Utah State University
DigitalCommons@USU

All Graduate Theses and Dissertations | Graduate Studies, School of

5-1-2009

Naive Prey versus Nonnative Predators: A Role for Behavior in Endangered Species Conservation

Stephanie A. Kraft
Utah State University

Recommended Citation
Kraft, Stephanie A., "Naive Prey versus Nonnative Predators: A Role for Behavior in Endangered Species Conservation" (2009). *All Graduate Theses and Dissertations*. Paper 442.
http://digitalcommons.usu.edu/etd/442

This Thesis is brought to you for free and open access by the Graduate Studies, School of at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.
Take a 1 Minute Survey- http://www.surveymonkey.com/s/BTVT6FR

NAIVE PREY VERSUS NONNATIVE PREDATORS: A ROLE FOR BEHAVIOR IN ENDANGERED SPECIES CONSERVATION

by

Stephanie A. Kraft

A thesis submitted in partial fulfillment
Of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Todd A. Crowl Major Professor	Charles P. Hawkins Committee Member
Kimberly Sullivan Committee Member	Byron Burnham Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2009

Copyright © Stephanie Kraft 2009

All Rights Reserved

ABSTRACT

Naive Prey Versus Nonnative Predators: A Role for

Behavior in Endangered Species Conservation

by

Stephanie A. Kraft, Master of Science

Utah State University, 2009

Major Professor: Dr. Todd A. Crowl
Program: Ecology

Fish are one of the most imperiled groups of vertebrates worldwide. Threats to fish fall into one of four general categories: physical habitat loss or degradation, chemical pollution, overfishing, and nonnative species introductions. Nonnative predatory fish often have a devastating impact on native prey, especially with endemic fish, whose restricted distribution and often limited evolutionary history with predators make them particularly susceptible to nonnative predators. One reason nonnative fish are often so efficient predators is that the native fish do not recognize the predator as a threat. Although many studies have examined the role of predator odor recognition, no fish have been shown to possess an innate recognition of the odor of predators unless they share a close co-evolutionary history. Many fish learn to identify novel predators through exposure to a predator's odor in conjunction with a conspecific alarm cue. Alarm cues are substances that are stored in the epidermis of many fish and are released when skin cells are broken. Exposure to novel predator odor in conjunction with alarm cue does not

necessarily require a fish to survive a close encounter with a predator to be able to learn to recognize the predator. Here I show that it is possible to train hatchery-raised fish (June sucker, *Chasmistes liorus*) to recognize a nonnative predator odor (largemouth bass, *Micropterus salmoides*) through exposure to the odor of a predator that has eaten June sucker. I also show that this training can translate into higher survival in subsequent encounters with predators. I propose that training hatchery-raised fish prior to stocking may increase survival of hatchery-raised fish through anti-predator behavior.

(77 pages)

ACKNOWLEDGMENTS

I would especially like to thank Dr. Todd A. Crowl and my committee members, Drs. Charles P. Hawkins and Kimberly A. Sullivan, for their support and assistance throughout this process. I would also like to thank the Utah Chapter of the American Fisheries Society and Utah State University's Ecology Center for financial support of my research.

I give special thanks to my husband, Erik Archer, without whose support I would never have completed this document. My family and friends have been particularly helpful as well. Specifically, I would like to thank my parents without whose support I would not have the strength to get here. I would also like to thank the members of the Crowl Aquatic Ecology Lab. I am grateful to the staff of the Utah Department of Wildlife's Fisheries Experiment Station, especially Doug Routledge, for supplying fish and invaluable advice.

Stephanie A. Kraft

CONTENTS

Page

ABSTRACT…… ii

ACKNOWLEDGMENTS…… v

LIST OF TABLES..... viii

LIST OF FIGURES…..... ix

INTRODUCTION…….……..... 1

PREVIOUS WORK—LITERATURE REVIEW….……..……..... 4

STUDY ORGANISM……..... 15

METHODS…….…….……..... 19

Preparation of Stimuli…….. 19
Initial trials……... 20
Alarm cue experiment...……... 20
Behavioral measurements……...…...……..…..... 21
Statistical analysis..... 22
Learning experiment..... 23
Survivorship experiment..... 24

RESULTS……..... 28

Alarm cue experiment……...……..... 28
Learning experiment..... 28

DISCUSSION……..……..... 35

LITERATURE CITED..... 42

APPENDICES……..……..... 60

Appendix A. Data from alarm cue experiment..... 61
Appendix B. Data from learning experiment..... 64
Appendix C. Data from survivorship experiment..... 67

LIST OF TABLES

Table Page

1 Species shown to respond to damage-released alarm signals……...11

2 Native fish of Utah Lake, Utah…….18

3 Nonnative fish established in Utah Lake, Utah…….19

4 Experimental treatments for experiment one……26

A.1. Data from alarm cue experiment..…….62

B.1. Data from learning experiment.....……66

C.1. Data from survivorship experiment……..69

LIST OF FIGURES

Figure Page

1 Illustration of the behavioral sequence initiated by the release of alarm cues during a predation event……...……..10

2 Experimental design for experiment two …….27

3 Time spent dashing (mean + SE) by treatment in the alarm cue experiment……30

4 Time spent freezing (mean + SE) for control and bass treatments in the alarm cue experiment……...31

5 Time spent freezing (mean + SE) by exposure history after two and ten days in the learning experiment……...……..32

6 The number of trials with and without predation for both trained and naïve fish……...33

7 Distribution of sucker consumed in survivorship experiment experiment trials……..…….34

INTRODUCTION

The loss of native species is a subject of concern for conservationists and managers worldwide. Fish represent one of the most specios vertebrate groups on the planet (Helfman et al. 1997). Over the last few decades the number of threatened and endangered fish has increased dramatically. The number of fish listed as threatened, endangered or extinct on the International Union for the Conservation of Nature's (IUCN) Red List has gone from 734 in 1996 to 1275 in 2008. Some estimates suggest 35% of fish native to North America are threatened (Helfman 2007). Of 377 vertebrate species and subspecies on the United States Endangered Species List, 138 are fish (U.S. Fish and Wildlife Service 2008). Freshwater fish are particularly threatened (Bruton 1995). In North America alone, there have been at least 42 documented extinctions of freshwater fish species and subspecies (Dextrase & Mandrak 2006).

The decline of freshwater fish can be linked to four general threats: physical habitat degradation and alteration, chemical pollution, overexploitation, and nonnative species introductions (Warren & Burr 1994; Bruton 1995). Nonnative species can affect native fish in many ways, including habitat alteration, competition, introduction of disease, hybridization, and predation (Dextrase & Mandrak 2006). Predation is often the most harmful effect of nonnative fish. Often when nonnative predatory fish become established in freshwater systems, the result is rapid population decline in native fish, sometimes leading to local extinction (McIntosh et al. 1994; Lodge et al. 1998; Mills et al. 2004).

The negative effects of nonnative species can be exaggerated in freshwater systems due to isolation and lack of refuge for native species. Nonnative predators are particularly

effective in reducing populations of endemic fish (Bruton 1995). Freshwater fish exhibit high levels of endemism due to the difficulty of dispersion within and between watersheds. The isolation that facilitated the evolution of endemic species may also explain why they are so susceptible to nonnative predators. The limited distribution of endemic fish makes it likely that the whole population will be affected by a single event (Angermeier 1995; Lodge et al. 1998). Endemic fish have often evolved in the presence of a stable, defined community. A defined community, or a community which changes very little over evolutionary time, leads to a naiveté towards nonnative predators and predation strategies (Cox & Lima 2006). Failure to recognize a potential predator usually has fatal consequences (Lind & Cresswell 2005). The devastation of two-thirds of Lake Victoria's endemic cichlids by the introduced Nile perch is one of the most dramatic examples of the effects of introduced species in the world (Witte et al. 1992).

Increasingly, conservation and management plans include restocking programs as a recovery tool (Marsh & Brooks 1989; Rakes et al. 1999; Bearlin et al. 2002). The goal of these programs is to supplement natural spawning populations while habitat is restored and improved and nonnative species control activities are pursued. Unfortunately, removal of nonnative predators is not feasible in many water bodies where threatened native fish occur. The inability to remove nonnative predators creates a situation where many stocked fish are immediately lost to predation (Marsh & Brooks 1989). Losses of stocked fish due to predation decrease the effectiveness of restocking as a recovery tool. The behavior and physiology of the animals we are trying to conserve may provide important insights into methods to decrease loss of stocked fish to predation.

Aquatic organisms, much like their terrestrial counterparts, identify predation threat through their senses. Although all senses play a role in the identification of predators, odors often play a large role due to their ability to convey species and threat-specific information over long distances. Fish, specifically, use olfaction to identify predation threat in two ways: through recognition of the odor of a predator, and conspecific chemical alarm cues. Chemical alarm cues were first discovered by Karl von Frisch in 1938. Through a series of experiments, von Frisch determined that the fish olfactory system mediated the reaction and the alarm substance was stored in the skin (von Frisch 1938, 1941). These alarm cues are released when the skin is broken, often during a predation event (Pfeiffer 1977). The release of an alarm substance allows conspecifics to initiate anti-predator defenses and to learn to identify new predators. This learned association can occur through both visual and chemical recognition of the novel predator (Brown 2003).

PREVIOUS WORK—LITERATURE REVIEW

Predator-prey interactions have been the subject of countless studies (Vermeij 1994). Predator-prey interactions can play a critical role in structuring communities (Sih et al. 1985), and the presence of predators has been cited as a catalyst for morphological and evolutionary change in prey species (Bronmark & Miner 1992; Laforsch et al. 2006). Prey species in both terrestrial and aquatic systems are constantly balancing the risk of predation with their need to forage and reproduce (Lima & Dill 1990; Lind & Cresswell 2005). The most successful individuals will maximize their fitness by allocating the most time to foraging and reproduction while effectively avoiding predation. For the optimal allocation of time to occur, prey species must have a reliable way of identify the presence of predators and posses effective antipredator behaviors once a predation threat is perceived (Abrahams 2006).

Prey species identify the presence of predators through their senses: visual, olfactory, auditory, gustation, tactile, and electroreception (Dominy et al. 2004; Abrahams 2006). Although most prey species rely on a combination of the information received by several senses to form a more accurate picture of the current predation threat, the main senses that each species relies on depend on the specific evolutionary history of the species as well as the environment in which it lives. In aquatic systems, visual and chemosensory cues often relay the most accurate information (Abrahams 2006); therefore, much research has been focused on determining the role of each sense in determining antipredator behavior (Dodson et al. 1994; Chivers & Smith 1998; Kats & Dill 1998; Dicke & Grostal 2001; Brown 2003).

Both chemical and visual cues have advantages and disadvantages. Visual cues can relay accurate species and threat-specific information, but often only over relatively short distances. Visual cues become nearly ineffective for nocturnal organisms or those that live in structurally complex or turbid environments. Additionally, the distance at which an individual may rely on visual information is directly related to the size of the eye (Abrahams 2006). In aquatic systems, most prey species are considerably smaller than their predators (Persson et al. 1996). The size difference typically results in prey species being at a distinct visual disadvantage to their predators.

Chemical cues, including both kairomes and pheromones, can convey species and threat-specific information over relatively large distances (Dodson et al. 1994; Chivers & Smith 1998; Abrahams 2006). Kairomones are commonly defined as any cues that transfer information between species and confer beneficial information to the receiver but not necessarily to the sender. Kairomones are typically passively released and are often referred to simply as odors (Dodson & Hanazato 1995; Chivers & Smith 1998). Pheromones are intended for intraspecific communication, are often actively released (though not always), and often provide a benefit to both the sender and receiver (Chivers et al. 1996a; Hamdani & Døving 2007). The physics of the aquatic environment results in dramatically different diffusion and persistence rates than those in terrestrial systems (Abrahams 2006). As a consequence, aquatic environments are often full of chemical cues, and false alarms can be common. For chemical cues to be effective, prey species must be able to accurately identify potential predators and assess the risk that potential predators pose at any given moment.

Many prey species across a wide range of taxa have developed a similar strategy for accurately identifying predation risk: damage-released alarm cues (Dodson et al. 1994; Chivers & Smith 1998; Kats & Dill 1998, Table 1). In fish, damage-released alarm cues (hereafter referred to as alarm cues) were first discovered by Karl von Frisch in 1938. Von Frisch discovered alarm cues accidentally while conducting a study on the auditory sense of a minnow, *Phoxinus phoxinus* (von Frisch 1938; Døving et al. 2005). He noticed that other fish exhibited a strong fright response to fish he had marked by placing small cuts on the caudal section. Through a series of experiments, olfaction was determined to mediate the signal, and the cue was found to reside in the epidermis (von Frisch 1938, 1941). Von Frisch termed the alarm substance *schreckstoff* and the alarm response *schreckreaktion* (Døving et al. 2005). Although schreckstoff/schreckreaktion specifically refers to the alarm cues found in fish in the super-order Ostariophysii, alarm cues have been found in many species outside of this super-order (Table 1).

