

**SOCIALLY LEARNED RECOGNITION OF PREDATION RISK AND NON-
RISK: A THEORETICAL MODEL AND EMPIRICAL TEST OF LEARNING
ABILITY IN THE CONVICT CICHLID (*AMATITLANIA SIQUIA*)**

by

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Abstract

Avoiding predators, though clearly fitness enhancing, may be costly in terms of the time and energy it requires. Effectively mediating the trade-off between the cost of antipredator behaviour and the cost of getting eaten requires an ability to assess changes in predation risk; an ability that can be enhanced by learning. Here, I investigated the role of learning in predation risk assessment. I developed an individual-based model to examine the conditions favouring social over asocial learning in the context of risk assessment, and explored, using a laboratory experiment, the possibility that some animals might socially learn *not* to fear novel cues in their environment. I found that in the context of risk assessment, social learning was more advantageous than asocial learning under a wide range of conditions. In the experimental study, I found no evidence that my study animals could socially learn not to fear novel cues in their environment.

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Chapter 1

General Introduction

In response to predation risk, disturbance, or even novelty, many animals will exhibit some form of 'antipredator' behaviour such as fleeing, hiding, increased vigilance, altered habitat use, or reduced activity (Lima and Dill 1990, Godin 1997, Frid and Dill 2002). These behavioural responses may benefit the responding animal by reducing its immediate risk of predation, but are also presumed to entail costs in terms of the time and energy that they require (Ydenberg and Dill 1986, Lima and Dill 1990, Godin 1997, Lima 1998). Assuming spatial or temporal variation in predation risk and at least some cost to antipredator behaviour, selection should favour mechanisms allowing animals to match their expression of antipredator behaviour to real-time changes in ambient predation risk (Sih 1992, Lima and Bednekoff 1999). This would first require that animals have the ability to assess changes in predation risk; particularly, to distinguish cues indicative of risk from cues unrelated to predation risk.

The ability to recognize cues indicative of risk may be innate (Veen et al. 2000, Hawkins et al. 2007), learned (Berger et al. 2001, Leduc et al. 2007), or some combination of the two (Magurran 1990, Epp and Gabor 2008). Innate recognition abilities have the advantage of functioning on the very first encounter with a novel cue, but are slow to respond to environmental change (e.g. the introduction of a novel predator species) given the relatively long time required for genetic evolution (Mery and Burns 2010). In contrast, learned recognition requires at least one encounter with a cue prior to functioning, but potentially allows for a rapid response to environmental change (e.g. Chivers and Smith 1995). Given that the nature and degree of predation risk experienced by a given population are likely to vary spatially and temporally, both within and between generations (Werner and Gilliam 1984, Lima and Bednekoff 1999), it is perhaps

not surprising that the ability for learned predator recognition is widespread among animals (reviewed in Griffin 2004).

In the context of predator recognition, I define learning as a change in the expression of antipredator behaviour by an individual toward a given cue with experience. Two basic categories of learning are possible: an increase (e.g. Suboski et al. 1990, Ferrari and Chivers 2009) or a decrease (e.g. Deecke et al. 2002, Vennesland 2010) in the expression of antipredator behaviour toward a cue over time. For convenience, throughout this thesis I will occasionally use the term ‘fear’ to indicate the expression of antipredator behaviour by an individual toward a given cue. My use of this term refers only to an observable behavioural outcome, and not necessarily to a motivational or emotional state. Learning to fear a cue therefore entails an increase in antipredator behaviour with experience (= learned recognition of risk), and learning not to fear a cue entails a decrease in antipredator behaviour toward that cue with experience (= learned recognition of non-risk). Below, I discuss these two categories of learning separately because they appear to involve distinct mechanisms.

Learning About Predation Risk

Learned recognition of risk occurs when an individual expresses increased antipredator behaviour toward a novel cue following an experience in which that cue is spatially and temporally associated with a cue indicative of risk (Griffin 2004, 2008). For example, Ferrari et al. (2008a) found that larval mosquitoes (*Culex restuans*) expressed increased antipredator behaviour in response to salamander odour after having been simultaneously exposed to the salamander odour (= novel cue) and chemical cues from

crushed conspecifics (= cue indicative of risk). Chemical cues from crushed conspecifics are presumed to be indicative of predation risk because they will only be detected when nearby conspecifics are injured or killed (Chivers and Smith 1998) and because mosquitoes have an innate ability to recognize and express antipredator behaviour toward such cues (Ferrari et al. 2007). In the psychological literature, a similar type of learning is referred to as Pavlovian or classical conditioning (Rescorla 1988, Heyes 1994). In a classical conditioning framework, the cue indicative of risk would represent an unconditional stimulus (US) and the novel cue a conditional stimulus (CS). The term 'conditional' implies that an individual's response to the CS is conditional on prior experience, whereas the US will unconditionally elicit a particular response. Classical conditioning occurs if an individual learns to respond to a CS after simultaneously experiencing that CS and a relevant US. This type of learning is referred to as 'associative' because it seems to entail a learned association between two cues. For convenience, and because some properties of learned recognition of risk appear to differ from properties of classical conditioning (Suboski 1990, Griffin 2008), I will not ascribe to classical conditioning terminology in this thesis. Instead, I will refer to cues that an individual could hypothetically learn to fear or not fear as 'learnable cues' (LCs), and cues involved in learning but not necessarily learned about as 'indicator cues' (ICs). Indicator cues are so named because they may be indicative of risk or indicative of non-risk. I avoid the term 'unconditional' because in the context of learned recognition of risk, ICs may themselves be learned about (Magrath et al. 2009), and behavioural responses toward ICs may be context and condition-dependent (Ferrari et al. 2007).

In the context of learning about predation risk, an IC may derive either from a predator, in which case the recognition of risk is ‘asocially’ learned, or from a nearby con- or heterospecific, in which case the recognition of risk is ‘socially’ learned. For instance, Shriner (1999) found that free-living golden-mantled ground squirrels (*Spermophilus lateralis*) expressed increased antipredator behaviour toward a novel sound after simultaneously experiencing the novel sound (= LC) and the appearance of a hawk (= IC). In this example, learned recognition of risk occurred asocially given that the IC derived directly from a predator, with no social influence. In contrast, socially learned recognition of risk involves ICs deriving from con- or heterospecifics, such as alarm calls (McLean et al. 1999), fright responses (Suboski et al. 1990), or mobbing behaviour (Curio et al. 1978). For example, Curio et al. (1978) found that European blackbirds (*Turdus merula*) would mob a harmless stuffed bird (= LC) after witnessing the bird being mobbed by conspecifics (= IC). In some cases, learned recognition of risk may involve an interaction between asocial and social ICs. For example, chemical alarm cues are released following injury or mechanical damage to the dermis of many aquatic animals (Chivers and Smith 1998). Although these cues are commonly regarded as social cues, the presence of chemical alarm cues seems to require an interaction between predators and prey. Chemical alarm cues are unique from social ICs in that they are probably a completely reliable indicator of nearby predation, whereas other social ICs may not be quite so reliable (Beauchamp and Ruxton 2007, Barrera et al. 2011).

Learning About Non-Risk

While it may seem as though animals only need to learn about risk, ample evidence suggests that animals can also acquire a learned recognition of non-risk, sometimes referred to as learned non-predator recognition (Ferrari and Chivers 2011). For example, many animals have the ability to learn via habituation (a form of non-associative learning), entailing a decrease in antipredator behaviour toward once-novel cues with repeated exposure (e.g. Csanyi 1985, Huntingford and Coulter 1989, Deecke et al. 2002, Stankowich and Blumstein 2005, Hemmi and Merkle 2009, Vennesland 2010). The ability to learn about novel cues via habituation requires neophobia, the expression of antipredator behaviour toward novel cues. To understand why, consider an individual that is not neophobic and therefore does not exhibit any antipredator behaviour toward novel cues. Assuming a lower limit to the expression of antipredator behaviour (i.e. zero), habituation, or a decrease in antipredator behaviour toward a novel cue, would not be possible for a non-neophobic individual.

Just like any antipredator behaviour, neophobic responses to novel cues are presumed to entail energetic and opportunity costs (Ydenberg and Dill 1986, Lima and Dill 1990, Godin 1997, Lima 1998). If the novel cue happens to be genuinely indicative of risk, then the benefit of a neophobic response in terms of risk reduction may outweigh the presumed costs. However, if the novel cue happens to be unrelated to predation risk, then neophobia is likely to be locally maladaptive (assuming some cost to antipredator behaviour). In reality, indiscriminate neophobia may be an adaptive cognitive strategy given that an animal can never have perfect information about all cues in the environment (e.g. Foster and Kokko 2009), and failing to avoid a predator cue is potentially more

costly than mistakenly avoiding a non-predator. Despite this asymmetry in costs, as long as there is some cost to antipredator behaviour and neophobia, an individual may benefit from the ability to accurately recognize and *not* respond to cues unrelated to predation risk (i.e. the ability to habituate to or otherwise learn about non-risky cues in the fewest number of encounters).

Social Learning

In learning about predators, and in many other aspects of life, animals can acquire information about their environment by attending to the behaviour of others (Danchin et al. 2004, Galef and Laland 2005, Valone 2007). For example, observing the reproductive success of others might provide information about local habitat quality (Danchin et al. 1998), and witnessing the mate choice of others might provide information about the quality of potential mates (Pruett-Jones 1992). Empirical evidence suggests that many biological traits can be influenced by the behaviour of others, including song dialect, courtship behaviour, foraging technique, predator recognition, and preferences for particular mates, migration routes, breeding sites, and food items (reviewed in Rendell and Whitehead 2001, Griffin 2004, Galef and Laland 2005, Laland and Janik 2006, Laland and Galef 2009, Godin 2010).

Given that the same types of information can often be acquired through both asocial and social learning, a number of authors have wondered why animals should ever rely on social learning (Barnard and Sibly 1981, Boyd and Richerson 1985, Pruett-Jones 1992, Schlag 1998), which seems to be the more error-prone of the two forms (Laland and Williams 1998, Giraldeau et al. 2002). For example, instead of copying the mate

choice or foraging patch choice of a conspecific (who might themselves be unlikely to select high quality mates or foraging patches), why not sample the environment and determine for one's self which mate or foraging patch is best? A great deal of theory has been developed to address this very question, most of which assumes that social learning is less costly than asocial learning given that the acquisition of asocial information requires sampling of the environment (Boyd and Richerson 1985, Rogers 1988, Vickery et al. 1991, Dugatkin and Hoglund 1995, Stöhr 1998). Presumably, environmental sampling involves risks and a costly investment of time and energy that social learners forego. Models of social learning generally predict that given a heterogeneous environment, a population of asocial and social learners will evolve to a mixed equilibrium (e.g. Rogers 1988). This occurs because, when rare, social learners acquire accurate information from asocial learners while avoiding the costs of personal sampling, and therefore have higher fitness than asocial learners. However, as the frequency of social learners increases, their fitness decreases because there are fewer asocial learners in the population producing up-to-date information. Given that there are many different forms of social learning (Galef and Laland 2005), each with potentially unique properties, it is currently unclear whether the predictions of theoretical models of social learning apply to the socially learned recognition of risk and non-risk, which have yet to receive theoretical investigation.

Thesis Overview

The general aim of this thesis is to explore the role of learning in predation risk assessment, and to understand if and when various approaches to learning about

predation risk and non-risk might be used. More specifically, my objectives are to develop a theoretical framework for understanding the evolution of socially learned recognition of predation risk, and to test for socially learned recognition of both risk and non-risk in a small freshwater fish, the convict cichlid (*Amatitlania siquia*). In Chapter 2, I review theoretical investigations into the evolution of social learning, identifying similarities and differences between the assumptions made by this body of theory and the empirical properties of socially learned recognition of risk. I suggest a number of unique properties of learning about risk that are relevant to evolutionary analyses, and develop an individual-based model to explore the conditions under which the ability for socially learned recognition of risk might evolve. In Chapter 3, I describe an experiment testing for socially learned recognition of both risk and non-risk by juvenile convict cichlids. Although there is extensive empirical evidence for socially learned recognition of risk in many animal taxa (Appendix Table A.1), to my knowledge, all investigations into the learned recognition of non-risk to date have focused on asocial learning (e.g. Csanyi 1985, Huntingford and Coulter 1989, Deecke et al. 2002, Stankowich and Blumstein 2005, Hemmi and Merkle 2009, Vennesland 2010). Given the importance of learning about non-risk (e.g. Deecke et al. 2002, Rodriguez-Prieto et al. 2010, Ferrari and Chivers 2011), and the efficiency and generality of social learning mechanisms (Griffin 2004), I sought to explore whether animals could learn about non-risk by attending to the behaviour of conspecifics. Finally, in Chapter 4, I discuss the results of both my theoretical and experimental analyses, and identify outstanding questions in the study of predation risk assessment. In general, I find that much of the theory on the evolution of social learning may not be especially relevant to socially learned recognition of risk and

non-risk. The further development of a conceptual framework that would integrate both the asocial and social learning of predation risk and non-risk would provide a great deal of cogence to the study of risk assessment, and a fruitful avenue for future research.

Chapter 2

A theoretical analysis of socially learned recognition of predation risk

Abstract

Experimental and observational studies have demonstrated that many animals can learn to recognize and avoid cues that are indicative of predation risk, and habituate to cues that are learned not to be indicative of risk. This learning may occur via personal interaction with the environment (= asocial learning), or through attention to the behaviour of nearby conspecifics (= social learning). Here, I develop a conceptual framework and mathematical model for studying the evolution of social learning about predation risk. Specifically, I review theory relating to the evolution of various types of social learning, describe some of the properties of learning about predation risk that are relevant to evolutionary analyses, and explore an individual-based model examining the conditions under which the ability for socially learned recognition of predation risk might evolve. My analysis indicates that some of the assumptions common among models of social learning do not necessarily apply to the socially learned recognition of risk. Assuming that the detection of risk-related cues is largely independent of learners, I found that initially rare alleles for social learning about risk could increase in frequency and even completely replace asocial learning alleles under a wide range of conditions.

Introduction

Few failures... are as unforgiving as the failure to avoid a predator. Being killed greatly decreases future fitness. – S. L. Lima and L. M. Dill (1990)

Despite the intuition that animals should have an innate ability to recognize and avoid potential predators, a great deal of research has demonstrated just the opposite; that is, many animals rely on experience and learning to determine which cues in their environment are indicative of predation risk, and which are neutral (e.g. Curio et al. 1978, Csanyi 1985, Huntingford and Coulter 1989, Magurran 1990, Suboski et al. 1990, Deecke et al. 2002, Ferrari and Chivers 2009). Hypothetically, such learning may proceed in one of two ‘directions’: the intensity of antipredator behaviour that an individual expresses toward a given cue may either decrease (= learned recognition of non-risk; e.g. Csanyi 1985) or increase (= learned recognition of risk; e.g. Curio et al. 1978) with experience. In addition to these two directions of learning, some authors distinguish between learning that occurs via personal interaction with the environment (= asocial learning; e.g. Deecke et al. 2002), and learning that is influenced by the behaviour of social companions (= social learning; reviewed in Griffin 2004). Although both the learned recognition of non-risk and risk and both asocial and social learning about risk are possible, studies on the learned recognition of non-risk tend to focus exclusively on asocial learning (e.g. Csanyi 1985, Huntingford and Coulter 1989, Deecke et al. 2002, Stankowich and Blumstein 2005, Vennesland 2010), while studies on the learned recognition of risk tend to focus on social learning (see Appendix Table A.1). It is currently unclear whether this pattern results from research biases or represents an

underlying biological relationship between the direction (recognition of non-risk or risk) and nature (asocial or social) of risk assessment learning.

Despite the large number of empirical studies on the learned recognition of non-risk and risk, to my knowledge, there has been no attempt to develop a theoretical framework for studying the evolution of these learning abilities. To date, much of the research on recognition learning has focused on the content and psychological properties of learning (reviewed in Griffin 2004), or functional constraints on learning (e.g. Acquistapace et al. 2003, Hazlett 2003, Ferrari and Chivers 2006), with little attention devoted to the evolution of different predation risk assessment strategies. For example, I am not aware of any investigation into the conditions that would favour learned recognition of risk or non-risk over innate recognition, or social learning over asocial learning. Here, I develop a conceptual framework for studying the evolution of learning in the context of predation risk assessment, with an emphasis on understanding the conditions that would favour social learning of predation risk over asocial learning of risk. Specifically, I briefly review existing theoretical models of the evolution of social learning, describe some of the properties of recognition learning that are relevant to evolutionary analyses, and develop an individual-based model examining the conditions under which the ability for socially learned recognition of predation risk might evolve.

Social Learning Theory

Social learning is ubiquitous in animals and is known to influence behavioural traits such as song dialect, mate preference, mating site preference, foraging technique, antipredator behaviour, migration route preference, and a variety of human behaviours

from handedness to language (reviewed in Rendell and Whitehead 2001, Laland and Janik 2006, Laland and Galef 2009, Godin 2010). There has been a great deal of theoretical investigation into the evolution of social learning, especially in relation to social foraging (Beauchamp and Giraldeau 1996, Dubois et al. 2010), mate-choice copying (Dugatkin and Hoglund 1995, Stöhr 1998), and proto-human culture (Boyd and Richerson 1985, Rogers 1988). The models resulting from this body of theory generally demonstrate that a population of asocial and social learners will evolve to a mixed equilibrium, given a heterogeneous or temporally changing environment. This equilibrium results from the negative frequency dependence of social learning. When rare, social learners acquire accurate information from asocial learners while avoiding the costs associated with personal sampling, and therefore have higher fitness than asocial learners. However, as the frequency of social learners increases, their fitness decreases because there are fewer asocial learners in the population producing up-to-date information. Although this finding holds in many models of social learning, the various theoretical approaches to understanding the evolution of social learning require diverse assumptions, and vary widely in their generality. For example, some models describe specific types of learning, such as Stöhr's (1998) account of the evolution of mate-choice copying in a lekking grouse, and some describe more abstract and general forms of learning, such as Rogers' (1988) account of culture in the imaginary 'Snerdwump'. Below, I briefly review the theory underlying various models of social learning, focusing on similarities and differences in the assumptions that they make and the outcomes that they predict.

