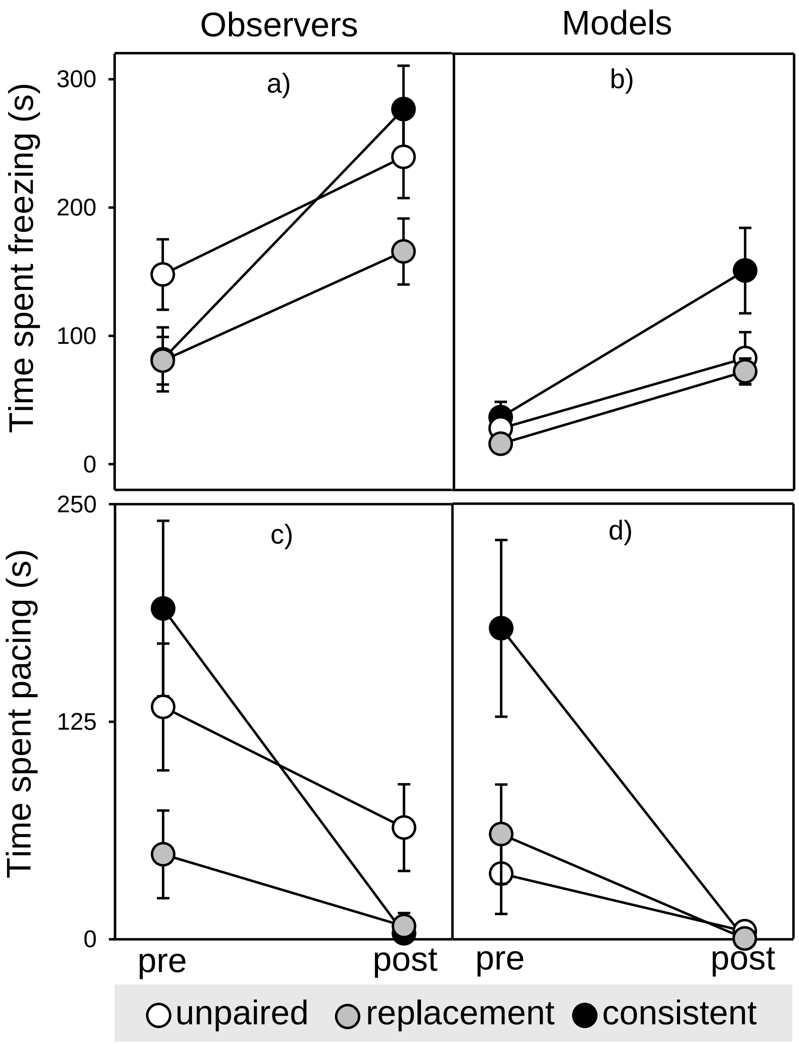

Figure 6.2. Mean (± SE) time spent freezing (a and b) and time spent pacing (c and d) when tested alone, before (pre) and after (post) exposure to a novel odour. Steeper slopes (upward for time spent freezing and downward for time spent pacing) represent stronger behavioural changes in response to the odour. Observers had prior experience with a high-risk regime. Then, during a 9-d conditioning phase, high-risk observers were paired with calm models: either consistently, with the model replaced every 3 d (replacement), or where the observer and model were not paired (unpaired). Testing of observers and models occurred 1 d following the conditioning period.

Socially-transmitted effects on models

As expected, models were influenced by their treatment (baseline: *p*=0.029, Table 6.2a; neophobia: *p*=0.017, Table 6.2d; Figs. 6.2b and 6.2d). At the end of the 9-d treatment period, the final replacement models behaved similarly to the low-risk unpaired (control) models (replacement vs. unpaired: baseline: α=0.025, *p*=0.66, Table 6.2c; neophobia: α=0.025, *p*=0.77, Table 6.2f), whereas the consistently paired models acquired socially-transferred fear (consistent vs. unpaired: baseline: α=0.025, *p*=0.017, Table 6.2b; neophobia: α=0.025, *p*=0.006, Table 6.2e). However, replacement models behaved differently depending on the timing of their pairing with observers (baseline: *p*<0.001, Table 6.3a; neophobia: *p*=0.001, Table 6.3d, Fig. 6.3a and 6.3b), becoming calmer over time. Compared to the first model, the second model was significantly calmer (d 4–6 vs. d 1–3: baseline: α=0.025, *p*=0.005, Table 6.3b; neophobia: α=0.025, *p*=0.021, Table 6.3e), and the final model appeared to continue this trend, although not significantly (d 7–9 vs. d 4–6: baseline: α=0.025, *p*=0.70, Table 6.3c; neophobia: α=0.025, *p*=0.18; Table 6.3f).

Table 6.2. Results for models following pairings with observers: statistical test output for baseline responses and neophobia (pre vs. post as repeated-measures) across modelling treatments (unpaired, consistent pairings, or replacement pairings). Significant terms of interest are in bold type.