Immediately after discovery of the alarm cue, researchers attempted to identify the specific chemical responsible for inducing the fright reaction observed. Pfieffer (1960) discovered the presence of specially shaped club cells in the epidermis of fish which had been shown to possess alarm cues. It is thought that the active alarm substance is stored in these club cells and released when the skin is broken, as in a predation event (Døving et al. 2005, Figure 1). Pfieffer and others have attempted to identifying the active compound that induces a fright response, and many substances have been proposed, but a consensus has yet to be reached (Pfeiffer 1963; Pfeiffer et al. 1985; Brown et al. 2000; Brown et al. 2003; Døving et al. 2005). One reason researchers may have had such difficulty determining a single active compound in the alarm substance is the species

specificity of the alarm cue (Schutz 1956). Although some species recognize heterospecific alarm cues, the alarm cues recognized tend to originate from either closely related species, or species with a close evolutionary history (Mathis & Smith 1993; Chivers et al. 1995b; Chivers & Smith 1998; Mirza & Chivers 2001; Dalesman et al. 2007).

Although alarm cues are helpful to conspecifics of the releaser, on first glance they seem to provide little to no benefit to the individual releasing the cue. While the ostariophysan alarm cue was traditionally touted as the classic example of a fish alarm pheromone, because of the apparent lack of benefit to the releaser there has been considerable debate whether the substance is actually a pheromone (Wilson & Bossert 1963; Magurran et al. 1996; Smith 1997; Chivers & Smith 1998; Abrahams 2006).

Regardless of whether or not the alarm cue is a pheromone, it can facilitate accurate identification of potential predators in two specifics ways. Fish can learn to recognize the odors of novel predators through exposure to alarm cues either during direct release of alarm cue during a predation event or as the predator exudes alarm cue after consumption of an alarm cue-producing organism. The potential for fish to use alarm cue to learn novel predator odors was recognized not long after their initial discovery (Göz 1941). After Goz's initial study, not much attention was paid to alarm cue-assisted learning for over 40 years. In recent years there has been intense interest in investigating the ability of fish to learn from exposure to alarm cues (Magurran 1989; Chivers & Smith 1994a; Brown 2003).

The ability to learn to associate novel predator odors with predation risk allows fish to recognize potential predators through chemical stimuli without the need for the alarm

cue to be present. While it may not be advantageous to flee an area or otherwise employ extreme antipredator behavior, in response to learned predator odors alone, fish may increase awareness and increase visual scans after smelling a learned predator, which would decrease the fish's reaction time if other senses confirm the presence of a strong immediate threat.

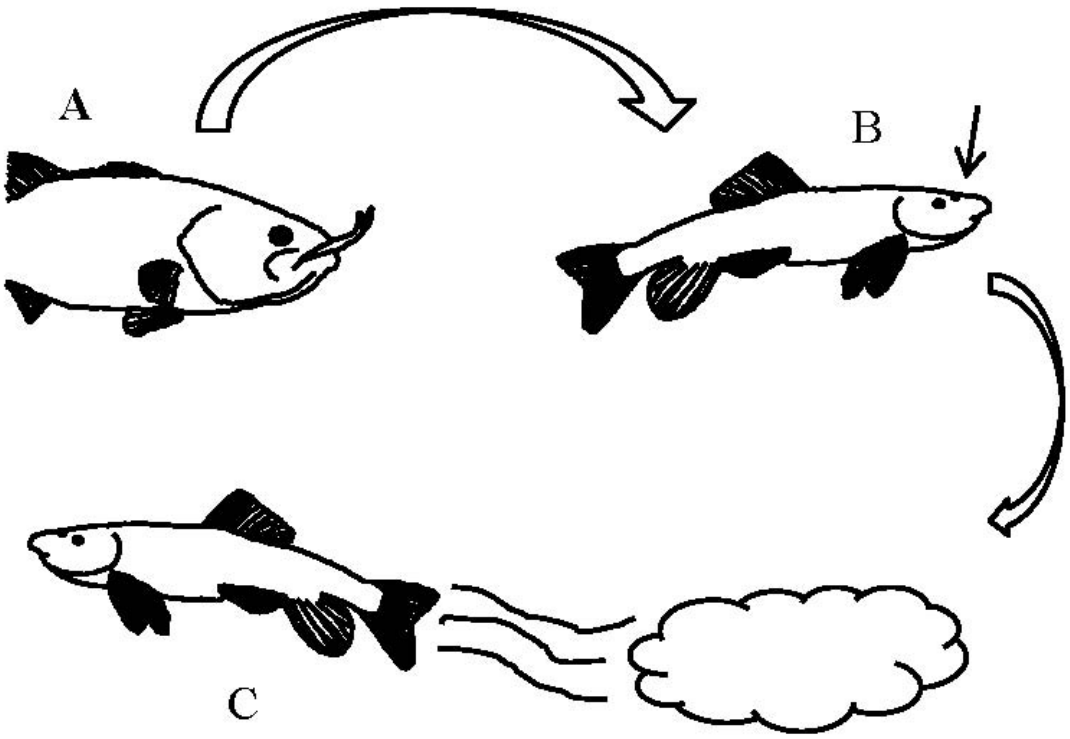

FIGURE 1. Illustration of the behavioral sequence initiated by the release of alarm cues during a predation event. A) A predation even occurs, skin cells are broken, and alarm cue is released into the water. B) Alarm cue and predator odor reach the olfactory organs of conspecifics of the prey in the area. C) Anti-predator behaviors are initiated.

TABLE 1. Species shown to respond to damage-released alarm signals. Species are arranged alphabetically under Phylum and Class

Taxa	Reference
Phylum cnidaria	
Anthopleura elegantissima	Howe & Sheikh 1975, Howe (1976)
Phylum mollusca	
Class Gastropoda	
Australorbis glabrutus	Kempendorff 1942
Littorina sitkana	Yamada et al 1998
Nassarius obsoletus, N. vibex, N. trivittatus	Atema & Burd 1975; Atema and Stenzler (1977); Stenzler & Atema (1977)
Physella virgata	Crowl & Covich (1990)
Pomacea paludosa, P. doliodes	Snyder & Snyder (1971)
Thais lamellosa	Appleton& Palmer (1988)
Phylum arthropoda	
Class Insecta	
Culex pipiens	Sih (1986)
Damselfly larvae: Enalagma spp.	Chivers et al. (1996b); Wisenden et al. (1997)
Mayfly larvae: Ephemerella aurivilli	Scrimgeour et al. (1994)
Baetis tricausatus	Scrimgeour et al. (1944)
Class Crustacea	
Calcinus laevimanus	Hazlett (1990)
Clibanarius vittatus	Rittschof et al. (1992)
Gammarus lacustris	Wudkevich et al. 1997
Gammarus pseudolimnaeus	Williams & Moore (1985)
Orconectes virilis	Hazlett (1994)
Pagurus longicarpus	Rittschof et al. (1992)
Pagurus pollicaris	Rittschof et al. (1992)
Phyilyra laevis	Mckillup & McKillup (1992)
Phylum echinodermata	
Diadema antillarium	Snyder and Snyder (1970)
Pycnopodia helianthoides	Lawrence (1991)
Strongylocentrotus droebachiensis	Mann et al. (1984)
Phylum Chordata	
Class Osteichthyes	
Abramites microcephalus	Pfieffer (1977)
Acanthopththalmus kuhlii	Pfieffer (1977)
Alburnoides bipunctatus	Pfieffer (1977)

Alburnus alburnus	Pfieffer (1977)
Alestes nurse	Pfieffer (1977)
Anostomus anostomus	Pfieffer (1977)
Anostomus trimaculatus	Pfieffer (1977)
Aphyocharaz rubropinnis	Pfieffer (1977)
Asterropterys semipunctatus	Smith (1989)
Astyanaz bimaculatus	Pfieffer (1977)
Atherinops affinis	Pfieffer (1977)
Brachydanio rerio	Pfieffer (1977); Jakobsen and Johnsen (1989)
Brachygobius sabanus	Smith et al. (1991); Smith and Lawrence (1992)
Brycon sp.	Pfieffer (1977)
Carassius auratus	Zhao et al. (2006)
Carassius carassius	Pfieffer (1977)
Carnegialla vesca	Pfieffer (1977)
Carnegiella marthae	Pfieffer (1977)
Carnegiella strigata	Pfieffer (1977)
Catostomus catostomus	Pfieffer (1977)
Catostomus macrocheilus	Pfieffer (1977)
Cheirodon axelrodi	Pfieffer (1977)
Chicholsoma nigrofasciatum	Wisenden and Sargent (1997)
Chondrostoma nasus	Pfieffer (1977)
Chrosomus erythrogaster	Pfieffer (1977)
Clarias sp.	Pfieffer (1977)
Clinostomus funduloides	Pfieffer (1977)
Copeina arnoldi	Pfieffer (1977)
Copeina guttata	Pfieffer (1977)
Corydoras palaeatus	Pfieffer (1977)
Corynopoma riisei	Pfieffer (1977)
Couesius plumbeus	Pfieffer (1977)
Culaea inconstans	Mathis & Smith (1993); Chivers & Smith (1994b); Chivers et al. (1995a)
Cyprinus carpio	Pfieffer (1977)
Danio malabaricus	Pfieffer (1977)
Ephippicharax orbicularis	Pfieffer (1977)
Esomus lineatus	Pfieffer (1977)
Etheostoma (ammocrypta) beani	Smith (1982)
Etheostoma exile	Smith (1979)
Etheostoma nigrum	Smith (1979)

Etheostoma swani	Smith (1982)
Fundulus olivaceus	Pfieffer (1977); Reed (1969)
Gambusia affinis	Pfieffer (1977); Reed (1969); Garcia et al. (1992)
Gasteropelecus laevis	Pfieffer (1977)
Gastrosteus aculeatus	Brown and Godin (1997)
Gnathopogon elongates	Pfieffer (1977)
Gnatholepis anjerensis	Smith (1989)
Gobio gobio	Pfieffer (1977)
Gryinocheilus aumonieri	Pfieffer (1977)
Gymnocorymbus ternetzi	Pfieffer (1977)
Hemigrammus armstrongi	Pfieffer (1977)
Hemigrammus caudovittatus	Pfieffer (1977)
Hemigrammus erythrozonus	Pfieffer (1977); Wisenden et al. (2008); Brown et al. (1999); Brown and Godin (1999b); Darwish et al. (2005)
Hemigrammus ocellifer	Pfieffer (1977)
Hemmigrammus rhodostomus	Pfieffer (1977)
Heterandria formosa	Pfieffer (1977)
Homalopterus sp.	Pfieffer (1977)
Hybognathus hankinsoni	Pfieffer (1977)
Hybopsis aestivalis	Pfieffer (1977)
Hybopsis biguttata	Pfieffer (1977)
Hyphessobrycon hertaxelrodi	Pfieffer (1977)
Hyphessobrycon innesi	Pfieffer (1977)
Hyphessobrycon pulchipinnis	Pfieffer (1977)
Hyphessobrycon scholzei	Pfieffer (1977)
Hyphessobrycon serape	Pfieffer (1977)
Ictalurus nebulosus	Pfieffer (1977)
Kneria maydelli	Pfieffer (1977)
Kryptopterus bicirrhis	Pfieffer (1977)
Labeo bicolor	Pfieffer (1977)
Lepomis cyanellus	Brown & Brennan (2000)
Lepomis gibbosus	Golub et al. (2005)
Leporinus affinis	Pfieffer (1977)
Leucaspius delineates	Pfieffer (1977)
Leuciscus cephalus	Pfieffer (1977)
Leuciscus idus	Pfieffer (1977)
Leuciscus leuciscus	Pfieffer (1977)
Leuciscus souffia	Pfieffer (1977)

Megalamphodus megalopterus	Pfieffer (1977)
Microglanis parahybae	Pfieffer (1977)
Mimagoniates microlepis	Pfieffer (1977)
Moenkhausia oligolepis	Pfieffer (1977)
Mylocheilus caurinus	Pfieffer (1977)
Nannaethiops unitaeniatus	Pfieffer (1977)
Noemacheilus barbatulus	Pfieffer (1977)
Notropis atherinoides	Pfieffer (1977)
Notropis cornutus	Pfieffer (1977)
Notropis rubellus	Pfieffer (1977)
Notropis spilopterus	Pfieffer (1977)
Notropis texanus	Pfieffer (1977)
Notropis venustus	Pfieffer (1977)
Oligocottus maculosa	Hugie et al. (1991); Houtman and Dill (1994)
Onchorhynchus mykiss	Brown and Smith (1998)
Oreochromis mossambicus	Jaiswal and Waghray (1990)
Percina nigrofasciata	Smith (1982)
Phoxinus phoxinus	Pfieffer (1977)
Phractolaemus ansorgei	Pfieffer (1977)
Pimelodella gracilis	Pfieffer (1977)
Pimephales promelas	Pfieffer (1977); Lawrence and Smith (1989); Chivers and Smith (1993)
Poecilia reticulata	Pfieffer (1977); Brown and Godin (1999a)
Pristella riddlei	Pfieffer (1977)
Ptychocheilus oregonensis	Pfieffer (1977)
Puntius holotaenia	Pfieffer (1977)
Puntius tetrazona	Pfieffer (1977)
Rasbora heteromorpha	Pfieffer (1977)
Rhinichthys atratulus	Pfieffer (1977)
Rhinichthys cataractae	Pfieffer (1977)
Rhodeus ocellatus	Pfieffer (1977)
Rhodeus sericeus	Pfieffer (1977)
Richardsonius balteatus	Pfieffer (1977)
Roeboides microlepis	Pfieffer (1977)
Rutilus rutilus	Pfieffer (1977)
Scardinius erythrophthalmus	Pfieffer (1977)
Semotilus atromaculatus	Pfieffer (1977)
Synodontis nigriventris	Pfieffer (1977)