Many investigations into the evolution of social learning have employed models of gene-culture coevolution, which simultaneously track both the genetic and experiential acquisition of biological traits (Boyd and Richerson 1985, Rogers 1988, Feldman and Laland 1996, Henrich and McElreath 2003, Kendal et al. 2009a). In these models, individuals acquire biological traits via experience with the environment (i.e. learning), and how individuals learn (i.e. asocially or socially) depends on which genetic allele they carry at a given locus. It is assumed that the environment occasionally changes state at some fixed probability u , with each possible state having a unique optimal behaviour that yields a fitness benefit b . Individuals that carry an asocial learning allele are assumed to always learn the most adaptive behaviour at some cost c , and individuals with an allele for social learning are assumed to forego cost c by simply copying the behaviour of a randomly selected ‘model’ from the previous generation. The probability of a social learner acquiring the adaptive behaviour therefore depends on the proportion of individuals expressing that behaviour in the previous generation. For mathematical convenience, gene-culture coevolutionary models commonly assume that cultural evolution occurs much more rapidly than genetic evolution, such that in a given generation, genetic selection acts only on the equilibrium proportion of socially learned behaviours (Boyd and Richerson 1985).

The general predictions resulting from gene-culture coevolutionary analyses can be summarized as follows (from Rogers 1988). The fitness of asocial learners is frequency independent, and depends only on the relative costs and benefits of asocial learning. When rare, social learners are likely to copy (at no cost) an asocial learner that has acquired up-to-date and optimal behaviour, and therefore the fitness of social learners

may exceed that of asocial learners if the rate of environmental change is sufficiently low. However, if the population consists entirely of social learners or if the rate of environmental change is high, social learners will have relatively low fitness because they cannot track environmental change and will therefore express outdated, non-optimal behaviour. The fitness of social learners is therefore negatively frequency dependent and a function of the rate of environmental change.

A second approach to investigating the evolution of social learning involves the multi-armed bandit problem, a framework employed in a variety of fields to study optimal learning strategies (Schlag 1998, Bolton and Harris 1999, McElreath et al. 2008, Rendell et al. 2010, Abbott and Sherratt 2011). In the multi-armed bandit, individuals may express one of a finite number of possible behaviours, with each behaviour corresponding to an arm of the bandit that yields a certain fitness payoff. Environmental change can be modeled by assuming that the payoffs associated with a given behaviour change at some fixed probability u . At any given time, individuals choose between the mutually exclusive actions of exploration (learning) and exploitation (expressing a learned behaviour and receiving the corresponding fitness payoff). Some authors have incorporated social learning into the multi-armed bandit problem by assuming that individuals can also choose between the mutually exclusive forms of learning – asocial and social (Bolton and Harris 1999, Rendell et al. 2010). In these models, asocial learning provides an individual with accurate information about the payoff associated with a randomly selected behaviour, whereas social learning provides ‘noisy’ (i.e. sometimes inaccurate) information about the payoff associated with a behaviour that was expressed (exploited) by a randomly selected conspecific in the previous generation.

Social learners tend to learn about behaviours with relatively high payoffs because the conspecifics they learn from are motivated to express the behaviour within their repertoire associated with the highest expected payoff (Rendell et al. 2010, 2011).

A third framework for understanding the evolution of social learning involves the producer-scrounger game, an evolutionary game theory approach applied primarily to the analysis of social foraging behaviour (Barnard and Sibly 1981, Vickery et al. 1991, Beauchamp and Giraldeau 1996, Giraldeau and Caraco 2000, Dubois et al. 2010). The producer-scrounger game models scramble competition for food in an environment with distinct food patches, each containing a finite number of food items. Producers (similar to asocial learners) independently search for food patches at some cost c , whereas scroungers (similar to social learners) exploit the discoveries made by producers at no immediate cost. Environmental change is not explicitly modeled in the producer-scrounger game, but rather is implicit given a finite amount of food per patch. When a patch becomes depleted, individuals that were previously foraging there must search for a new one.

Unlike models of gene-culture coevolution and multi-armed bandit problems, producer-scrounger models assume that scroungers cannot learn from other scroungers (given that scroungers only occur at patches that were initially discovered by producers) (Giraldeau and Caraco 2000). Nonetheless, producer-scrounger models predict that the fitness of scroungers is negatively frequency dependent for two inter-related reasons. First, as the frequency of scroungers increases, the total number of food patches discovered decreases because only producers can discover food patches. At the extreme, a population consisting entirely of scroungers would starve because they would be

waiting in vain for a food patch to be discovered. A second reason that the fitness of scroungers (and also producers) decreases with an increasing frequency of scroungers is that with fewer patches discovered, more individuals must share the finite food resources in any given patch. Therefore, the mean energy intake and fitness of both scroungers and producers decreases as the frequency of scroungers increases. However, the fitness of scroungers decreases at a greater rate because producers do not suffer (directly) from the reduction in patch discovery rate that accompanies an increase in the frequency of scroungers (Beauchamp and Giraldeau 1996). Like models of gene-culture coevolution, the producer-scrounger game predicts that, under most conditions, the proportions of producers and scroungers will evolve to a mixed equilibrium (Giraldeau and Caraco 2000).

Finally, a number of authors have developed population genetic or game theoretic models to understand the conditions under which mate-choice copying might evolve (Losey et al. 1986, Pruett-Jones 1992, Dugatkin and Høglund 1995, Stöhr 1998). These models vary in scope and application, but generally assume that females are faced with the problem of choosing a mate among males that vary in quality. Choosers (asocial learners) are assumed to pay a search or assessment cost c and receive some fitness benefit b if they choose to mate with a male of better than average quality. Copiers (social learners) forego the cost of searching or personal assessment and simply copy the choice of another female. The fitness of choosers therefore depends on their ability to assess male quality, whereas the fitness of copiers depends on the assessment ability of whichever female they copy. Even without a cost to choosing, copiers (when rare) can have higher fitness than choosers if copiers are able to observe and integrate the mate

choices of more than one female model (Losey et al. 1986). Similar to gene-culture coevolutionary models, models of mate-choice copying predict that the fitness of choosers is frequency independent, whereas the fitness of copiers is negatively frequency dependent (e.g. Pruett-Jones 1992).

One feature that may distinguish mate-choice copying from other forms of social learning is its susceptibility to indirect selection. Even without direct benefits to the copier, copying alleles can increase in frequency if they become associated with alleles that are common in high quality males (Servedio and Kirkpatrick 1996, Tramm and Servedio 2008). This occurs because the presence of copying in a population will by definition increase the variation in mating success among males (Wade and Pruett-Jones 1990). When copiers exist, males who mate at least once are likely to get more matings with copying females, and therefore have higher than average lifetime fitness. On average then, female copiers mate with males that have high lifetime fitness due to increased female preference, even if these males have no other qualities giving them a higher probability of survival or reproduction than other males. This frequent mating between copying females and males with high total lifetime fitness therefore explains how a copying allele and a high quality male allele may become associated and increase in frequency (Servedio and Kirkpatrick 1996, Tramm and Servedio 2008).

In summary, despite a wide variety of applications and assumptions, theoretical models used to investigate the evolution of social learning generally make similar predictions; namely, that the fitness of social learners is negatively frequency dependent. In the following section, I discuss properties of the learned recognition of predation risk (and non-risk) that may be relevant to evolutionary analyses. I highlight some of the

ways in which learned recognition of risk differs from the models of social learning described above, and attempt to incorporate some of the ideas and assumptions of social learning theory into a new model of the evolution of socially learned recognition of predation risk.

Learning about Predation Risk and Non-Risk

A fundamental property of learning in the context of predation risk assessment is that it seems to depend on the presence or absence of external cues (hereafter referred to as indicator cues, ICs); that is, cues that are involved in learning but are not directly learned about. For instance, the socially learned recognition of risk (or non-risk) requires the pairing of a cue that a given individual could hypothetically learn to fear (or not-fear) (hereafter a learnable cue, LC) and a social IC indicative of risk (or non-risk). In comparison, the asocial learning of non-risk (habituation) involves repeat exposure to a LC in the absence of ICs indicative of risk. The association between a LC and IC is less obvious in the context of asocial learning of risk. For example, if an individual learns to fear a novel predator after narrowly escaping an attack, what are the LCs and ICs that might have been involved in recognition learning? I suggest that, even in this scenario, learning will involve distinct LCs and ICs. For instance, the sight, smell, or sound of a given predator can be considered a LC, as many animals can learn to express antipredator behaviour toward purely visual, chemical, or auditory representations of their predators (e.g. Curio et al. 1978, Chivers and Smith 1995, Barrera et al. 2011). However, experience with these LCs alone is not sufficient for a learned recognition of risk (e.g. Csanyi 1985, Ferrari et al. 2008a), which therefore depends on an external IC (perhaps

mechanical abrasion or a rapidly approaching object, for example). Note that the LC and IC involved in a given learning event may derive from the same source, namely, the predator. I consider these two cues to be distinct because it is possible for potential prey to occasionally or perhaps quite often experience one without the other. The associative nature of recognition learning means that the probability of an individual learning about a given LC depends on the probability of it simultaneously detecting that LC and a relevant IC.

The ICs involved in recognition learning may take a variety of forms, but can roughly be categorized into cues deriving directly from predators (asocial ICs) and cues deriving from social companions (social ICs). In the learned recognition of risk, asocial ICs might include a rapidly approaching object (Dill 1974), mechanical abrasion, stalking behaviour (Brown and Warburton 1997), or the sight of certain visual features (Karplus and Algom 1981, Shriner 1999), whereas social ICs may include chemical alarm cues (Chivers and Smith 1994), alarm calls (McLean et al. 1999), mobbing behaviour (Curio et al. 1978), predator inspection behaviour (Godin and Davis 1995), or stereotypical fright responses (Godin et al. 1988, Suboski et al. 1990) by other individuals. There may also be cases where learning involves both asocial and social ICs. For example, if an individual were to observe a conspecific being chased or consumed by a predator, learning might be said to involve an interaction between asocial and social ICs.

Another important feature of learning about predation risk and non-risk in relation to theoretical analyses is that the detection of both LCs and ICs is likely to be largely independent of the learner. Presumably, animals do not generally go looking for cues that might be indicative of risk. Admittedly, behaviours such as inspection (Godin and

Davis 1995), vigilance (Beauchamp 2008), and even different propensities for sociality (Krause and Ruxton 2002) might influence an individual's likelihood of detecting LCs or ICs. Nonetheless, in developing a framework for studying the learned recognition of risk and non-risk, I make the simplifying assumption that the detection of LCs and ICs is entirely independent of the learner. I additionally assume that learning is obligate and occurs anytime an individual simultaneously detects a LC and a relevant IC (or absence of an IC in the case of habituation). What follows from these two assumptions is that there is no inherent difference in the costs of asocial and social learning about risk (assuming similar neuro-physiological costs). Unlike the models of social learning described in the previous section, individuals that learn about risk asocially do not pay sampling or assessment costs that social learners avoid.

In models of gene-culture coevolution, producer-scrounger games, and game-theoretic analyses of mate-choice copying, social learners are found to have higher fitness than asocial learners only when social learning is rare (Pruett-Jones 1992, Boyd and Richerson 1985, Giraldeau and Caraco 2000). When rare, social learners avoid the costs of asocial learning, but still indirectly acquire accurate information about their environment because most of their models are asocial learners who have invested time and energy to acquire accurate information. The aforementioned approaches to studying the evolution of social learning suggest that the fundamental problem faced by learners is that acquiring accurate information about the environment is costly. Given my assumption that asocial and social learning about predation risk carry equivalent costs, what is the problem or trade-off faced by learners in the context of learning about predation risk? I suggest that the challenge faced by individuals learning about risk

involves a trade-off between the quality and quantity of available information. Social ICs are presumably more common than asocial ICs, at least for animals that aggregate or live in social groups. Therefore, social learners may have more information available to them and be more likely than asocial learners to acquire information about predators and non-predators in a timely fashion, which would contribute to the known antipredator benefits of living in social groups (Krause and Ruxton 2002). However, as discussed in Chapter 3, social ICs may be less reliable than asocial ICs because they are physically distinct from the associated LC, and may occasionally occur in the absence of genuine predation risk (Beauchamp and Ruxton 2007, Barrera et al. 2011). Such occurrences could lead to type I learning errors (borrowing from statistical terminology), which occur when animals learn to fear cues that are not associated with predation risk.

Another fundamental characteristic of learning about risk and non-risk is that asocial and social learning are unlikely to be incompatible, even at a specific point in time. Consider a pure social learner that narrowly avoids an attack by a novel animal with orange stripes, in the absence of social ICs. It is difficult to imagine that an individual would fail to subsequently avoid orange stripes because of an allele dictating that the individual *only* learn via social ICs. My assumption that the presence of ICs is independent of learners means that opportunities for asocial and social learning will occur at different times. Even if both asocial and social ICs are present during a given predation attempt, there is no reason why an ability for social learning would prevent an individual from detecting asocial ICs, or vice versa. I therefore emphasize two learning strategies in subsequent analyses: pure asocial learners (individuals that only learn to fear LCs that are detected alongside asocial ICs), and mixed social learners (individuals that

learn to fear LCs that are detected alongside asocial *or* social ICs). For comparative reasons, I also consider a pure social learning strategy (only learn to fear LCs that are detected alongside social ICs).

A final feature of learning about risk that is relevant to evolutionary analysis is that social learners can potentially learn from both asocial and social learners. Unlike producer-scrounger games where only asocial learners produce information about food patches (Giraldeau and Caraco 2000), I assume that both asocial and social learners can produce information about risk. For example, both types of learners might produce a social IC when they detect a LC that they previously learned to fear. Alternatively, even without learning, any individual may ‘inadvertently’ provide information about a LC if they happen to respond to another cue to which that LC is spatially or temporally associated. Consider again an individual faced with a rapidly approaching object with orange stripes. Even if the individual being attacked is not capable of learning, and does not fear orange stripes, it may still flee from a rapidly approaching object (e.g. Dill 1974). This antipredator behaviour could presumably act as a social IC indicative of predation risk for nearby conspecifics, who might then learn to avoid orange stripes. Therefore, in subsequent analyses I assume a baseline occurrence of ‘inadvertent’ social ICs that is independent of any learning within the population.

In the following section, I develop an individual-based model for studying the evolution of socially learned recognition of predation risk. The general objective is to explore some of the conditions that might favour social learning of risk (both pure and mixed strategies) over asocial learning of risk. My model ignores the learned recognition

of non-risk for the sake of brevity, but such learning could easily be incorporated in the future.

Methods

I considered a population of n individuals inhabiting an environment with l learnable cues (LCs). A fixed proportion T of the LCs represented a genuine predation threat, and $1-T$ were neutral. For simplicity, I assumed that all threats were equally dangerous. In each generation (= round of the simulation), each individual encountered a randomly selected LC, which they either feared or did not fear, and received a fitness payoff W that depended on their response and whether the LC encountered was a threat or non-threat (Table 2.1).

Immediately after the payoff was received, individuals had an opportunity to learn about the cue they encountered. As mentioned above, I modeled three learning strategies: pure asocial learning, pure social learning, and mixed asocial and social learning (hereafter mixed social learning). Each learning strategy corresponded to an allele at a single genetic locus. Asocial learners learned to fear the encountered LC if they simultaneously detected an asocial IC, whereas social learners acquired fear only if they simultaneously detected a social IC. Mixed learners learned to fear an encountered LC if either type of IC was detected. The conditional probability of detecting an asocial IC given a threatening LC was $i_{A|T}$, and the conditional probability of detecting an asocial IC given a non-threatening LC was $i_{A|NT}$. In contrast to the fixed probability of detecting asocial ICs, the probability of detecting a social IC (i_S) is a function of the number of other individuals that fear a particular LC. To model social learning, I assumed that a

Table 2.1 Matrix of assigned fitness payoffs (W) for individuals responding to learnable cues in their environment. In all simulations $W_{NF|NT} \geq W_{F|NT} > W_{F|T} > W_{NF|T}$.

		Learnable Cue Type	
		Threat (T)	Non-Threat (NT)
Response	Fear (F)	$W_{F T} = -10$	$W_{F NT} = -9, -5, 0$
	Non-Fear (NF)	$W_{NF T} = -40$	$W_{NF NT} = 0$

focal social (or mixed social) learner would randomly select m individuals from the previous round as ‘models’ or social companions. If at least r of those models feared the encountered LC, then i_S was set to $i_S = 1$. However, if less than r of the models feared the encountered LC, then i_S was set to $i_S = i_{S-B}$, representing a fixed baseline probability of ‘inadvertent’ alarm responses among nearby conspecifics (i.e. alarm responses that are independent of any learning within the population).

One of the commonly assumed costs of social learning is that it can lead individuals to acquire outdated information following environmental change. In the context of learning about predation risk, the acquisition of outdated information might occur if an individual learns to fear a neutral cue that at some point in the past represented a threat. Such learning would be locally maladaptive unless the neutral cue was to revert back to a threat at some point in the future. In the above scenario, environmental change entails a change in the status of a given cue (e.g. from threat to non-threat). Although this type of environmental change might be plausible, I chose to model environmental change by allowing novel cues to occasionally replace cues of the same status (e.g. invasive predator Y replaces native predator X), and required that the status (threat or non-threat) of a particular cue remain fixed. Specifically, I assumed a fixed probability u that a given LC would change in a given round. Individuals that feared the outgoing LC did not transfer that fear to the replacement LC.

Evolutionary dynamics were realized through randomly inflicted mortality. In each round of the simulation, individuals were killed and replaced with probability k . The genotype of replacement offspring was selected in proportion to the total fitness of each genotype (= summed payoffs to individuals with a given genotype) in the previous

round. As was the case for all individuals entering the simulation in generation 1, replacement offspring entered the simulation not fearing any of the LCs. My choice to inflict mortality at random and make reproduction a function of W (the payoff associated with behavioural responses to LCs) was arbitrary. Evolutionary dynamics could also have been realized by making mortality, or both mortality and reproduction, a function of W .

An overview of the above-described simulation is provided in Figure 2.1. To simulate the evolution of social learning, I played each of the social learning strategies (separately) against a pure asocial learning strategy for 10,000 generations (rounds). In all simulations, the population size was $n = 3,000$ individuals and the initial proportion of social learners was set to 0.01. To understand how the specific parameters in my model influenced the dynamics of social learning, I systematically varied the values of four parameters that I thought would be most likely to influence the evolution of socially learned recognition of risk in nature. These parameters were the number of models available to social learners (m), the baseline probability of inadvertent social ICs (i_{S-B}), the fitness cost of fearing a non-threat (W_{FNT}), and the proportion of LCs that were a threat (T). All other model parameters were constant (Table 2.2). For each combination of parameter values, I performed 10 replicate simulations (separately for pure and mixed social learners) and calculated the mean proportion of pure or mixed social learners, and the mean relative fitness of pure or mixed social learners (= mean fitness of social learners in a given generation - mean fitness of asocial learners across all 10,000 simulated generations), in each generation.

