PHYSIOLOGICAL AND BEHAVIORAL DRIVERS OF ANGLING VULNERABILITY IN FRESHWATER SPORTFISH

BY

MICHAEL JEFFREY LOUISON

DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2018

Urbana, Illinois

Doctoral Committee:

Associate Professor Cory Suski, Chair
Dr. Jeffrey Stein, Director of Research
Associate Professor Alison Bell
Assistant Professor Zachary Cheviron

ABSTRACT

A large body of research has documented evolutionary change in fish populations as a result of selective harvest, a process known as Fisheries-Induced Evolution (FIE). Much of this research has focused on commercially-harvested marine populations, though recent work has also shown that FIE can also occur in freshwater systems targeted by recreational hook-and-line anglers. For FIE to occur as a result of recreational angling, it is necessary that particular traits (for instance, aspects of an individual fish's behavior or physiology) are associated with an increased likelihood of capture by anglers, leading to selective harvest that causes directional evolution away from that trait. For researchers and managers to accurately predict the outcomes of FIE in freshwater, it is therefore imperative that selected traits are identified, particularly in heavily fished species. While some work has been done previously in this area, several behavioral and physiological characteristics that could be linked with angling vulnerability have yet to be fully explored.

In this dissertation, I present a series of experiments examining a set of behavioral and physiological traits and their role in driving angling vulnerability in fish. Each experiment utilizes one of two highly sought-after freshwater species, the largemouth bass *Micropterus salmoides* or the bluegill *Lepomis macrochirus*. In each experiment, a given set of characteristics is evaluated in individuals of the species in question, and paired with results from actual angling experiments conducted on those same individuals in a naturalistic pond setting.

In chapter 2, I examine the role of boldness, metabolic rate (standard metabolic rate, maximum metabolic rate, and aerobic scope) and stress responsiveness in driving angling vulnerability. A set of largemouth bass from a suite of lines selected for differing vulnerability to angling were assessed for boldness in a standard open-field test. Following this, individuals had blood samples taken before and after an air exposure challenge to assess both baseline and post-stress levels of the primary stress hormone, cortisol. All assessed fish were then stocked into a pond where angling took place. At the conclusion of angling trials, a subset of captured and uncaptured fish were assessed for metabolic rate using intermittent-flow respirometry. Results showed a highly significant association between stress responsiveness and angling vulnerability, specifically that individuals captured by anglers showed a smaller rise in cortisol levels after the air exposure challenge compared to uncaptured fish. Boldness and metabolic rate did not predict angling vulnerability. Because high stress responsiveness has been linked previously to a propensity to freeze in response to challenges (as well as other behavioral traits), selective capture in largemouth bass could lead to evolutionary pressure favoring passive and reactive behavior in exploited systems.

In chapter 3, I examined the role of metabolic phenotype in driving angling vulnerability in bluegill. Similar methods were used to assess metabolic rate as in chapter 2, with an additional examination of anaerobic capacity in the form of excess post-exercise oxygen consumption (EPOC). Fish were first angled, with a subset of fish assessed for metabolic phenotype afterwards. Results showed no difference in metrics of metabolic phenotype (standard and maximal metabolic rates, aerobic scope, EPOC, metabolic recovery time) between captured and uncaptured fish, indicating that, in bluegill, metabolic characteristics are likely not under selective pressure from angling.

Chapter 4 examined the relationships between individual sociability, aggression, and angling vulnerability in bluegill. For this chapter, bluegill were first subjected to angling, with a subset of captured and uncaptured fish then assessed for sociability and aggression in the laboratory. Assessment for sociability consisted of placing an individual bluegill in a large tank divided in half by a transparent barrier that separated the focal fish from a shoal of conspecifics. Sociability was defined as the time spent by the focal fish near the divider, associating with the conspecifics. Following this, focal fish were size-matched and assessed for aggression and dominance in dyadic trials. Results showed a significant effect of time spent near the divider on angling vulnerability, with captured bluegill being more social than uncaptured bluegill. Aggression was not a significant predictor of vulnerability, though a non-significant trend was found whereby captured fish tended to be less aggressive.

While chapter 4 examined bluegill sociability on an individual basis (i.e. each focal fish was examined in isolation), Chapter 5 sought to quantify sociability within the context of interactions within a group of individuals. In addition, swimming performance was assessed for the purpose of determining if this physiological trait was linked with either angling vulnerability or social behavior. For this, groups of 6 individuals were size-matched and placed into a common tank, where they were evaluated for sociability and aggression over three days of observation. Pooled behavior from all three days was then analyzed using methods derived from Social Network Analysis. Each fish was then assessed for swimming performance (critical swimming speed - U_{crit}) in a Brett-style swim tunnel before being stocked into a pond for angling. The results showed that, while only fish size predicted whether or not a fish was captured (larger fish were more likely to be caught at least once), more social and less aggressive individuals were found to be the most vulnerable. Specifically, high sociability/low aggression predicted whether an individual was caught multiple times, and also predicted capture order with highly social individuals being captured first. Swimming performance did not predict any aspect of angling vulnerability. These results, combined with the results from chapter 4, indicate that

social behavior is indeed a key determinant of angling vulnerability in bluegill, and that angling selection may evolutionarily favor fish that are both more aggressive and less social.

In chapter 6, I examined the role of learning performance and proactivity in driving angling vulnerability in largemouth bass. For this experiment, a set of largemouth bass was assessed for learning performance on an active-avoidance task. For this task, each fish was put into an individual tank that was divided in two by an opaque barrier. The barrier included a small opening for shuttling between sides of the tank. Over a set of trials, an observer first shined a light over the fish, which was followed by chasing with an aquarium net. When fish successfully shuttled to the other side of the tank in response to the light (but before the onset of chasing), this was considered successful learning. From there, each fish was assessed for proactivity in a restraint test, where fish were scored based on the number of attempts each fish made to leap from a container when held out of water. Following angling, it was found that learning performance was significantly linked with angling vulnerability, with high performing individuals being more likely to be captured. Within the framework of "cognitive syndromes", this result indicates that individuals that learn tasks quickly and are, therefore often prone to mistakes, may be under selective pressure in angled populations of largemouth bass.

Collectively, this research has identified several behavioral and physiological characteristics that drive vulnerability to angling, however the characteristics differed between species. While largemouth bass vulnerability was driven by characteristics broadly related to proactive behavior (rapid learning, low stress responsiveness), for bluegill it was social and unaggressive individuals that were found to be the most vulnerable. Overall, this means that heavily fished populations could experience behavioral evolution as a result of selective capture on these traits, however the traits under selection may differ depending on the species.

ACKNOWLEDGEMENTS AND DEDICATION

To begin, I would like to thank my advisors, Drs. Jeffrey Stein and Cory Suski, for their guidance, help, and general support during this process. I also would like to thank all members of the Suski and Stein labs who have been friends, colleagues, and helpers on my research projects. These include Caleb Hasler, Jen Jeffrey, Kelly Hannan, John Tix, Cody Sullivan, Adam Wright, Eric Schneider, Toniann Keiling, Ian Bouyoucos, Emi Tucker, Steve Midway, Josh Sherwood, Austin Rundus, Sarah King, Sarah Molinaro, and Scott Cleary. I would make special mention of two additional people: Justin Rondón, who helped out with nearly every single thing I did here at UIUC and basically facilitated all of the research in this dissertation, and Shivani Adhikari, who was my research “partner in crime” for my first two years and basically kept me afloat early on when things didn’t always go according to plan. I also thank my Master’s Degree advisor, Dr. Robert Stelzer. While he didn’t assist on any of the projects in this dissertation, it was his guidance and help that put me on the road to taking on the challenge of this doctorate.

Finally, and most importantly, I thank with all my heart my wife, Sandy. It’s been a twisting road for us to get here, one we didn’t foresee when we were both teaching high school in Central Wisconsin eight years ago. Obviously everything I have in my life currently extends from her support and encouragement, including the professional things I’ve accomplished here at the University of Illinois. I also dedicate this dissertation to my grandmother Vivian and my Great Aunt Norma, as even though they are no longer with us physically, I’d like to believe that they find me getting this degree to be a great thing.