Thanichthys albonubes	Pfieffer (1977)
Thayeria obliquus	Pfieffer (1977)
Thayeria sanctaemariae	Pfieffer (1977)
Tinca tinca	Pfieffer (1977)
Tribolodon hakonensis hakonensis	Pfieffer (1977)
Tribolodon hakonensis tazanowskii	Pfieffer (1977)
Class Amphibia	
Bufo americanus	Petranka (1989)
Bufo boreas	Hews and Blaustein (1985); Hews (1988))
Bufo bufo	Eibl-Eibesfeldt (1949); Hrbacek (1950); Kulzer (1954); Pfeiffer (1960)
Bufo calamita	Pfieffer (1966)
Cynops pyrrhogaster	Marvin and Hutchison (1995)
Notophthalmus viridescens	Marvin and Hutchison (1995); Woody and Mathis (1997)
Rana aurora	Wilson and Lefcort (1993)
Rana cascadae	Hews and Blaustein (1985)
Rana perezi	Gonzalo et al.(2007)

STUDY ORGANISM

Suckers in the family Catostomidae are primarily endemic to North America (Helfman et al. 1997). More than half of the approximately 70 described species can be found on either the Canadian, U.S., or Mexican endangered species lists (Helfman 2007). Lake Suckers (genus *Chasmistes*) are particularly threatened. There are four described species of *Chasmistes*: cui-ui (*Chasmistes cujus*), shortnose sucker (*C. brevirostris*), June sucker (*C. liorus*), and the Snake River sucker (*C. muriei*). Each lake sucker is endemic to one of four hydrologic basins in the Western United States. The snake river sucker is thought to be extinct, and the three extant species are on the U.S. endangered species list (Scoppettone & Vinyard 1991; U.S. Fish and Wildlife Service 1999; Helfman 2007).

The June sucker is endemic to Utah Lake, Utah (Whitney & Belk 2000). Utah Lake is thought to once have been a clear, macrophyte-dominated, shallow lake that supported a community of 13 native fish (Table 2). Today the lake is eutrophic, with macrophytes (mostly nonnative) relegated to the near shore, and all but two native fish have been extirpated from the lake. The native species have been replaced with 16 nonnative fish, including the top-level predators walleye (*Sander vitreum*), white bass (*Morone chrysops*), and largemouth bass (*Micropterus salmoides*) (Whitney & Belk 2000; Belk et al. 2001; Billman & Crowl 2007, Table 3). On April 30, 1986, the June sucker was listed as endangered with critical habitat (U.S. Fish and Wildlife Service 1986). A restocking program began in 1994 and to date has stocked over 100,000 June sucker into Utah Lake (Utah Department Wildlife Resources 2008). Very few of the stocked fish have appeared in the spawning population (Rasmussen, personal communication).

In this study, I investigated the possibility of using learned recognition of novel predator odors to increase survival of hatchery-reared fish. I tested five specific hypotheses. 1) Hatchery-raised sucker do not have an innate recognition of bass odor. If hypothesis one is true, I would not expect to see a measurable fright reaction in response to exposure to bass odor alone. 2) Sucker do produce and react to a conspecific chemical alarm cue. If hypothesis two is true, I would expect to see an intense fright reaction when fish are exposed to homogenized sucker skin cells. 3) Sucker can recognize conspecific alarm cue in the odor of a bass that has eaten sucker. If hypothesis three is true, I would expect to see a fright response when fish are exposed to the odor of bass that have consumed sucker. 4) Sucker can learn to associate bass odor with the threat of predation. If hypothesis four is true, I could expect fish that have previously smelled the odor of a bass that had eaten sucker to show a fright response when they are later exposed to bass odor alone. 5) Training sucker to recognize bass odor will increase survival in a later encounter with a bass. If hypothesis five is true, I would expect trained sucker to have a higher survival rate than naïve sucker in short-term exposures to a bass.

TABLE 2. Native fish of Utah Lake, Utah

Species	Current Status in Utah Lake
June Sucker, *Chasmistes liorus*	Present
Utah Sucker, *Catostomus ardens*	Present
Utah Lake Sculpin, *Cottus echinatus*	Absent
Bonneville Cutthroat Trout, *Onchorhynchus clarkii utah*	Absent
Least Chub, *Iotichthys phlegethontis*	Absent
Bonneville Redside Shiner, *Richardsonius balteatus hydrophlox*	Absent
Mottled Sculpin, *Cottus bairdi*	Absent
Leatherside Chub, *Gila copei*	Absent
Utah Chub, *Gila atraria*	Absent
Speckled Dace, *Rhinichthys osculus*	Absent
Longnose Dace, *Rhinichthys cataractae*	Absent
Mountain Whitefish, *Prosopium williamsoni*	Absent
Mountain Sucker, *Catostomus platyrhyncus*	Absent

TABLE 3. Nonnative fish established in Utah Lake, Utah

Species	Year Introduced
Black Bullhead, *Ameiurus melas*	1871
Common carp, *Cyprinus carpio*	1881
Goldfish, *Carassius auratus*	1889
Green Sunfish, *Lepomis cynellus*	1890
Bluegill Sunfish, *Lepomis machrochirus*	1890
Largemouth Bass, *micropterus salmoides*	1890
Black Crappie, *Pomoxis nigromaculatus*	1890
Yellow Perch, *Perca flavescens*	1890
Channel Catfish, *Ictalurus punctatus*	1911
Smallmouth Bass, *Micropterus dolomieu*	1912
Red Shiner, *Cypinella lutrensis*	1920
Western Mosquitofish, *Gambusia affinis*	~1930
Walleye, *Sander vitreum*	1952
White Bass, *Morone chrysops*	1956
Fathead Minnow, *Pimephales promelas*	1968
Grass Carp, *Ctenopharyngodon idella*	~1990

METHODS

All trials were conducted at the Utah State University Millville Aquatic Research Facility in Millville, Utah. Sucker were obtained from Utah Division of Wildlife's Fisheries Experiment Station located in Logan, Utah. Largemouth bass were used as predators and were captured from Mantua Reservoir, Mantua, Utah. Swordtail (*Xiphophorus helleri*) were used to allow collection of predator odor alone and were purchased from commercial pet stores in Ogden, Utah.

Preparation of Stimuli

All stimuli were prepared and administered in concentrations well above those thought to be necessary for detection (Brown et al. 2001; Døving et al. 2005). To collect water containing alarm cue without the presence of any predator odor (hereinafter alarm cue, Table 4), four sucker were euthanized via a blow to the head. The sucker were then filleted and the skin area measured. The fillets were immediately homogenized with chilled distilled water at a concentration of 0.1 cm^2/1 ml H_2O. The homogenized mixture was then filtered through glass wool, divided into 60 ml aliquots and frozen for future use.

Predator odor alone and predator odor with alarm cue present were prepared similarly. Two groups of four bass were fed either swordtail (hereinafter predator odor, Table 4) or sucker (hereinafter predator odor plus alarm cue, Table 4) ad libitum for ten days. Swordtail do not produce an alarm cue recognizable by most fish (Golub & Brown 2003). On the tenth day, one hour after feeding, the bass were removed from their

holding tank, rinsed with distilled water, and placed into 150 L tanks by feeding history. The tanks were aerated but not filtered. After 24 hours the bass were removed. The remaining water was divided into 60 ml aliquots and frozen for future use.

Initial trials

This experiment was designed to test hypotheses one through three via a 2 x 2 factorial design with predator odor and June sucker alarm cue as the main factors. Eighteen 190 L experimental tanks were encircled with a curtain to remove any visual stimuli. Experimental tanks were fiberglass on three sides with a class front with a gravel bottom and one plastic aquarium plant. Tanks were aerated but not filtered. Water was kept between 18 and 21°C. One meter of 0.25 centimeter inside-diameter plastic tubing was secured to the airstone tubing and extended through the curtain. This tube was used to inject stimulus during the trial. Five one-year-old, naïve sucker were placed into each tank. The sucker placed into the fiberglass experimental tanks did not return to normal swimming behavior within 96 hours. Because the sucker never acclimated to the experimental tanks, the fiberglass tanks were abandoned and new glass tanks were purchased.

Alarm cue recognition experiment

This experiment was designed to test hypotheses one through three via a 2 x 2 factorial design with predator odor and June sucker alarm cue as the main factors (Table 4). Treatments were randomized among tanks. Twelve replicates were conducted for each

of the four treatment combinations. Trials were conducted between 10-17 November 2007 and 14-16 March 2008.

Four 150 L experimental tanks were encircled with a curtain to remove any visual stimuli. An opaque barrier was placed in between the tanks to visually separate the tanks. Tanks were aerated but not filtered. Water was kept between 18 and 21°C. One meter of 0.25 centimeter inside-diameter plastic tubing was secured to the airstone tubing and extended through the curtain. This tube was used to inject stimulus during the trial. Tanks were drained, rinsed, dried, and refilled between each trial.

Five one-year-old, naïve sucker were placed into each tank and allowed to acclimate for 24 hours. Acclimation was defined as a return to normal swimming behavior. A total of 240 sucker were used (mean = 177.34, SD = 25.99). Each fish was used only once to avoid any learning bias. Prior to the start of each trial, 60 ml of water was drawn out of the tank with a syringe through the injection hose and discarded to remove any water in the hose. Another 60 ml of water was then drawn out and was used to flush the stimulus completely through the tube. Trials were 10 minutes in duration. Sixty milliliters of stimulus was injected 5 minutes into the trial creating a concentration of 4×10^{-4} ml of stimulus per ml of tank water. Data were collected during the 5-minute pre-exposure and 5-minute post-exposure periods.

Behavioral measurements

Sucker were observed prior to the beginning of experiments to identify typical fright reaction behavior. Two fright reactions, dashing and freezing, were recorded in both alarm cue recognition and learning experiments. Dashing was defined as rapid,

undirected swimming. Dashing was considered the most extreme response, and I expected to see this only when an immediate threat was perceived. Freezing was defined as cessation of any movement for at least 15 seconds. Freezing was considered a less extreme response; therefore I expected to see freezing when a lesser threat was perceived and after an initial fright response involving dashing. The variable recorded for each behavior was the amount of time, in seconds, when any fish in the tank was exhibiting the behavior. To avoid overlap in variable measurement if fish in the tank were exhibiting both dashing and freezing behavior, the time was assigned to dashing. I performed behavioral analysis from video using Observer XT® software. I calculated the amount of time used in statistical analysis by subtracting pre-exposure values from post-exposure values. Subtracting pre-exposure values from post-injection values allowed me to control for differences in fish behavior by trial.

Statistical analysis

Time spent dashing was log transformed to meet the assumption of normality of residuals. I compared treatments using analysis of variance (ANOVA). Post hoc mean comparisons were done using the Ryan-Einot-Gabriel-Welsch (REGWQ) method. Sucker exposed to stimulus two did not spend a significantly longer time dashing than the control. Therefore, I compared time spent freezing between stimulus 2 and the control in a paired t-test. All analyses were performed with SAS version 9.1.3 for personal computers (SAS Institute 2004).

Learning experiment

This experiment was designed to test whether sucker learned to associate bass odor with predation risk after one exposure to bass odor in conjunction with conspecific alarm cue (hypothesis four). I exposed two groups of 80 one-year-old sucker to either bass odor alone (hereafter referred to as naïve) or odor of bass fed sucker (hereafter referred to as trained). Sucker were initially exposed in 230 L aerated flow through tanks. Flow was temporarily stopped and 240 ml of the appropriate stimulus was added to the tank creating a concentration of .001 ml of stimulus per ml of tank water. The concentration of stimulus was higher than that used in the first trial to ensure detection by all fish. After 30 minutes flow was resumed.

Two days after initial exposure, 40 fish from each exposure history were placed into experimental tanks in groups of five. Experimental tanks were set up identically to experiment one. The order of testing was randomized. Fish were allowed to acclimate before trials. I followed the same procedure with the remaining fish ten days after initial exposure (Fig. 2). Trials were conducted as described in the alarm cue recognition experiment, except all fish were exposed to bass odor alone. Sucker were initially exposed on 14 July 2008 and trials were conducted on 16 and 24 July 2008. A total of 160 sucker were used (mean = 198.29, SD = 25.28). Each fish was only used once.

Behavioral variables were recorded following the same methods as experiment one. There was no significant dashing behavior observed. Therefore, time spent freezing was compared between exposure history and days since exposure using ANOVA. Because the interaction term was significant, a Tukey adjustment for multiple

comparisons was used to determine which treatment combinations were significantly different.