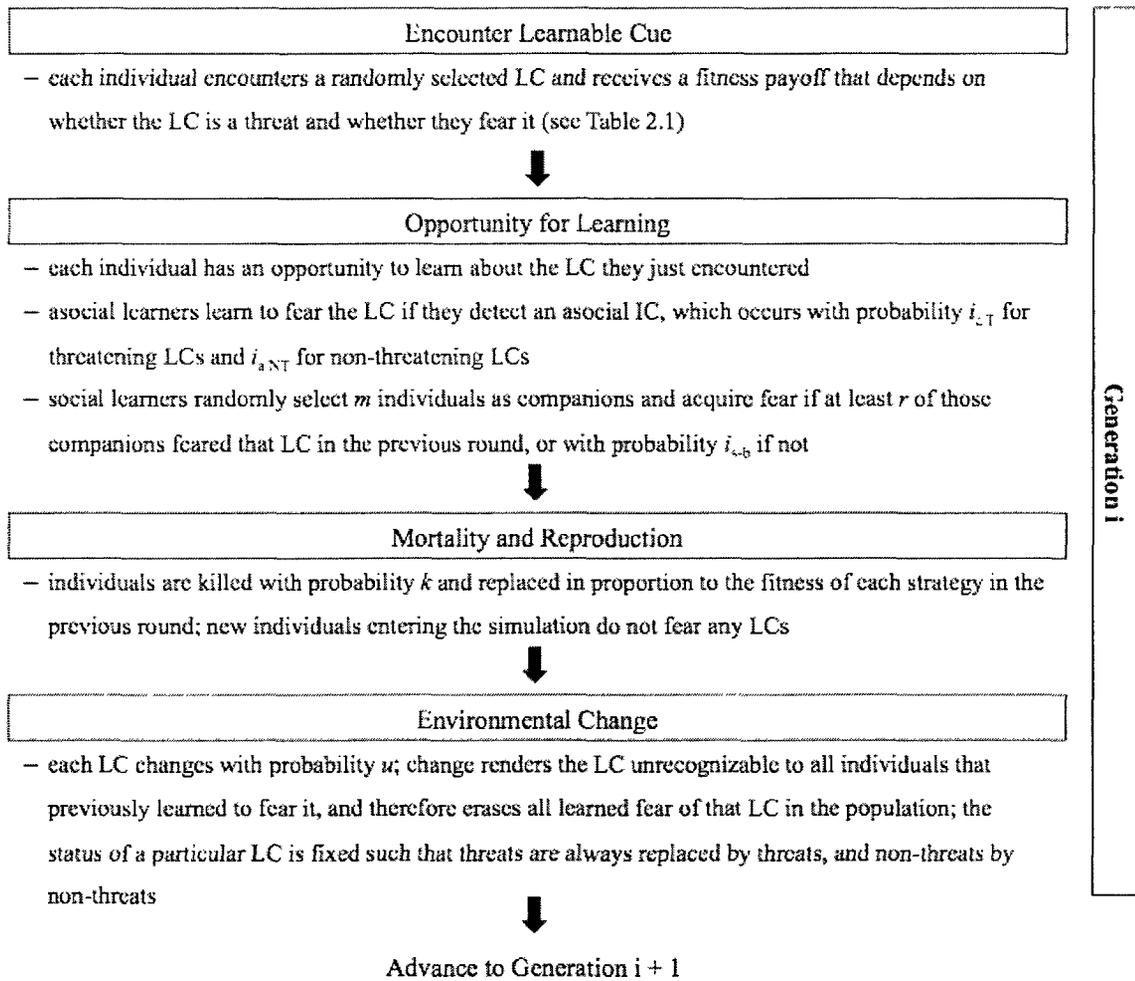


Figure 2.1 Overview of the algorithm used to simulate the evolution of learned recognition of predation risk.

Table 2.2 Description of model parameters. Parentheses indicate parameter values that I systematically varied, and boldface indicates default parameter values.

Parameter	Description	Value(s)
n	population size	3,000
l	number of learnable cues	10
T	proportion of learnable cues that represent a threat	(0.2, 0.4 , 0.6)
W_{FIT}	fitness payoff for fearing a threat	-10
W_{NFIT}	fitness payoff for not fearing a threat	-40
W_{FINT}	fitness payoff for fearing a non-threat	(0, -5 , -9)
W_{NFINT}	fitness payoff for not fearing a non-threat	0
$i_{A T}$	probability of asocial indicator given threat	0.6
$i_{A NT}$	probability of asocial indicator given non-threat	0.01
i_S	probability of social indicator	1 or i_{s-b}
i_{S-B}	baseline probability of inadvertent social indicator	(0.00, 0.05 , 0.10)
u	rate of environmental change	0.01
k	mortality rate	0.2
m	number of models available to social learners	1, 5, 10
r	threshold # of fearful models required for learning	1
g	number of simulated generations	10,000

Results and Discussion

My model demonstrates that in a population of asocial learners, an initially rare allele for either pure or mixed social learning can increase in frequency, even to fixation, under a range of conditions (Figures 2.2, 2.3, and 2.4). This finding contrasts with the common theoretical prediction that social learners can never completely replace asocial learners due to the negative frequency dependence of social learning (Pruett-Jones 1992, Boyd and Richerson 1985, Giraldeau and Caraco 2000). I suggest that this novel finding – that is, a frequency independent fitness advantage to social learners – relates to unique properties of predator recognition learning that might not be consistent with other types of social learning; particularly, the independence of learners and cues involved in learning, and the ability of social learners to produce social ICs indicative of predation risk in the absence of asocial learners, as discussed below.

In all of the simulations that I performed, the mean fitness of mixed social learners was greater than or equal to the mean fitness of asocial learners for at least 10,000 generations. In contrast, pure social learners occasionally had lower fitness than asocial learners, and even went extinct under a number of conditions (e.g. panels a-c in Figures 2.2, 2.3, and 2.4). In particular, pure social learners went extinct in all of the simulations where the number of models available to them was minimal (i.e. $m = 1$). When $m = 1$, pure social learners can only learn from a single randomly selected model (e.g. a social companion). When this occurs, the social transmission of fear is ‘unbiased’ given that pure social learners will learn to fear cues in direct proportion to the number of potential models already fearing those cues (e.g. Kendal et al. 2009a). Ignoring inadvertent social ICs, unbiased transmission means that in a given generation, the

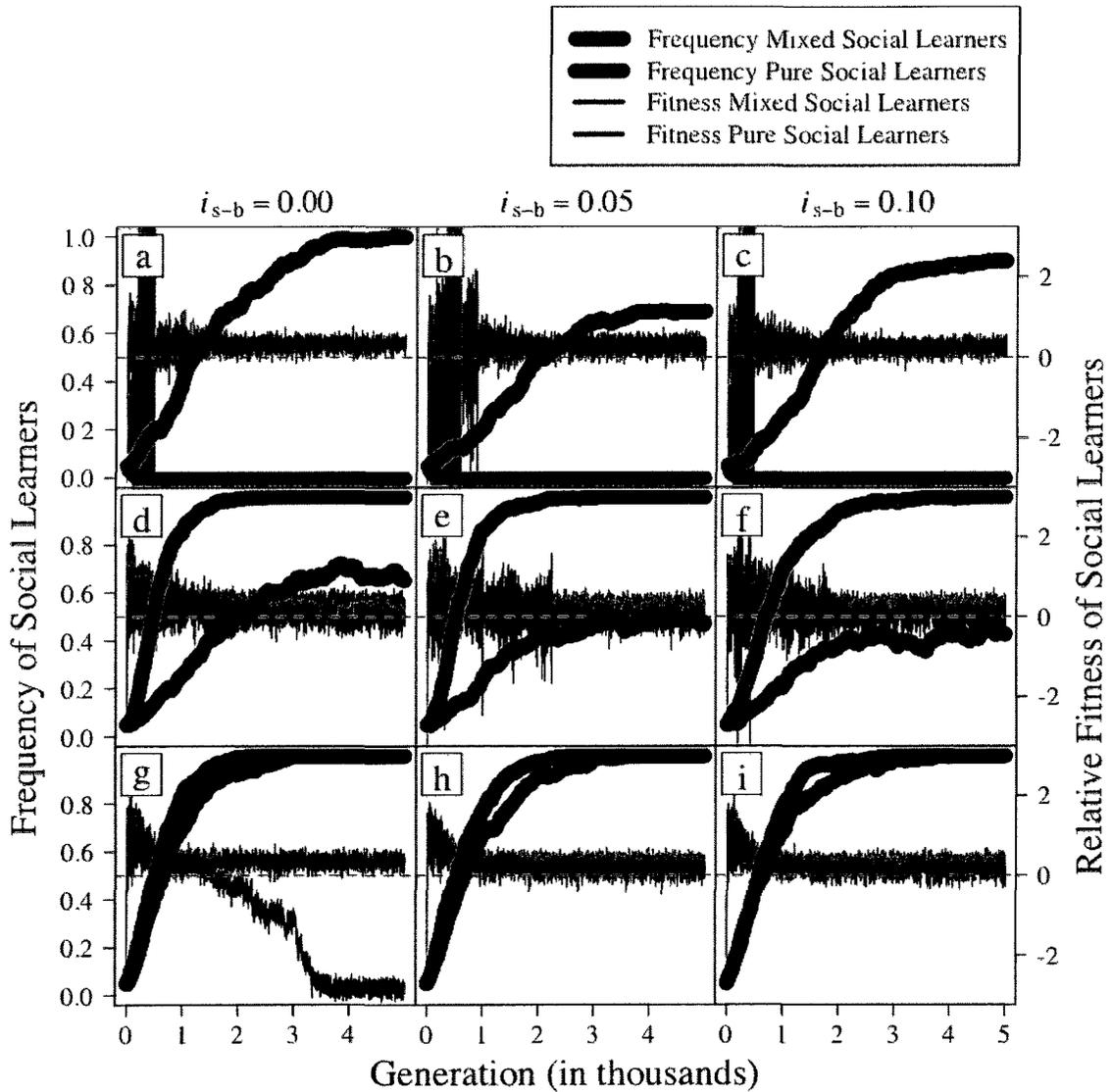


Figure 2.2 Simulated changes in the frequency (thick lines; primary y-axis) and relative fitness (thin lines; secondary y-axis) of an initially rare mixed (blue) or pure (red) social learning strategy when played against a pure asocial learning strategy. Points greater than zero on the secondary y-axis indicate a fitness advantage to social learners, whereas points below zero indicate a fitness advantage to asocial learners. Parameters varied in these simulations included the number of models available to social learners ($m = 1$ in panels a-c, $m = 5$ in panels d-f, $m = 10$ in panels g-i), and the baseline probability of inadvertent social indicators (i_{s-B}). All other parameter values are specified in Table 2.2. The depicted data represent mean values from 10 replicate simulations.

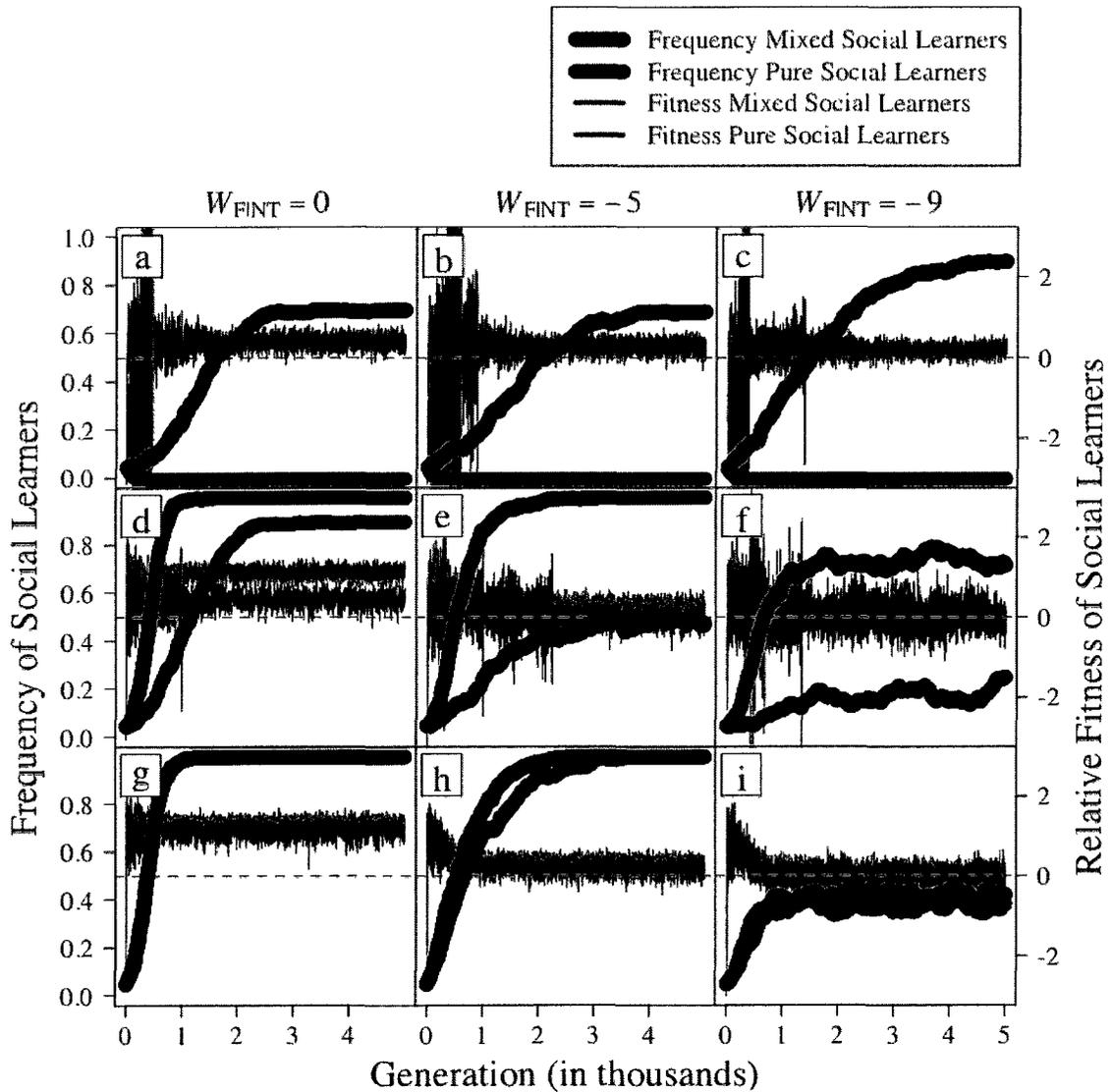


Figure 2.3 Simulated changes in the frequency (thick lines; primary y-axis) and relative fitness (thin lines; secondary y-axis) of an initially rare mixed (blue) or pure (red) social learning strategy when played against a pure asocial learning strategy. Points greater than zero on the secondary y-axis indicate a fitness advantage to social learners, whereas points below zero indicate a fitness advantage to asocial learners. Parameters varied in these simulations included the number of models available to social learners ($m = 1$ in panels a-c, $m = 5$ in panels d-f, $m = 10$ in panels g-i), and the fitness payoff for fear given a non-threat (W_{FINT}). All other parameter values are specified in Table 2.2. The depicted data represent mean values from 10 replicate simulations.

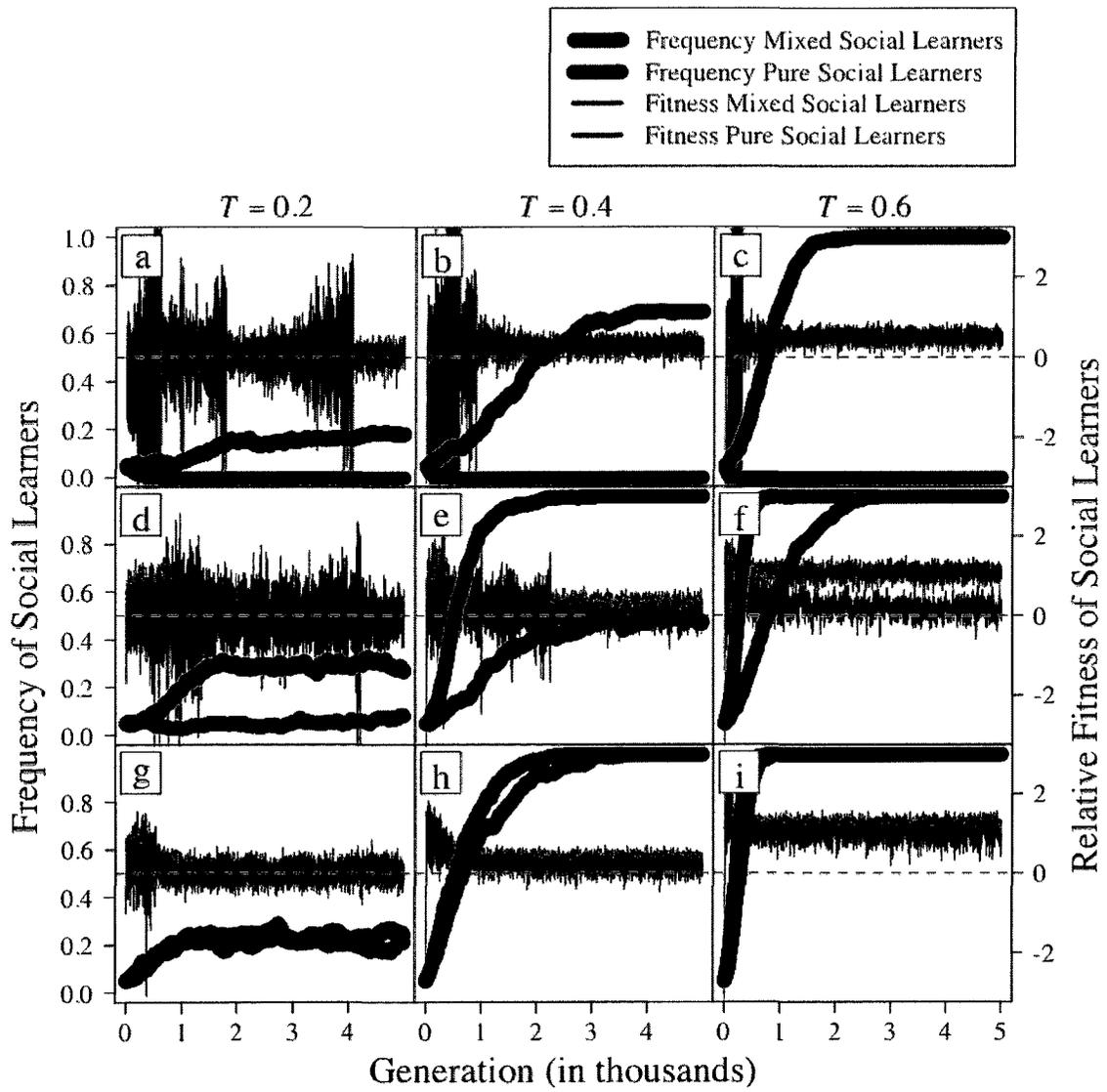


Figure 2.4 Simulated changes in the frequency (thick lines; primary y-axis) and relative fitness (thin lines; secondary y-axis) of an initially rare mixed (blue) or pure (red) social learning strategy when played against a pure asocial learning strategy. Points greater than zero on the secondary y-axis indicate a fitness advantage to social learners, whereas points below zero indicate a fitness advantage to asocial learners. Parameters varied in these simulations included the number of models available to social learners ($m = 1$ in panels a-c, $m = 5$ in panels d-f, $m = 10$ in panels g-i), and the proportion of learnable cues that are a threat (T). All other parameter values are specified in Table 2.2. The depicted data represent mean values from 10 replicate simulations.

proportion of pure social learners that fear a LC cannot exceed the proportion of asocial learners fearing that same LC (e.g. Enquist et al. 2010). In my simulations (and presumably in nature), the relative payoff for fearing a threat was greater than the relative payoff for not-fearing a non-threat (i.e. not fearing a threat, a type II error, was more costly than fearing a non-threat, a type I error). Therefore, when $m = 1$, despite making fewer type I errors, pure social learners were disadvantaged compared to asocial learners because they were always less likely to respond correctly when facing a threat. It is possible that a higher cost of type I errors or a higher probability of inadvertent social ICs could outweigh the learning disadvantage faced by pure social learners when $m = 1$; however, this possibility was not fully explored in the current study.