TABLE OF CONTENTS

CHAPTER 1: GENERAL INTRODUCTION 1

CHAPTER 2: HORMONAL RESPONSIVENESS TO STRESS IS NEGATIVELY ASSOCIATED WITH VULNERABILITY TO ANGLING CAPTURE IN FISH 7

CHAPTER 3: METABOLIC PHENOTYPE IS NOT ASSOCIATED WITH VULNERABILITY TO ANGLING IN BLUEGILL SUNFISH 27

CHAPTER 4: SOCIABLE BLUEGILL (*LEPOMIS MACROCHIRUS*) ARE SELECTIVELY CAPTURED *VIA* RECREATIONAL ANGLING.................................49

CHAPTER 5: FORTUNE FAVORS THE ANGRY: SOCIAL AND UNAGGRESSIVE BLUEGILL ARE CAPTURED EARLY AND OFTEN BY RECREATIONAL ANGLERS 71

CHAPTER 6: QUICK LEARNING, QUICK CAPTURE: LARGEMOUTH BASS THAT RAPIDLY LEARN AN ASSOCIATION TASK ARE MORE LIKELY TO BE CAPTURED BY RECREATIONAL ANGLERS...101

CHAPTER 7: SUMMARY AND CONCLUSIONS..124

REFERENCES 129

CHAPTER 1: GENERAL INTRODUCTION

Evolutionary change drives the diversity of life on earth. While “natural” cycles of climatic change, continental drift, cataclysmic events, and competition among species have shaped the form and function of today’s flora and fauna, for today’s species a new evolutionary force, human activity, has emerged as a major driver of both extinction and evolutionary change. The challenges placed on species by recent human activity have been so extreme that the present age is often referred to as the “Anthropocene”, a period where human activity shapes the course of life even more than natural forces (Sarrazin and Lecomte 2016). Indeed, recent analyses have described the rate of evolution due to human activity as exceeding all other evolutionary drivers (Palkovacs et al. 2012). Evolutionary changes in response to human activity include changes in morphology to cope with altered habitats (Templeton et al. 2001; Riesch et al. 2015), alterations in vocalization to effectively communicate in disturbed environments (Smith et al. 2008), and changes to behavior to either avoid humans entirely or take advantage of new opportunities (Sih et al. 2011; Sol et al. 2013). In addition, humans are an all-too-frequent conduit for the spread of non-native species, which frequently cause both decline and evolutionary change in native species (Mooney and Cleland 2001; Berthon 2015). Collectively, these evolutionary changes are drastically changing the ecology of numerous species, and understanding how these changes will impact fitness and resilience of these species is therefore crucial for researchers and wildlife managers alike.

Human activity is capable of driving evolutionary change in a variety of ways, including through the selective harvest of food and game species. It has been widely demonstrated that hunting and fishing can induce evolution by selectively capturing/killing individuals with certain traits that render them more vulnerable (Kuparinen and Merila 2007; Palkovacs et al. 2012;

Allendorf et al. 2014). For wild game animals, susceptible traits are often those that make the animal more of a target for hunters, for instance research has shown that selective harvest of "trophy" bighorn sheep *Ovis Canadensis* is at least partially responsible for a decline in mean horn size (Coltman et al. 2003; Hedrick 2011), leading to a concurrent decline in growth rate and fitness (Hengeveld and Festa-Bianchet 2011). In addition, individuals that behave in a particular way (for instance, be being more active) may be more conspicuous to hunters or more likely to encounter fishing gear, leading to their capture/harvest (Biro and Post 2008; Ciuti et al. 2012). This selective capture has been shown to not only evolutionarily alter the trait that is the direct target of selection, but also a host of additional characteristics through their covariance with that trait (Coltman et al. 2003; Cooke et al. 2007; Diaz Pauli and Sih 2017). These changes can have major ramifications for the fitness of these populations, leaving them vulnerable to potential collapse and eventual extinction (Palkovacs et al. 2012; Kuparinen and Festa-Bianchet 2016). Predicting such consequences is not only important from an ecological perspective, but also an economic perspective as many local communities rely on spending by hunters and fishers in order to persist (Eikeset et al. 2013). Therefore, understanding the impacts of harvest-induced evolution has merit both from a basic scientific point of view, but also from the perspective of human interests as well.

Among harvested taxa, the induced evolution of fish has been the most heavily studied, a process known specifically as Fisheries-Induced Evolution (FIE). Study of FIE has largely focused on commercially harvested species, with a frequent finding that extensive harvest leads to early maturation, reduced overall fecundity, and lower growth (Kuparinen and Hutchings 2012; Audzijonyte et al. 2013; Kokkonen et al. 2015). These impacts are the result of both the selective harvest of larger individuals, as well as the imposition of a high-mortality environment that creates a selective advantage for individuals that reach maturation sooner (Dunlop et al. 2015; Feiner et al. 2015). While these impacts have been found in commercially targeted fishes, some recent work also indicates that similar impacts can also occur in species targeted by hook-and-line anglers (Consuegra et al. 2005; Edeline et al. 2007; Saura et al. 2010). As a result, the extensive management and research into FIE that is suggested for marine species (Jorgensen et al. 2007) may be necessary for recreationally targeted species as well. However, currently our knowledge of the potential impacts of FIE in recreational systems lags behind our knowledge of commercially targeted species.

With regards to FIE in recreationally angled species, target traits will almost certainly be those that cause individual fish to be more likely to strike a fishing lure, leading to capture. To answer the question of why some individuals may be more likely to strike fishing lures than others, previous research has examined the role of individual behavioral characteristics. Indeed, an abundance of research has demonstrated that individuals within a species may differ consistently in various aspects of their behavior, with the suite of characteristics specific to an individual being referred to as its 'behavioral type' or 'personality' (Bell 2007; Mittelbach et al. 2014). These personalities are often broken down into five distinct axes of behavior: Boldness, exploratory tendency, activity, sociability, and aggression (Reale et al. 2007; Conrad et al. 2011). An individual's personality may also be associated with other aspects of its behavior, for instance its ability to learn novel tasks (Sih and Del Giudice 2012; Bensky et al. 2017). Studies of which behavioral types may be more likely to be caught by anglers have often focused on the first three axes, with a common finding that bolder (Klefoth et al. 2013, 2017), more explorative (Harkonen et al. 2014, 2016), and/or more active (Alós et al. 2012; Villegas-Rios et al. 2014) individuals are more vulnerable to angling, though these findings are not universal (Wilson et al.

2011). While boldness and exploration have indeed been studied in the context of angling vulnerability, no work has examined whether sociability or aggression is linked with vulnerability. In addition, links between personality and learning ability have only recently been explored in animals (Sih and Del Giudice 2012), and no research has examined whether learning ability is predictive of angling vulnerability. The lack of work on these aspects of animal behavior leaves a gap in our knowledge of how fish personality may evolve in response to recreational angling selection.

Personality in fish and other animals is often correlated with physiological characteristics, many of which may also be impacted by angling selection. Metabolic rate, for instance, has been linked with bold behavior, under the hypothesis that individuals with high metabolic rates will need to forage more (including under risk) to meet their higher metabolic demands (Stamps 2007). Given that boldness has been linked with angling vulnerability in some species (Klefoth et al. 2017; Lennox et al. 2017) it might therefore be expected that individuals with high metabolic rates would be more vulnerable to capture. Studies have shown that angling selection has resulted in lower metabolic rates in experimental and wild populations with heritable differences in angling vulnerability (Redpath et al. 2010; Hessenauer et al. 2015). In fish, metabolic rates have been linked with swimming performance and other traits that are relevant to individual fitness in natural environments (Reidy et al. 2000). Furthermore, these metabolic and behavioral characteristics have often been found (separately or together) to be linked to an individual’s hormonal physiology, specifically their response to stress (Koolhaas et al. 1999). Generally speaking, bolder behavior and high metabolic rates are associated with low stress responsiveness, as indicated by levels of stress hormones (particularly cortisol) in the blood and muscle following the onset of a stressor (Koolhaas et al. 1999; Careau et al. 2008). The combination of physiological and behavioral responses to a stressor or challenge is referred to as an individual's "stress coping style", with individuals possessing this combination of traits (bold behavior, high metabolic rates, and low stress responsiveness) referred to as "proactive stress copers", while those with the opposite characteristics are referred to as "reactive stress copers" (Koolhaas et al. 1999). While the covariances among these traits have been described, the role of these physiological correlates of behavior in driving angling vulnerability have not been given the same attention as behavioral axes, even though physiological changes as a result of FIE could be highly consequential for exploited populations (Hollins et al. 2018). Understanding how these physiological characteristics may evolve in response to angling pressure is therefore highly important, and will allow for accurate predictions as to the consequences of FIE in recreationally angled systems.