Survivorship experiment

Two 1500 L experimental tanks were aerated but not filtered and the water was kept between 18 and 21°C. Gravel was placed on the bottom of the tanks. One group of five plastic aquarium plants was positioned in the tank to provide shelter. Five one-year-old sucker were placed into a 150 L aerated flow-through tank. Flow was temporarily stopped and 60 ml of either bass odor alone (hereafter referred to as naïve) or bass odor plus alarm cue (hereafter referred to as trained) was added to the tank. After 30 minutes flow was resumed. A total of 80 sucker were used (mean = 92.58, SD = 17.73). Each fish was only used once. Sucker used in this experiment were raised from the larval stage at Millville Aquatic Research Facility.

One hour after exposure, sucker were placed into the experimental tank and allowed to acclimate for several hours. Three bass were used (287, 300, and 298 mm SL). Each bass was kept in an individual holding tank and starved for 24 hours prior to use. This time period should be sufficient for full gastric evacuation, therefore alarm cue should not be detectable from previously eaten sucker (Hayward & Bushmann 1994). One bass was then removed from the holding tank, rinsed, and added to the experimental tank. After 90 minutes the bass was removed and the surviving sucker were counted. I chose Ninety minutes to minimize the possibility of in-tank learning. Between trials, the tanks were drained, rinsed for 20 minutes, and refilled. Eight trials of each exposure

history were conducted from 7-17 October 2008. Trials were randomized with respect to exposure history, experimental tank, and bass used.

The number of sucker that survived was the response measured. All trained sucker survived, which allowed me to treat the mean survival of trained sucker as a constant. The mean survival of naïve sucker was compared to this constant in a one tailed t-test.

TABLE 4. Experimental treatments for experiment one

	Alarm cue absent	Alarm cue present
Predator odor absent	Distilled water (control)	Crushed sucker skin cells (alarm cue)
Predator odor present	Bass fed swordtail (bass odor)	Bass fed sucker (bass odor plus alarm cue)

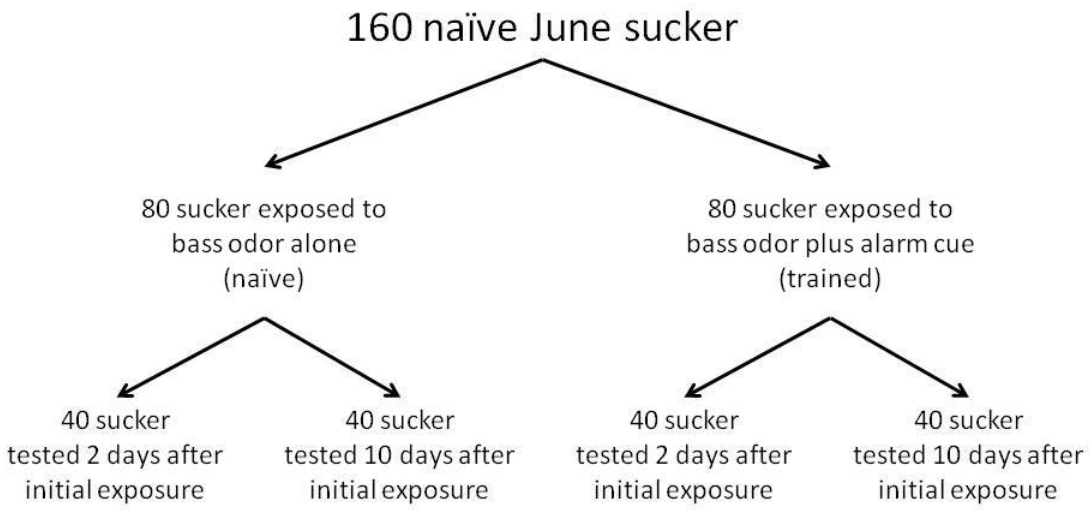

FIGURE 2. Experimental design for experiment two.

RESULTS

Alarm cue recognition experiment

There was no evidence that predator-naïve sucker have an innate recognition of bass odor. Exposure to bass odor alone did not result in higher levels of time spent dashing than the control (adjusted $p > 0.05$, Fig. 3). The absence of dashing behavior indicates that a strong immediate threat was not conveyed through bass odor alone. Time spent freezing, which should increase if a lesser threat was perceived, was also similar between sucker exposed to bass odor alone and the control ($t_{22}=0.73$, $p=0.4713$, Fig. 4).

Although sucker did not show an innate recognition of bass odor alone, they were able to detect alarm cues in the odor of bass which had eaten conspecifics ($F_{3,44}=15.52$, $p<0.0001$, REGWQ $\alpha=0.05$, Fig. 3). Application of both stimuli where alarm cues were present resulted in higher levels of time spent dashing than the control ($p<0.05$, Fig. 3). While conspecific alarm cues alone elicited the highest levels of dashing behavior, sucker exposed to bass plus alarm cue exhibited dashing behavior 15 times higher than those exposed to bass odor alone. The raw data collected can be found in Table A.1.

Learning experiment

There was evidence that sucker form short-term associations between odors. Two days after exposure, trained sucker showed recognition of bass odor as a threat (time spent freezing, $F_{3,28} = 6.31$, $p=0.0021$, Fig. 5). By day 10, trained sucker no longer showed any recognition of bass odor (trained vs naïve at 10 days, $p = 1.0000$). Freezing behavior of naïve sucker was similar between days two and 10 ($p=0.7600$). There was no

evidence that sucker in any treatment combination recognized the bass odor alone as a strong immediate threat (time spent dashing, $F_{3,28}$=0.42, p=0.7434). The raw data collected can be found in Table B.1.

Survivorship experiment

Previously exposing June sucker to the odor of bass fed June sucker (hereafter referred to as training) resulted in increased survival of sucker when exposed to a bass for 90 minutes. One hundred percent of trained sucker survived the encounter with a bass, while 82.5 % of naïve sucker survived and a predation event occurred in 50% of trials with naïve sucker (Fig. 6). In three of four trials where predation occurred one sucker was consumed, two sucker were consumed in the fourth trial (Fig. 7). Mean survival of naïve sucker was significantly less than trained sucker (t_7=-2.497, p=0.0206). The raw data collected can be found in Table C.1.

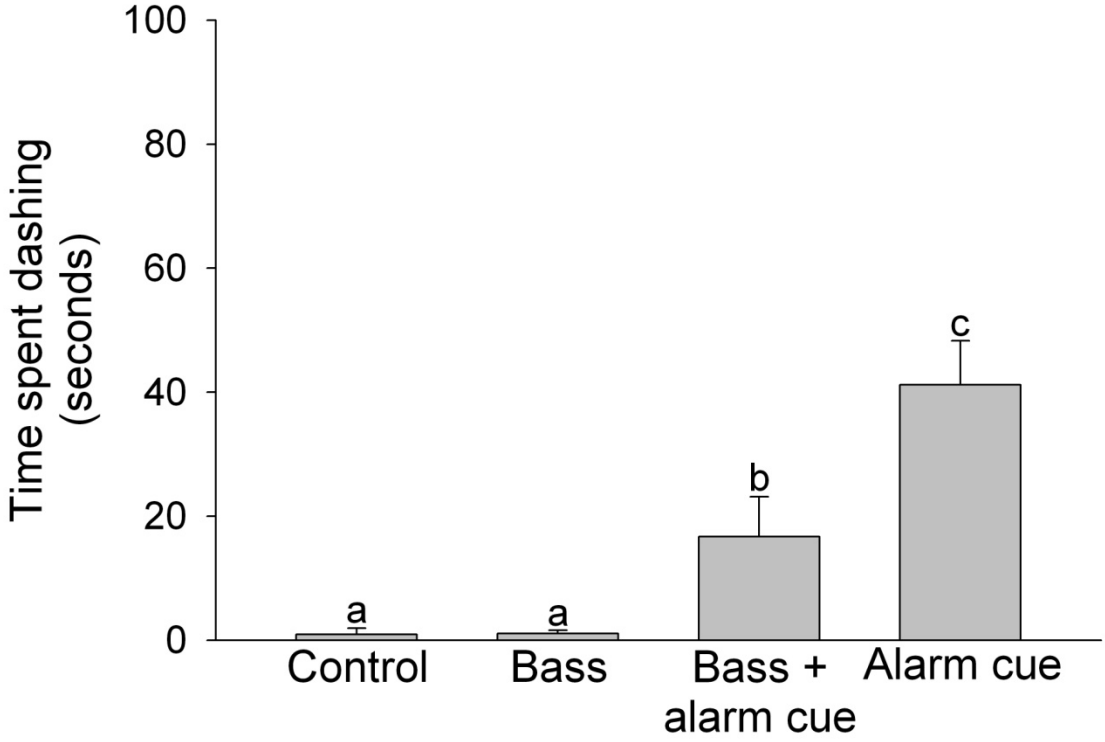

FIGURE 3. Time spent dashing (mean + SE) by treatment in experiment one. Time spent dashing was calculated by subtracting pre-exposure from post-exposure values for each trial. Significance was determined using ANOVA ($F_{3,44} = 15.52$, $p < 0.0001$). Letters above bars indicate significant differences among treatments identified by REGWQ post hoc mean comparison ($p < 0.05$).

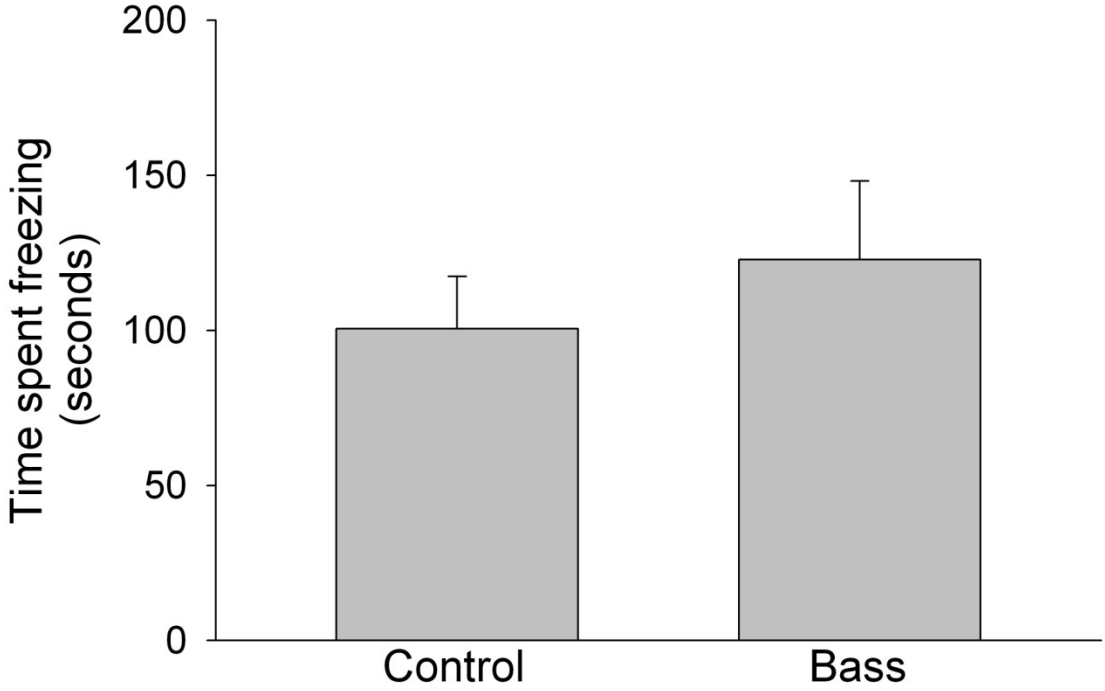

FIGURE 4. Time spent freezing (mean + SE) for control and bass treatments in experiment one. Time spent freezing was calculated by subtracting pre-exposure from post-exposure values for each trial. Means were compared using a paired t-test ($t_{22} = 0.73$, $p = 0.4713$).