In my analysis, negative frequency dependence occurred under a number of conditions. In particular, when the baseline probability of an inadvertent social IC was set to $i_{S-B} = 0$, somewhat paradoxically, an allele for pure social learning became fixed despite strong negative frequency dependence that resulted in pure social learners having lower fitness than asocial learners following fixation (Figure 2.2g). This drop in fitness following the loss of asocial learners occurred because environmental change eventually rendered all socially learned information obsolete, and social learners therefore lost all fear of all LCs (e.g. Figure 2.5). Without asocial learners or inadvertent social ICs, pure social learners cannot track environmental change. Because environmental change occurred infrequently in the above-described simulation, social learners were able to maintain higher fitness than asocial learners right up until a few generations following fixation of the pure social learning allele. Presumably, a higher rate of environmental

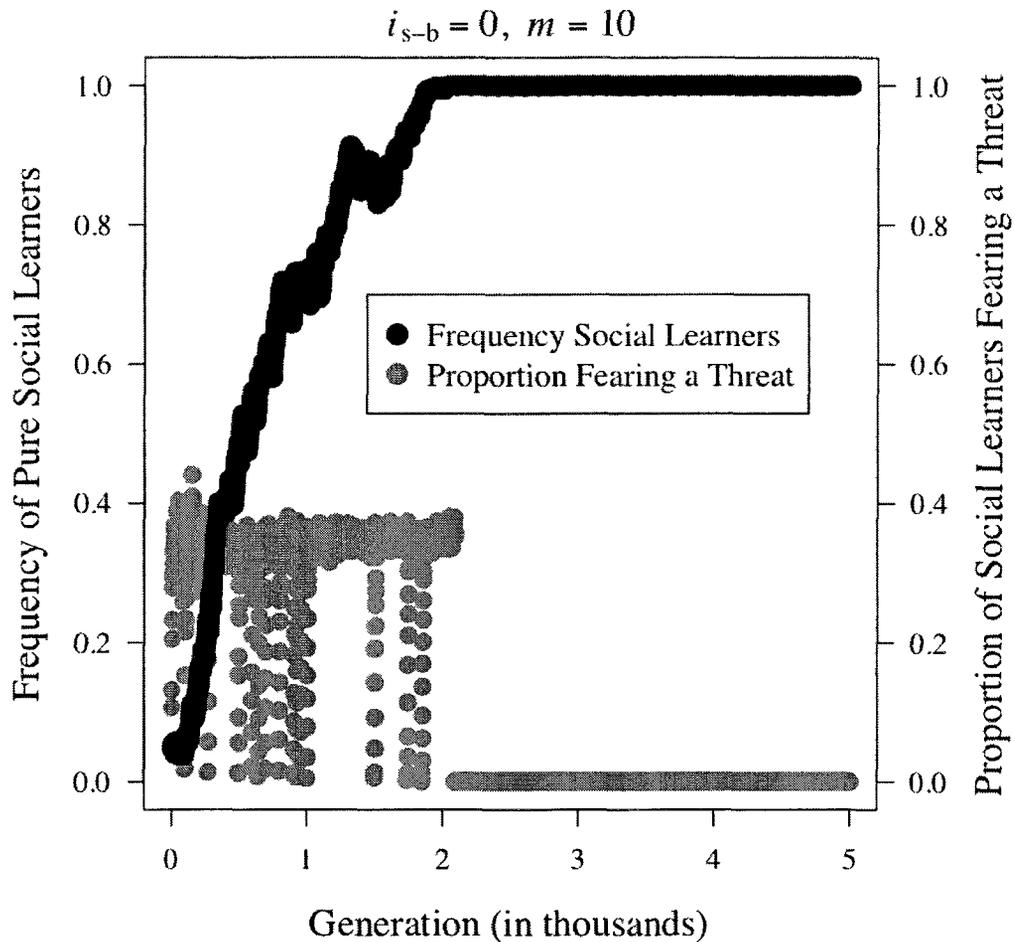


Figure 2.5 Example of changes in the proportion of pure social learners fearing a threat following the fixation of an allele for pure social learning at Generation = 2009. In this simulation (corresponding to the simulations depicted in Figure 2.2g), the baseline probability of inadvertent social indicators was set to $i_{s-B} = 0$, and the number of models available to social learners was $m = 10$. All other parameter values are specified in Table 2.2.

change would have prevented fixation of pure social learning alleles when $i_{S-B} = 0$, but this possibility was not explored in the current study.

Negative frequency dependence also occurred to a lesser extent in many conditions when i_{S-B} was > 0 , for both mixed and pure social learners (e.g. when $m = 10$; panels g-i in Figures 2.2, 2.3, and 2.4). In these cases, as the proportion of either type of social learner increased, the likelihood of social learners fearing a non-threat also increased (e.g. Figure 2.6). This frequency dependent increase in the likelihood of social learners fearing a non-threat was due to the baseline probability of inadvertent social ICs (i_{S-B}) being greater than the probability of asocial ICs given a non-threat ($i_{A|NT}$), meaning that independent of their respective frequencies, social learners were always more likely than asocial learners to fear non-threats (except when $i_{S-B} = 0$, and negative frequency dependence occurred for different reasons, as described above). Because social learners copy the fear of others, the likelihood of social learners fearing a non-threat increased with the frequency of social learners for both the mixed and pure strategies. Note that the only time that the above-described effect did not result in negative frequency dependence was when there was no cost to fearing a non-threat (Figure 2.3g).

The socially learned recognition of predation risk appears to be somewhat distinct from other types of social learning. In particular, the challenge in learning about risk is not so much that acquiring accurate information is costly, but rather that the most abundant form of information available (i.e. social information) is potentially the least reliable form (Beauchamp and Ruxton 2007, Barrera et al. 2011). In the simulations that I conducted, successful learning strategies were almost always the ones that resulted in the most rapid acquisition of fear, even though individuals playing these successful

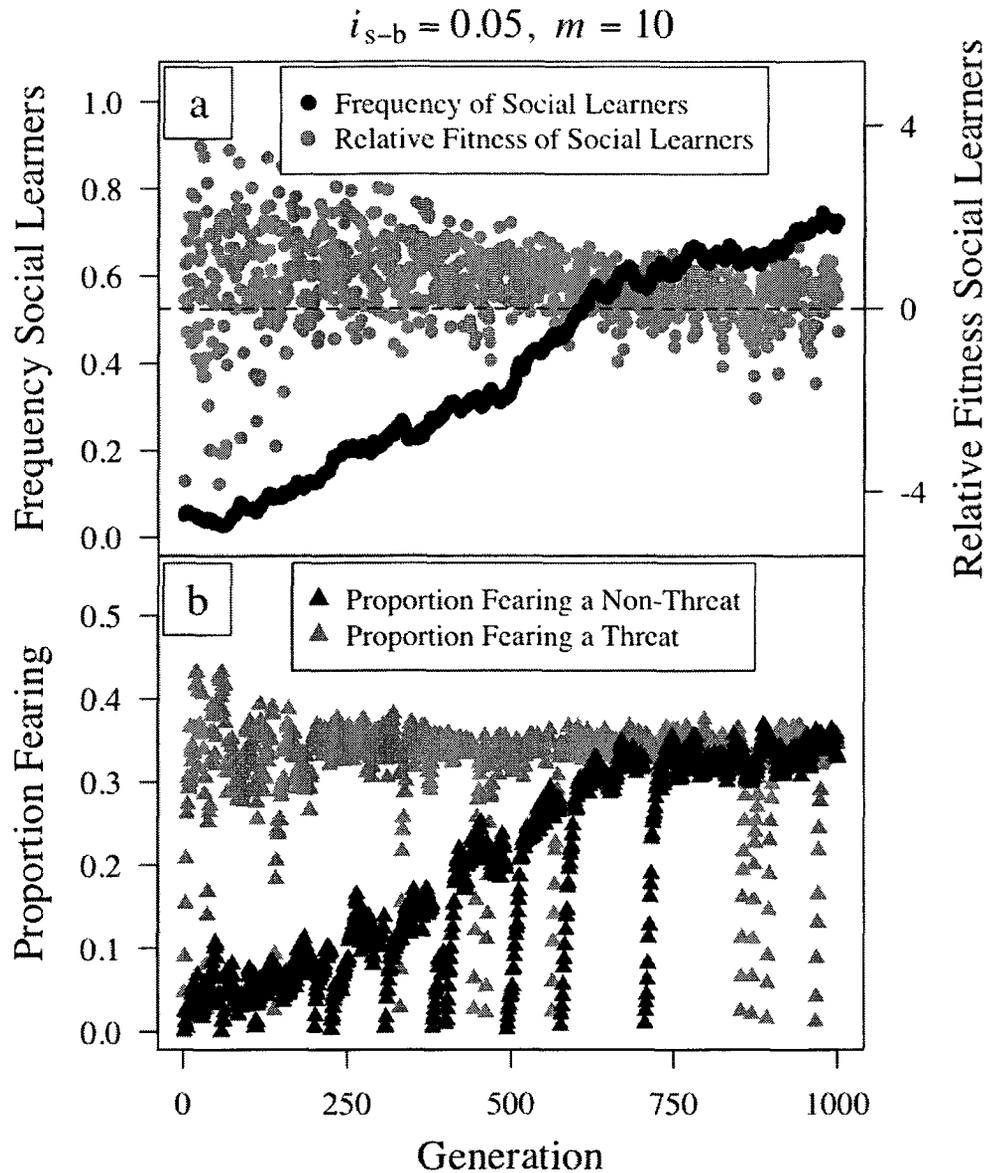


Figure 2.6 Example of changes in the proportion of pure social learners fearing a threat and non-threat (panel b) as the frequency of social learners increases and their relative fitness decreases (panel a). Note that points greater than zero on the secondary y-axis (panel a) indicate a fitness advantage to pure social learners, whereas points below zero indicate a fitness advantage to pure asocial learners. In this simulation (corresponding to the simulations depicted in Figure 2.2h), the baseline probability of inadvertent social indicators was set to $i_{s-B} = 0.05$, and the number of models available to social learners was $m = 10$. All other parameter values are specified in Table 2.2.

strategies were often more likely to develop a fear of non-threats. This makes sense given the relatively low cost of fearing a non-threat (type I error) compared to not fearing a threat (type II error). However, the range of parameter space that I explored was quite small, and it is possible that the fitness costs of type I errors might have a greater influence on evolutionary dynamics under some conditions. For example, when the proportion of threatening LCs was much lower than the proportion of non-threatening LCs, the relative importance of not-fearing a non-threat increased and the fitness of pure and mixed social learners therefore decreased (Figure 2.4). Even though the cost of failing to avoid a predator is high relative to the time and energy wasted in mistakenly avoiding a non-predator, the fitness advantage of risk-aversion will clearly depend on the probability of encountering predators (Sih 1992).

Although many theoretical analyses of social learning have assumed that social and asocial learning are mutually exclusive (e.g. Richerson and Boyd 1965, Rogers 1988, Rendell et al. 2010), this assumption does not make sense in the context of learning about predation risk, given that opportunities for each type of learning may arise at different times. In understanding the evolution of social learning about risk, it is therefore more pertinent to ask when a mixed asocial and social learning strategy could be favoured over a pure asocial strategy, as I have done here. Unlike social learners in other analyses, the mixed social learners that I modeled could have higher fitness than asocial learners even at a frequency of 1. This was possible because mixed social learners could still produce information in the absence of asocial learners. In the context of learning about predation risk, even pure social learners may be able to produce information in the form of ‘inadvertent’ social ICs. It is therefore theoretically possible for the fitness of pure social

learners to exceed that of pure asocial learners, independent of their respective frequencies (assuming $i_{S-B} > 0$; e.g. Figures 2.3g, 2.4i).

In conclusion, my theoretical analysis has demonstrated that the socially learned recognition of predation risk can evolve, even to fixation, under a range of conditions. Social learning about predation risk may be fundamentally different from other types of social learning, especially if the detection of LCs and ICs is truly independent of learners as I have assumed here. Although this assumption will be difficult to test empirically, I contend that in the context of learning about risk, the independence of learners and the cues involved in learning more accurately reflects reality than an assumption of complete dependence. I suggest that future research should further explore the conditions under which socially learned recognition of predation risk (and non-risk) might evolve, potentially within an analytical framework. Further exploration of this theory will hopefully lead to testable predictions regarding, for example, relationships between the frequency of social learning and the frequency of inadvertent social ICs, the ratio of predators to non-predators in the environment, or rates of environmental change.

Chapter 3

Testing for socially learned recognition of risk and non-risk in juvenile convict cichlids (*Amatitlania siquia*)

Abstract

For many animals, the ability to recognize cues from potential predators is not entirely innate, but rather is learned and improved with experience. Such learning may entail increases in antipredator behaviour toward cues that are learned to be indicative of predation risk (= learned recognition of risk), or decreases in antipredator behaviour toward cues that are learned to be safe (= learned recognition of non-risk). These two forms of learning appear to be mechanistically distinct; that is, increases in antipredator behaviour with experience tend to occur via associative social learning, whereas decreases in antipredator behaviour occur via habituation, a form of non-associative asocial learning. Here I tested whether animals can acquire a learned recognition of both risk and non-risk via associative social learning. I exposed juvenile convict cichlids (*Amatitlania siquia*) simultaneously to a novel visual cue and a social cue indicative of either risk or non-risk, or a control treatment with no social cue. Cichlids conditioned with the paired novel cue and social cue indicative of risk subsequently expressed slightly increased antipredator behaviour toward the novel cue compared to cichlids in the other two conditioning treatments. However, I found no difference in subsequent response to the novel cue between cichlids conditioned with a social cue indicative of non-risk and those conditioned without a social cue. These results indicate that juvenile convict cichlids in this study may have acquired a recognition of risk, but not non-risk, via associative social learning.

Introduction

Avoiding predators, though clearly fitness-enhancing, may entail an opportunity cost in that time and energy spent on antipredator behavior cannot be spent on other activities such as foraging and mating (Ydenberg and Dill 1986, Lima and Dill 1990, Godin 1997, Lima 1998). Assuming such a cost, selection should favour mechanisms allowing animals to selectively express antipredator behaviour during only those periods in which there is a genuine risk of predation (Sih 1992, Lima and Bednekoff 1999). This selectivity would first require that animals have the ability to assess predation risk; particularly, to recognize and distinguish between cues indicative of risk and cues unrelated to predation risk.

The ability to distinguish predators from non-predators can be innate (Veen et al. 2000, Hawkins et al. 2007), learned (Berger et al. 2001, Leduc et al. 2007), or some combination of the two (Magurran 1990, Epp and Gabor 2008). Owing to the variable nature and degree of predation risk over multiple spatial and temporal scales (Werner and Gilliam 1984, Lima and Bednekoff 1999), innate recognition abilities are not likely to be advantageous in all circumstances. For example, a population that relies entirely on innate predator recognition might fare poorly against a novel invasive predator given the relatively long time required for mutation and selection to act on genetically determined traits. In contrast to innate recognition abilities, the ability to learn about predators entails flexibility and may allow individuals to adaptively adjust antipredator behaviour to changing local conditions in a much shorter time frame (Kieffer and Colgan 1992, Mery and Burns 2010). Learning may therefore improve the ability of individuals to

effectively mediate the trade-off between avoiding predation and participating in other fitness-enhancing activities.

There is a continuum of potential approaches by which animals may learn to distinguish cues indicative of risk from those unrelated to risk. For illustrative purposes, I consider two extremes. First, an animal might initially express intense antipredator behaviour toward all cues of a certain type and subsequently learn which cues are not indicative of risk (= learned recognition of non-risk; e.g. Csanyi 1985). Alternatively, an individual might initially express zero antipredator behaviour toward all cues of a certain type and allow experience to dictate which cues *are* indicative of risk (= learned recognition of risk; e.g. Mirza et al. 2006). In reality, I suggest that animals are likely to express intermediate antipredator behaviour toward a wide range of novel cues, and use both the learned recognition of risk and non-risk to distinguish threat from non-threat.