	F	***df***	***p***
a) overall MANOVA for baseline behaviour			
treatment	2.78	4, 152	**0.029**
b) post-hoc MANOVA for baseline behaviour: unpaired vs. consistent			
treatment	4.45	2, 44	**0.017**
c) post-hoc MANOVA for baseline behaviour: unpaired vs. replacement			
treatment	0.43	2, 58	0.66
d) overall RM-MANOVA for neophobia			
Within subjects			
time	34.93	2, 75	<0.001
time × treatment	3.10	4, 152	**0.017**
Between subjects			
treatment	3.34	4, 152	0.012
e) post-hoc RM MANOVA for neophobia: unpaired vs. consistent			
Within subjects			
time	23.99	2, 44	<0.001
time × treatment	5.87	2, 44	**0.006**
Between subjects			
treatment	5.20	2, 44	0.009
f) post-hoc RM MANOVA for neophobia: unpaired vs. replacement			
Within subjects			
time	23.59	2, 58	<0.001
time × treatment	0.27	2, 58	0.77
Between subjects			
treatment	0.34	2, 58	0.71

Table 6.3. Results for replacement models: statistical test output for baseline responses and neophobia (pre vs. post as repeated-measures) for models paired with observers during days 1–3, 4–6, or 7–9. Significant terms of interest are in bold type.

	F	***df***	***p***
a) overall MANOVA for baseline behaviour			
period	5.28	4, 186	**<0.001**
b) post-hoc MANOVA for baseline behaviour: days 1-3 vs. days 4-6			
period	5.90	2, 61	**0.005**
c) post-hoc MANOVA for baseline behaviour: days 4-6 vs. days 7-9			
period	0.35	2, 61	0.70
d) overall RM-MANOVA for neophobia			
Within subjects			
time	61.69	2, 92	<0.001
time × period	4.83	4, 186	**0.001**
Between subjects			
period	7.68	4, 186	<0.001
e) post-hoc RM MANOVA for neophobia: days 1-3 vs. days 4-6			
Within subjects			
time	50.79	2, 61	<0.001
time × period	4.13	2, 61	**0.021**
Between subjects			
period	7.67	2, 61	0.001
f) post-hoc RM MANOVA for neophobia: days 4-6 vs. days 7-9			
Within subjects			
time	29.69	2, 61	<0.001
time × period	1.77	2, 61	0.18
Between subjects			
period	1.35	2, 61	0.27

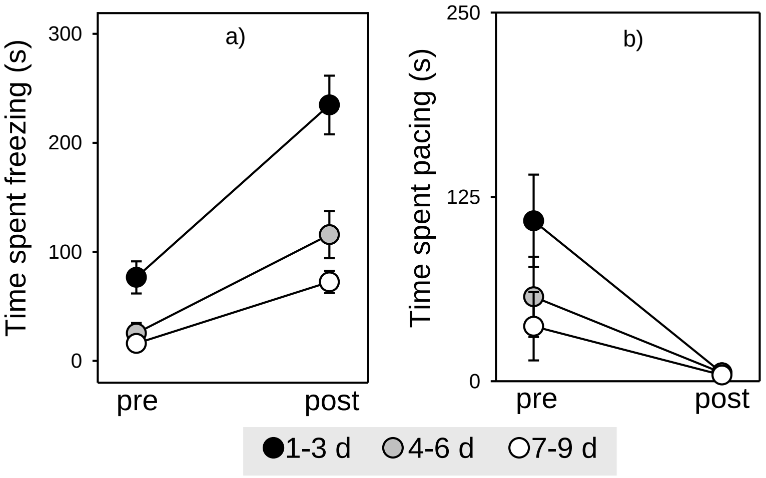

Figure 6.3. Baseline and neophobic behaviour of replacement models after interacting with observers at different time periods. Mean (± SE) time spent freezing and time spent pacing when tested individually both before (pre) and after (post) exposure to a novel odour. Replacement models were paired with high-risk observers either days 1–3, 4–6, or 7–9 following the observers' risk exposure. All models were tested 1 d after their removal from the observers' tanks. Steeper slopes (upward for time spent pacing and downward for time spent freezing) represent stronger behavioural changes in response to the odour.

6.5. Discussion

This study provides further evidence that social experiences with calm models can weaken the high-risk phenotype. Moreover, this study demonstrated that such experiences can minimize the social transfer of fear. I found that replacing models experiencing socially-transferred fear with new calm models significantly weakened the high-risk phenotype in observers. While the first model experienced a high level of socially-transferred fear, subsequent models experienced significantly less. Thus, new replacement models were better demonstrators of safety and more likely to influence observers. It was the second model (i.e., first replacement model) that made the largest impact, with the final model furthering this effect. In contrast, the high-risk phenotype of observers was unaffected when paired consistently with one model. Thus, social information coming from multiple models (3 vs. 1 in this case), even in succession and not together, was convincing to observers that their new environment was safe. This is consistent with Chapter 5 and most previous studies assessing observer-to-model ratios (e.g., Ferrari & Chivers 2008; Reebs 2000).

As in Chapter 4, socially-transferred fear was stronger in intensity than in Chapter 3 where the social pairing occurred for a shorter duration of time (48 h less than in this experiment). However, the intensity of the high-risk phenotype was again weaker when socially-transferred vs. being directly acquired, especially in terms of freezing (see Fig. 6.2a vs. Fig. 6.2b). Although I did not directly compare models and observers because models were moved into new tanks whereas observers were not, this confounding factor (a stressful disturbance) should have affected models more than observers in terms of promoting fear behaviours. Thus, I can conclude that socially-transferred fear in this study was indeed less intense than directly-acquired fear, as was also documented in Chapters 3 and 4 (see the following chapter for applications to human fear-psychology).