The goal of this dissertation is to define behavioral and physiological characteristics that may be associated with angling vulnerability, with special attention towards characteristics that have not been assessed in previous work. All data chapters (2-6) in this document consist of a similar framework in which behavior and physiology is evaluated in a laboratory setting, with the results coupled with live angling conducted in a naturalistic pond setting to determine if the traits assessed were linked with whether or not fish were captured during angling trials. Each of the five studies were conducted utilizing one of two highly popular recreational sportfish species: The largemouth bass *Micropterus salmoides*, or the bluegill *Lepomis macrochirus*. Chapters 2 and 3 fall within a theme of evaluating the components of individual stress coping style (boldness, stress responsiveness, and metabolic rate). Chapter 2 includes individual assessments for boldness, stress responsiveness, and the aerobic aspects of metabolic phenotype (standard and maximum metabolic rate, aerobic scope) in largemouth bass, while chapter 3 focuses on metabolic phenotype in bluegill exclusively, with the addition of an assessment of anaerobic metabolic capacity in the form of post-exercise oxygen consumption (EPOC). Chapters 4 and 5 examine the role of social behavior and aggression in driving angling vulnerability in bluegill, using two separate experimental designs. In chapter 5, swimming performance is also assessed to determine if a relationship between angling vulnerability, social behavior, and swimming performance is found in this species. Finally, chapter 6 examines the role of learning performance on a standardized active-avoidance test and overall proactivity (as assessed with a restraint test) in driving angling vulnerability in largemouth bass. The cumulative results of these studies will shed valuable light on the factors that may be drivers of angling vulnerability, and thus be subject to FIE in recreationally-angled systems. Through the use of two separate species, this research also provides an opportunity to evaluate whether characteristics that make individuals of one species vulnerable necessarily lead to vulnerability in the other, allowing for predictions of the impacts of FIE to be tailored to specific species and angling contexts.

CHAPTER 2: HORMONAL RESPONSIVENESS TO STRESS IS NEGATIVELY ASSOCIATED WITH VULNERABILITY TO ANGLING CAPTURE IN FISH.

Introduction

A large body of research has documented the alteration of exploited fish populations *via* selective capture of particular phenotypes, a phenomenon known as fisheries-induced evolution (FIE) (Jorgensen et al. 2007; Devine et al. 2012). The majority of these studies have focused on the alteration of life history traits (Kuparinen and Hutchings 2012), including decreases in growth rate, lower total reproductive output, and reduced age-at-maturity in populations of marine species that have been subjected to commercial harvest (Kuparinen and Merila 2007; Devine et al. 2012). Similar processes may also be occurring in freshwater fisheries primarily targeted by recreational hook-and-line anglers (Nussle et al. 2009; Kendall and Quinn 2011), which may reduce the overall fitness of individuals in the population (Sutter et al. 2012). Whether in freshwater or marine ecosystems, FIE has the potential to greatly alter the ecology of the affected populations.

While alterations in growth rate, reproductive rate, and the timing of maturation have been identified as outcomes of FIE in exploited populations, it has been posited that inter-individual differences in behavior are the proximate mechanisms responsible for FIE, specifically those behaviors that predispose individuals to capture by commercial or recreational gears (Biro and Post 2008; Uusi-Heikkila et al. 2008). Consistent behavioral differences among individuals, which are alternatively referred to as ‘behavioral syndromes, ‘personalities’, or ‘stress coping styles’, have been thoroughly studied in a host of animal taxa (Sih et al. 2004a). These differences among individuals are typically parsed into behavioral axes, including boldness, aggression, and activity levels (Reale et al. 2007), and the physiological mechanisms that underpin many of these behavioral differences have also been defined. For instance, studies of stress coping styles have examined the relationship between levels of boldness and neuroendocrine responsiveness to stress, with ‘proactive’ individuals being marked by bolder behavior and a less pronounced hypothalamic-pituitary-adrenal (hypothalamic-pituitary-interrenal in teleost fish and amphibians) axis response to stress, as measured by cortisol concentrations in the blood (Koolhaas et al. 1999; Overli et al. 2005). Levels of boldness and/or aggression have also been linked with metabolic rate and aerobic capacity (Careau et al., 2008; Metcalfe et al., 1995), under the presumption that individuals with intrinsically high metabolic demands will need to behave more boldly and/or more aggressively to acquire and defend sufficient resources to satisfy higher energetic requirements (Stamps 2007; Biro and Stamps 2010).

For FIE to influence the physiology or behavior of recreationally targeted species, the traits in question must be linked to a propensity to strike a fishing lure. At present, links between physiological traits and angling vulnerability within individuals have been relatively unexplored, although some studies have made comparisons among lines artificially selected for differing angling vulnerability (Cooke et al. 2007; Redpath et al. 2010). Direct causal links between behavioral type and angling have, however, been studied more frequently. For example, previous work has shown that bolder and more active individuals may be more likely to be caught on hook-and-line (Klefoth et al. 2013; Harkonen et al. 2014), while individuals with higher growth rates have been found to be more vulnerable to commercial netting (Biro and Post 2008). Important to note here is, while previous work has independently examined the correlation of boldness (Wilson et al. 2011) as well as metabolic rate (Redpath et al. 2010) with angling vulnerability, no studies have taken an integrative approach to simultaneously examine the relative influence of behavior, metabolic rate, and hormones in driving the likelihood of capture. Defining these relationships is of critical importance in determining which characteristics may be under selective pressure, and what types of evolutionary alterations we can expect to see in populations exploited by recreational anglers.

The goal of this chapter is to define physiological and behavioral mechanisms responsible for driving the vulnerability of fish to recreational angling capture. To accomplish this goal, I utilized a population of largemouth bass *Micropterus salmoides* artificially selected to vary in their vulnerability to angling (Philipp et al. 2009). Several studies have examined these selected lines for differences in their metabolic characteristics/growth (Cooke et al. 2007; Redpath et al. 2009, 2010), reproductive output (Sutter et al. 2012), foraging ecology (Binder et al. 2012), and daily activity (Binder et al. 2012). However, none of these studies have attempted to link characteristics to angling vulnerability on the individual level, instead focusing on between-line comparisons. These approaches, while highly useful, ignore the fact that angling vulnerability and its associated characteristics may still vary within each line. In this chapter, I am therefore looking to quantify factors driving vulnerability to angling in individuals, rather than by comparing lines to draw inferences. In addition, boldness and hormonal/physiological characteristics may possibly play a major role in determining whether an individual is vulnerable to capture (Cooke et al. 2009; Biro and Sampson 2015), but have been understudied with respect to angling vulnerability in fish. I predicted that individuals with lower neuroendocrine responsiveness to stress (as indicated by plasma cortisol levels), greater levels of boldness, and higher metabolic rates (i.e., proactive copers) would be more likely to be captured by hook-and-line angling. This hypothesis was formulated due to the greater rates of exploration, aggression, and feeding motivation in individuals with these characteristics in prior studies (Koolhaas et al. 1999; Stamps 2007; Killen et al. 2014). Results from this chapter will enhance our knowledge of the factors (especially physiological factors) driving angling vulnerability that has been unexplored to date.

Methods

Study Animals

This chapter makes use of a population of largemouth bass that has been the subject of an artificial selection experiment to produce lines of fish that differ in their vulnerability to angling (Philipp et al. 2009). Beginning in 1976 and ending in 1980, a population of wild Largemouth Bass from Ridge Lake near Charleston, IL, was angled to divide the population into individuals that were captured numerous times (hereafter high vulnerability bass, HVB) and not vulnerable to capture (hereafter low vulnerability bass, LVB). Both HVB and LVB were subsequently removed from the lake, given fin clips to identify assignment to HVB and LVB lines, and returned to the Illinois Natural History Survey's (INHS) aquatic research facility in Champaign, IL, where they were held in a set of identical, earthen-bottom ponds. HVB and LVB fish were allowed to breed within their respective lines, and offspring were similarly marked with a fin clip to identify HVB and LVB individuals. Angling to further select LVB and HVB based on catchability continued for an additional three generations. Following the third generation of selection, the selection regime was halted (no additional angling). However within-line breeding was continued to produce additional generations of pure HVB and LVB, as well as reciprocal hybrid lines (H×L and L×H). This chapter utilized the 6th generation of largemouth bass (spawned in 2012) derived from this selection experiment, and was conducted in 2015.