Learned recognition of risk occurs when an individual expresses increased antipredator behaviour toward a particular cue (a learnable cue, LC) after experiencing that cue concurrently with another cue that is known to be indicative of risk (an indicator, IC). This type of learning is referred to as ‘associative learning’ given that learning appears to depend on an association between two cues (Griffin 2004). Although an IC may derive either from a predator or from a social companion (or some combination of the two), the vast majority of studies on learned recognition of risk have focused exclusively on ICs deriving from social companions and therefore the socially learned recognition of risk (reviewed in Kelley and Magurran 2003, Griffin 2004).

Socially learned recognition of risk appears to be widespread throughout the animal kingdom and has been demonstrated via both laboratory experiments and

experimental manipulation under natural conditions (see Appendix Table A.1). This type of learning is efficient given that it often occurs with a single pairing of the LC and IC (Griffin 2004), and general given that learning may involve virtually any combination of sensory modalities (Vieth et al. 1980, Suboski et al. 1990, Chivers and Smith 1994, Arai et al. 2007, Wisenden et al. 2008). The high degree of efficiency and generality characterizing socially learned recognition of risk has led some authors to speculate about the potential for animals to learn to fear cues that are unrelated to predation risk – a type I error in statistical terminology (Hazlett 2003, Ferrari and Chivers 2011, Mitchell et al. 2011). Such errors are common under controlled laboratory conditions, where animals have been conditioned to fear cues such as red lights (Yunker et al. 1999), artificial noises (Wisenden et al. 2008), Plexiglas boxes (Cook and Mineka 1987), synthetic chemicals (Suboski et al. 1990), plastic disks (Wisenden and Harter 2001), stuffed animals (Mineka et al. 1984), and live non-predators (Chivers and Smith 1994). However, it is currently unknown whether similar learning errors occur under natural conditions.

In contrast to the associative learning paradigm involved in learned recognition of risk, the learned recognition of non-risk tends to occur via habituation, a form of non-associative asocial learning, entailing a decrease in antipredator behaviour toward once-novel cues with repeat exposure (e.g. Csanyi 1985, Huntingford and Coulter 1989, Deecke et al. 2002, Stankowich and Blumstein 2005, Hemmi and Merkle 2009, Vennesland 2010). For example, Csanyi (1985) found that paradise fish (*Macropodus opercularis*) exhibited inspection and aggressive behaviours toward satiated northern pike (*Esox lucius*) in an initial staged encounter, but that this response consistently

declined throughout five subsequent encounters. This finding raises two interesting issues. First, habituation in this example would seem to be locally maladaptive given that the northern pike in this experiment could and sometimes did prey upon paradise fish. Although these two species do not co-occur, is it possible that animals might learn not to fear cues that are genuinely indicative of risk (a type II error in statistical terminology) in their natural environment? Another interesting finding from Csanyi (1985) is that, unlike the relatively instantaneous learning involved in socially learned recognition of risk (e.g. Mirza et al. 2006), habituation by paradise fish to the northern pike occurred progressively over the course of five 5-min trials. Presumably, this difference in the speed of learning asocially about non-risk versus learning socially about risk relates to the reliability of the cues involved and the relative cost of making a type I error versus a type II error. For example, detecting a LC (e.g. the sight of a northern pike) in the absence of an IC is not necessarily a reliable indicator of non-risk, and failing to avoid an actual threat is probably more costly than mistakenly avoiding a non-threat. The asymmetry in cue reliability and relative cost of mistakes may explain why learning about non-risk appears to occur more gradually than learning about risk. However, to my knowledge, this possibility remains unexplored.

Despite the potential asymmetry in cost of mistakes and cue reliability between learning about non-risk and learning about risk, given that non-associative learning via habituation is relatively inefficient compared to the single-trial associative learning process characterizing the learned recognition of risk, I suggest that some animals might possess an ability to learn about non-risk via associative learning. The associative learning of non-risk would require an IC that is reliably indicative of non-risk – an IC that

is only likely to be detected during periods of relatively low predation risk. One such IC might be the sight of active or actively foraging conspecifics. Reductions in activity and foraging rates are common antipredator responses in a variety of species (reviewed in Lima and Dill 1990). Furthermore, in some species, the sight of active or actively foraging conspecifics can facilitate activity and foraging in nearby observers (Ryer and Olla 1991), just as the sight of conspecific alarm responses can facilitate alarm responses in nearby observers (Magurran and Higham 1988, Cordi et al. 2005). Therefore, the sight of active or actively foraging conspecifics may be reliably indicative of a relative lack of local predation risk.

The objective of the current study was to test for learned recognition of both risk and non-risk via associative social learning. Specifically, I tested the hypotheses that individuals simultaneously presented with a novel object (= LC) and a social cue indicative of either risk or non-risk (= IC) would subsequently express increased or decreased antipredator behaviour toward the novel object, respectively. To test these hypotheses, I conducted a laboratory experiment using juvenile convict cichlids (*Amatitlania siquia*), a freshwater species native to streams and lakes of Central America. Juvenile convict cichlids are known to exhibit decreased activity and foraging rates in response to predation risk (Wisenden and Sargent 1997, Brown et al. 2006), and have the ability to learn about novel objects via habituation (*pers. observation*). I was therefore able to generate social ICs indicative of risk (demonstrators trained to decrease activity and foraging rates in response to a novel object) and social ICs indicative of non-risk (demonstrators trained via habituation to maintain high activity and foraging rates in response to a novel object). Although the antipredator behaviour of convict cichlids has

been previously documented (e.g. Lavery and Colgan 1991, Alemadi and Wisenden 2002, Brown et al. 2004, Foam et al. 2005, Pollock et al. 2005, Ferrari et al. 2008b), to my knowledge, the current study is the first one testing for learned recognition of risk in this species and for learned recognition of non-risk via associative learning in any animal species.

Methods

Test Subjects

My experimental subjects were juvenile (range in age: 4-14 months; total length: 31-58 mm) convict cichlids from a laboratory population housed at Carleton University (Ottawa, Canada) that was originally derived from wild adults collected in the Rio Cabuyo, Costa Rica. Broods were taken from their parents approximately one month after hatching and transferred to 80 l stock aquaria (2-5 broods per aquarium) containing continuously filtered tap water (24-26°C), a gravel substrate, an artificial plant, and a flowerpot refuge. The aquaria were exposed to overhead fluorescent lighting on a 13 h L : 11 h D cycle. Cichlids were fed ad libitum twice per day, once with frozen brine shrimp or live brine shrimp nauplii and once with crushed commercial food granules (Tetra Cichlid Mini Granules, Tetra Holding Inc., Blacksburg, VA), and were maintained in the same stock aquaria until the time of testing.

Experimental Protocol

Overview

Each experimental trial spanned three consecutive days and was divided into three phases: training, conditioning, and recognition. In the initial training phase (Day 1), groups of ‘demonstrator’ cichlids were either habituated to, or trained to fear, one of two novel objects (object A or object B; see Figure 3.1). Subsequently, in the conditioning phase (Day 2), groups of ‘observer’ cichlids were simultaneously exposed to one of the two novel objects (object A or object B) and one of three social cues or treatments (habituated demonstrators, no demonstrators, or fearful demonstrators), and were thus given an opportunity to form a learned association between a novel object and a social cue. Finally, in the recognition phase (Day 3), I quantified the behavioural response of the same groups of observers when exposed to a novel object alone (always object B) to determine whether observers learned about the novel object during the previous conditioning phase. For each of the six treatment \times object combinations, I conducted a total of 15 replicate trials over a four-month period, yielding a total sample size of 90.

For both demonstrators and observers, each group (the experimental unit) comprised four size-matched individuals. I chose to make the experimental unit a group of four individuals because pilot studies suggested that individuals or groups of fewer than four individuals were likely to remain motionless and under shelter for the duration of the trial, which would make it difficult to assess their response to a novel object. Similar effects of group size on activity budgets and foraging rates are commonly documented in the behavioural literature (e.g. Pitcher and Parrish 1993, Beauchamp 1998, Krause and Ruxton 2002). My use of groups as an experimental unit necessitates the assumption that learning, a property of individuals, can be understood in terms of the average behaviour expressed by a group of individuals.

Object A

Object B

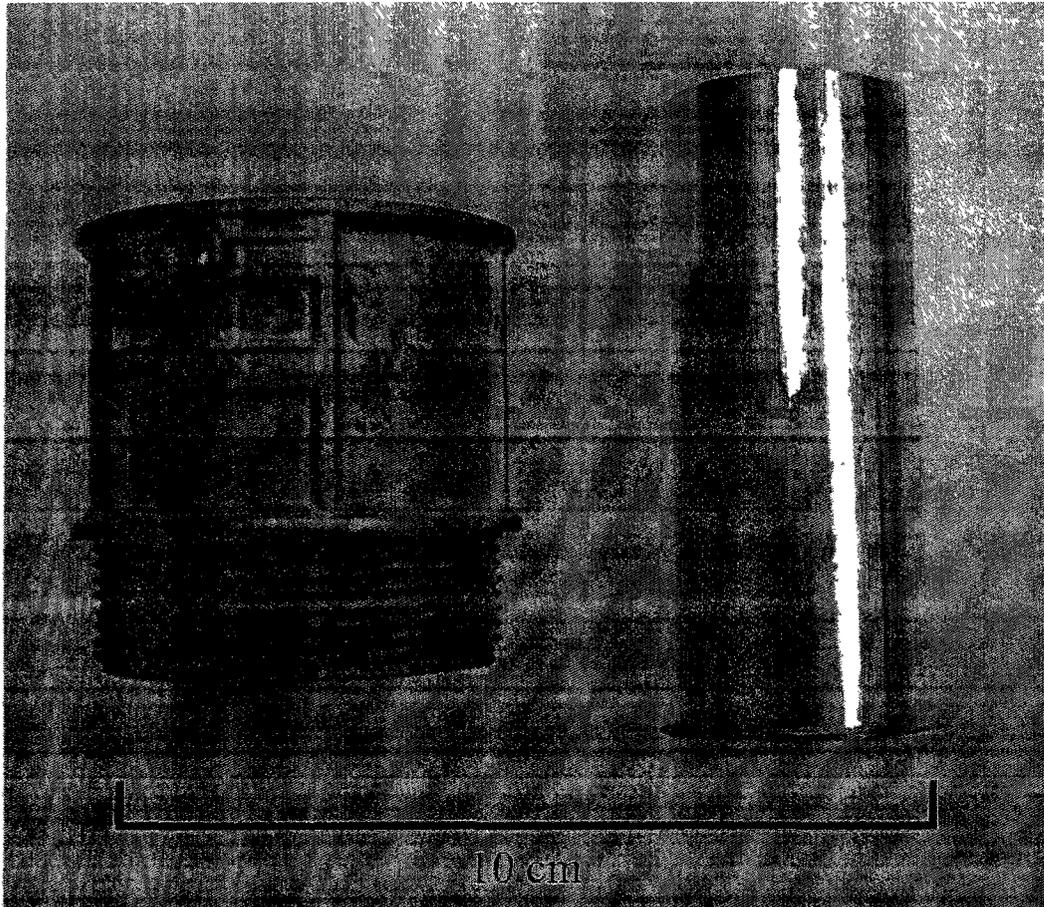


Figure 3.1 The two novel objects used in the current study. Object A was an 8×6 cm steel cylinder (EMT Set Screw Connector, Model BC-5016, Thomas and Betts Corporation, Memphis, TN) and object B was a 10×4 cm brass cylinder (Rough Brass Sink Tailpiece, Model R-812-4RB, Oakville Stamping and Bending, Oakville, ON).

Apparatus

The experimental apparatus consisted of two adjacent 20 l aquaria – one for demonstrators and the other for observers (Figure 3.2). Both aquaria contained a gravel substrate, a heater, an air-stone, and a shelter constructed by affixing three 20 ml scintillation vials (the legs of the shelter) to an 8 × 15 cm sheet of white Plexiglas (the roof of the shelter) using aquarium silicone. The demonstrator aquarium also contained a remotely moveable opaque Plexiglas partition that divided the aquarium into a large compartment for the demonstrators and a smaller compartment where the novel object was placed (see Figure 3.2). Two additional opaque partitions separated the demonstrator aquarium from the observer aquarium. The longer partition completely separated the two aquaria, whereas a second shorter partition was just long enough to prevent observers from seeing into the smaller compartment of the demonstrator aquarium that contained the novel object. Each of the partitions could be remotely removed and replaced at different points throughout the experiment, as explained below.

Each test aquarium also contained a number of items that were present for only certain portions of the experiment (as described in the following subsections), including a novel object opposite the shelter and a microscope slide covered with crushed commercial food granules affixed to the slide via a thin coating of gelatin. This food was the same as that fed to the cichlids in their holding aquaria. Food slides were placed atop the substrate and leaning up against the front glass pane of the aquarium. Novel object A was an 8 × 6 cm steel cylinder (EMT Set Screw Connector, Model BC-5016, Thomas and Betts Corporation, Memphis, TN) and novel object B was a 10 × 4 cm brass cylinder (Rough Brass Sink Tailpiece, Model R-812-4RB, Oakville Stamping and Bending,

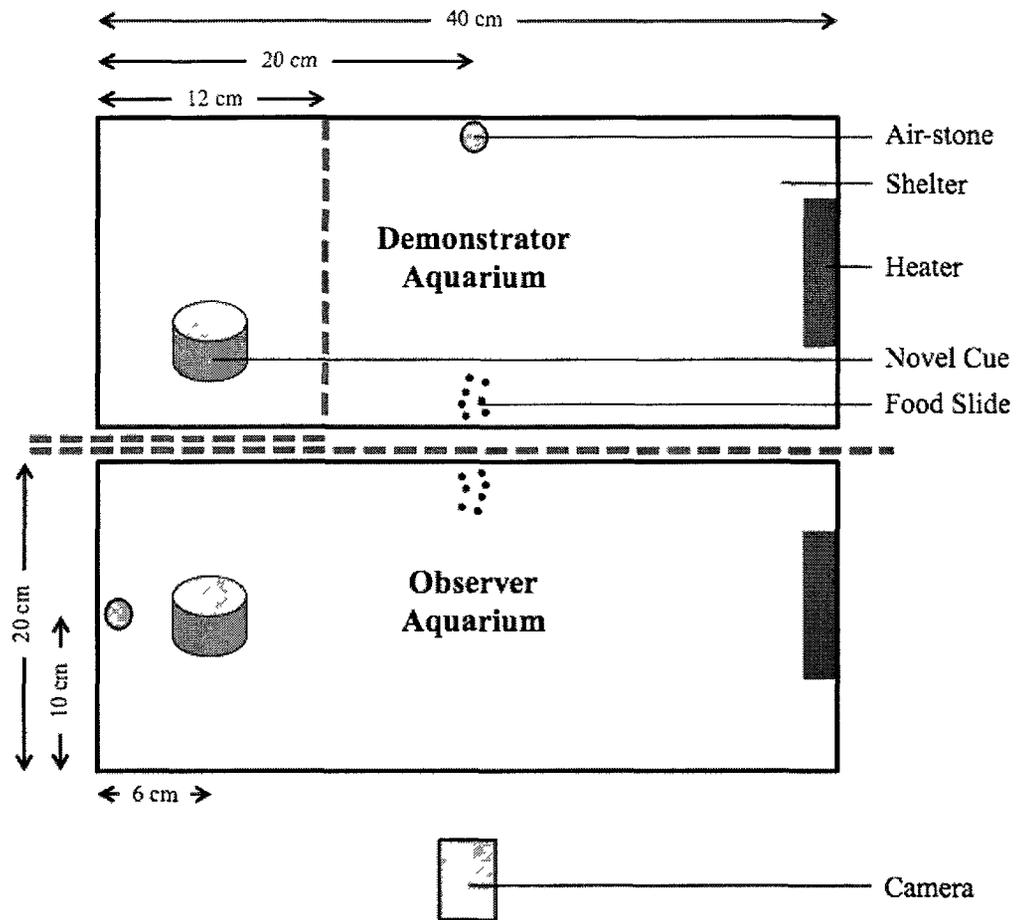


Figure 3.2 Top-view schematic representation of the experimental apparatus. The dashed lines represent three opaque partitions that were each remotely removed at different points during an experimental trial, as described in the text. Likewise, the novel objects and food slides were added to and removed from the apparatus as described in the text. The roof of the artificial shelter was approximately 5 cm above the substrate, and was supported by legs (20-ml glass scintillation vials) that were 6 cm in height and slightly buried into the substrate. Both aquaria were 25 cm deep and filled with approximately 20 l of aged, dechlorinated water maintained at 24-26°C.

Oakville, ON) (Figure 3.1). The objects were chosen arbitrarily with the intention that they would be entirely novel to the cichlids, and be similar enough to illicit equivalent behavioural responses but different enough to prevent a learned generalization from one object to the other (e.g. Griffin et al. 2001, Ferrari et al. 2007).

Acclimatization

The day before experimental trials began, groups of observers and demonstrators were transferred from stock aquaria into their respective test aquaria (assignment was randomized with respect to treatment and novel object) between 16:00 and 19:00 hrs and left undisturbed to acclimatize overnight. The following morning (Day 1 of the experiment), a single food slide was placed into each experimental aquarium between 09:00 and 11:00 hrs. All experimental cichlids were accustomed to foraging from a gelatin-coated food slide, as similar slides were regularly placed in the stock aquaria. Throughout the acclimatization phase of the experiment, demonstrators and observers remained visually isolated from each other as an opaque partition was placed between their respective aquaria. Demonstrators were also visually isolated from the novel object (located behind an opaque partition; see Figure 3.2) in their aquarium, and the observer aquarium lacked a novel object until the recognition phase on Day 3.

For a given trial, all four individuals within a test aquarium (i.e. all four observers or all four demonstrators) were taken from the same stock aquarium, but demonstrators and observers within a given trial were always from different stock aquaria. Therefore, individuals were always familiar with and possibly akin to the other individuals in the same test aquarium, but were never familiar with the individuals in the adjacent

aquarium. This process of ensuring demonstrators and observers came from different stock aquaria was done to prevent the potential confounding effects of prior social familiarity on behaviour (e.g. Chivers et al. 1995, Wiley et al. 1999). I chose to make demonstrators and observers unfamiliar rather than familiar with each other because it would have occasionally been impossible to obtain eight size-matched individuals from the same stock aquarium. The selection and size-matching of experimental subjects from stock aquaria was performed haphazardly and without actually measuring the fish prior to experimentation to minimize stress (fish were measured at the end of each experimental trial).