Chapter 7: Discussion and applications to fear recovery[7]

7.1. Summary of findings in a cognitive ecology framework

In this thesis, I explored factors that potentially influence learning about risk and safety in minnows. I found that two mechanisms – alarm-cue learning and social learning – can have similar learning outcomes. However, when new information conflicted with prior information, social information about risk was more persuasive, completely overriding previous information about safety (Chapter 2). Conversely, previously-learned risk was difficult to override via the opportunity to learn safety, presumably because an incorrect response to risk is much more costly than an incorrect response to safety. In Chapter 4, I found little evidence that safety demonstration by an experienced model could influence fear in an observer in a one-on-one setting. However, in Chapters 5 and 6, I showed that the presence of multiple models, when behaving calmly, could override fear in observers, but this influence was lessened when previously learned fear had been socially reinforced.

I induced uncertainty about risk by exposing individuals repeatedly to general predation cues without any specific information. Indeed, this caused minnows to display neophobic behaviour. However, individuals that were provided with information about a specific threat within a high-risk environment also displayed neophobia, and at a fairly similar intensity (Chapter 4). Individuals that were repeatedly exposed to risk, regardless of whether they had specific information, displayed increased baseline fear behaviours in addition to neophobia, which I have collectively referred to as the 'high-risk phenotype'. This phenotype was even more intense when minnows experienced risk in isolation. I also found no evidence that uncertain individuals were more influenced by experienced models. These outcomes, taken together,

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[7] A portion of this chapter comes from a manuscript currently in press:

Crane AL, Ferrari MCO (in press). Learning of safety by a social fish: applications for studying post-traumatic stress in humans. Animal Behaviour.

indicate that the high level of risk, rather than uncertainty, was the fundamental driver of behaviour in my experiments.

When given an opportunity to learn a specific threat from neophobic models, observer minnows did not learn correctly, instead acquiring the high-risk phenotype from models (Chapters 3 and 4). Hence, a potential mechanism for the failed learning of safety in Chapter 4 is that, despite being experienced with safety, models became poor demonstrators of such because they acquired socially-transferred fear from observers. Hence, in this social learning framework, the observer and model influence each other in a contradirectional transfer of information, with the naive observer having an opportunity to learn safety from an experienced model, but instead the model learning risk from the observer. In Chapter 5, I found that a large group of models was necessary to counteract the social transfer of fear from observer to model, which allowed models to influence observers to behave as though the environment was now safe. Likewise, in Chapter 6, I found that when a model had experienced socially-transferred fear, its removal and replacement with a new unaffected model was influential in weakening the high-risk phenotype of the observer.

I conducted these studies to better understand social learning of risk and safety, but from my early work came a goal of applying my results to a human problem – the acquisition of post-traumatic stress (PTS) and behavioural therapy. Indeed, the social environment appears critical for the susceptibility and recovery of PTS (Charuvastra & Cloitre 2008). In this chapter, I make the case that non-human animals, and specifically prey fishes, can be valuable in furthering our understanding the ‘social ecology’ of PTS in humans, hopefully stimulating new ideas for recovery strategies.

7.2. Animal models for human post-traumatic stress

Like other animal species, humans exposed to danger can develop long-term alterations in the neurobiological responses to stress, resulting in severe psychological problems (Garbarino & Kostelny 1996; Kaysen, Resick & Wise 2003; Nutt 2000). For instance, combat veterans and victims of sexual assault often experience post-traumatic stress (PTS), whereby they exhibit intense symptoms of emotional distress, social withdrawal, nervousness, hypervigilance, and fear of the unexpected, among other effects (Charuvastra & Cloitre 2008). These symptoms can be debilitating, providing no benefit in low-risk environments, such as when returning home from combat. However, from an evolutionary perspective, these traits may be exactly the optimal response in high-risk environments, where extra caution toward unordinary events, and increased preparedness for danger, can increase survival (Cantor 2009). This has led some experts to no longer refer to PTS as a disorder (PTSD).

Performing controlled, randomized experiments on humans to understand PTS source-therapy interactions (i.e., how symptoms acquired in different ways affect the outcomes of different therapies) is generally not ethically viable. However, animal models allow researchers to test such questions, but the main drawback of animal models is that they are often limited in how well they represent humans (Borghans & Homberg 2015; Goswami et al. 2013). Three basic criteria must be met for animal models to be considered valid in terms of human applications. The model must reproduce symptoms that parallel those seen in humans (‘face validity’) and predict the treatment outcomes seen in humans (‘predictive validity’) (Belzung & Lemoine 2011). There must also be confidence that tests of the model are measuring the intended response (‘construct validity’), in this case, a fear response (Maximino, de Brito & Gouveia Jr 2010). Studies using animal models typically induce PTS-like symptoms using one of two basic methods, either via exposure to painful stressors or to predation risk (Goswami et al. 2013). Unlike exposure to painful stressors, such as shock or simulated drowning, exposure to predation risk is more ecologically relevant and has shown several advantages in modelling the human disorder (Goswami et al. 2013). There is extensive evidence that predation-risk methods yield high face validity for PTS symptoms across animal taxa (Clinchy et al. 2011; Clinchy et al. 2013; Goswami et al. 2013). Behavioural changes in animals exposed to risk (e.g., avoidance behaviour, reduced activity, aggression, hypervigilance, neophobia) often parallel those of PTS sufferers. The classic example of severe and long-lasting PTS-like behaviours was demonstrated in rats, *R. norvegicus*, following exposure to a predator, *Felis catus* (Adamec & Shallow 1993).