All largemouth bass used in this chapter were held in one of several 0.12 ha ponds at the INHS aquatic research facility from the time they were spawned until the outset of experiments. Ponds at this facility were maintained in an identical fashion, with similar vegetative cover, fish density, and abundance of forage (fathead minnows, *Pimphales promelas*), such that the effects of differential experience and habitat availability on behavior and physiology were minimized (Brydges and Braithwaite 2009). Prior to experimental trials, ponds containing fish were drained, and each fish was checked for a fin clip to identify lineage then implanted with a passive integrated transponder (PIT) tag (Biomark Inc., Boise, ID, USA) for individual identification. Fish were then moved to one of eight circular 1135 L holding tanks connected to an adjacent pond with a flow-through system providing a continuous supply of fresh water where they were held for a period of five days to recover from handling. While being held fish were fed fathead minnows *ad libitum*. All procedures described were approved by the University of Illinois Institutional Care and Use Committee (IACUC), protocol #14230.

Boldness and Stress Responsiveness

A total of 113 largemouth bass (N=23 HVB, 26 LVB, 37 H×L, 27 L×H; mean total length = 230.9 mm, range = 211-255 mm; mean total weight = 159.8 g, range = 118-223 g) were assessed for boldness and stress responsiveness. No difference in size was present across lines (analysis of variance, ANOVA on weight, df = 3, F = 0.967, *P* = 0.41). Prior to boldness assessment trials, each fish was PIT-identified and isolated overnight indoors in a 27 L opaque plastic holding tank provided with a continual supply of re-circulating water. Temperature for all indoor tanks was maintained at 23ºC by a TK 500 Heater-Chiller (Teco, Revenna, Italy), with dissolved oxygen levels maintained above 8.0 mg/L by an air stone connected to an air compressor.

At the outset of the experiment, largemouth bass were first assessed for boldness. The arena to test boldness consisted of a 180 × 65 cm opaque rectangular tank filled to a depth of 35 cm and transected into four equally-sized zones. The first "refuge" zone was separated from the three remaining zones (the "open area") by an opaque plexiglass divider. The refuge was covered with naturally colored gravel and artificial aquarium plants, while the open area contained no substrate or vegetative cover. Prior to the start of each trial, a focal fish was quickly netted from its individual holding tank and placed into the refuge zone of the arena. The fish was allowed to acclimate in the refuge for a period of 10 minutes before the divider was raised *via* a pulley system from behind a blind, allowing the fish to swim about the arena for 30 minutes. Each trial was videotaped from above using a GoPro^{TM} 3 camera, and three measures of boldness were quantified – the latency for the fish's entire body to cross the line separating the refuge zone from the rest of the arena, the amount of time spent by fish in the open area, and the total number of zone lines crossed by the fish. Each fish was assessed only once for boldness. While repeatability of behavior is necessary to identify that behavior as consistent and intrinsic to an individual (Bell et al. 2009), previous work has shown fish behavior with open field tests is repeatable (Webster et al. 2009; Kortet et al. 2014; Mazue et al. 2015). In addition, I was concerned that repeatedly testing each fish would result in a loss of novelty of the environment on the second test (i.e., habituation), which can alter what behaviors are actually being assessed compared to the first test (Reale et al. 2007; Dingemanse et al. 2012).

After its boldness trial, the fish was returned to its individual holding tank where it was again held overnight. The following day, two blood draws were taken from each fish to quantify cortisol concentration before and after a stressor, following procedures previously used for largemouth bass (Cook et al. 2011). In each case, the fish in question was quickly removed from its individual holding tank and a blood sample (baseline) was acquired within 2 minutes *via* caudal puncture using a 23 gauge heparinized needle. The fish was then given an air-exposure challenge in a container lined with wet towels for a period of 3 minutes, and was subsequently held in a 68 L tank filled with fresh pond water for a period of 25 minutes to allow cortisol levels to peak. Following this period, a second, post-stress blood sample was acquired in a fashion identical to the baseline sample. All blood samples were immediately centrifuged at 6,000 RPM for 2 minutes to extract plasma, which was temporarily stored in liquid nitrogen prior to transport to the laboratory where they were permanently stored at -80º C. Cortisol was quantified using an enzyme-linked immunosorbent assay (ELISA, Kit # ADI-901-071, Enzo Life Sciences®, Farmingdale, NY) previously validated for use in largemouth bass (Sink et al. 2008). Stress responsiveness was defined as the difference between post-stress and baseline cortisol concentrations for each individual. Blood draw sets (pre- and post- air exposure) were conducted only once, as recent work in largemouth bass has shown stress responsiveness to be repeatable (Cook et al. 2011), and I wanted to avoid excess stress resulting from multiple handling events. Following blood collection, all fish were stocked into a single 0.12 ha pond containing abundant fathead minnows and held for a period of one month before angling trials commenced.

Angling Trials

Angling trials began in July of 2015 and consisted of 10 two-hour angling sessions performed over the course of 7 days. Each session took place at one of three times as determined by random selection: morning (6:00-8:00 AM), midday (12:00-2:00 PM) or evening (6:00-8:00 PM). All angling was performed by a pair of experienced anglers. Medium-action rods spooled with 2.7 kg Berkley Trilene ® monofilament line, commonly used by anglers targeting largemouth bass, were used for all three lure presentations, which included a 7.6 cm watermelon colored plastic worm (Gary Yamamoto Custom Baits^{TM}) rigged “wacky” style on a size 2 Eagle Claw ® J-hook, a Strike King ® 1 g white single-bladed spinnerbait tipped with a 0.95 cm white curly tail grub, and a single size 2 J-hook baited with a live nightcrawler *Lumbricus terrestris* L. suspended from a slip-bobber. I chose to use multiple lure types as fish with different behavior types may have preferences for striking certain types of lures (Wilson et al. 2015), and the three lure types used here allowed for a range of presentation speeds (the spinnerbait was retrieved quickly, the plastic worm was retrieved slowly, and the live nightcrawler was static) to maximize catch rates. The pond was divided into six equal sections (60 m × 20 m), and the two anglers simultaneously fished a different section during each of three 40-minute periods within a two-hour angling session. Following each period, the anglers moved to a new section and switched lures as determined by random selection. Thus, during each two hour session (which contained three periods), each section of the pond was fished once, and each angler used each of the three lure types. Upon capture, each largemouth bass was identified via PIT tag before being quickly released back to the pond. No bleeding or other injury was observed in any captured fish. At the conclusion of the angling trials, the pond was drained and 88 of the original 113 fish were recovered. Unrecovered fish, which had presumably died (N=25), did not differ from the collected fish in boldness, cortisol levels, or weight, (Student T-test, $p > 0.3$ for all tests). Because none of the unrecovered fish had been captured previously, I also assumed that those fish had died prior to the start of angling trials. For consistency, only the 88 recovered fish (19 HVB, 23 LVB, 26 H×L, 20 L×H) were considered in subsequent analyses.

Metabolic Rate Assessment

Due to the length of time that would be needed to process all 88 fish, metabolic rate assessment was performed only on a subsample of 40 fish: 20 that had been captured 1 or more times, and 20 that had not been captured. Specifically, sampling all 88 fish would have required sampling to continue well into October, when cooling weather conditions and decreasing photoperiod could potentially influence my results (Evans 1984). Fish weight did not differ across experimental groups (ANOVA, $p > 0.05$). All metabolic assessments took place six weeks following the completion of angling (fish were held in the meantime in a 0.12 ha pond stocked with fathead minnows), and were performed using static, intermittent-flow respirometry (Loligo Systems^{TM}, Tjele, Denmark) following the methods of Redpath et al. (2010) with a few modifications (5.26 L respirometry chambers were used, and measurement cycles were lengthened to a 20 minute "flush", 2 minute "wait", and 10 minute measurement phase). During measurements, all chambers were submerged in a 500 L square tank. Oxygen saturation in the tank was maintained near 100% by a pair of air stones, and kept at 23º C using heater-chillers. Measurements of oxygen saturation in the chambers were taken every 5 s during the measurement phase by a fiber-optic dissolved oxygen probe (calibrated regularly during the study) that allowed for the calculation of oxygen consumption (M_{O2}, in mg O_2 consumed /weight of fish in kg/hr).