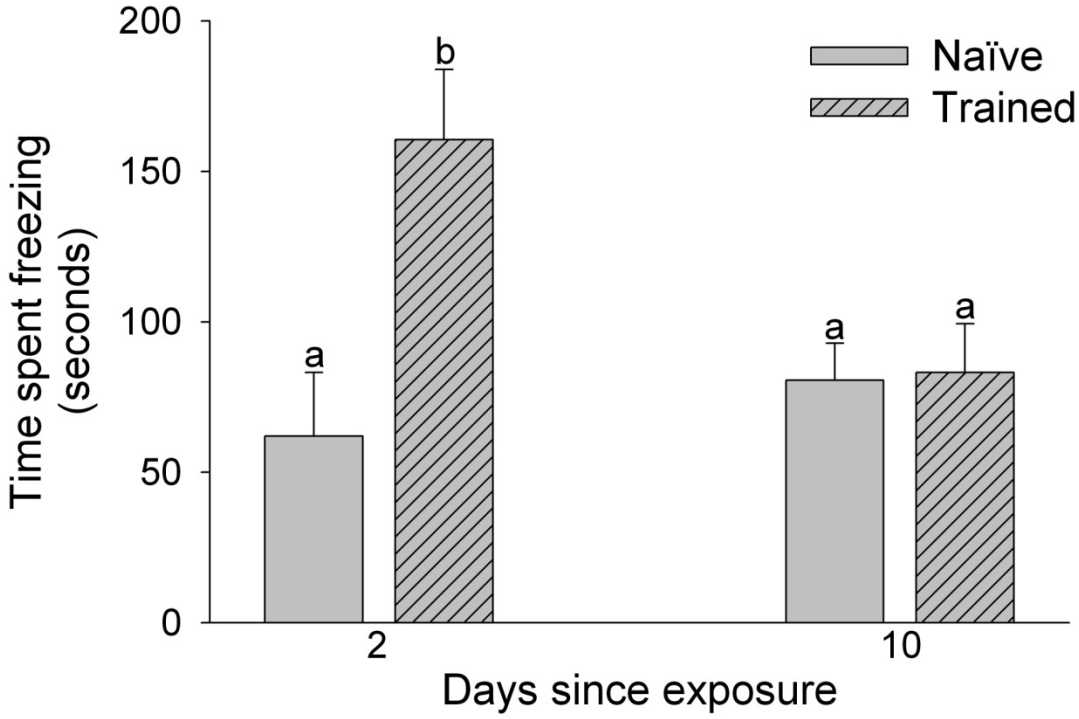

FIGURE 5. Time spent freezing (mean + SE) by exposure history after two and ten days in experiment two. Time spent freezing was calculated by subtracting pre-exposure from post-exposure values for each trial. Significance was determined using ANOVA ($F_{3,28}$ = 6.31, $p < 0.0021$). Letters above bars indicate significant differences among treatments identified by Tukey post hoc test ($p < 0.03$).

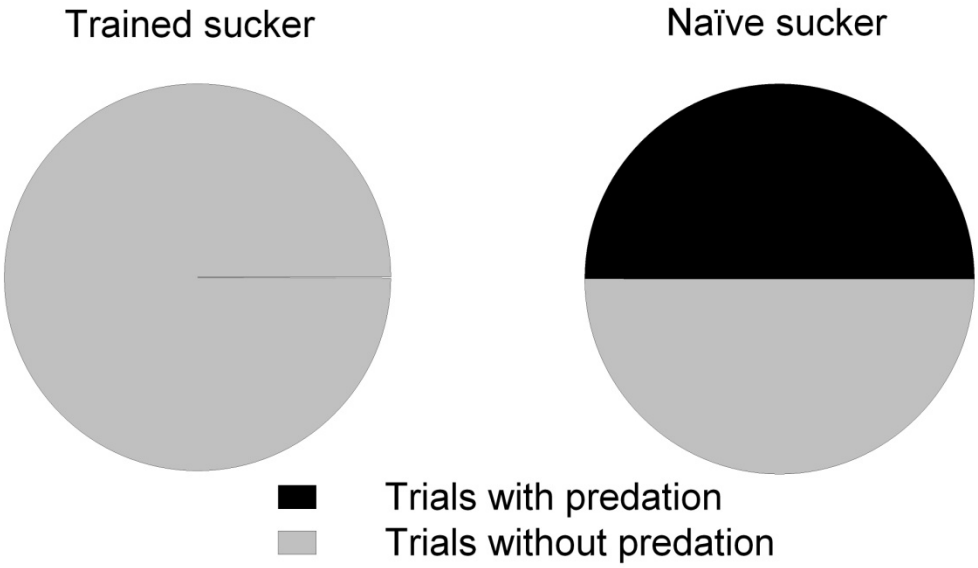

FIGURE 6. The number of trials with and without predation for both trained and naïve fish .

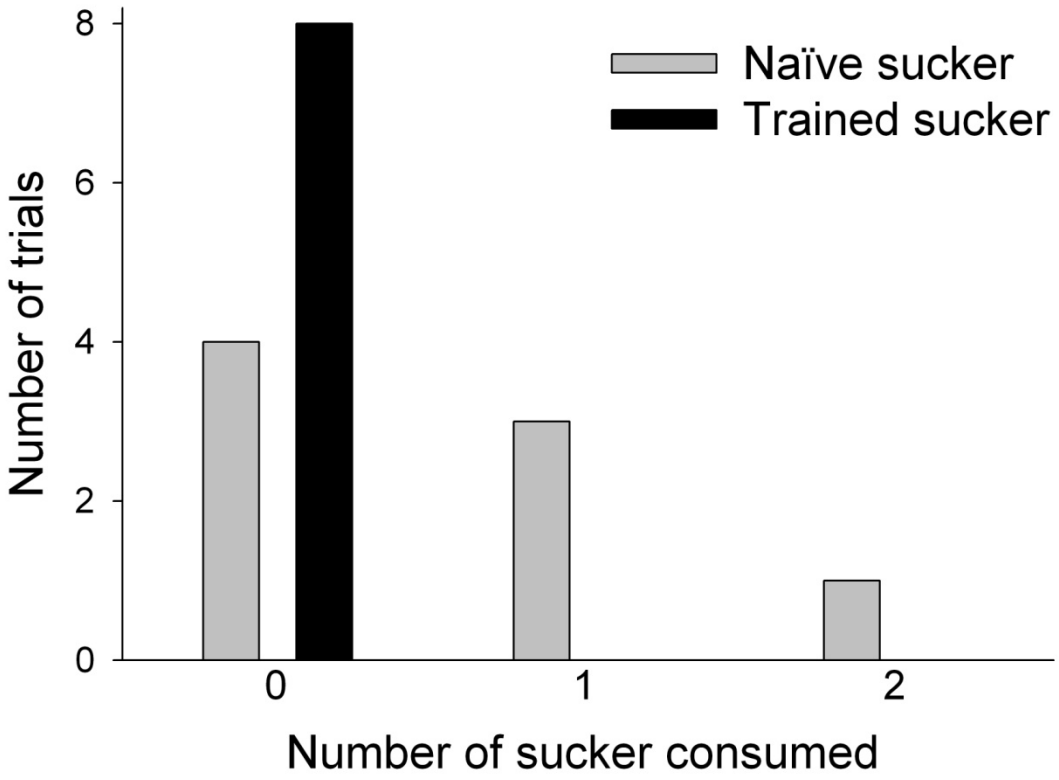

FIGURE 7. Distribution of sucker consumed in survivorship experiment experiment trials.

DISCUSSION

Incorporating behavior into the study of conservation biology has been a topic of interest for some time (see Behavioural ecology as a tool in conservation biology, *Oikos* 77:2). Antipredator behavior, specifically ways to combat native prey naïveté, is an area that is potentially useful for managers (Shumway 1999; Caro 2007). As captive propagation programs increase in fisheries management, interest in training hatchery-raised fish in everything from natural feeding to antipredator behavior has also increased (Suboski & Templeton 1989; Brown & Laland 2001; Wisenden et al. 2004).

In my experiments I found evidence to support my first hypothesis that June sucker do not have an innate recognition of bass odor. I saw no difference in the behavior of sucker exposed to predator odor alone and the control. Naïveté towards a novel predator's odor is consistent with other studies (Brown 2003). Hatchery-raised rainbow trout (*Oncorhynchus mykiss*) have been shown to be naïve to the odor of both cutthroat trout (*Oncorhynchus clarkii*) and northern pike (*Esox lucius*) (Brown & Smith 1998; Mirza & Chivers 2003). Yet some hatchery raised fish do appear to retain an innate recognition of a predator's odor with whom they share a co-evolutionary history. Atlantic salmon (*Salmo salar*) have been shown to possess an innate recognition of the danger posed by northern pike (Hawkins et al. 2007b). Chinook salmon (*Oncorhynchus tshawytscha*) have also been shown to possess an innate recognition of northern pikeminnow (*Ptychocheilis oregonensis*). Similarly, arctic charr (*Salvelinus alpines*) were shown to respond innately to the odor of brown trout (*Salmo trutta*) (Vilhunen & Hirvonen 2003).

My second hypothesis, that June sucker produce and react to a conspecific alarm cue, was also supported by my data. Sucker exposed to June sucker alarm cue alone exhibited the highest levels of dashing behavior. Production of conspecific alarm cue is one of the characteristics of the super-order Ostariophysi (Helfman et al. 1997). Suckers are a member of the ostariophysan super-order; thus my results were expected.

I also found support for the hypothesis that June sucker can recognize conspecific alarm cue in the odor of a largemouth bass which has eaten June sucker. I saw significantly higher levels of dashing in fish exposed to the odor of largemouth bass which had eaten June sucker than in those exposed to distilled water. The amount of time spent dashing was significantly higher in those sucker exposed only to alarm cue compared to those exposed to bass odor plus alarm cue. One possible explanation for this is that the concentration of alarm cue would be much higher in the alarm cue only stimulus simply because the bass plus alarm cue treatment contains both predator odor and alarm cue. Concentration of alarm cue may serve as an indicator of the proximity of the predation event or the threat posed by the approaching predator (Mirza & Chivers 2003; Zhao et al. 2006). If concentration does convey information about proximity or threat level a stimulus which contains a higher concentration of the alarm cue would be expected to elicit higher levels of fright response. Hawkins et al. (2007b) found that the fright response of Atlantic salmon to pike increased as concentration increased. Similarly, Zhao et al. (2006) found that the fright response of goldfish (*Carassius auratus*) to pike odor and goldfish alarm cue increased as the concentration of the stimulus was increased.

My fourth hypothesis, that sucker can learn to associate bass odor with the threat of predation was also supported by my data. Although my results showed June sucker can

learn to associate largemouth bass odor with the threat of predation, this association disappeared by 10 days after exposure. The short length of time that June sucker retain a fright response to predator odor may be due to a lack of reinforcement of the association. More research is needed to investigate the effectiveness of coupling chemical cue training with visual reinforcement of a predation event in increasing the length of retention. The short retention length makes sense considering the "odor cocktail" in which fish live in the natural environment. There are a wide variety of odors which would be present at any given time in addition to the predator odor and alarm cue. It would be not be to the fish's advantage to form a permanent association between every odor present and danger after a single exposure to conspecific alarm cue. Therefore, fish may retain a short association, and in the absence of reinforcement, the association may disappear.

Examples of learned recognition of a novel predator odor are abundant in the literature. The length of retention of the learned recognition appears to vary significantly between species. Rainbow trout have been shown to retain a fright response to a learned predator odor for 21 days, brook trout (*Salvelinus fontinalis*) have only been found to retain an association for 10 days (Brown & Smith 1998; Mirza & Chivers 2000). In many species that have been shown to learn from alarm cues (ex. Chinook salmon, walleye, glowlight tetras, goldfish, Atlantic salmon) the duration of association has not been tested (Berejikian et al. 1999; Darwish et al. 2005; Zhao et al. 2006; Leduc et al. 2007).

Despite the short duration of the association, training June sucker to recognize largemouth bass odor did increase survival in a later encounter with a bass. The increase in survival supports my fifth hypothesis: Training sucker to recognize bass odor will increase survival in a later encounter with a bass. Although statistically significant the

difference in survival between trained and naïve fish may not appear staggering. The small difference may be explained by the nature of the trials. In a tank with no filtration, once a predation event occurs it is reasonable to assume alarm cue would be released into the water. From the results of the alarm cue recognition experiment, it is reasonable to conclude that release of alarm cue would elicit a strong fright response in the sucker remaining in the tank. If the anti-predator behavior of the sucker is effective against the predation strategy employed by largemouth bass, no further predation would be expected.

My study is not the first to show an increase in survival after predator odor training of hatchery-raised fish. Mirza and Chivers (2000) found that brook trout trained to recognize chain pickerel (*Esox niger*) odor had higher survival in subsequent encounters with chain pickerel in both laboratory and field experiments. Fathead minnows trained to recognize a heterospecific's alarm cue were less likely to be attacked when exposed to a novel predator which had consumed the heterospecific species they were trained to recognize than those with no training (Chivers et al. 2002). Berejikian et al. (1999) compared the survival of juvenile Chinook trained to recognize the odor of cutthroat trout. The Chinook were raised in both traditional and complex hatchery environments. The results of their study were mixed, although there was evidence that recognition of cutthroat trout odor increased survival when the juveniles were placed in a natural stream. Not all studies investigating possible survival benefits of training hatchery raised fish to recognize predator odors have found positive results. Hawkins et al. (2007a) found no difference between the survival of naïve juvenile hatchery raised Atlantic salmon and those trained to recognize pike odor. Studies of survival benefit are complex and it is

difficult to control for all sources of mortality in field studies, which may account for some of the variability in results.

The production of an alarm cue is essential for this type of predator-recognition training to be applicable in management situations. Ostariophysan fish make up approximately 64% of all freshwater fish species worldwide, and research has shown that the production of alarm cue is not limited to the Ostariophysan order (Mathis & Smith 1993; Chivers & Smith 1998). The wide spread nature of alarm cues suggests that training captively propagated fish may be applicable to a wide variety of native, threatened fish.