Another strength of predation-risk models is high construct validity (Cantor 2009; Clinchy et al. 2011; Clinchy et al. 2013) due to the phylogenetic conservation of the fear neural pathways involved with PTS. Indeed, prey exposed to predation risk display neurological and hormonal changes (e.g., Barcellos et al. 2007; Egan et al. 2009) that are similar to those in humans, which is how construct validity is typically judged (Siegmund & Wotjak 2006). As for the predictive validity of animal PTS models, studies have targeted reduced anxiety via fear conditioning (e.g., in mice, *Mus musculus*) (Golub et al. 2009), or exposure to anxiolytic drugs (e.g., in fishes, including minnows: Cachat et al. 2010; Maximino et al. 2014; Rehnberg et al. 1989; Richendrfer et al. 2012; Wong et al. 2010).

7.3. Prey fishes as PTS models

All animal models have limitations. However, long-term psychological stress can cause chronic effects considered directly comparable to those in humans, even for far less cognitively advanced species (Clinchy et al. 2013). Indeed, fishes have already shown a moderate degree of face validity for a PTS model based upon the PTS-specific criteria of Yehuda and Antelman (1993) that I outline here: (1) There is substantial variability in who acquires PTS and its severity, and likewise, there is rich literature on inter-individual variability in fear reactions in fishes and other non-human animals (e.g., Bell & Sih 2007; Brown et al. 2015a). (2) In humans, the behavioural changes associated with PTS can be expressed in a bidirectional fashion, as has been found for fish (e.g., see Chapters 4–6 where activity increased in the form of pacing and decreased in the form of freezing). (3) The intensity of symptoms should be ‘dose dependent’, meaning that exposure to higher levels of risk causes intensified symptoms, as has again been demonstrated in fishes (Brown et al. 2014; Brown et al. 2015a; Brown et al. 2015b). (4) These behavioural changes often persist for many years in humans. In fishes, little work has examined the longevity of the high-risk phenotype, but Brown et al. (2015a) demonstrated its persistence for a few weeks in cichlids, *Amatitlania nigrofasciata*. Another study with this species indicated that repeated exposures to alarm cues (12 times) caused neophobia to persist only for three weeks (Joyce et al. 2016). The study by Brown et al. (2015a), however, revealed that further increasing the level of risk will cause even longer retention. Other species and longer durations should be tested, and the length of duration relative to lifespan may be a consideration for animal models. (5) Brief exposures to risk (e.g., a one-time sexual assault) can induce PTS. In fishes, this criterion has yet to be explored, so studies assessing fear after surviving an actual predator attack would be valuable, here, if ethically viable.

Using fish as human models has aided research on cardiovascular metabolism (Chico, Ingham & Crossman 2008), genetic disease (Lieschke & Currie 2007), cancer (Amatruda et al. 2002), and behavioural neuroscience (Blaser, Chadwick & McGinnis 2010; Stewart et al. 2012). In addition, fish models show predictive validity for PTS pharmaceutical treatment (Caramillo et al. 2015; Gerlai 2011; Maximino et al. 2014; Richendrfer et al. 2012; Stewart et al. 2014). The use of fish as PTS models can provide some advantages relative to other animal models. For instance with fish, researchers can consistently induce PTS-like symptoms using their alarm cues, which is more ethically satisfying than other methods, such as causing physical pain to the animals (Braithwaite & Boulcott 2007; Sneddon 2011). Moreover, the abundance of small prey fishes allows for multi-factorial and manipulative experiments that can increase our understanding of source-treatment interactions with statistical reliability from large sample sizes. Like others (Borghans & Homberg 2015), I posit that the best way to obtain the optimal reflection of PTS is by combining what we learn from multiple animal models.

7.4. Secondary trauma

Unfortunately for people living or working with PTS sufferers, their symptoms can be vicariously transmitted. This phenomenon, while receiving much less attention than the direct acquisition of PTS, has been described as 'secondary traumatic stress', 'vicarious traumatization', 'burnout', and 'compassion fatigue' (Canfield 2005; Elwood et al. 2011). While these terms have slightly different defining criteria, their similarity has led to using the term 'secondary trauma' to encompass this overall phenomenon (Elwood et al. 2011; Whitfield & Kanter 2014). As of the late 1990s, evidence for secondary trauma was scarce, and there was debate surrounding whether it was actually a real issue. Today, difficulties still remain in determining whether secondary trauma results from interaction with the direct-trauma sufferer or simply from the stressful nature of their own lives (Sabin-Farrell & Turpin 2003). However, a substantial amount of literature has documented secondary trauma in recent years (Canfield 2005; Knight 2010). Examples are widespread among professional and non-professional interactions, including therapists (Canfield 2005), clinicians working with victims of terrorism (Bauwens & Tosone 2010), nurse examiners (Maier 2011), Holocaust survivors (Baranowsky et al. 1998), family members of war veterans (Arzi, Solomon & Dekel 2000), war journalists (Feinstein, Owen & Blair 2002), and individuals that frequently view trauma-related media content (Holman, Garfin & Silver 2014). While data are limited within different therapeutic fields, a comparison study across fields found evidence that social workers developed the highest levels of secondary trauma, whereas psychologists experienced the lowest levels (Manning-Jones, de Terte & Stephens 2016). My work with minnows indicates that prey fishes are well suited for addressing questions about secondary trauma. Much like secondary trauma in humans, the high-risk phenotype in minnows can be indirectly acquired simply by interacting with individuals that already display the phenotype (Chapters 3-6 and Fig. 7.1). My results in Chapter 3 were the first causal evidence for this phenomenon in any species, adding to the face validity of prey fishes for modelling PTS.