Training Phase [Demonstrators Only]

The purpose of the training phase was to generate groups of demonstrators that would respond in one of two manners to a novel object (half were trained with object A and the other half with object B). Demonstrators in the ‘habituated’ treatment were trained not to respond to the novel object, potentially indicating to observers that the object was safe, whereas ‘fearful’ demonstrators were trained to exhibit an avoidance or antipredator response (as reflected in a reduction in activity and foraging rate, and movement away from the object and toward shelter) when the object was presented, potentially indicating to observers that the novel object represented a threat. The third treatment was a control with no demonstrators present and therefore no training.

The training phase comprised three separate training sessions conducted between 15:00-17:00 hrs on Day 1, 08:00-10:00 hrs on Day 2, and 11:00-13:00 hrs on Day 2, respectively. Demonstrators and observers remained visually isolated throughout the

training phase via the same opaque partitions previously described. To train demonstrators in the habituated treatment, I remotely raised the opaque partition previously separating them from the novel object in their test aquarium, and then left the demonstrators alone until one hour prior to the beginning of the next session, at which time the partition was gently replaced. I did not account for which side of the aquarium the demonstrators were in when the partition was replaced, except after the final training sessions when I ensured that all demonstrators were in the larger compartment (occasionally this required gentle coaxing with the partition). The total time that habituated demonstrators were exposed to the novel object was approximately 20 h, 55% of which was at night.

To train demonstrators in the fearful treatment, I remotely raised the opaque partition separating them from the novel object and then repeatedly passed a dipnet through their aquarium in a standardized manner every 30 s for 3 min, after which time the partition was replaced. Each pass of the dipnet lasted approximately 5 s and consisted of the following process: I inserted the dipnet into the demonstrator aquarium near the novel object, rapidly moved it across the length of the tank eventually bumping it up against the shelter, slowly moved the dipnet back toward the novel object, and repeated this process once more. Throughout this process, I was visually isolated from the demonstrators except for the part of my hand holding the dipnet handle. When I replaced the partition after each training session, all demonstrators were invariably underneath the shelter and therefore did not need to be coaxed away from the novel object.

The decision to use a dipnet to train demonstrators in the fearful treatment was based on my personal observation that cichlids avoided the dipnet more strongly than any

other object I introduced into their aquaria, even realistic predator models. Others have similarly used dipnets to simulate predation risk and test for antipredator responses in fishes (e.g. Evans and Magurran 2000). Pilot trials conducted prior to the experiment suggested that the above training regime was effective; fearful demonstrators tended to reduce their activity and foraging rate and take shelter upon post-training presentation of the novel object they were trained with, whereas habituated demonstrators did not appear to respond in any way to the object following training. I acknowledge the possibility that demonstrators were not responding to the novel object per se, but rather to the raising of the partition. However, this would not affect my interpretation of results because during the recognition phase, the novel object was presented to observers without the use of a partition.

Conditioning Phase [Observers and Demonstrators]

The purpose of the conditioning phase was to present observers with an opportunity to learn about a novel object based on the behavioural response of trained demonstrators toward that object. Five minutes prior to the start of conditioning, I removed the larger of the two opaque partitions separating the demonstrators and observers, thus allowing the two groups to visualize each other (except in control treatments where there were no demonstrators) and to acclimatize to their new surroundings. The other two partitions remained in place so that both demonstrators and observers were visually isolated from the compartment within the demonstrator aquarium containing the novel object. Immediately after removing the partition, I placed a food slide in the centre of the demonstrator aquarium, leaning against the long face of the

aquarium nearest the observer aquarium (see Figure 3.2). Typically, demonstrators would begin foraging within seconds and observers would rapidly swim against the wall of their own aquarium nearest the adjacent demonstrators and food slide. Even in the control trials where there were no demonstrators, observers would often swim against the wall of their aquarium, seemingly attempting to access the food in the adjacent demonstrator aquarium.

The conditioning trials were conducted between 15:00 and 17:00 hrs on Day 2, and were each 6 min in duration. In each conditioning trial, the behaviour of both observers and demonstrators (except in the control treatment where there were no demonstrators) was videotaped from a side-on-view (see Figure 3.2) using a digital HD video camera (Sony HandyCam HDR-HC7, Sony Electronics Inc., San Diego, CA). Conditioning began 5 min after the removal of the long partition (described above), and consisted of a 3-min pre-object period to establish the baseline behaviour of both observers and demonstrators, followed by the remote removal of the remaining two partitions and a 3-min post-object period, during which observers could witness the behaviour of demonstrators toward the novel object. At the end of the post-object period, the long partition separating observers from demonstrators was gently replaced, and demonstrators had no further role in the experiment.

Recognition Phase [Observers Only]

The purpose of the recognition phase was to assess the post-conditioning response of observers toward a novel object (always object B) to determine whether observers learned about the novel object during the previous conditioning phase. These trials were

conducted between 09:00 and 12:00 hrs on Day 3 of the experiment, and were videotaped in the same manner as for the conditioning trials. Approximately 1 min prior to the beginning of the trial, a food slide was introduced into the observer aquarium halfway between the shelter and the location of the novel object (see Figure 3.2). The recognition trials began after observers initiated foraging and consisted of a 3-min pre-object period followed by a 3-min post-object period (total trial time was thus 6 min). At 3 min into the trial, object B was remotely lowered into the aquarium via a pulley system utilizing monofilament nylon line. The object had until that point been hidden behind the overhead lighting approximately 1 m above the experimental aquaria. Following the recognition phase, all fish were digitally photographed (for length measurement) and then transferred to new stock aquaria or euthanized with an overdose of the anesthetic MS-222. The fish were not reused in subsequent trials.

Behavioural Measures

To understand how the response of observers toward object B during the recognition phase was influenced by the conditioning treatment, object type, and relevant covariates, I chose to model a single dependent variable – the change in median horizontal position of all four observers between pre- and post-object periods of the recognition phase (subsequently referred to as ΔMHP_O). I assumed that horizontal position of observers relative to the edge of the shelter was a good proxy for perceived risk because the experimental aquaria were setup such that the shelter and novel object were at opposing (horizontal) ends with the food slide in between (see Figure 3.2).

Physical avoidance of the novel object or an increase in usage of the shelter following presentation of the novel object should therefore correlate positively with ΔMHP_O .

The dependent variable ΔMHP_O was quantified based on an analysis of still images extracted from video footage at 5-s intervals for the duration of each recognition trial. I extracted these images manually using the screen capture function in Mac OS X v10.5.8 (Apple Inc., Cupertino, CA), and then used the free software package ImageJ v1.43u (<http://rsb.info.nih.gov/ij/>) to determine the horizontal distance between each fish and the shelter side of the aquarium for each still image (72 images per trial; 36 pre-object and 36 post-object). For each period of the recognition phase (pre-object and post-object), I calculated the median horizontal distance between observers and the shelter side of their aquarium (I used medians instead of means because distributions of horizontal distance were often skewed). The difference between these two medians (pre-object median distance from shelter side - post-object median distance from shelter side) was the dependent variable ΔMHP_O , representing the change in median horizontal position of observers between the pre- and post-object periods. Positive ΔMHP_O scores indicated movement away from the object and toward the shelter side of the aquarium.

The covariates that I suspected might explain variation in the dependent variable, aside from treatment and object, included water temperature during the recognition phase and mean body length of observers. Even small increases in temperature have been shown to affect behavioural traits in fishes, including activity, boldness, and aggressiveness (e.g. Biro et al. 2010). In general, many behavioural and physiological traits of ectothermic animals are affected by ambient temperature (Clarke and Johnston 1999, Brodie and Russell 1999, Pruitt et al. 2011). Likewise, many behavioural and

physiological traits have been shown to vary with body size and age (e.g. Werner and Gilliam 1984, Krause et al. 1998, Clarke and Johnston 1999, Dowling and Godin 2002).

Finally, to ensure that demonstrators behaved as anticipated, I quantified changes in the median horizontal position of demonstrators during the conditioning phase (subsequently referred to as ΔMHP_D) in exactly the same manner as for observers in the recognition phase. This was done only for the habituated and fearful treatments, as there were no demonstrators in the control treatment.

Statistical Analyses

The statistical paradigm I employed to make inferences about the likelihood of competing hypotheses was one of model selection via an information-theoretic criterion (reviewed in Burnham and Anderson 2002, Johnson and Omland 2004, Garamszegi et al. 2009, Symonds and Mousalli 2011), as opposed to the traditional frequentist or null hypothesis significance testing (NHST) approach. Although the model selection approach is presently less commonly used than NHST (Stephens et al. 2006), especially in behavioural ecology (Richards et al. 2011), many authors have recently presented forceful arguments for its adoption (Buckland et al. 1997, Burnham and Anderson 2002, Burnham et al. 2011), even in purely experimental studies (Lukacs et al. 2007, Richards et al. 2011). Articles in a recent special issue of the journal *Behavioural Ecology and Sociobiology* discussed many of the advantages (and limitations) of model selection and information theoretic approaches, and generally argued for their increased application in behavioural ecology (Garamszegi 2011).

The limitations of NHST methods (particularly relating to P -values) have been extensively documented (a list of >400 citations critical of NHST can be found at <http://warnercnr.colostate.edu/~anderson/thompson1.html>, accessed 10 July 2011). The major limitation of NHST, at least with respect to the current study, is that the result of a significance test (i.e. a P -value) is uninformative. A P -value represents the probability of obtaining the observed data (or data 'more extreme') assuming that the null hypothesis is true, but says nothing about the likelihood of the null or alternative hypotheses. There is no logical or mathematical relationship between a P -value and the probability of the associated hypothesis (Berkson 1942, Gibbons and Pratt 1975, Carver 1978, Berger and Sellke 1987). The information-theoretic criterion I employ here, the Akaike Information Criterion (AIC), can be used to estimate the relative support for any number of competing hypotheses, given the observed data (Akaike 1973, 1974). Although the general outcome of model selection via AIC may only rarely differ from the outcome of a NHST approach for experimental studies (e.g. Richards et al. 2011), I contend that model selection via AIC is a more informative approach for making inference using the scientific method.

All of the statistical methods subsequently described were performed using the freely available statistical software R (R Development Core Team 2011). To understand which variables influenced the response of observers toward object B during the recognition phase, I constructed generalized linear models (GLMs) relating ΔMHP_O to all possible combinations of the predictor variables (treatment, object, treatment \times object, water temperature during the recognition phase, and mean total body length of observers). The global model (i.e. a model relating the dependent variable to all five predictors) was generated using the `glm` function in R assuming a Gaussian error

structure and identity link. I then derived an all-subsets set of sub-models (including a null model with only an intercept) using the dredge function implemented in the *MuMIn* package (Barton 2011). The dredge function specifies models for each possible combination of predictors, with the condition that models including an interaction term must also include the associated main effects. The total number of competing models, including the global and null models, was therefore 20.

For each model in the set, I calculated the AIC value corrected for small sample size, AIC_C , and relevant statistics (Burnham and Anderson 2002). The AIC_C value associated with a given model is inversely related to model fit (calculated as the maximized log-likelihood of the model given the data), and positively related to model complexity (i.e. the number of parameters). The ‘best’ models within a set are therefore the ones with the lowest AIC_C values. Within a set, models can be readily compared via the ΔAIC_C statistic, which rescales all AIC_C values in a set such that the lowest is zero (i.e. $\Delta AIC_{C_i} = AIC_{C_i} - AIC_{C_{min}}$). The final statistic I calculated for each model was the Akaike weight, W_i , which indicates the ‘weight of evidence’ for model i , and sums to 1 across the set of models. An Akaike weight can be thought to represent the approximate probability that model i is the best model in the set given the observed data (Burnham and Anderson 2002; but see slightly different interpretations in Richards 2005, Link and Barker 2006). To make inferences about the best models within a set, and specifically about the relative importance of the independent variables in explaining ΔMHP_O , I focused primarily on the ΔAIC_C of competing models in relation to that of the null model. I avoid ascribing to a particular threshold ΔAIC_C that would indicate ‘significance’, but rather interpret ΔAIC_C values with some consideration to published ‘guidelines’ such as

$\Delta AIC_C \leq 2$ indicates substantial support, $4 \leq \Delta AIC_C \leq 7$ indicates less support, and $\Delta AIC_C \geq 10$ indicates almost no support (Burnham and Anderson 2004).

Due to the uncontrollable nature of demonstrator behaviour during the conditioning phase, I conducted two additional analyses examining: a) whether demonstrators behaved as expected during the conditioning phase, and b) whether demonstrator behaviour during conditioning influenced the behaviour of observers during the recognition phase (independent of the specific treatment). Both issues were addressed using an identical approach to the one described above. First, to examine whether demonstrators behaved as expected during the conditioning phase, I constructed a set of GLMs with ΔMHP_D as the dependent variable, and all possible combinations of the independent variables treatment, object, and treatment \times object. To examine whether the behaviour of demonstrators during conditioning influenced the subsequent behaviour of observers during the recognition phase, I constructed another set of GLMs with ΔMHP_O as the dependent variable, and all combinations of the independent variables ΔMHP_D , object, and $\Delta MHP_D \times$ object. Both model sets ($n = 5$ models in each set) described above assumed a Gaussian error structure and identity link, included a null model with only an intercept, and were again derived under the condition that models with an interaction must also include the associated main effects. I assessed the relative evidence for each of the models within its set using AIC_C and relevant statistics, as was previously described.

Results

In the conditioning phase, demonstrators in the fearful treatment exhibited a greater ΔMHP_D (mean \pm SE $\Delta\text{MHP}_D = 7.4 \pm 1.0$ cm) than those in the habituated treatment (1.4 ± 0.9 cm) (Figure 3.3). Likewise, all three GLMs for ΔMHP_D that incorporated a treatment effect had substantially more support (differences in $\text{AIC}_C > 20$) than the null model (Table 3.1). These results suggest that during conditioning, fearful demonstrators avoided the novel object more strongly than habituated demonstrators.

There was no effect of object type on ΔMHP_D (mean \pm SE ΔMHP_D : object A = 4.5 ± 1.4 cm, object B = 4.4 ± 1.2 cm; Figure 3.3), as indicated by the object-only model receiving the least statistical support (Table 3.1). There was, however, an interactive effect of treatment and object on the behaviour of demonstrators during conditioning, such that habituated demonstrators trained with object A responded less strongly than those trained with object B (mean \pm SE ΔMHP_D : object A = 0.0 ± 0.4 cm, object B = 2.9 ± 1.2 cm), whereas fearful demonstrators trained with object A responded more strongly than those trained with object B (mean \pm SE ΔMHP_D : object A = 8.9 ± 1.0 cm, object B = 6.0 ± 1.0 cm) (Figure 3.3). This interaction between treatment and object was statistically supported given that the global model for ΔMHP_D , containing treatment and object effects and a treatment \times object interaction, was ranked the best in the set, receiving moderately more support than the treatment-only model (difference in $\text{AIC}_C = 5$; Table 3.1). These results collectively suggest that my training regime for demonstrators was generally effective given the expected treatment effect and lack of an object effect during the conditioning phase. However, the observed interaction between treatment and object indicates that training was more effective (i.e. the effect of treatment

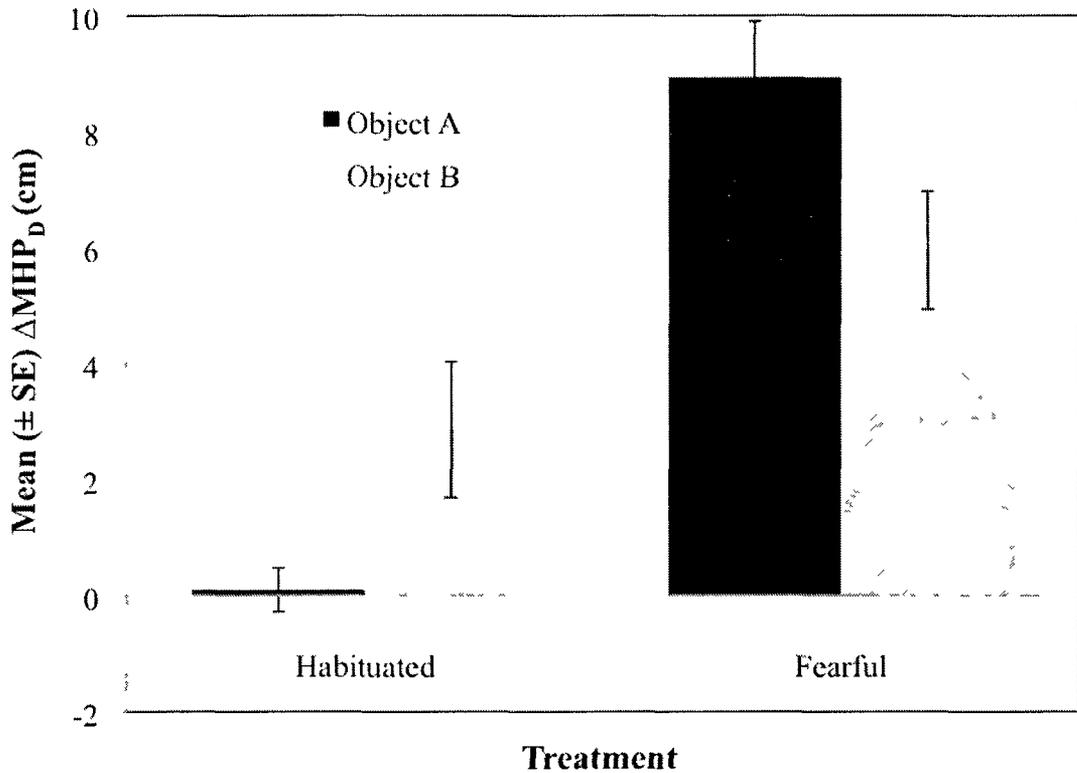


Figure 3.3 Difference score (ΔMHP_D) representing the change in median horizontal position of demonstrators between the pre-object and post-object periods of the conditioning phase (positive ΔMHP_D indicates post-object movement of the demonstrators toward the shelter). Demonstrators had previously been either habituated to, or trained to fear, one of two novel objects – object A (black bars) or object B (grey bars). During the conditioning phase, demonstrators were always presented with the object that they had previously been trained with.