Prior to implementation of a training program for hatchery-raised fish, several other questions need to be addressed. Many studies have found that chemical pollution and an altered pH can negatively impact the ability of fish to detect chemical cues (McPherson et al. 2004; Olivier et al. 2006; Mandrillon & Saglio 2007). For fish that are being reintroduced to chemically impacted water bodies trials should be conducted in water collected from the body of water where the reintroduction is intended. Also, many systems where nonnatives are a significant threat to the continued existence of native fish have more than one nonnative predator. To my knowledge, only one study has been conducted testing the ability of fish to learn the odors of several predators at once (Darwish et al. 2005). Darwish et al. found that glowlight tetras (*Carassius auratus*) were able to learn to recognize several novel predator odors from a single exposure to a stimulus containing the odor of 3 predators and the glowlight tetra alarm cue. The ability to learn from exposure to novel odors in conjunction with conspecific alarm cue varies

greatly across species. Therefore species-specific studies should be conducted before implication of a training program.

To reestablish or recover native fish, removal of nonnative predators is often the most desirable goal, but is likely not achievable. My research shows that it may be possible to train naive, hatchery-raised fish to recognize predators prior to stocking and decrease losses due to predation. Training native fish combined with control of nonnative predator may reduce predation losses enough to allow stocked fish to contribute to the spawning population, which is the goal of most captive propagation programs.

Just as understanding the ecology and genetics of the species of concern is essential to designing an effective management strategy, understanding an organism's behavior can often give insights into how to make conservation efforts more effective and efficient. Some conservation efforts have faltered due to a lack of incorporating the known behavior of the organism into the conservation efforts. For example, efforts to establish a migrating population of the endangered whooping crane (*Grus Americana*) were hampered by an oversight in accounting for the early-life sexual imprinting behavior of the whooping crane. During the reintroduction project, whooping cranes hatched in captivity were raised by sandhill cranes (*Grus Canadensis*), with the idea that the migratory sandhill cranes would teach their migration behavior and route to the young whooping cranes, eventually establishing a self-sustaining breeding population of whooping cranes. This strategy would have worked if whooping cranes did not learn to mate with sandhill cranes by visually imprinting on them. This behavior resulted in a cohort of whooping cranes that would not display to conspecifics, which led to failure of the reintroduction (U.S. Fish and Wildlife Service 1997). This example highlights the

importance of taking the behavior of the organism into account when designing management strategies.

My work is one example of combining behavioral knowledge with management and conservation goals to increase the effectiveness of programs that are already in place. Predation by nonnatives has long been recognized as an obstacle to effective reintroduction and stocking efforts for native fish (Marsh & Brooks 1989). Unfortunately, nonnatives are notoriously difficult to remove once they are established, either due to logistical constraints or public opinion. My results suggest that training may decrease predation on newly stocked hatchery-raised June sucker.

LITERATURE CITED

Abrahams, M. 2006. The physiology of antipredator behaviour: what you do with what you've got. Pages 79-109 in K. A. Sloman, R. W. Wilson, and S. Balshine, editors. Behaviour and physiology of fish. Elsevier Academic Press, San Diego, CA.

Angermeier, P. L. 1995. Ecologica attributes of extinction-prone species - loss of fresh-water fishes of virginia. Conservation Biology **9**:143-158.

Appleton, R. D., and A. R. Palmer. 1988. Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in a marine gastropod. Proceedings of the National Academy of Sciences of the United States of America **85**:4387-4391.

Atema, J., and D. Stenzler. 1977. Alarm substance of marine mud snail, nassarius obsoletus - biological characterization and possible evolution. Journal of Chemical Ecology **3**:173-187.

Bearlin, A. R., E. S. G. Schreiber, S. J. Nicol, A. M. Starfield, and C. R. Todd. 2002. Identifying the weakest link: simulating adaptive management of the reintroduction of a threatened fish. Canadian Journal of Fisheries and Aquatic Sciences **59**:1709-1716.

Belk, M. C., M. J. Whitney, and G. B. Schaalje. 2001. Complex effects of predators: determining vulnerability of the endangered june sucker to an introduced predator. Animal Conservation **4**:251-256.

Berejikian, B. A., R. J. F. Smith, E. P. Tezak, S. L. Schroder, and C. M. Knudsen. 1999. Chemical alarm signals and complex hatchery rearing habitats affect antipredator behavior and survival of chinook salmon (oncorhynchus tshawytscha) juveniles. Canadian Journal of Fisheries and Aquatic Sciences **56**:830-838.

Billman, E. J., and T. A. Crowl. 2007. Population dynamics of a june sucker refuge population. Transactions of the American Fisheries Society **136**:959-965.

Bronmark, C., and J. G. Miner. 1992. Predator-induced phenotypical change in body morphology in crucian carp Science **258**:1348-1350.

Brown, C., and K. Laland. 2001. Social learning and life skills training for hatchery reared fish. Journal of Fish Biology **59**:471-493.

Brown, G. E. 2003. Learning about danger: chemical alarm cues and local risk assessment in prey fishes. Fish and Fisheries **4**:227-234.

Brown, G. E., J. C. Adrian, N. T. Naderi, M. C. Harvey, and J. M. Kelly. 2003. Nitrogen oxides elicit antipredator responses in juvenile channel catfish, but not in convict cichlids or rainbow trout: conservation of the ostariophysan alarm pheromone. Journal of Chemical Ecology **29**:1781-1796.

Brown, G. E., J. C. Adrian, and M. L. Shih. 2001. Behavioural responses of fathead minnows to hypoxanthine-3-n-oxide at varying concentrations. Journal of Fish Biology **58**:1465-1470.

Brown, G. E., J. C. Adrian, E. Smyth, H. Leet, and S. Brennan. 2000. Ostariophysan alarm pheromones: laboratory and field tests of the functional significance of nitrogen oxides. Journal of Chemical Ecology **26**:139-154.

Brown, G. E., and S. Brennan. 2000. Chemical alarm signals in juvenile green sunfish (lepomis cyanellus, centrarchidae). Copeia:1079-1082.

Brown, G. E., and J. G. J. Godin. 1997. Anti-predator responses to conspecific and heterospecific skin extracts by threespine sticklebacks: alarm pheromones revisited. Behaviour **134**:1123-1134.

Brown, G. E., and J. G. J. Godin. 1999a. Chemical alarm signals in wild trinidadian gunnies (poecilia reticulata). Canadian Journal of Zoology-Revue Canadienne De Zoologie **77**:562-570.

Brown, G. E., and J. G. J. Godin. 1999b. Who dares, learns: chemical inspection behaviour and acquired predator recognition in a characin fish. Animal Behaviour **57**:475-481.

Brown, G. E., J. G. J. Godin, and J. Pedersen. 1999. Fin-flicking behaviour: a visual antipredator alarm signal in a characin fish, hemigrammus erythrozonus. Animal Behaviour **58**:469-475.

Brown, G. E., and R. J. F. Smith. 1998. Acquired predator recognition in juvenile rainbow trout (oncorhynchus mykiss): conditioning hatchery-reared fish to recognize chemical cues of a predator. Canadian Journal of Fisheries and Aquatic Sciences **55**:611-617.

Bruton, M. N. 1995. Have fishes had their chips - the dilemma of threatened fishes. Environmental Biology of Fishes **43**:1-27.

Caro, T. 2007. Behavior and conservation: a bridge too far? Trends in Ecology & Evolution **22**:394-400.

Chivers, D. P., G. E. Brown, and R. J. F. Smith. 1995a. Acquired recognition of chemical stimuli from pike, esox-lucius, by brook sticklebacks, culaea inconstans (osteichthyes, gasterosteidae). Ethology **99**:234-242.

Chivers, D. P., G. E. Brown, and R. J. F. Smith. 1996a. The evolution of chemical alarm signals: attracting predators benefits alarm signal senders. American Naturalist **148**:649-659.

Chivers, D. P., R. S. Mirza, and J. G. Johnston. 2002. Learned recognition of heterospecific alarm cues enhances survival during encounters with predators. Behaviour **139**:929-938.

Chivers, D. P., and R. J. F. Smith. 1993. The role of olfaction in chemosensory-based predator recognition in the fathead minnow, pimephales promelas. Journal of Chemical Ecology **19**:623-633.

Chivers, D. P., and R. J. F. Smith. 1994a. Fathead minnows, pimephales promelas, aquire predator recognition when alarm substance is associated with the sight of unfamiliar fish Animal Behaviour **48**:597-605.

Chivers, D. P., and R. J. F. Smith. 1994b. Intrapsecific and interspecific avoidance of areas marked with skin extract from brook sticklebacks (culaea inconstans) in a natural habitat. Journal of Chemical Ecology **20**:1517-1524.

Chivers, D. P., and R. J. F. Smith. 1998. Chemical alarm signalling in aquatic predator-prey systems: a review and prospectus. Ecoscience **5**:338-352.

Chivers, D. P., B. D. Wisenden, and R. J. F. Smith. 1995b. The role of experience in the response of fathead minnows (pimephales promelas) to skin extract of iowa darters (etheostoma exile). Behaviour **132**:665-674.

Chivers, D. P., B. D. Wisenden, and R. J. F. Smith. 1996b. Damselfly larvae learn to recognize predators from chemical cues in the predator's diet. Animal Behaviour **52**:315-320.

Cox, J. G., and S. L. Lima. 2006. Naivete and an aquatic-terrestrial dichotomy in the effects of introduced predators. Trends in Ecology & Evolution **21**:674-680.

Crowl, T. A., and A. P. Covich. 1990. Predator-induced life-history shifts in a fresh-water snail Science **247**:949-951.

Dalesman, S., S. D. Rundle, D. T. Bilton, and P. A. Cotton. 2007. Phylogenetic relatedness and ecological interactions determine antipredator behavior. Ecology **88**:2462-2467.

Darwish, T. L., R. S. Mirza, A. Leduc, and G. E. Brown. 2005. Acquired recognition of novel predator odour cocktails by juvenile glowlight tetras. Animal Behaviour **70**:83-89.

Dextrase, A. J., and N. E. Mandrak. 2006. Impacts of alien invasive species on freshwater fauna at risk in canada. Biological Invasions **8**:13-24.

Dicke, M., and P. Grostal. 2001. Chemical detection of natural enemies by arthropods: an ecological perspective. Annual Review of Ecology and Systematics **32**:1-23.

Dodson, S. I., T. A. Crowl, B. L. Peckarsky, L. B. Kats, A. P. Covich, and J. M. Culp. 1994. Nonvisual communication in fresh-water benthos - an overview. Journal of the North American Benthological Society **13**:268-282.

Dodson, S. I., and T. Hanazato. 1995. Commentary on effects of anthropogenis and natural organic-chemicals on development, swimming behavior, and reproduction of daphnia, a key member of aquatic ecosystems Pages 7-11.

Dominy, N. J., C. F. Ross, and T. D. Smith. 2004. Evolution of the special senses in primates: past, present, and future. Anatomical Record Part a-Discoveries in Molecular Cellular and Evolutionary Biology **281A**:1078-1082.

Døving, K. B., E. H. Hamdani, E. Höglund, A. Kasumyan, and A. O. Tuvikene. 2005. Review of the chemical and physiological basis of alarm reactions in cyprinids. Pages 133-163 in K. Reutter and B. G. Kapoor, editors. Fish chemosenses. Science Publishers, Inc., Enfield, NH.

Eibl Eibesfeldt, I. 1949. Uber das vorkommen von schreckstoffen bei erdkrotenquappen. Experientia **5**:236-236.

Garcia, C., E. Rolanalvarez, and L. Sanchez. 1992. Alarm reaction and alert state in gambusia affinis (pisces, poeciliidae) in response to chemical stimuli from injured conspecifics. Journal of Ethology **10**:41-46.

Golub, J. L., and G. E. Brown. 2003. Are all signals the same? Ontogenetic change in the response to conspecific and heterospecific chemical alarm signals by juvenile green sunfish (lepomis cyanellus). Behavioral Ecology and Sociobiology **54**:113-118.

Golub, J. L., V. Vermette, and G. E. Brown. 2005. Response to conspecific and heterospecific alarm cues by pumpkinseeds in simple and complex habitats: field verification of an ontogenetic shift. Journal of Fish Biology **66**:1073-1081.

Gonzalo, A., P. Lopez, and J. Martin. 2007. Iberian green frog tadpoles may learn to recognize novel predators from chemical alarm cues of conspecifics. Animal Behaviour **74**:447-453.

Göz, H. 1941.Űberden art-und individualgeruch bie fischen. Zeitschrift fur Vergleichende Physiologie **29**:1-45.

Hamdani, E. H., and K. B. Døving. 2007. The functional organization of the fish olfactory system. Progress in Neurobiology **82**:80-86.

Hawkins, L. A., J. D. Armstrong, and A. E. Magurran. 2007a. A test of how predator conditioning influences survival of hatchery-reared atlantic salmon, salmo salar, in restocking programmes. Fisheries Management and Ecology **14**:291-293.

Hawkins, L. A., A. E. Magurran, and J. D. Armstrong. 2007b. Innate abilities to distinguish between predator species and cue concentration in atlantic salmon. Animal Behaviour **73**:1051-1057.

Hayward, R. S., and M. E. Bushmann. 1994. Gastric evacuation rates for juvenile largemouth bass. Transactions of the American Fisheries Society **123**:88-93.