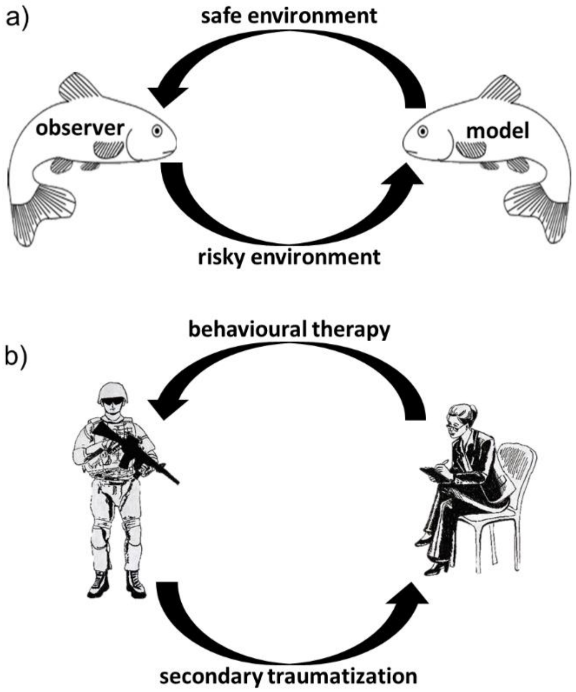

Figure 7.1. Linking social learning theory to fear recovery in humans. In minnows (a), a high-risk observer has the opportunity to learn safety from a conspecific model, but also conveys to the model that the environment is dangerous. Because social information about fear can override safety in a one-on-one setting, models can acquire high-risk behaviours from observers without being exposed to risk directly. In humans (b), a behavioural therapist may work with a PTS sufferer (*Monson et al. 2006* ***) to help alleviate their symptoms. Often these therapists experience symptoms of secondary trauma (*** *Sabin-Farrell & Turpin 2003* ***).***

In humans, the severity of secondary trauma correlates with the time spent interacting with the direct trauma victim (e.g., in therapists: Cohen et al. 2004; Killian 2008), and likewise, I found evidence for this association in minnows (Chapter 3 vs. 4 and 6). The research community still knows little, however, about how secondary trauma compares to direct trauma, or factors affecting the persistence of acquired symptoms (Arzi et al. 2000; Baranowsky et al. 1998). A review of secondary trauma among trauma clinicians found that low-level symptoms were common, and not restricted only to trauma-focused therapies, but ‘clinically significant’ levels of secondary trauma were rare (Elwood et al. 2011). In Chapters 3, 4, and 6, I found similar results, where socially-transferred fear occurred at lower levels than that displayed by individuals directly exposed to alarm cues. However, a few studies in humans indicate, that in some rare cases, the symptoms of secondary trauma can actually be more severe than direct-trauma symptoms (Arzi et al. 2000; Feinstein, Audet & Waknine 2014). For example, Feinstein et al. (2014) found that war journalist who photographed violent events in person had lower levels of PTS than the journalist who conducted the image processing. Interestingly, the frequency of viewing the images had a stronger effect than the viewing duration. In contrast, factors thought to prevent secondary trauma are age, experience, and emotional independence (Arzi et al. 2000; Knight 2010), although these are not always correlated with the severity of symptoms (Levin et al. 2011). Other studies indicate that having background social support, such as working closely with a supervisor or working in teams, helps to prevent secondary trauma (Coles, Dartnall & Astbury 2013; Killian 2008; Williams, Helm & Clemens 2012), as does the lack of trauma exposure during early life (Williams et al. 2012).