Each fish was loaded into a chamber in the afternoon and held overnight to collect data to determine Standard Metabolic Rate (SMR), which was calculated as the mean of the five lowest M_{O2} values (Nelson and Chabot 2011). The following morning, fish were removed from their chambers and temporarily placed in a 550 L tank where they were exercised to exhaustion by manual chasing with a net for 5 minutes (Suski et al. 2007) before being returned back to their chambers for an additional 4 measurement cycles. The highest individual M_{O2} value from these measurements was taken as the fish's Maximum Metabolic Rate (MMR) and aerobic scope (AS) was defined as the difference between MMR and SMR for each fish (Redpath et al. 2010). All equipment (chambers, pumps, and tubing) was sterilized between trials with a 10% bleach solution, and final M_{O2} values were corrected to account for background metabolic activity (Rodgers et al. 2016).

Statistical Analysis

To simplify measurement of boldness, Principal Components Analysis (PCA), was performed based on the correlation matrix derived from the three individual boldness metrics (latency to emerge, time spent in the open, number of zones crossed). Principal components with eigenvalues over 1 were extracted using varimax rotation on the maximum likelihood solution (Kaiser 1960). To determine the effect of boldness, baseline cortisol, stress responsiveness, fish weight, and/or selected line on whether a fish was captured, I ran logistic regression models on all possible combinations of predictors (including models that included predictors independently, as well as full and null models). Logistic regression models were then compared using Akaike's Information Criterion, adjusted for small sample sizes (AIC_C), with top models selected based on ΔAIC_C values at or lower than 2 (Arnold 2010).

To assess whether capture was size selective, fish weight was compared between captured and uncaptured fish using t-tests. All other metrics measured (baseline cortisol, stress responsiveness and boldness for the full set of 88 fish, and SMR, MMR, and AS for the subset of 40 fish assessed with respirometry) were compared across captured and uncaptured fish using t-tests. Normality of data was assessed *via* examination of residual quantile-quantile plots, and homogeneity of variances was assessed by visual examination of fitted residuals (Anscombe and

Tukey 1963). All analyses were performed using R version 3.2.1 (R Core Team, Vienna, Austria) and the level of significance (α) was set at 0.05.

Results

Ten angling sessions resulted in a total of 92 fish captures, with 38 captures occurring in the first angling session. Of the lures used, the plastic worm proved to be the most effective (57 captures), followed by the spinnerbait (28 captures) and the live nightcrawler (7 captures). Thirty largemouth bass, out of the total population of 88, were not captured. Fifty-eight of the 88 recovered largemouth bass were captured at least once, with 25 of those being captured multiple times. Fish captured once did not differ from those captured multiple times in boldness, stress responsiveness, or metabolic rate (ANOVA, $p > 0.44$ in all cases).

PCA revealed that the three boldness metrics were highly correlated. Only a single component was extracted (PC1, hereafter referred to as the "boldness score") with an eigenvalue greater than 1; this single component explained over 70 % of the variation in boldness behavior (Table 2-1). Individuals with high boldness scores tended to leave the refuge sooner, spend more time exploring open zones and cross more lines relative to fish with lower boldness scores.

Stress responsiveness (i.e., the difference between post-stress and baseline cortisol concentration) alone was the top model explaining whether or not a fish was captured by anglers, and stress responsiveness was featured as a predictor variable in all of the top ten models (Table 2-2). No additional models had a ΔAIC_C value lower than 2 (Table 2-2). However, models that contained stress responsiveness along with boldness score and baseline cortisol concentration had ΔAIC_C values of 2.02 and 2.04, respectively, suggesting some possible role for these factors in influencing vulnerability to angling (Table 2-2). Selected line did not factor into any of the top 7 models, indicating that a fish's line in this experiment did not influence whether or not it was captured (Table 2).

Stress responsiveness differed significantly between captured and uncaptured fish (Table 2-3). Baseline cortisol concentration across all fish was 20.47 ng ml^{-1} and did not differ between captured and uncaptured fish, and instead the difference in stress responsiveness was driven by post-stress cortisol concentrations that were 48% higher in uncaptured fish (Figure 2-1). Angling was not size selective, indicated by the fact that size was not included in any of the top logistic regression models, and also by the fact that weight did not differ statistically between captured and uncaptured fish (Table 2-3). Captured and uncaptured fish did not differ in any other metric assessed, including boldness, SMR, MMR, or AS (Table 3; Fig. 2-1C).

Discussion

Data from this chapter indicate that neuroendocrine stress responsiveness was the strongest driver of angling vulnerability in largemouth bass when compared against other behavioral or physiological parameters. More specifically, largemouth bass that were captured by anglers showed a lower rise in plasma cortisol levels following an air-exposure challenge compared to largemouth bass that were not captured. Cortisol is the primary stress hormone in fish, which rises in response to stressors to mobilize energy reserves for use in responding to an external challenge (Bonga 1997). High stress responsiveness, as defined by relatively large rises in cortisol following a stressor, is associated with the 'reactive' stress coping style in many studies of animal behavior (Overli et al. 2005). This high responsiveness has been linked to shyer and less aggressive behavior (Archard et al. 2012), as well as increased flexibility and learning capacity in dealing with environmental change (de Lourdes Ruiz-Gomez et al. 2011). In the case of largemouth bass in this chapter, highly responsive individuals were less likely to be captured, which may be linked in part to shyer and less aggressive behavioral tendencies. Reduced vulnerability may also be related to a tendency to freeze and/or not respond aggressively to sudden appearance of a fishing lure nearby, as freezing behavior has also been shown to be linked with high stress responsiveness (Koolhaas et al. 1999). Regardless of what behavior is being affected by underlying physiology, it appears that stress responsiveness is negatively associated with angling vulnerability.

Interestingly, boldness had little influence on vulnerability to capture, with no difference in boldness score found between captured and non-captured fish. Boldness is typically defined by a propensity to take risks, whether in exploring novel environments or continuing to be active in the face of threats (Bell and Sih 2007). Previous work has sought to link this risk-taking behavior to angling vulnerability, and results have been inconsistent. Some studies indicate that bolder and more exploratory individuals are more vulnerable to capture by anglers (Klefoth et al. 2013; Harkonen et al. 2014, 2016), other work has found bold individuals to be less vulnerable to angling (Wilson et al. 2011), and still other work has found no connection between boldness and angling vulnerability (Kekalainen et al. 2014; Vainikka et al. 2016). Inconsistent findings linking boldness to angling vulnerability may be due to differences in methodology across studies (Beckmann and Biro 2013), or that a relationship between boldness and vulnerability is context-dependent and may fluctuate depending on factors such as the species in question or time of year (for instance, during spawning season vulnerability to angling may depend to a greater degree on factors related to aggressiveness, see Sutter et al., 2012). If the latter is the case, then study of how behavioral and physiological characteristics affect angling vulnerability should take this into account so that these context-driven patterns may be better understood.

In contrast to my predictions, it was found that metabolic phenotype (SMR, MMR, and AS) was not an important predictor of angling vulnerability. This finding was contrary to my initial predictions, which were based on a number of previous studies documenting that high metabolic rates may increase the likelihood of a fish being captured, albeit *via* different gear types (Biro and Post 2008). Other work has also indicated that angling pressure may lead to a reduction in metabolic rate in exploited populations, likely as a result of the selective capture of individuals with higher metabolism (Hessenauer et al. 2015). Alterations to metabolic phenotype *via* the selective capture and removal of individuals with high metabolic rates has the potential to have fitness related outcomes for exploited populations, as metabolism is closely linked to growth rate and overall productivity as well as the likelihood of mortality (Biro and Stamps 2008; Myles-Gonzalez et al. 2015). Not all experiments have indicated that this metabolic alteration will occur as a result of FIE in exploited populations. For instance, an artificial selection experiment performed on zebrafish *Danio rerio* Hamilton resulted in no alteration in metabolic rate associated with simulated size-selective capture (Uusi-Heikkila *et al.* 2015). The context in which angling occurs may be an important factor in determining the evolutionary changes imparted by the selective capture of certain individuals in a population, as some angling techniques may preferentially capture individuals with higher metabolic rates while other techniques do not. In a similar vein to my conclusions regarding the role of boldness in driving angling vulnerability, a compelling future avenue of research resides in the need to determine how different contexts (variable temperatures, seasons, capture techniques and/or targeted species) may lead to the capture-driven selection for or against different physiological traits.