Hazlett, B. A. 1990. Disturbance pheromone in the hermic-crab calcinus laevimanus (randall, 1840) Crustaceana **58**:314-316.

Hazlett, B. A. 1994. Alarm responses in the crayfish orchonectes virilis and orconectes propinquus. Journal of Chemical Ecology **20**:1525-1535.

Helfman, G. S. 2007. Fish conservation: a guide to understanding and restoring global aquatic biodiversity and fishery resources. Island Press, Washington, DC.

Helfman, G. S., B. B. Collette, and D. E. Facey 1997. The diversity of fishes. Blackwell Science, Inc., Malden, Massachusetts.

Hews, D. K. 1988. Alarm response in larval western toads, bufo boreas - release of larval chemicals by a natural predator and its effect on a predator capture efficiency. Animal Behaviour **36**:125-133.

Hews, D. K., and A. R. Blaustein. 1985. An investigation of the alarm response in bufo boreas and rana cascadae tadpoles. Behavioral and Neural Biology **43**:47-57.

Houtman, R., and L. M. Dill. 1994. The influence of substrate color on the alarm response of tidepool sculpins (oligocottus maculosus, pisces, cottidae). Ethology **96**:147-154.

Howe, N. R. 1976. Behavior of sea anemones evoked by alarm pheromone anthopleurine. Journal of Comparative Physiology **107**:67-76.

Hrbacek, J. 1950. On the flight reaction of tadpoles of the common toad caused by chemical substances. Experientia **6**:100-102.

Hugie, D. M., P. L. Thuringer, and R. J. F. Smith. 1991. The response of the tidepool sculpin, oligocottus maculosus, the chemical stimuli from injured conspecifics, alarm signaling in the cottidae (pisces). Ethology **89**:322-334.

Jaiswal, S. K., and S. Waghray. 1990. Quantification of defense reactions of cichlid fish, oreochromis mossambicus (peters) trewavas, in response to warning chemicals. Indian Journal of Animal Sciences **60**:1137-1145.

Jakobsen, J., and G. H. Johnsen. 1989. The influence of alarm substance on feeding in zebra danio fish (brachydanio rerio). Ethology **82**:325-327.

Kats, L. B., and L. M. Dill. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience **5**:361-394.

Kulzer, E. 1954. Üntersuchungen uber die schreckreaktion der erdkrotenkaulquappen (bufo bufo l). Zeitschrift fur Vergleichende Physiologie **36**:443-463.

Laforsch, C., L. Beccara, and R. Tollrian. 2006. Inducible defenses: the relevance of chemical alarm cues in daphnia. Limnology and Oceanography **51**:1466-1472.

Lawrence, B. J., and R. J. F. Smith. 1989. Behavioral response of solitary fathead minnows, pimephales promelas, to alarm substance. Journal of Chemical Ecology **15**:209-219.

Lawrence, J. M. 1991. A chemical alarm response in pycnopodia helianthoides (echinodermata, asteroidea). Marine Behaviour and Physiology **19**:39-44.

Leduc, A., E. Roh, C. Breau, and G. E. Brown. 2007. Learned recognition of a novel odour by wild juvenile atlantic salmon, salmo salar, under fully natural conditions. Animal Behaviour **73**:471-477.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation - a review and prospectus. Canadian Journal of Zoology-Revue Canadienne De Zoologie **68**:619-640.

Lind, J., and W. Cresswell. 2005. Determining the fitness consequences of antipredation behavior. Behavioral Ecology **16**:945-956.

Lodge, D. M., R. A. Stein, K. M. Brown, A. P. Covich, C. Bronmark, J. E. Garvey, and S. P. Klosiewski. 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Australian Journal of Ecology **23**:53-67.

Magurran, A. E. 1989. Acquired recognition of predator odor in the europoean minnow (phoxinus phoxinus). Ethology **82**:216-223.

Magurran, A. E., P. W. Irving, and P. A. Henderson. 1996. Is there a fish alarm pheromone? A wild study and critique. Proceedings of the Royal Society of London Series B-Biological Sciences **263**:1551-1556.

Mandrillon, A. L., and P. Saglio. 2007. Herbicide exposure affects the chemical recognition of a non native predator in common toad tadpoles (bufo bufo). Chemoecology **17**:31-36.

Mann, K. H., J. L. C. Wright, B. E. Welsford, and E. Hatfield. 1984. Responses of the sea urchin strongylocentrotus droebachiensis (muller, o.F.) to water-borne stimuli from potential predators and potential food algae. Journal of Experimental Marine Biology and Ecology **79**:233-244.

Marsh, P. C., and J. E. Brooks. 1989. Predation by ictalurid catfishes as a deterrent to re-establishment of hatchery-reared razorback suckers. Southwestern Naturalist **34**:188-195.

Marvin, G. A., and V. H. Hutchison. 1995. Avoidance-response by adult newts (cynops-pyrrhogaster and notophthalmus-viridescens) to chemical alarm cues. Behaviour **132**:95-105.

Mathis, A., and R. J. F. Smith. 1993. Intraspecific and cross-superorder responses to chemical alarm signals by brook stickleback. Ecology **74**:2395-2404.

McIntosh, A. R., T. A. Crowl, and C. R. Townsend. 1994. Size-related impacts of introduced brown trout on the distribution of native common river galaxias. New Zealand Journal of Marine and Freshwater Research **28**:135-144.

McKillup, S. C., and R. V. McKillup. 1992. Inhibition of feeding in response to crushed conspecifics by the pebble crab philyra laevis (bell). Journal of Experimental Marine Biology and Ecology **161**:33-43.

McPherson, T. D., R. S. Mirza, and G. G. Pyle. 2004. Responses of wild fishes to alarm chemicals in pristine and metal-contaminated lakes. Canadian Journal of Zoology-Revue Canadienne De Zoologie **82**:694-700.

Mills, M. D., R. B. Rader, and M. C. Belk. 2004. Complex interactions between native and invasive fish: the simultaneous effects of multiple negative interactions. Oecologia **141**:713-721.

Mirza, R. S., and D. P. Chivers. 2000. Predator-recognition training enhances survival of brook trout: evidence from laboratory and field-enclosure studies. Canadian Journal of Zoology-Revue Canadienne De Zoologie **78**:2198-2208.

Mirza, R. S., and D. P. Chivers. 2001. Learned recognition of heterospecific alarm signals: the importance of a mixed predator diet. Ethology **107**:1007-1018.

Mirza, R. S., and D. P. Chivers. 2003. Response of juvenile rainbow trout to varying concentrations of chemical alarm cue: response thresholds and survival during encounters with predators. Canadian Journal of Zoology-Revue Canadienne De Zoologie **81**:88-95.

Olivier, A., H. C. Leduc, E. Roh, M. C. Harvey, and G. E. Brown. 2006. Impaired detection of chemical alarm cues by juvenile wild atlantic salmon (salmo salar) in a weakly acidic environment. Canadian Journal of Fisheries and Aquatic Sciences **63**:2356-2363.

Persson, L., J. Andersson, E. Wahlstrom, and P. Eklov. 1996. Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. Ecology **77**:900-911.

Petranka, J. W. 1989. Response of toad tadpoles to conflicting chemical stimuli - predator avoidance versus optimal foraging. Herpetologica **45**:283-292.

Pfeiffer, W. 1960. Uber die schredckreaktion bei fischen und die herkunft des schreckstoffes. Zeitschrift fur Vergleichende Physiologie **43**:578-614.

Pfeiffer, W. 1963. Alarm substances. Experientia **19**:113-123.

Pfeiffer, W. 1966. Die verbreitung der schreckreaktion bei kaulquappen und die herkunft des schrecktoffes. Zeitschrift fur Vergleichende Physiologie **52**:79-&.

Pfeiffer, W. 1977. Distribution of fright reaction and alarm substance cells in fishes. Copeia:653-665.

Pfeiffer, W., G. Riegelbauer, G. Meier, and B. Scheibler. 1985. Effect of hypoxanthine - 3(n)-oxide and hypoxanthine-1(n)-oxide on central nervous excitation of the black tetra gymnocorymbus ternetzi (characidae, ostariophysi, pisces) indicated by dorsal light response. Journal of Chemical Ecology **11**:507-523.

Rakes, P. L., J. R. Shute, and P. W. Shute. 1999. Reproductive behavior, captive breeding, and restoration ecology of endangered fishes. Environmental Biology of Fishes **55**:31-42.

Reed, J. R. 1969. Alarm substances and fright reaction in some fishes from southeastern united states. Transactions of the American Fisheries Society **98**:664-&.

Rittschof, D., D. W. Tsai, P. G. Massey, L. Blanco, G. L. Kueber, and R. J. Haas. 1992. Chemical mediation of behavior in hermit crabs - alarm and aggregation cues Journal of Chemical Ecology **18**:959-984.

SAS Institute. 2004. Sas 9.1.3 service pack 4. SAS Institute, Cary, NC.

Schutz, F. 1956. Vergleichende untersuchengen uber die schreckreaktion bei fischen und deren verbreitung Zeitschrift fur Vergleichende Physiologie **38**:84-135.

Scoppettone, G. G., and G. Vinyard. 1991. Life history and management of four endangered lucastrine suckers. Pages 359-377 in W. L. Minckley and J. E. Deacon, editors. Battle against extinction: native fish managment in the american west. The University of Arizona Press, Tucson, AZ.

Scrimgeour, G. J., J. M. Culp, and K. J. Cash. 1994. Antipredator responses of mayfly larvae to conspecific and predator stimuli. Journal of the North American Benthological Society **13**:299-309.

Shumway, C. A. 1999. A neglected science: applying behavior to aquatic conservation. Environmental Biology of Fishes **55**:183-201.

Sih, A. 1986. Antipredator responses and the perception of danger by mosquito larvae. Ecology **67**:434-441.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities - a review of field experiments. Annual Review of Ecology and Systematics **16**:269-311.

Smith, R. J. F. 1979. Alarm reaction of iowa and johnny darters (etheostoma, percidae, pisces) to chemical from injured conspecifics. Canadian Journal of Zoology-Revue Canadienne De Zoologie **57**:1278-1282.

Smith, R. J. F. 1982. Reaction of percina nigrofasciate, ammocrypta beani, and etheostoma swaini (percidae, pisces) to conspecific and intergeneric skin extracts. Canadian Journal of Zoology-Revue Canadienne De Zoologie **60**:1067-1072.

Smith, R. J. F. 1989. The response of asterropteryx semipunctatus and gnatholepis anjerensis (pisces, gobiidae) to chemical stimuli from injured conspecifics, an alarm response in gobies. Ethology **81**:279-290.

Smith, R. J. F. 1997. Does one result trump all others? A response to Magurran, Irving and Henderson. Proceedings of the Royal Society of London Series B-Biological Sciences **264**:445-450.

Smith, R. J. F., and B. J. Lawrence. 1992. The response of a bumblebee goby, brachygobius sabanus, to chemical stimuli from injured conspecifics. Environmental Biology of Fishes **34**:103-108.

Smith, R. J. F., B. J. Lawrence, and M. J. Smith. 1991. Cross reaction to skin extract between 2 gobies, asterropteryx semipunctatus and brachygobius sabanus. Journal of Chemical Ecology **17**:2253-2259.

Snyder, N., and H. Snyder. 1970. Alarm response of diadema antillarum. Science **168**:276-&.

Snyder, N. F. R., and H. A. Snyder. 1971. Defenses of florida apple snail pomacea paludosa. Behaviour **40**:175-&.

Stenzler, D., and J. Atema. 1977. Alarm response of marine mud snail, nassarius obsoletus, specificity and behavioral priority. Journal of Chemical Ecology **3**:159-171.

Suboski, M. D., and J. J. Templeton. 1989. Life skills training for hatchery fish - social-learning and survival. Fisheries Research **7**:343-352.

U.S. Fish and Wildlife Service. 1986. Final rule determining june sucker (chasmistes liorus) to be end. Species w/ crit. Hab. 51 fr 10851-10857. Pages 10851-10857. U.S. Fish and Wildlife Service, Denver, CO.

U.S. Fish and Wildlife Service. 1997. Final rule to designate the whooping cranes of the rocky mountains as experimental nonessential and to remove whooping crane critical habitat designations from four locations. Federal Register **62**:3982-3989.

U.S. Fish and Wildlife Service. 1999. June sucker (chasmistes liorus) recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado.

U.S. Fish and Wildlife Service. 2008. Endangered species program http://www.Fws.Gov/endangered/wildlife.Html.

Utah Department Wildlife Resources. 2008. Fish stocking information, http://www.Wildlife.Utah.Gov/stocking/. Division of Wildlife Resources.

Vermeij, G. J. 1994. The evolutionary interaction among species - selection, escalation, and coevolution. Annual Review of Ecology and Systematics **25**:219-236.

Vilhunen, S., and H. Hirvonen. 2003. Innate antipredator responses of arctic charr (salvelinus alpinus) depend on predator species and their diet. Behavioral Ecology and Sociobiology **55**:1-10.

von Frisch, K. 1938. On the psychology of the fish shoal. Naturwissenschaften **26**:601-606.

von Frisch, K. 1941. About schreckstoff substance in fish skin and its biological significance. Zeitschrift fur Vergleichende Physiologie **29**:46-145.