7.5. PTS growth and therapy

Post-traumatic growth is the process of overcoming trauma-related symptoms (Samios, Rodzik & Abel 2012). The term ‘resilience’ (Yehuda et al. 2006) is also frequently used for such. For some PTS sufferers, medication (e.g., anxiolytics and antidepressants) can alleviate their symptoms (Mohamed & Rosenheck 2008; Sharpless & Barber 2011), as in fishes (Caramillo et al. 2015). The primary anxiolytics used to treat PTS are benzodiazepines, or ‘benzos’, including clomipramine (Anafranil), diazepam (Valium), chlordiazepoxide (Librium), and alprazolam (Xanax), whereas selective-serotonin reuptake inhibitors, such as sertraline (Zoloft) and fluoxetine (Prozac), are commonly prescribed antidepressants. In contrast, various psychotherapies are also used to treat PTS. One form of psychotherapy is eye-movement desensitization and reprocessing, which is a growing therapeutic method where the patient optically focuses on a moving stimulus during trauma-memory recall (Shapiro 1989). However, there has been some controversy as to whether the eye movements have any benefit vs. the trauma recall alone (Davidson & Parker 2001; Lee & Cuijpers 2013). In more traditional behavioural therapy, patients may simply focus on their present environment (present-focused therapy) (Bisson et al. 2007; Classen et al. 2001; Foy et al. 2002; Monson et al. 2006; Rizvi, Vogt & Resick 2009; Sharpless & Barber 2011). This can occur in a one-on-one setting or alongside other patients in a group (Classen et al. 2001; Foy et al. 2002). In Chapter 3, I attempted to use a one-time safety conditioning in a one-on-one setting to reduce the high-risk phenotype, finding some evidence that fear was reduced toward the conditioned stimulus but not toward novel stimuli. In contrast, 'prolonged exposure' is a trauma-focused therapy in humans where patients must recall trauma memories over numerous sessions until they eventually become desensitized to the memories (McLean, Asnaani & Foa 2015), consistent with the Risk Allocation Hypothesis (Ferrari et al. 2009; Lima & Bednekoff 1999b). However, in Chapter 3, I also attempted to weaken the high-risk phenotype via fear conditioning (exposure to risk from an experienced model), but to no avail with only a one-time exposure.

Although only a few studies have assessed the effectiveness of group therapy (Bisson et al. 2007), it appears largely beneficial to sufferers of PTS when acquired in isolation (e.g., physical or sexual abuse) (Bradley & Follingstad 2003; Classen et al. 2001; Resick et al. 1988). However, for patients with PTS that was acquired in groups (common in military conflicts), the effects have been only modest, despite often having less severe symptoms than victims of isolated trauma. In one study on combat veterans, the dropout rate was nearly half (Schottenbauer et al. 2008), which is a common occurrence in these studies, but participants that continued therapy did show weakened symptoms (Schnurr et al. 2003). In another study, group therapy reduced PTS symptoms, but other defensive behaviours remained unaffected (Britvić, Radelić & Urlić 2006). However, these anecdotal patterns may be driven by confounding factors. For instance, studies on single-trauma victims generally involve women who may be more comfortable with a therapist or have more social attachment (see: O'Connor & Elklit 2008) relative to group-trauma victims – primarily men exposed to combat.

Another type of therapy is "modelling", where patients have opportunities to learn by imitating the actions of other individuals (the models) (Jaffe & Carlson 1972; Swney 2013). A behavioural change or skill develops by observing the model exhibit the desired behaviour. Again, this type of therapy can occur in a one-on-one situation or within a group of models. However, I am not aware of any current evidence that supports modelling as an effective therapy for PTS, but whether the lack of evidence is due to the therapy's ineffectiveness or simply a lack of study remains unclear. Because social withdrawal is a typical symptom of PTS, sufferers may be unlikely to spend much time with a calm group of people, whereas individuals that live with the PTS sufferers (e.g., spouses) may not serve as ‘calm models’ because they have become secondarily traumatized (e.g., Arzi et al. 2000). There is evidence in humans, however, that specific phenotypes – general levels of anxiety and social withdrawal – are reduced via modelling therapy (Jaffe & Carlson 1972; O'connor 1972; Swney 2013).

My results in Chapter 5 demonstrated that group modelling weakened the high-risk phenotype for observers but was more persuasive for those that had experienced background risk in isolation, rather than in a group, despite the tendency for isolated individuals to be more fearful initially. Experiencing risk in a group appeared to reinforce fear and override the calm model. These findings are in line with anecdotal comparisons of group vs. isolated trauma in humans (mentioned above), and thus, the social reinforcement of fear appears to limit the effectiveness of treatment in humans and in minnows. Moreover, in my study, I used both sexes in each treatment, and thus sex was not a confounding factor, unlike the human anecdotes. However, group therapy for humans involves other symptomatic individuals alongside a therapist (Bober & Regehr 2006), whereas in my study the members of each group of models were either all calm or all un-calm. Hence, the recovery of human patients in groups of symptomatic individuals may be limited by the social reinforcement of fear, whereas therapists working in these groups could experience intensified secondary trauma by being out-numbered by traumatized individuals (Canfield 2005; Samios et al. 2012).

In Chapter 6, I modelled outcomes for fearful observers when their models were replaced after experiencing socially-transferred fear. In humans, changing therapists can be a stressful event for patients, especially when the change is unplanned (Bostic, Shadid & Blotcky 1996). It can cause tension and expressions of anger, loss, and resentment in patients (Dinnen & Bell 1972). In the psychological literature, some attention has gone toward what has been referred to as ‘substitute therapists’ or ‘replacement therapists’. Dinnen and Bell (1972) assessed patients with epilepsy, and found that replacement therapists did not hinder the progress of patients. For overcoming alcoholism, the rotation of therapists has been essential, attributed to increased therapeutic relationships for patients (Krampe et al. 2004). However, in both cases the patients’ symptoms are not socially transferred, and thus, replacement therapy for fear recovery should work differently. I am not aware of any human studies on such, but in my work with minnows (Chapter 6), I found evidence that periodic replacement of a therapist would be beneficial in helping a patient overcome fear.