My results showed no role of selected line in driving vulnerability to angling. The lines of fish used in this chapter were generated based on their response to recreational angling over 3 generations (Philipp et al. 2009), but selection pressures had stopped for 3 generations prior to being used in this chapter. The selection regime had previously resulted in numerous differences between HVB and LVB as determined by studies of the 3rd-5th generations, with HVB showing higher rates of recovery from exercise (Cooke et al. 2007), higher maximum metabolic rates and aerobic scopes (Redpath et al. 2010), higher gonadosomatic indices (Redpath et al. 2009), greater aggression and angling vulnerability while nesting (Sutter et al. 2012) and lower rates of prey rejection (Nannini et al. 2011). The failure to detect a line effect with respect to capture likelihood in this chapter is likely due to differences in my classification of fish as vulnerable relative to the criteria used to establish the selected lines. In this chapter, a vulnerable individual was defined as being captured once within a 10-day angling experiment, whereas HVB in the original selection regime were defined as being captured three or more times over an entire summer (Philipp *et al.* 2009). Also, this chapter utilized different lure types and presentation styles compared to previous work, a difference that may have allowed for the capture with a wider range of behavioral and physiological traits compared to fish captured by a single lure types, thus muting the line effect of catchability (Wilson et al. 2015). It is also possible that differences in angling vulnerability have become less distinct between HVB and LVB over the past three unselected generations due to a relaxation of the selection regime. However, a reversal of the aforementioned differences after only 3 generations of no angling would be quite rapid based on work that suggests human-induced evolutionary changes should take longer to reverse than induce (Conover et al. 2009). In summary, the lack of differences between the lines in catchability may be simply due to how the word "catchability" is defined, with different characteristics being associated with the propensity to be caught via different lure types.

Results from this chapter provide a number of new insights into the role of physiological characteristics driving capture vulnerability in recreational fisheries, and some of the potential long-term consequences of harvest by recreational anglers. It has been demonstrated previously that stress responsiveness and its behavioral and physiological correlates may be linked to fitness and overall productivity (Biro and Stamps 2008). Because stress responsiveness is a heritable trait (Overli et al. 2005), the potential therefore exists for this trait to be under selective pressure in recreationally angled populations through selective harvest and/or angling-induced mortality. While this pattern would hold significance in these populations, the actual degree of negative consequence of this is not entirely clear. On one hand, populations that have experienced harvest and/or mortality due to angling may experience a selective alteration of physiological and behavioral traits, with selection leaving behind fish that respond reactively (for instance by freezing) to threats such as predators, territorial intrusions, and attempts at predation of their nests. This, of course, could have cascading effects on the overall fitness of the population, especially in environments where greater fitness would otherwise be imparted by the maintenance of more proactive characteristics (Sutter et al. 2012). On the other hand, selection favoring reactive individuals could actually impart some fitness benefits in the form of increased behavioral flexibility in changing environments (Groothuis and Carere 2005), which is a characteristic often found in individuals with higher levels of stress responsiveness (Ruiz-Gomez et al. 2008; Ruiz-Gomez et al. 2011). This ability of an individual to adjust its behavior in the face of changing environments may be especially important in the face of the rapid environmental change brought on by human activity. (Sih 2013). Regardless of the outcome, it is likely that fisheries selection on physiology will have an impact on fitness levels in exploited populations, which will need to be closely examined and monitored in the years to come.

TABLES AND FIGURE

Table 2-1: Factor loadings and variance explained following Principal Components Analysis (PCA) on boldness metrics for largemouth bass (N=88). Largemouth bass were assessed for latency to emerge from a refuge in a novel arena, the number of zones crossed, and the amount of time spent away from the refuge within a 30 minute trial.

Factor	PC1 Loadings	PC2 Loadings
Time Spent in Open (s)	0.881	0.256
Number of Zone Lines Crossed	0.871	0.307
Latency to Emerge from Refuge (s)	-0.761	0.649
Eigenvalue	2.11	0.58
% Variance Explained	70.45%	19.35%

Table 2-2: Top 10 binary logistic models comparing baseline cortisol concentration, stress responsiveness (post-stress cortisol concentration minus baseline concentration), boldness score, fish weight, and selected line on whether or not a largemouth bass was captured during angling trials (N=88). Comparisons were made using Akaike's Information Criterion, adjusted for small sample sizes (AIC_C). -2 log likelihood scores and Model Likelihoods (W_i) are also given.

Model	AIC_C	Δ AIC_C	-2 log likelihood	W_i
Stress Responsiveness	109.68	0	105.54	0.46
Stress Responsiveness + Boldness	111.70	2.02	105.41	0.17
Stress Responsiveness + Baseline Cortisol	111.72	2.04	105.43	0.16
Stress Responsiveness + Fish Weight	111.78	2.10	105.49	0.16
Stress Responsiveness + Fish Weight + Boldness	113.70	4.02	105.22	0.06
Stress Responsiveness + Baseline Cortisol + Boldness	113.75	4.07	105.27	0.06
Stress Responsiveness + Fish Weight + Baseline Cortisol	113.85	4.17	105.37	0.06
Stress Responsiveness + Line	114.35	4.67	108.06	0.04
Stress Responsiveness + Fish Weight + Baseline Cortisol + Boldness	115.81	6.13	105.08	0.02
Stress Responsiveness + Fish Weight + Line	116.33	6.65	107.85	0.02

Table 2-3: Statistical outputs of Student's t-tests comparing captured and uncaptured largemouth bass for baseline cortisol, stress responsiveness, boldness score, standard metabolic rate (SMR), maximum metabolic rate (MMR), aerobic scope (AS), and fish weight following assessment and experimental angling trials. Variables that differed significantly between captured and uncaptured fish are given in bold.

Variable Measured	t	p	df
Baseline Cortisol (ng ml^{-1})	-0.80	0.42	87
Stress Responsiveness	**2.80**	**0.006**	**87**
Boldness Score	-0.36	0.71	87
SMR (mg O_2 kg^{-1} hr^{-1})	-1.00	0.32	38
MMR (mg O_2 kg^{-1} hr^{-1})	-0.52	0.60	38
AS (mg O_2 kg^{-1} hr^{-1})	-0.22	0.81	37
Fish Weight (g)	-0.56	0.57	87