Table 3.1 Selection results for candidate models explaining variation in ΔMHP_D , which represents the change in median horizontal position of demonstrators between the pre-object and post-object periods of the conditioning phase. The model set includes GLMs (assuming Gaussian error and identity link) relating ΔMHP_D to all combinations of treatment, object, and treatment \times object, including a null model with only an intercept.

Model	k	RSS	AIC _C	ΔAIC_C	W_i
treatment, object, treatment \times object	5	727.3	331.09	0.00	0.90
treatment	3	854.7	336.09	5.00	0.07
treatment, object	4	854.6	338.38	7.29	0.02
null	2	1395.0	363.26	32.18	0.00
object	3	1394.9	365.48	34.39	0.00

Notes: k = number of estimated parameters; RSS = residual sum of squares; $\text{AIC}_C = -2 \times \log\text{-likelihood} + 2k(k+1)/(n-k-1)$, where n = sample size; $\Delta\text{AIC}_C = \text{AIC}_{C_i} - \text{AIC}_{C_{\text{min}}}$; $W_i = e^{(-0.5 \times \Delta\text{AIC}_{C_i})} / \sum e^{(-0.5 \times \Delta\text{AIC}_{C_i})}$

was greater) for demonstrators trained and presented with object A than for those trained and presented with object B.

In the recognition phase, observers that had been conditioned with fearful demonstrators avoided object B more strongly (mean \pm SE Δ MHP_O = 7.8 \pm 1.2 cm) than those in both the control (6.7 \pm 1.2 cm) and habituated (6.5 \pm 1.3 cm) treatments (Figure 3.4). Within object types, this trend occurred only among observers conditioned with object B (mean \pm SE Δ MHP_O: fearful = 9.7 \pm 0.9 cm; control = 6.8 \pm 1.2 cm; habituated = 7.1 \pm 1.5 cm), whereas there was no apparent effect of treatment among observers conditioned with object A (mean \pm SE Δ MHP_O: fearful, 5.8 \pm 1.3 cm; control, 6.5 \pm 1.2 cm; habituated, 5.9 \pm 1.1 cm) (Figure 3.4). Despite these trends, I found only weak statistical evidence for an effect of treatment on Δ MHP_O, given that only two models containing a treatment effect received more support than the null model, both of which were more complex versions of the two best models (i.e. length + object, and length-only; Table 3.2). Likewise, I found no evidence for a treatment \times object interaction, as all models containing an interaction term received less support than the null model (Table 3.2). Collectively, these results provide no evidence that observers conditioned with object B and habituated demonstrators subsequently responded less strongly to object B during the recognition phase than observers in the other treatment groups (i.e. no evidence for a learned recognition of non-risk), and weak evidence that observers conditioned with object B and fearful demonstrators subsequently responded more strongly to object B during the recognition phase than observers in the other treatment groups (i.e. weak evidence for a learned recognition of risk).

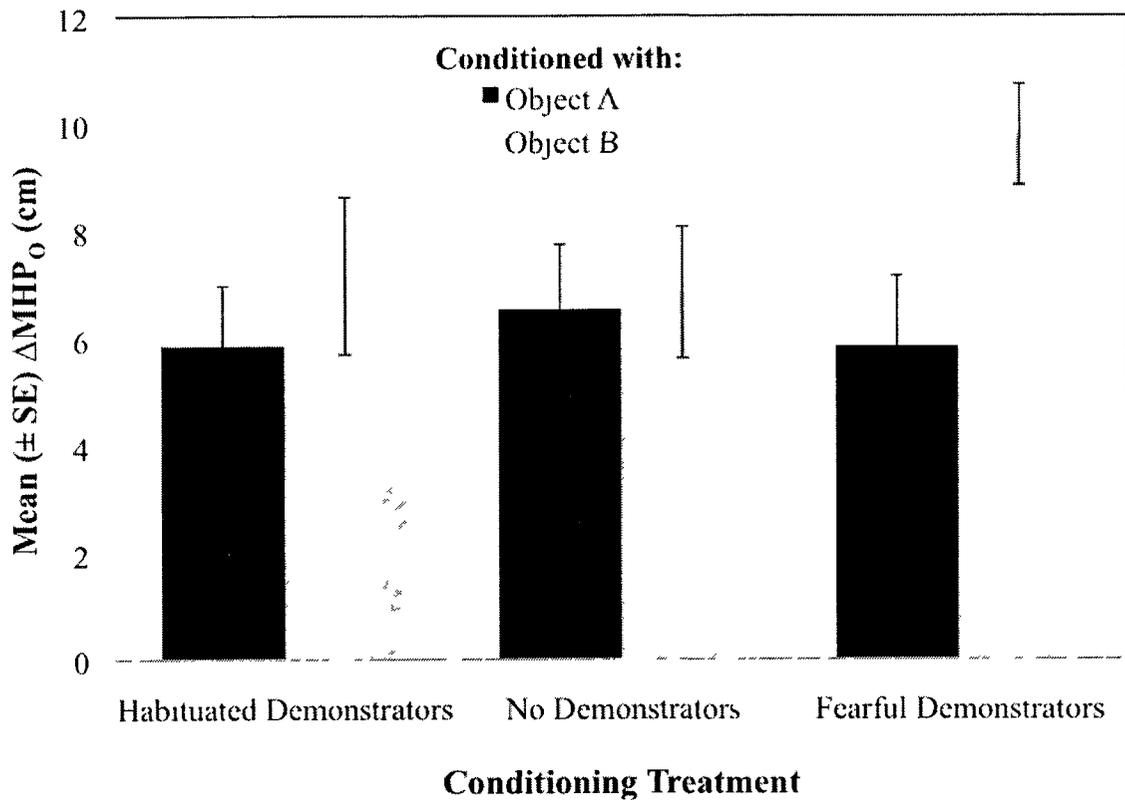


Figure 3.4 Difference score (ΔMHP_O) representing the change in median horizontal position of observers between the pre-object and post-object periods of the recognition phase (positive ΔMHP_O indicates post-object movement of observers toward the shelter). During the recognition phase, all observers were presented with object B. One day before testing (during the conditioning phase), observers had been simultaneously exposed either to object A (black bars) or object B (grey bars), and to one of three social cues (habituated demonstrators, a control treatment with no demonstrators, or fearful demonstrators).

Table 3.2 Selection results for the set of candidate models explaining variation in ΔMHP_O , which represents the change in median horizontal position of observers between the pre-object and post-object periods of the recognition phase. The model set includes GLMs (assuming Gaussian error and identity link) relating ΔMHP_O to all combinations of object, treatment (treat), object \times treatment, water temperature in the observer aquarium during the recognition phase (temp), and mean total body length of observers (length), and includes a null model with only an intercept.

Model	k	RSS	AIC _C	ΔAIC_C	W_1
length, object	4	1842.4	535.59	0.00	0.36
length	3	1925.9	537.39	1.80	0.15
length, object, temp	5	1841.1	537.77	2.18	0.12
length, object, treat	6	1811.4	538.60	3.02	0.08
object	3	1967.5	539.31	3.72	0.06
length, temp	4	1925.8	539.58	3.99	0.05
length, treat	5	1895.1	540.37	4.78	0.03
null	2	2044.6	540.63	5.04	0.03
length, object, treat, temp	7	1811.4	540.96	5.37	0.02
length, object, treat, object \times treat	8	1764.9	541.03	5.44	0.02
object, temp	4	1963.7	541.33	5.74	0.02
object, treat	5	1937.3	542.36	6.77	0.01
length, treat, temp	6	1892.4	542.54	6.95	0.01
temp	3	2044.3	542.76	7.17	0.01
length, object, treat, temp, object \times treat	9	1764.6	543.49	7.90	0.01
treat	4	2014.4	543.62	8.03	0.01
object, treat, object \times treat	7	1884.3	544.51	8.92	0.00
object, treat, temp	6	1936.9	544.63	9.04	0.00
treat, temp	5	2013.9	545.84	10.25	0.00
object, treat, temp, object \times treat	8	1884.2	546.92	11.33	0.00

Notes: k = number of estimated parameters; RSS = residual sum of squares; $\text{AIC}_C = -2 \times \log\text{-likelihood} + 2k(k+1)/(n-k-1)$, where n = sample size; $\Delta\text{AIC}_C = \text{AIC}_{C_i} - \text{AIC}_{C_{\min}}$; $W_1 = e^{(-0.5 \times \Delta\text{AIC}_{C_i})} / \sum e^{(-0.5 \times \Delta\text{AIC}_{C_i})}$

There was a small effect of object type on the behaviour of observers, whereby observers conditioned with object B subsequently exhibited greater avoidance of object B during the recognition phase (mean \pm SE $\Delta\text{MHP}_O = 7.9 \pm 1.3$ cm) than those conditioned with object A (6.1 ± 1.2 cm), especially in the fearful treatment (mean \pm SE ΔMHP_O : object A = 5.8 ± 1.3 cm; object B = 9.8 ± 0.9 cm) (Figure 3.4). This effect of object on ΔMHP_O was statistically supported given that object occurred in four of the seven models more strongly supported than the null, including the best model (difference in AIC_C between best model and null model = 5.0; Table 3.2).

The covariate influencing ΔMHP_O most strongly was the mean total length of observers, as demonstrated by the inclusion of length in six of the seven models receiving more support than the null model, including the best (length + object) and second best (length-only) models (Table 3.2). Across all trials, mean total length of observers in a given group ranged from 3.3 to 4.6 cm, with an overall mean \pm SE of 4.0 ± 0.03 cm. The model-averaged coefficient for length (\pm unconditional standard error) from the seven models receiving more support than the null model was -3.9 ± 1.7 cm, indicating a decrease in ΔMHP_O of -3.9 ± 1.7 cm for every 1.0 cm increase in mean total length of observers (Table 3.3). That is, smaller fish showed a stronger avoidance response toward object B during the recognition phase than larger fish. In contrast to the strong effect of length on ΔMHP_O , there was no evidence for an effect of water temperature during the recognition phase on ΔMHP_O , given that temperature was included in only two of the seven models receiving greater support than the null, both of which were more complex versions of the two best models (Table 3.2). Across all trials, temperature ranged from 22.8 to 28.5°C, with a mean \pm SE of 25.1 ± 0.1 °C.

Table 3.3 Model averaged statistics from the seven models of ΔMHP_O that received greater support than the null model (full model set shown in Table 3.2).

Parameter	Estimate (ϑ)	Unconditional SE	Confidence Interval	Relative Importance
(intercept)	21.3	11.50	(-1.21, 43.80)	
length	-3.89	1.65	(-7.13, -0.66)	0.93
object (B)	1.93	0.99	(-0.01, 3.87)	0.73
temperature	-0.12	0.79	(-1.66, 1.42)	0.20
treatment (habituation)	-0.71	1.24	(-3.13, 1.71)	0.13
treatment (fearful)	0.73	1.23	(-1.68, 3.13)	0.13

Notes: treatment (control) and object (A) were reference categories; Estimate (ϑ) = $\sum W_i \vartheta_i$, where ϑ_i is the maximum likelihood estimator from model i ; Unconditional SE of $\vartheta = \{ \sum W_i [\text{var}(\vartheta_i | i) + (\vartheta_i - \vartheta)^2]^{1/2} \}^2$, Relative Importance = proportion of models that include the given parameter

Finally, I found no evidence for an effect of ΔMHP_D on ΔMHP_O among those observers conditioned with demonstrators (habituated and fearful treatments combined; Figure 3.5), given that ΔMHP_D appeared in only one model (object + ΔMHP_D) receiving more support than the null model (Table 3.4). Furthermore, the object + ΔMHP_D model was a more complex version of the best model (object-only), and received only slightly more support than the null model (difference in $\text{AIC}_C = 0.47$; Table 3.4). This result suggests that there was no or only a very weak effect of ΔMHP_D on ΔMHP_O . Likewise, I found no statistical evidence for an interaction between object and ΔMHP_D (Table 3.4). Collectively, these results suggest that the behaviour of observers toward object B during the recognition phase was not directly correlated with the behaviour of the demonstrators they witnessed during conditioning.

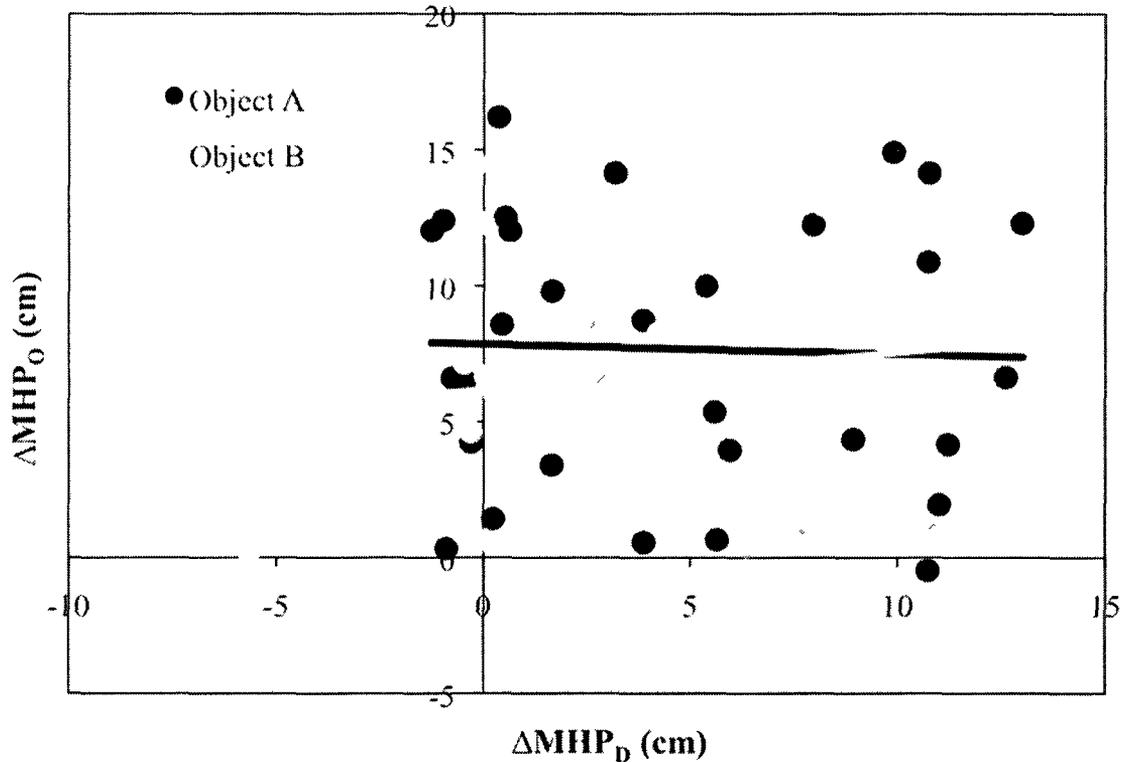


Figure 3.5 Relationship between the change in median horizontal position of observers during the recognition phase (ΔMHP_O), and that of demonstrators during the conditioning phase (ΔMHP_D). Note that positive ΔMHP scores indicate movement of the fish toward the shelter following presentation of the novel object. The depicted relationship is based on all trials for which there were demonstrators (i.e. habituated and fearful treatments combined, $n = 60$). ΔMHP scores for groups exposed to object A during the conditioning phase are shown in black, whereas scores for those exposed to object B during the conditioning phase are depicted in grey. The lines represent lines of best fit based on linear regression for each novel object type respectively. The R^2 value of the regression line was 0.001 for the object A group and 0.02 for the object B group.

Table 3.4 Selection results for candidate models examining the relationship between ΔMHP_O and ΔMHP_D . The model set includes GLMs (assuming Gaussian error and identity link) relating ΔMHP_O to all combinations of object, ΔMHP_D , and object \times ΔMHP_D , and includes a null model with only an intercept.

Model	k	RSS	AIC _C	ΔAIC_C	W_1
object	3	1314.0	361.89	0.00	0.49
object, ΔMHP_D	4	1304.3	363.74	1.85	0.19
null	2	1417.3	364.22	2.32	0.15
object, ΔMHP_D , object \times ΔMHP_D	5	1279.1	364.96	3.07	0.11
ΔMHP_D	3	1410.9	366.16	4.27	0.06

Notes: k = number of estimated parameters; RSS = residual sum of squares; $\text{AIC}_C = -2 \times \log\text{-likelihood} + 2k(k+1)/(n-k-1)$, where n = sample size; $\Delta\text{AIC}_C = \text{AIC}_{C_i} - \text{AIC}_{C_{\text{min}}}$; $W_1 = e^{(-0.5 \times \Delta\text{AIC}_C)} / \sum e^{(-0.5 \times \Delta\text{AIC}_C)}$

Discussion

Juvenile convict cichlids in the current study did not acquire a socially learned recognition of non-risk, but there was weak evidence that they acquired a socially learned recognition of risk. In particular, observers that were conditioned with a novel object and a social IC indicative of risk subsequently expressed increased antipredator behaviour toward that object compared to the relevant control groups. However, this apparent effect received little statistical support, and it therefore remains somewhat ambiguous whether convict cichlids are capable of learning about predation risk.

Despite the possible effect of learning on the behaviour of observers during the recognition phase in the current study, the variable influencing the behaviour of observers most strongly was body length. Independent of the conditioning treatment, movement toward the shelter following presentation of object B was inversely related to the mean body length of observers, suggesting that smaller observers were more risk averse or more wary of object B than larger observers. This pattern may reflect changes in metabolic requirements or susceptibility to predation that are known to correlate with body size in fishes. In particular, teleost fish often experience decreased predation risk with increasing body size (Godin 1997, Sogard 1997), which could explain why larger convict cichlids in my study were less wary of object B. To my knowledge, there are no studies documenting a relationship between body size and predation risk among convict cichlids within the size range (3.3 - 4.6 cm) used in the current study; however, there is evidence that predation risk is inversely related to body size among convict cichlids that are still dependent on parental care (0.5 - 1.0 cm in length; Wisenden and Keenleyside 1992, 1994).