In the context of recovery from secondary trauma, therapists experiencing such symptoms are recommended to first cease their interaction with the patient, and allow a new therapist to counsel the trauma victim. The next step is to adopt self-care strategies such as exercising, eating and sleeping regularly, taking more personal time, and undergoing stress management training (Osofsky, Putnam & Lederman 2008). However, little is known regarding the success of these strategies for actually alleviating secondary trauma (Bober & Regehr 2006; Motta 2008). In fact, a recent review of the literature on the efficacy of interventions to help mental health workers with secondary trauma found that no randomized experimental studies have been conducted (Bercier & Maynard 2015). The authors viewed the observational studies as being plagued by small sample sizes due to low participant recruitment and high drop-out rates. The authors proceeded to highlight the need for more rigorous research, underscoring that we should not assume that therapy for PTS sufferers will work in the same way for alleviating secondary trauma (Bercier & Maynard 2015).

Again, my work on socially-transferred fear in minnows suggests they could be a good model for assessing recovery from secondary trauma. I did not test such in this thesis, but I did explore how the removal and replacement of models could affect their own fear behaviours (Chapter 6). My results indicate that a therapist experiencing secondary trauma could become ineffective if they are unable to mask their symptoms. Although the initial model experienced socially-transferred fear, their removal resulted in a shortened interaction time with the directly exposed individual. In humans, a shorter interaction correlates with faster recovery from secondary trauma (e.g., Cohen et al. 2004; Killian 2008). In fishes, we know that higher intensities of the high-risk phenotype persist longer than lower intensities, at lease when acquired directly by individuals from similar social backgrounds (e.g., Brown et al. 2014; Brown et al. 2015a; Brown et al. 2015b). This presumably holds true for indirect acquisition as well. Hence, the replacement of therapists experiencing secondary trauma could be beneficial to the therapists involved, in addition to their patients. Often, however, a therapist may feel compelled to continue their interactions with a patient after experiencing secondary trauma, attempting to hide their symptoms (Osofsky et al. 2008). My data suggest that such a decision could be harmful to the therapist and their patient in the long-term, but the impact of masking secondary trauma is a topic of future interest.

7.6. Other potential applications

My primary focus was to apply my work to post-traumatic stress; however, there is a parallel between social learning in high-risk environments and another topic in human psychology. ‘Helicopter parenting’ is a behaviour where parents ‘hover’ over their children regardless of whether this oversight is actually needed (Locke, Campbell & Kavanagh 2012). This phenomenon has received a substantial amount of media attention, yet there has been little research on the topic, and the literature is mostly speculative (Ungar 2009). Some psychologists think that helicopter parents are so overprotective that their children do not learn the natural consequences of actions (Locke et al. 2012). Some children will become overly anxious, accept that everything is dangerous, and withdraw, and others will not be able to filter out irrelevant information (Ungar 2009). In Ungar’s (2009) view, overprotecting children in low-risk environments (e.g., stable, well-resourced homes) is what causes the negative consequences. He adds that “the level of protection should match the level of actual risk”. The current state of the literature is biased toward middle-class North Americans, even though they are unlikely to suffer from extreme risk (Hoffman 2010). Hence, our view of helicopter parenting may not reflect different ethnic backgrounds or social groups. Future research on vertical transmission (parent to offspring) of the high-risk phenotype in fishes under different background environments could be an innovative approach for exploring outcomes of helicopter parenting.

Behavioural problems related to fear are also commonly seen in companion animals like domestic dogs and cats (Marder 1991). In dogs, for example, aggressiveness, separation (isolation) anxiety, and generalized anxiety are common (Talegón & Delgado 2011). Generalized anxiety is often seen in abused individuals (McMillan et al. 2015), those living in shelters (Tod, Brander & Waran 2005), and those with working roles such as guarding, contraband detection, and medical alert – all roles where fear recovery is critically important (Rooney, Clark & Casey 2016). Standard medications are often used to reduce anxiety (Marder 1991), as is artificial selection for individuals with fewer fear problems (Rooney et al. 2016). Although human therapy for dogs is common (e.g., Coppola, Grandin & Enns 2006), as is using dogs in therapy for humans (e.g., Altschuler 1999), I am not aware of any studies that intentionally use intraspecific social therapy for dogs or other companion animals. However, some studies on dogs have used a conspecific chemical cue (‘dog-appeasing pheromone’ secreted during lactation) to reduce anxiety behaviours such as vigilance and pacing (Kim et al. 2010; Tod et al. 2005). Rooney et al.

(2016) argued that future research on fear recovery in dogs should explore new methods involving social learning, stressing that the influence of calm conspecific models needs to be evaluated.

7.7. Future directions

The way uncertainty affects social learning processes remains a fundamental question. I explored uncertainty via the lack of information about a predator's identity, but incomplete information regarding when or where attacks occur also deserves attention. At least in minnows, assessing uncertainty when induced by repeated exposures to risk poses a challenge for researchers, due to the acquisition of the high-risk phenotype and its social transmission. How much, if any, of these outcomes should be attributed to uncertainty? Perhaps lower threat levels, fewer risk exposures, or more time between exposures would facilitate a phenotype of uncertainty in response to novel cues without inducing a consistent fearful state. Determining how social information is incorporated into fear responses over a longer time scale could be valuable. For instance, when uncertain individuals learn socially, do they retain their learned responses for the same duration of time as those with complete information? Evidence for such a pattern exists in tadpoles, *L. sylvaticus,* in a non-social context (Ferrari & Chivers 2013).