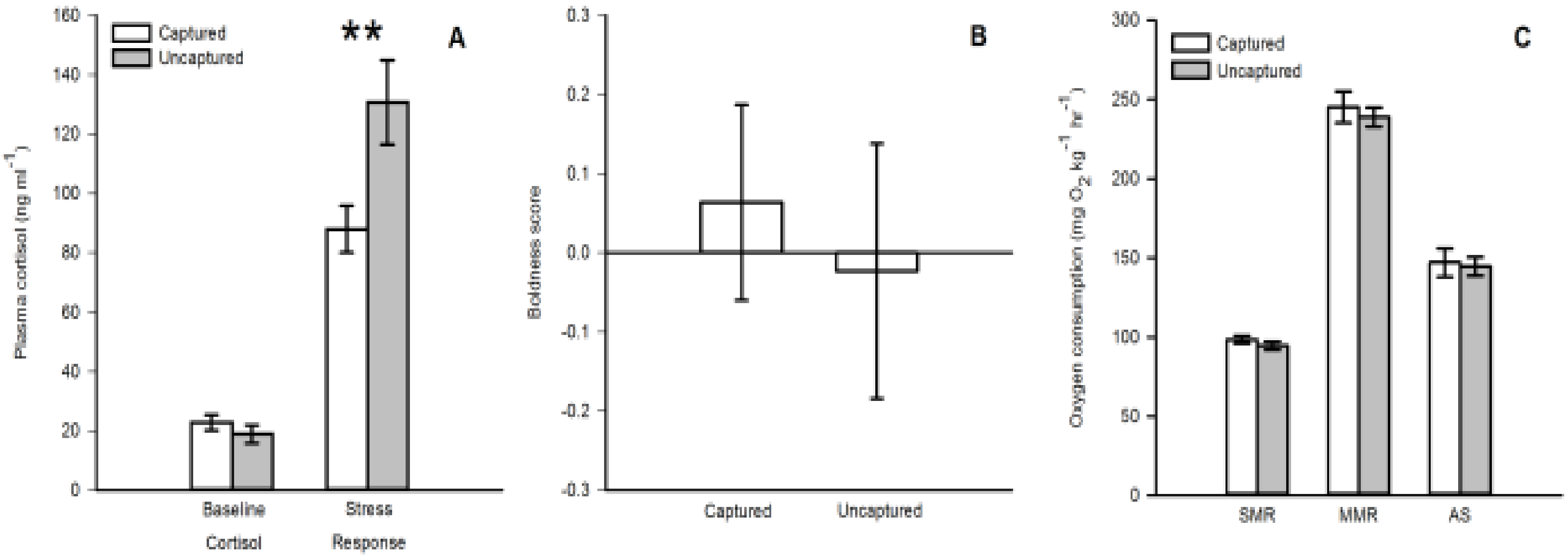

Figure 2-1: Comparison of A) baseline and post-stress cortisol, B) boldness scores, and C) metabolic variables (Standard Metabolic Rate, Maximum Metabolic Rate, Aerobic Scope) for largemouth bass that were either captured or not captured during experimental angling trials. For each fish, a baseline and post-stress plasma sample was taken, similarly for metabolic rate a single measurement of SMR and MMR was taken. Significant differences between captured and uncaptured fish for a given metric are denoted by asterisks (**). All bars are shown as means ± S.E.M. For cortisol concentrations and boldness score N = 58 captured and 30 uncaptured fish; for metabolic rate N=20 captured and 20 uncaptured fish.

CHAPTER 3: METABOLIC PHENOTYPE IS NOT ASSOCIATED WITH VULNERABILITY TO ANGLING IN BLUEGILL SUNFISH

Introduction

Behavioral decisions by individuals are influenced by a host of factors associated with their physiology. Energy reserves, for instance, can be a major driver of behavior, with starving individuals likely to forage in riskier situations to acquire necessary energy (Dingemanse and Wolf 2010; Sih et al. 2015; Näslund and Johnsson 2016). Alternatively, high energy reserves may lead to more aggressive and/or bold behavior (defined as a willingness to take risks) by facilitating faster growth, resulting in larger body size that lowers vulnerability to predators or aggressive competitors (Luttbeg and Sih 2010; Wolf and Weissing 2010). The amount of energy an organism has in reserve is determined by both its foraging success as well as its intrinsic metabolic rate, which dictates the pace at which acquired energy stores are utilized (Metcalfe et al. 1995; Houston 2010). Individuals with high metabolic rates often tend to take more risks while foraging to acquire enough food to satisfy metabolic demands (Stamps 2007; Biro and Stamps 2010). This expectation has been validated in several studies that found a highly integrated relationship between metabolism and bolder behavior (Killen et al. 2012; Herrera et al. 2014; Myles-Gonzalez et al. 2015; Binder et al. 2016), though this conclusion is not unanimous (Houston 2010). What is clear, however is that an organism's metabolic phenotype (standard metabolic rate, maximum metabolic rate and its scope for aerobic and anaerobic activity (Metcalfe et al. 2016)) is capable of underpinning numerous aspects of its behavior.

The behavioral decisions made by individuals may have fitness consequences, particularly when applied to encounters with humans. Bolder behavior, for example, which may have provided fitness benefits in an undisturbed environment, may suddenly become maladaptive if that bold behavior leads to death at the hands of humans (Sih 2013). One context in which this possibility has been previously studied is within the realm of fisheries, where evolution (hereafter referred to as fisheries-induced evolution) can occur in exploited populations as a result of selective harvest of individuals with certain behavioral/physiological/life history characteristics (Uusi-Heikkila et al. 2008; Sutter et al. 2012; Diaz Pauli and Sih 2017). In the case of recreational angling, which utilizes so-called “passive gears” that require a fish to make a decision to approach a lure and strike, it has often been posited that bolder individuals will be more likely to be captured (Harkonen et al. 2014; Alós et al. 2016; Arlinghaus et al. 2016). If bold individuals are more likely to be captured, then high metabolic rates should also be positively associated with capture likelihood if indeed boldness and metabolic characteristics are linked. Indeed, prior work has found that fish populations exploited by anglers undergo downward shifts in metabolic phenotype resulting from the selective capture of individuals with high metabolic rates (Redpath et al. 2010; Hessenauer et al. 2015). This evidence collectively suggests that metabolic phenotype is a physiological variable of interest in terms of driving capture by recreational anglers.

While prior work has indicated that metabolic phenotype may be altered in exploited fish populations, work that directly quantifies whether certain phenotypes are more vulnerable to angling is lacking. Due to potential links between metabolism, behavior and feeding/foraging, aspects of metabolic phenotype may be responsible for fish striking lures and being captured (Cooke et al. 2007; Lennox et al. 2017). Alternatively, anglers may selectively capture individuals based on an unknown variable connected to metabolic rate, which leads to metabolic phenotype being altered even though it isn’t the proximal driver of selection (Ketterson and Nolan, Jr. 1999). In addition, whether angling-driven selection alters metabolic phenotype in multiple species targeted by recreational anglers is not known. Work demonstrating alterations in metabolic phenotype as a result of recreational harvest have largely been performed using largemouth bass *Micropterus salmoides* (Cooke et al. 2007; Redpath et al. 2010; Hessenauer et al. 2015), and no other work has quantified the role of metabolic phenotype in driving angling vulnerability for any other species. More work is necessary to define links between metabolic phenotype and angling vulnerability in additional contexts, especially in additional species that may be subject to the effects of fisheries-induced evolution in freshwater systems.

The goal of this chapter is to define whether metabolic phenotype drives capture likelihood in bluegill sunfish *Lepomis macrochirus*. This species is an ideal candidate for study because it is an extremely popular species targeted by recreational anglers throughout much of the eastern and central portions of the United States and Canada (Gaeta et al. 2013), and little work to this point has been done examining how individual traits may relate to capture vulnerability in this species (but see Wilson et al. 2011). In addition, positive relationships between boldness and metabolic characteristics have been previously described for this species (Binder et al. 2016), allowing us to extrapolate likely behavioral traits of bluegill based on their metabolic phenotype. I experimentally angled lake-reared bluegill held in an earthen pond to establish captured and uncaptured groups, which I then assessed for differences in metabolic phenotype. I also assessed whether metabolic phenotype was connected to the order in which fish were captured, predicting that individuals with high metabolic rates would be captured early in the angling process. Assessing capture order in addition to whether or not the fish was captured may provide insights into whether metabolic rate is connected with hook-avoidance learning in fish. For instance, if individuals with certain metabolic phenotypes are captured in later angling sessions (after the threat of angling has been established), that may indicate that those phenotypes have a more difficult time learning to avoid striking fishing lures. I hypothesized that, in congruence with prior work on largemouth bass, individuals with high standard metabolic rates and aerobic scopes would be more vulnerable to capture. If metabolic phenotype is indeed a driver of capture likelihood in bluegill, this finding combined with previous work would indicate that metabolic phenotype may be a key trait under selection in a larger set of contexts. This could have major impacts on not only the metabolic physiology of exploited populations, but on the ecologically relevant behaviors that are themselves linked to metabolic phenotype.

Materials and Methods

Fish and Holding Conditions

A total of 160 bluegill sunfish were acquired from Jake Wolf Hatchery in Topeka, IL, in fall 2015. The hatchery environment for these fish was in a natural lake setting, where they were able to forage for natural prey items and avoid predators (both piscine and avian), thus eliminating the possibility of fish behavior being altered as a result of rearing in typical sterile hatchery conditions (Lee and Berejikian 2008). After being acquired from the hatchery, fish were transported to the Illinois Natural History Survey's Aquatic Research Facility near Champaign, IL. This facility consists of a wet lab and a series of earthen-bottom experimental ponds, all of which feature natural macrophyte cover and stocked fathead minnows *Pimphales promelas*, along with natural macroinvertebrate forage. Following arrival at the facility, all fish were implanted with a Passive Integrated Transponder (PIT) tag for individual identification, and subsequently stocked into a single 0.04 ha pond where they were held for eight months. In spring 2016, the pond was drained and 115 bluegill (mean total weight ± standard error of the mean (SEM) = 100.0 ± 2.7 g) were recovered. These fish were then stocked into a second pond (hereafter, the "angling pond"), which featured nearly identical conditions to the original pond, and were the subjects of this chapter.