Warren, M. L., and B. M. Burr. 1994. Status of fresh-water fishes of the united-states - overview of an imperiled fauna. Fisheries **19**:6-17.

Whitney, M., and M. C. Belk. 2000. Threatened fishes of the world: chasmistes liorus jordan, 1878 (catostomidae). Environmental Biology of Fishes **57**:362-362.

Williams, D. D., and K. A. Moore. 1985. The role of semiochemicals in benthis community relationships of the lotic amphipod gammarus pseudolimnaeus - a laboratory analysis. Oikos **44**:280-286.

Wilson, D. J., and H. Lefcort. 1993. The effect of predator diet on the alarm response of red-legged from, rana aurora, tadpoles. Animal Behaviour **46**:1017-1019.

Wilson, E. O., and W. H. Bossert. 1963. Chemical communication among animals. Recent Progress in Hormone Research **19**:673-716.

Wisenden, B. D., D. P. Chivers, and R. J. F. Smith. 1997. Learned recognition of predation risk by enallagma damselfly larvae (odonata, zygoptera) on the basis of chemical cues. Journal of Chemical Ecology **23**:137-151.

Wisenden, B. D., J. Klitzke, R. Nelson, D. Friedl, and P. C. Jacobson. 2004. Predator-recognition training of hatchery-reared walleye (stizostedion vitreum) and a field test of a training method using yellow perch (perca flavescens). Canadian Journal of Fisheries and Aquatic Sciences **61**:2144-2150.

Wisenden, B. D., J. Pogatshnik, D. Gibson, L. Bonacci, A. Schumacher, and A. Willett. 2008. Sound the alarm: learned association of predation risk with novel auditory stimuli by fathead minnows (pimephales promelas) and glowlight tetras (hemigrammus erythrozonus) after single simultaneous pairings with conspecific chemical alarm cues. Environmental Biology of Fishes **81**:141-147.

Wisenden, B. D., and R. C. Sargent. 1997. Antipredator behaviour and suppressed aggression by convict cichlids in response to injury-released chemical cues of

conspecifics but not to those of an allopatric heterospecific. Ethology **103**:283-291.

Witte, F., T. Goldschmidt, J. Wanink, M. Vanoijen, K. Goudswaard, E. Wittemaas, and N. Bouton. 1992. The destruction of an endemic species flock - quantitative data on the deline of the haplochromine cichlids of lake victoria. Environmental Biology of Fishes **34**:1-28.

Woody, D. R., and A. Mathis. 1997. Avoidance of areas labeled with chemical stimuli from damaged conspecifics by adult newts, notophthalmus viridescens, in a natural habitat. Journal of Herpetology **31**:316-318.

Zhao, X. X., M. C. O. Ferrari, and D. P. Chivers. 2006. Threat-sensitive learning of predator odours by a prey fish. Behaviour **143**:1103-1121.

APPENDICES

Appendix A. Data from alarm cue experiment

Table A.1. Data from alarm cue experiment. Stimulus indicates the stimulus injected during the trial (dh20=control, js=alarm cue, bass= bass odor alone, bjs= bass odor plus alarm cue). Dashingpre indicates the amount of time where dashing behavior was observed during the pre-exposure period. Dashingpost indicates the amount of time where dashing behavior was observed during the post-exposure period. Dashingdiff is the difference between dashingpost and dashingpre. Freezepre indicates the amount of time where freezing behavior was observed during the pre-exposure period. Freezepost indicates the amount of time where freezing behavior was observed during the post-exposure period. Freezediff is the difference between freezepost and freezepre.

tank	date	stimulus	dashing pre	dashing post	dashing diff	freeze pre	freeze post	freeze diff
1	11/11/2007	bjs	0.00	0.00	0.00	0.00	105.81	105.81
2	11/11/2007	js	0.00	22.49	22.49	0.00	166.76	166.76
3	11/11/2007	dh20	0.00	0.00	0.00	130.58	288.16	157.58
4	11/11/2007	bass	0.00	5.78	5.78	22.93	141.24	118.31
1	11/12/2007	js	0.00	43.72	43.72	67.43	117.69	50.26
2	11/12/2007	dh20	0.00	5.62	5.62	71.72	167.73	96.01
3	11/12/2007	bass	29.68	31.59	1.91	191.72	115.85	-75.87
4	11/12/2007	bjs	0.00	21.50	21.50	0.00	144.58	144.58
1	11/14/2007	bass	14.41	15.17	0.76	12.18	200.31	188.13
2	11/14/2007	bjs	0.00	62.38	62.38	0.00	136.76	136.76
3	11/14/2007	js	0.00	81.37	81.37	0.00	123.73	123.73
4	11/14/2007	dh20	0.00	0.00	0.00	20.55	66.72	46.17
1	11/15/2007	bjs	0.00	9.69	9.69	142.77	175.00	32.23
2	11/15/2007	js	0.00	43.02	43.02	139.98	160.18	20.20
3	11/15/2007	dh20	0.00	0.00	0.00	234.06	279.37	45.31
4	11/15/2007	bass	0.00	0.00	0.00	0.00	168.47	168.47
1	11/17/2007	dh20	0.00	9.72	9.72	0.00	157.83	157.83
2	11/17/2007	bass	0.00	0.00	0.00	0.00	200.40	200.40
3	11/17/2007	bjs	0.00	0.00	0.00	64.36	17.06	-47.30
4	11/17/2007	js	0.00	38.85	38.85	0.00	167.93	167.93
2	11/18/2007	bjs	0.00	50.60	50.60	11.97	226.75	214.78
1	11/18/2007	bass	0.00	0.00	0.00	103.32	233.82	130.50
3	11/18/2007	js	0.00	0.00	0.00	285.70	300.00	14.30
4	11/18/2007	dh20	0.00	0.00	0.00	0.00	227.77	227.77
1	2/5/2008	bass	0.00	2.06	2.06	0.00	275.65	275.65
2	2/5/2008	bjs	0.00	0.00	0.00	5.00	5.00	0.00
3	2/5/2008	js	0.00	5.62	5.62	15.19	144.94	129.75
4	2/5/2008	dh20	4.31	0.00	-4.31	48.55	154.96	106.41
1	2/7/2008	js	0.00	73.03	73.03	35.69	195.70	160.01
2	2/7/2008	dh20	0.00	0.00	0.00	36.00	137.60	101.60

Table A.1. continued

tank	date	stimulus	dashing pre	dashing post	dashing diff	freeze pre	freeze post	freeze diff
3	2/7/2008	bass	0.00	2.42	2.42	0.00	94.63	94.63
4	2/7/2008	bjs	0.00	0.00	0.00	14.69	47.47	32.78
1	2/10/2008	dh20	0.00	0.00	0.00	0.00	24.34	24.34
2	2/10/2008	bass	0.00	0.00	0.00	120.61	187.77	67.16
3	2/10/2008	bjs	0.00	0.00	0.00	127.72	168.15	40.43
4	2/10/2008	js	0.00	47.65	47.65	0.00	20.28	20.28
1	2/16/2008	bjs	0.00	0.00	0.00	2.94	45.89	42.95
2	2/16/2008	js	0.00	43.10	43.10	5.50	55.64	50.14
3	2/16/2008	dh20	0.00	0.00	0.00	100.25	177.10	76.85
4	2/16/2008	bass	0.00	0.00	0.00	232.92	295.10	62.18
1	3/14/2008	bjs	0.00	18.87	18.87	54.15	147.08	92.93
2	3/14/2008	js	0.00	64.05	64.05	0.00	181.92	181.92
3	3/14/2008	dh20	0.00	0.00	0.00	66.98	124.76	57.78
4	3/14/2008	bass	0.00	0.00	0.00	0.00	92.55	92.55
1	4/18/2008	js	2.34	33.57	31.23	78.81	222.07	143.26
2	4/18/2008	dh20	0.00	0.00	0.00	30.88	140.03	109.15
4	4/18/2008	bjs	0.00	37.52	37.52	39.49	181.49	142.00
3	4/18/2008	bass	0.00	0.00	0.00	8.10	159.84	151.74

APPENDIX B. Data from learning experiment

Table B.1. Data from learning experiment. Time indicates the group (1-4) in which the trial was run. Trials in group one were run first, group two second, etc. Treat indicates the number of days since exposure. Exp indicated the stimulus injected during the trial (bass= bass odor alone, bjs= bass odor plus alarm cue). Dash pre indicates the amount of time where dashing behavior was observed during the pre-exposure period. Dash post indicates the amount of time where dashing behavior was observed during the post-exposure period. Dash diff is the difference between dash post and dash pre. Freeze pre indicates the amount of time where freezing behavior was observed during the pre-exposure period. Freeze post indicates the amount of time where freezing behavior was observed during the post-exposure period. Freeze diff is the difference between freeze post and freeze pre.

tank	time	date	treat	exp	dash pre	dash post	dash diff	freeze pre	freeze post	freeze diff
1	1	7/16/2008	2	bass	0.00	0.00	0.00	23.97	23.79	-0.18
2	1	7/16/2008	2	bass	1.85	0.00	-1.85	74.13	76.74	2.61
2	2	7/16/2008	2	bass	0.00	0.00	0.00	0.00	9.91	9.91
4	1	7/16/2008	2	bass	0.00	0.00	0.00	2.02	17.46	15.44
3	2	7/16/2008	2	bass	0.00	33.07	33.07	178.90	200.46	21.56
3	1	7/16/2008	2	bass	0.00	0.00	0.00	0.00	78.49	78.49
1	3	7/16/2008	2	bass	0.00	0.00	0.00	79.05	248.84	169.79
1	4	7/16/2008	2	bass	0.00	0.00	0.00	0.00	209.81	209.81
3	3	7/16/2008	2	bjs	0.00	0.00	0.00	175.15	260.03	84.88
4	2	7/16/2008	2	bjs	0.00	0.00	0.00	115.62	235.27	119.65
4	4	7/16/2008	2	bjs	0.00	17.01	17.01	16.98	179.74	162.76
3	4	7/16/2008	2	bjs	0.00	0.00	0.00	21.09	229.70	208.61
4	3	7/16/2008	2	bjs	0.00	0.00	0.00	50.20	278.03	227.83
1	2	7/16/2008	2	bjs	0.00	0.00	0.00	61.75	289.67	227.92
2	3	7/16/2008	2	bjs	0.00	0.00	0.00	48.43	277.84	229.41
2	4	7/16/2008	2	bjs	0.00	0.00	0.00	31.68	269.52	237.84
1	3	7/24/2008	10	bass	0.00	0.00	0.00	65.96	91.58	25.62
1	1	7/24/2008	10	bass	0.00	6.23	6.23	0.00	68.74	68.74
3	1	7/24/2008	10	bass	0.00	0.00	0.00	21.16	98.57	77.41
2	2	7/24/2008	10	bass	0.00	0.00	0.00	140.77	242.10	101.33
2	3	7/24/2008	10	bass	0.00	13.56	13.56	159.75	272.68	112.93
2	1	7/24/2008	10	bass	0.00	0.00	0.00	14.50	151.38	136.88
3	4	7/24/2008	10	bass	0.00	0.00	0.00	166.05	276.35	110.30
4	4	7/24/2008	10	bass	0.00	0.00	0.00	87.05	200.00	112.95
2	4	7/24/2008	10	bjs	0.00	0.00	0.00	255.28	253.56	-1.72
3	2	7/24/2008	10	bjs	0.00	0.00	0.00	132.65	167.77	35.12
1	2	7/24/2008	10	bjs	0.00	0.00	0.00	244.03	300.00	55.97
1	4	7/24/2008	10	bjs	0.00	0.00	0.00	202.44	297.92	95.48
4	2	7/24/2008	10	bjs	0.00	0.00	0.00	72.44	199.61	127.17

Table B.1. continued

tank	time	date	treat	exp	dash pre	dash post	dash diff	freeze pre	freeze post	freeze diff
4	3	7/24/2008	10	bjs	0.00	0.00	0.00	149.66	282.71	133.05
4	1	7/24/2008	10	bjs	0.00	0.00	0.00	62.34	195.44	133.10
3	3	7/24/2008	10	bjs	0.00	0.00	0.00	0.00	165.40	165.40

Appendix C. Data from survivorship experiment

Table C.1. Data from survivorship. Exphist refers to the exposure history of the sucker (bjs= bass odor plus alarm cue, bass=bass odor alone). Bass identifies the specific largemouth bass used in the trial.

day	exphist	bass	trial	tank	survived	eaten
1	bass	2	1	1	5	0
1	bass	1	1	2	3	2
2	bass	2	1	1	3	2
2	bjs	3	1	2	5	0
2	bjs	1	2	2	5	0
3	bass	3	1	2	5	0
3	bass	1	2	2	5	0
3	bjs	2	1	1	5	0
4	bass	2	1	1	4	1
4	bjs	3	1	2	5	0
4	bjs	1	2	2	5	0
5	bass	1	1	1	5	0
5	bjs	3	1	1	5	0
5	bjs	2	2	2	5	0
6	bass	3	1	1	3	0
6	bjs	1	1	2	5	0