More attention should also go to the reinforcement of social learning via multiple conditionings, particularly in the context of conflicting information between prior and current situations (e.g., how many individual experiences of safety are required to prevent subsequent social learning of risk? how many social experiences with safety are required to override one instance of socially-learned risk?). Moreover, some traits of observers and models have received little attention, such as age, dominance status, or social familiarity. With regards to age differences, for instance, does learning from a different-sized model cause uncertainty for observers, weaken learned responses, or even prevent learning? The outcome likely depends on whether different-sized models have different predator threats, and whether observers recognize such information. In my social learning experiments, observers and models fully interreacted, so determining how specific types of information (e.g., tactile, visual, chemical cues) were used is unknown. Social learning of risk in minnows is known to occur via visual cues in the absence of other information (Ferrari et al. 2005), whereas the release of non-injury chemical cues from models does not invoke learning in some species (Ferrari et al. 2008) but has yet to be tested in minnows. The way specific cue types affect the social transfer of generalized fear should be explored, as should whether minnows release any auditory cues or alarm calls when frightened. Across the board, more work is needed to understand the duration of the socially learned response, which has rarely been tested more than a few days after conditioning (see Mineka & Cook 1993 for an exception).

While not a focus of this thesis, research on social learning of predators may become increasingly important in a world that is rapidly changing. Physical alterations to habitats, in addition to biotic homogenization, can result in prey species encountering new predator species. The social transmission of predator-related information will likely play an important role in the evolutionary future of many prey species. Will a high-risk phenotype benefit species that experience new threats, despite the energetic costs of vigilance and reduced time spent on other fitness-related activities? These costs are preferable to being consumed, but if the chances of being consumed are low, as in safe environments, a high-risk phenotype becomes maladaptive. A few studies have found higher survival among neophobic individuals when novel predators were present (Benard & Fordyce 2003; Ferrari et al. 2015b). However, these studies revealed that neophobic behaviour can be an evolutionary trap when individuals contend with invasive predators that use hunting strategies unlike those of their native predators. From an evolutionary perspective, a plastic high-risk phenotype is an adaptive trait for success in risky environments (Brown et al. 2013). It helps animals survive their initial encounters with novel predators and facilitates the retention of information that is learned during the encounter (Mitchell et al. 2016). Inducing or reducing the high-risk phenotype may become increasingly useful for species management (e.g., enhancing food production), as well as for conservation efforts that rear and release animals to replenish natural populations.

Finally, I have proposed that my thesis work has applications to PTS in humans. However, clearly more work is needed to validate the use of prey fishes as a PTS model. Little is known regarding two criteria: (1) Can a one-time event induce PTS-like symptoms? Answering this question might involve individuals that survive an actual predator attack, or alternatively, for fishes, a one-time exposure to a concentration of alarm cues well higher than is ecologically relevant might work in similar fashion. Moreover, can a one-time event re-trigger PTS-like symptoms after waning? Indeed, another criterion for PTS validity is (2) the waning time of the symptoms. In prey fishes, we known that the high-risk phenotype can last for several days, but can researchers drive its longevity further, and for a duration that is comparable to humans when accounting for differences in lifespan?

Feedback from psychologists on this potential application will be valuable in targeting future work to address gaps in our understanding of PTS. From my perspective, there are several interesting avenues for investigation that deserve attention: (1) Can socially-transferred fear be more intense than fear from a direct event? My work herein showed that socially-transferred fear was weaker, as have most observational studies on humans. One recent exception however, was the journalists that processed war photos (Feinstein et al. 2014). It would be interesting to test minnows that are repeatedly exposed to multiple, new high-risk models. (2) Because the therapist is the leader of the therapist-patient pair, research should explore how the dominance/subordinate status of observers affects social transfer of the high-risk phenotype. (3) My work herein involved a fish species that is social. However, many fish species are asocial, and thus, they might not be good models for understanding social influences on fear. In contrast, there are other fish species that are considered even more social than minnows. Research exploring the social transmission of fear across fish species with different levels of sociality is needed. (4) There is some evidence in humans that the frequency of frightening stimuli is more influential in driving PTS symptoms than the duration of the frightening stimuli. Prey fishes can be an ideal model for experimentally testing such mechanisms. (5) Additional work on fear and safety conditioning should be conducted, but with multiple conditionings. Prolonged-exposure therapy could also be modelled in this way. (6) How parents with the high-risk phenotype affect their naïve offspring should be tested in prey fishes with parental care, and over generations.

The scientific community still has little non-correlational evidence for how various underlying factors affect the acquisition of PTS, treatment success, the reoccurrence of symptoms, or how medications and behavioural therapy interact. The same can be said for secondary trauma. I believe that a minnow model can help us to address such issues, hopefully providing us with beneficial ideas for recovery, while also increasing our understanding of the cross-taxa dynamics of social learning.

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