Another correlate of body size that may influence antipredator behaviour is mass-specific metabolic rate, which generally decreases with increasing body size (Wootton 1994, Clarke and Johnston 1999, Gillooly et al. 2001). Metabolic (i.e. energetic) requirements are known to influence the trade-off between foraging and predator avoidance such that individuals with higher metabolic requirements are more likely to accept higher predation risk while foraging (Kohler and McPeck 1989, Pettersson and Brönmark 1993, Krause et al. 1998, Dowling and Godin 2002). For example, Krause et al. (1998) found that food-deprived three-spined sticklebacks (*Gasterosteus aculeatus*) spent less time hidden in a refuge than control sticklebacks that were not deprived of food, and among those sticklebacks that were food-deprived, large individuals spent more time in the refuge than smaller ones. Given that mass specific metabolic requirements decrease with increasing body size, the results of Krause et al. (1998) collectively suggest that an individual's willingness to accept predation risk while foraging increases with mass-specific metabolic requirement, and decreases with body size. However, this trend is opposite to what was observed in the current study, where larger convict cichlids were more likely to accept predation risk (less likely to move toward the shelter) than smaller cichlids. It would therefore seem as though a decrease in susceptibility to predation with increasing body size is the best explanation for the observed influence of body size on the antipredator behaviour of observers during the recognition phase.

Although cichlids conditioned with fearful demonstrators and object B subsequently expressed increased antipredator behaviour toward object B, I found only a weak relationship between the behaviour of demonstrators during conditioning and the subsequent behaviour of observers during the recognition phase. This result may reflect

the relatively weak effect of treatment on the behaviour of both demonstrators and observers, or may suggest that my measure of fear, ΔMHP_D , did not adequately reflect the particular IC that was involved in learning. The major limitation of using live demonstrators to generate a visual IC is that the behaviour of live demonstrators is difficult to control, and it is difficult or impossible to isolate the specific IC or set of ICs that learners are actually responding to. One potential solution to this problem is to videotape the behaviour of demonstrators and present this IC to observers using high-resolution video monitors (e.g. Trainor and Basolo 2000). The development of movement analysis algorithms (Peters et al. 2002) and video-editing software might soon allow visual ICs to be artificially generated or manipulated, which would aid in the isolation of specific ICs that are involved in risk assessment learning (Griffin 2004).

While it is generally assumed that social learning allows animals to rapidly learn about their environment while avoiding the costs of personal sampling (Boyd and Richerson 1985, Galef 1995), a potential cost of social learning is its vulnerability to errors (Giraldeau et al. 2002). In the context of predator recognition, an error occurs when an individual learns to fear a LC not associated with predation risk (a type I error) or learns not to fear a LC that is a genuine threat (a type II error). In this study, I found weak evidence that cichlids learned to fear neutral cues (arbitrary objects that were in no way related to predation risk), and therefore may have made type I learning errors. Although such errors are commonly made under controlled, experimental conditions (e.g. Curio et al. 1978, Mineka et al. 1984, Chivers and Smith 1994, Yunker et al. 1999), it is unknown whether such learning errors occur in nature. Regardless, the question of how animals might avoid making type I errors in the context of predator recognition remains.

At least two mechanisms are potentially capable of preventing type I errors in predator recognition: preferential learning and latent inhibition, both of which act to prevent certain learned associations from forming. Preferential learning occurs when animals have innate predispositions to learn only about certain types of cues (Griffin 2004). For example, tammar wallabies (*Macropus eugenii*) could be conditioned to fear a model fox but not a model goat (Griffin et al. 2001, Griffin et al. 2002), and fathead minnows (*Pimephales promelas*) could learn to avoid moving objects but not stationary objects (Wisenden and Harter 2001). The literature on socially learned recognition of predation risk contains many similar examples of animals learning about some types of cues, but not others (e.g. Curio et al. 1978, Magurran 1989, Cook and Mineka 1990). It is therefore possible that juvenile convict cichlids do not make type I errors in nature because they are primed to learn only about those objects that genuinely indicate predation risk. For example, assume there exists a finite set of hypothetical objects that a cichlid could learn to fear, and another finite set of objects that actually occur in a cichlid's natural environment. If the intersection of these two sets consists entirely of objects that are genuinely indicative of predation risk, then cichlids would never make type I errors in their natural environment. Therefore, because the novel objects that cichlids may have learned to fear in the current study do not occur in nature, the learning errors that I observed might not be biologically relevant.

A second mechanism that may prevent type I learning errors in predator recognition is latent inhibition, which occurs when pre-exposure to a LC (in the absence of an IC) prevents an animal from subsequently learning to fear that LC (Acquistapace et al. 2003, Ferrari and Chivers 2006). Latent inhibition constrains the learned recognition

of risk to cues that are novel. For example, Ferrari and Chivers (2009) found that wood frogs (*Rana sylvatica*) could be conditioned to fear the odour of a tiger salamander (*Ambystoma tigrinum*) via a single pairing of salamander odour and a chemical alarm cue from injured conspecifics. However, the same conditioning regime had no effect on wood frogs that were pre-exposed to the salamander odour alone, suggesting that wood frogs pre-exposed to salamander odour had labeled it as 'safe' or 'irrelevant' (Ferrari and Chivers 2009). It is therefore possible that juvenile convict cichlids are in fact capable of making type I learning errors, as may have occurred in the current study, but are unlikely to make such errors in nature due to latent inhibition. That is, wild cichlids will be pre-exposed to many of the 'irrelevant' cues in their environment prior to simultaneously experiencing such cues alongside a social IC indicative of risk.

Given that the cost of making a type II error in predator recognition is potentially greater than that of a type I error, it is perhaps not surprising that animals would be more likely to learn about risk than non-risk. Despite the high cost of mistakenly labeling a predator as non-threatening (a type II error), there is ample evidence that animals can learn *not* to fear cues in their environment via non-associative asocial learning (Csanyi 1985, Huntingford and Coulter 1989, Deecke et al. 2002, Stankowich and Blumstein 2005, Vennesland 2010). Why then did the juvenile convict cichlids in the current study fail to acquire a learned recognition of non-risk? One possibility is that animals, or at least juvenile convict cichlids, are not capable of learning about non-risk via associative social learning, the learning paradigm employed in the current study. If this is the case, one might ask why animals can learn about non-risk via non-associative asocial learning, but not via associative social learning. I suggest two reasons. First, social cues may by

their nature be less reliable than asocial cues (Giraldeau et al. 2002, Laland 2004, Dall et al. 2005, Barrera et al. 2011). Consider the social IC in this study – the sight of actively foraging conspecifics. Although activity and foraging rates are known to decrease in the presence of predation risk (Lima and Dill 1990), the reliability of this social IC may depend on the experience, motivation, and detection ability of the individual from whom the IC derives. For example, a nearby social companion will only respond to a novel cue if that individual detects the cue, recognizes the cue to be a threat, and is motivated to respond, which will not always be the case. It is therefore possible that high activity and foraging rates, or any other cues deriving from the behaviour of social companions, are not reliably indicative of non-risk. A second potential disadvantage of associative social learning compared to non-associative asocial learning is that, regardless of cue reliability, associative learning requires that animals associate an IC to the correct (i.e. causal) LC, which may be difficult when numerous novel cues (i.e. potential LCs) are detected simultaneously. For these reasons, it is possible that animals simply do not learn about non-risk via associative social learning.

An alternative explanation for my failure to find evidence for a learned recognition of non-risk is that, as previously suggested, animals might have innate predispositions to learn only about certain types of cues – a phenomenon termed preferential learning (Griffin 2004). For example, it is possible that juvenile convict cichlids in the current study were in fact capable of learning about non-risk via associative learning, but were not predisposed to learn about the specific objects that I presented to them. Similar cases of preferential learning have been documented in the context of learned recognition of predation risk (Griffin et al. 2002, Wisenden and Harter

2001), and also in the learned recognition of non-risk via non-associative learning (Csanyi 1985). For example, Csanyi (1985) found that paradise fish (*Macropodus opercularis*) expressed similar initial antipredator behaviour toward both goldfish (*Carassius auratus*) and satiated northern pike (*Esox lucius*), but habituated to goldfish much more rapidly than to pike. Given the possibility for preferential learning, future research on the associative learning of non-risk should incorporate novel cues that animals are most likely to have the capacity to learn about. Such cues might include cues deriving from sympatric non-predator species, or various forms of abiotic debris that occur in the focal animal's natural environment.

Although I did not find evidence for socially learned recognition of non-risk among juvenile convict cichlids, I suggest, following Ferrari and Chivers (2011), that the ability to learn about non-risk is an underappreciated aspect of risk assessment. As an extreme example of the importance of learning about non-risk, some animal populations appear to learn about predation risk exclusively via decreases in antipredator behaviour toward cues that are learned not be indicative of risk (e.g. Deecke et al. 2002, Hemmi and Merkle 2009). For example, Deecke et al. (2002) found evidence that harbour seals (*Phoca vitulina*) initially express antipredator behaviour toward all underwater calls from killer whales, but selectively habituate to the calls of fish-eating killer whale populations. Instead of expressing a mild antipredator response to novel killer whale calls and selectively learning which calls to fear, harbour seals appear to express a strong antipredator response to novel killer whale calls, and selectively learn which calls *not* to fear. The widespread documentation of neophobia and habituation in many animal species (e.g. Csanyi 1985, Huntingford and Coulter 1989, Stankowich and Blumstein

2005, Hemmi and Merkle 2009, Vennesland 2010) suggests that, like harbour seals, many animals will initially express antipredator behaviour (to varying degrees) toward a wide range of novel cues and allow experience to slowly dictate which cues are safe.

Chapter 4

General Discussion

In all of the decisions that an animal might face, deciding how best to avoid predators has perhaps the most immediate fitness implications (Lima and Dill 1990). The most effective predator avoidance strategies (e.g. never come out of hiding, or always remain vigilant) are unlikely to be employed in nature given that, in addition to avoiding predators, animals must perform a wide range of activities such as foraging, defending territories, finding mates, and provisioning offspring (Lima and Dill 1990, Godin 1997, Lima 1998). Learning is one way to effectively mediate this trade-off between avoiding predators and partaking in other fitness-enhancing activities, because learning can improve an individual's ability to distinguish threat from non-threat. The aim of my thesis was to investigate the role of learning in predation risk assessment, and to understand if and when various learning strategies might be used.

In my theoretical analysis of socially learned recognition of predation risk, described in Chapter 2, I found that social learning strategies (both pure and mixed) often fared better than pure asocial learning strategies because social learners were able to learn about threats in their environment more rapidly than asocial learners. In contrast to the common theoretical prediction that social learners can never completely replace asocial learners (Pruett-Jones 1992, Boyd and Richerson 1985, Giraldeau and Caraco 2000), in my simulations, initially rare alleles for both pure and mixed social learning became fixed under a range of conditions. However, this fitness advantage to social learners was not absolute, and the negative frequency dependence of social learning occasionally resulted in a low equilibrium frequency of social learners. For example, the proportion of social learners (both pure and mixed) after 10,000 simulated generations decreased with a decreasing ratio of threatening to non-threatening LCs, and with an increasing cost of

fearing non-threats. I suggested that the pitfalls of social learning assumed in many theoretical accounts of its evolution might not be especially pertinent to learning about risk. In particular, asocial and social learning need not be mutually exclusive in the learned recognition of risk, and social learners might still be able to acquire information about predation risk in the absence of asocial learners. These apparently unique properties of learning about risk allow both pure and mixed social learning strategies to outcompete pure asocial learning strategies under a variety of conditions.

A slightly different approach to predation risk assessment involves treating all novel cues as threatening and selectively learning which cues *not* to fear, also known as learned recognition of non-risk. In Chapter 3, I described an experiment testing for socially learned recognition of both risk and non-risk in juvenile convict cichlids. Although all previous accounts of learning about non-risk were limited to asocial learning, I suggested that some animals might also learn about non-risk socially given the prevalence of social learning in the learned recognition of risk, and the relative efficiency and generality of social learning mechanisms. However, I did not find evidence for socially learned recognition of non-risk by juvenile convict cichlids, although some of the subjects in my study may have acquired a socially learned recognition of risk. I discussed the possibility that animals might rely exclusively on asocial information when learning about non-risk, given the potentially high cost of mistakenly learning not to fear a genuine threat.

Although many animals are known to learn via habituation, the role of learning about non-risk in the context of risk assessment has been largely ignored (but see Deecke et al. 2002, Hemmi and Merkle 2009). Somewhat paradoxically, the effects of

habituation are often accounted for in the experimental design of studies investigating predator recognition abilities (e.g. Olla and Davis 1989, Brown and Warburton 1997), and yet few authors have made the case that this type of learning might be important in nature. I suggest that a thorough understanding of predation risk assessment requires an understanding of how animals learn about both risk and non-risk, and how these two forms of learning relate to each other. For example, for a given individual, the fitness benefit associated with learning to fear a particular cue might depend on whether or not the individual has the ability to learn *not* to fear that cue. All else being equal, animals capable of making type II learning errors (mistakenly learning not to fear a threat) might benefit more from a rapid acquisition of fear than animals only capable of learning to fear. Although I did not incorporate learning about non-risk into the individual-based model I described in Chapter 2, the basic properties of learning about risk and non-risk seem to be similar; therefore, the learned recognition of both risk and non-risk might be studied simultaneously using a framework similar to the one I developed in this thesis.

As a result of the theoretical prediction that social learners cannot attain higher equilibrium fitness than asocial learners (due to negative frequency dependence; Boyd and Richerson 1985, Rogers 1988), a number of theorists have suggested that individuals should be selective in how and when they use social learning (Boyd and Richerson 1985, Laland 2004). For example, Laland (2004) describes a number of *when* learning strategies such as ‘use social learning when uncertain’, and *who* strategies such as ‘learn from individuals who have high fitness’ or ‘learn from the majority’. There is accumulating empirical evidence that social learners are in fact selective in their use of social learning in a variety of contexts (Webster and Laland 2008, Kendal et al. 2009b,

Pike and Laland 2010). For instance, when provided with conflicting social and asocial information about the quality of a food patch, Pike and Laland (2010) found that nine-spined sticklebacks (*Pungitius pungitius*) were disproportionately more likely to rely on social learning as the number of demonstrators at a given food patch increased. Control treatments indicated that this was not simply a shoaling response, suggesting that the fish employed a conformist (i.e. learn from the majority) social learning strategy.

Given the differences between learning about predation risk and other forms of social learning (described in Chapter 2), it is unclear whether animals might benefit from selective learning strategies in learning to recognize risk and non-risk. It seems plausible that some individuals may be more prone to produce false alarms than others, and therefore animals living in social groups might selectively learn from social ICs produced by the most ‘reliable’ conspecifics (e.g. Cheney and Seyfarth 1988, Blumstein et al. 2004). Alternatively, some animals might take into account the total number or proportion of individuals producing a social IC when learning socially about risk or non-risk. In the simulations I described in Chapter 2, the threshold number of fearful models required for learning to occur (r) was always set to $r = 1$. In future studies, the effect of conformity learning (i.e. a copy the majority social learning strategy) on the relative fitness of social learners could be investigated by systematically increasing r .

To conclude, the role of learning in predation risk assessment, especially with regard to learning about non-risk, is ripe for further theoretical and empirical investigation. Studies that simultaneously account for the learned recognition of risk and non-risk will be especially important for understanding how animals strike a balance between too much fear and too little fear in a heterogeneous and fluctuating environment.

Eventually, researchers might explore phylogenetic or ecological correlates of risk assessment strategies. For example, do certain ecological conditions favour extreme neophobia combined with an ability to learn about non-risk while other conditions favour boldness in the face of novelty combined with an ability to learn about risk? The development of a conceptual framework that would integrate both the social and asocial learning of risk and non-risk would serve as a starting point for the investigation of such patterns, and provide a great deal of cogence to the study of predation risk assessment.

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Appendix Table A.1 Selected examples of socially learned recognition of predation risk in a variety of animal taxa.

Taxa	Species	Novel Cue	Cue Indicative of Risk	Reference
Amphibian	American toad, <i>Bufo americanus</i>	Odour	Chemical Alarm Cue	Mirza et al. 2006
	Iberian green frog, <i>Rana perezi</i>	Odour	Chemical Alarm Cue	Gonzalo et al. 2007
	Wood frog, <i>Rana sylvatica</i>	Odour	Experienced Demonstrators	Ferrari et al. 2007
Bird	Carib grackle, <i>Quiscalus lugubris</i>	Predator Model	Alarm Call	Griffin and Galef 2005
	Indian mynah, <i>Acridotheres tristis</i>	Predator Model	Alarm Call	Griffin 2008
	New Zealand robin, <i>Petroica australis</i>	Predator Model	Alarm Call	McLean et al. 1999
	European blackbird, <i>Turdus merula</i>	Predator Model	Mobbing Behaviour	Curio et al. 1978
Fish	Fathead minnow, <i>Pimephales promelas</i>	Live Predator	Chemical Alarm Cue	Chivers and Smith 1994
	Rainbow trout, <i>Oncorhynchus mykiss</i>	Odour	Chemical Alarm Cue	Ferrari et al. 2008c
	Zebra danio, <i>Brachydanio rerio</i>	Odour	Fright Response	Suboski et al. 1990
	Arctic charr, <i>Salvelinus alpinus</i>	Odour	Experienced Demonstrators	Vilhunen et al. 2005
	Fathead minnow, <i>Pimephales promelas</i>	Odour	Experienced Demonstrators	Mathis et al. 1996
	Tetra, <i>Hemigrammus erythrozonus</i>	Auditory Cue	Chemical Alarm Cue	Wisenden et al. 2008
Invertebrate	Crayfish, <i>Orconectes virilis</i>	Odour	Chemical Alarm Cue	Hazlett 2003
	Damselfly, <i>Enallagma boreale</i>	Odour	Chemical Alarm Cue	Wisenden et al. 1997
	Flatworm, <i>Dugesia dorotocephala</i>	Odour	Chemical Alarm Cue	Wisenden and Millard 2001
	Mosquito, <i>Culex restuans</i>	Odour	Chemical Alarm Cue	Ferrari et al. 2008a
Mammal	Prairie dog, <i>Cynomys ludovicianus</i>	Live Predator	Experienced Demonstrators	Shier and Owings 2007
	Rhesus monkey, <i>Macaca mulatta</i>	Live Predator	Experienced Demonstrators	Mineka et al. 1984
	Tammar wallaby, <i>Macropus eugenii</i>	Predator Model	Experienced Demonstrators	Griffin and Evans 2003
	Tammar wallaby, <i>Macropus eugenii</i>	Predator Model	Simulated Capture	Griffin et al. 2002