Experimental Angling

Experimental angling to quantify angling vulnerability in bluegill occurred between July 8 and July 10, 2016, and consisted of five 90-minute angling sessions. On all three days, a morning angling session was conducted beginning at 7:00 AM, and on July 8 and July 9 an afternoon session was conducted beginning at 5:30 PM. For each angling session, the perimeter of the pond was divided in half, and one of two experienced anglers fished each half. Every 30 minutes during the 90 minute session (30 minute subunits are hereafter referred to as 'periods'), the anglers switched sides of the pond. Both anglers used identical gear commonly used by anglers targeting bluegill sunfish. This gear consisted of light-action spinning rods spooled with 1.8 kg Berkley® Trilene monofilament fishing line, tied to a single 12 Eagle Claw® J-Hook suspended from a slip-bobber. Hooks were baited with Berkley® Crappie Nibbles that were colored chartreuse, pink or white. During each 30-minute period, each angler used a different colored bait as determined by random selection and casted to all areas within the pond in an attempt to maximize catch rates. Fish captured via angling were identified by PIT tag before being released back into the pond within one minute of capture, and the color of lure and section of the pond where capture occurred were noted. All fish, with the exception of one, were hooked in the mouth with minimal tissue damage; the fish that was deep-hooked in the gullet failed to recover in a separate tank and was subsequently euthanized. While released fish were available to be potentially captured a second time, only two recapture events occurred over the five angling sessions. All fish that were captured at least once over the five angling sessions were considered vulnerable to angling for the purpose of the study. Following the angling sessions, a total of 34 bluegill were captured (two of which had been captured twice), and 81 bluegill were not captured. In addition to these captures, anglers also noted when a strike was detected, evidenced by the bobber being pulled below the surface of the water, but a fish was not successfully landed (e.g., situations where bluegill "nibbled" the lure and likely never fully ingested the hook into its mouth). These situations were considered "misses", in line with previous angling research on bluegill (Cooke et al. 2005).

Five days following the conclusion of angling, the pond was drained and 54 bluegill (24 captured, 30 non-captured) were randomly selected and transferred to a series of 1175 L circular holding tanks connected to a recirculating flow-through system that brought water in continuously from an adjacent pond. The remaining fish that were not used in the study were subsequently stocked into a separate on-site pond. Tanks were stocked at a density of nine fish per tank (four captured, five uncaptured). Water temperatures in the tanks matched ambient conditions in the ponds (daily mean temperature = 25.98º C ± 0.2º SEM). During holding, fish were fed daily with frozen bloodworms (Chironomidae). A total of 48 fish (N=23 captured fish, and 25 uncaptured) out of this group of 54 were then assessed for metabolic rate, beginning on July 20. I chose not to assess all 115 fish for metabolic phenotype because I was concerned that the photoperiod and ambient temperature would change over extended period required to conduct respirometry assessments on all fish, thus biasing assessments of metabolic rates (Biswas and Takeuchi 2002).

Metabolic Phenotype Assessment

The 48 bluegill randomly selected following angling trials were assessed for metabolic phenotype *via* intermittent flow respirometry (Metcalfe et al. 1995; Redpath et al. 2010; Nelson and Chabot 2011). Four fish were analyzed each day over the course of 12 d, beginning on July 21, 2016. During these 12 d, fish that had not yet been assessed for metabolic phenotype continued to be held in holding tanks described above. On the day before analyses, each bluegill was loaded into an individual 27 L black Perspex box fed by a flow-through recirculation system that maintained dissolved oxygen above 10 mg/L and temperature at 24^o C using an air stone and a heater-chiller (Teco®, Ravenna, Italy) in the reservoir tank that fed the system. This was done to ensure that all fish were fasted for 24 h before conducting respirometry trials (Nelson and Chabot 2011) and to allow fish an opportunity to acclimate to the water temperatures employed in the respirometry setup. On the day of the trial, each bluegill was removed from its individual container and placed into a 190 L tank and immediately exercised to exhaustion *via* "tail pinching" (Norin and Clark 2016), where an observer attempted to grab the tail of the fish forcing it to burst to escape. All fish were considered exhausted when they no longer made attempts to escape and could be easily grabbed by the observer without successive bursts. Immediately following exercise, fish were loaded into one of four 5.26 L individual respirometry cylinders immersed in a 585 L tank. Water temperatures in the tank were maintained at 24^{o}C using heater-chillers and dissolved oxygen in the tank was maintained near 100% saturation with a series of air stones. Dissolved oxygen levels in the cylinders were monitored continuously using fiber optic oxygen probes (Loligo Systems ®, Tjele, Denmark). The measurement cycle was determined following a series of pilot trials and went as follows: 10 minute flush, 5 minute wait, and 12 minute measurement, thus providing an individual measurement of metabolic rate ($MO_{2,}$ given in mg O_2 consumed/kg fish weight/hr.) every 27 minutes. All fish were held in respirometry chambers overnight before being removed the following morning (17-18 h later). Following removal, a measurement of background metabolic rate was taken by measuring oxygen consumption in the cylinders without the fish. Background respiration as a result of microbial activity was then corrected for each measurement based on a linear increase in MO_2 from the outset of the trial (when pilot trials previously showed background MO_2 values to be at zero) to the background MO_2 value obtained after removing the fish (Rodgers et al. 2016). To keep background respiration at a minimum, the entire setup (all tubing and chambers) were cleaned in a 10% bleach solution before each trial.

Calculation of metabolic phenotype metrics was performed following methods described in Killen et al. (2015). Standard Metabolic Rate (SMR) was calculated as the mean of the lowest tenth percentile of MO_2 values collected during overnight holding. Maximum Metabolic Rate (MMR) was determined as the single largest individual MO_2 obtained following exercise. Aerobic Scope (AS) was calculated as the difference between MMR and SMR for each fish, and Routine Metabolic Rate (RMR) was defined as the mean of all MO_2 measurements, excluding the first two hours after loading. The determination of RMR was then used to calculate Excess Post-Exercise Oxygen Consumption (EPOC). For this, a sixth-order polynomial recovery function was constructed that ran through all collected MO_2 values obtained following exercise and overnight. EPOC was then defined as the area under this curve and above RMR between the onset of the trial and the point where the recovery curve intersected with RMR (Killen et al. 2015b). Recovery time (T_s) was defined as the time needed before the fish had recovered 50% of its AS, as taken from MO_2 values. While I am conscious of prior studies that have shown that stressors can influence measures of metabolic phenotype, I found it unlikely that the process of being captured would have impacted measurements of metabolic phenotype as prior work has shown that fish can recover normal metabolic cardiovascular function within 12 h of the angling stressor (Milligan et al. 2000; Cooke et al. 2003).

Statistical Analysis

To reduce the number of variables assessed, and account for correlations among metabolic metrics (SMR, MMR, AS, T_s, and EPOC) Principal Components Analysis (PCA) based on the correlation matrix was performed. Component scores for each fish were varimax rotated based on the maximum likelihood solution, components with an eigenvalue over one were retained, and factor loadings with an absolute value ≥ 0.4 were considered significant contributors to each factor (Kaiser 1960, King et al. 2016). Once components were extracted, Pearson's Correlation Tests were run to determine if any components were associated with fish weight.

To determine if the two anglers were systematically capturing fish with different metabolic phenotypes, Student's T-tests were run comparing all extracted principal components between anglers. A Fisher's exact test was then used to determine if one angler captured a disproportionate number of fish relative to the other angler. A one-way analysis of variance (ANOVA) was used to determine if any extracted components for captured fish differed depending on the color of the lure on which they were captured.

To determine if angling selected for particular metabolic characteristics, a binary logistic regression was run to determine if any extracted components or fish weight were associated with capture status. In addition, an ordinal regression was performed to determine if metabolic metrics influenced the order in which fish were captured. For this analysis, only captured fish were assessed, and fish capture was binned by angling session. This approach was taken, rather than running the analysis based on the actual order of capture (for instance, the 1st, 2nd, 3rd fish captured, and so on), to account for the fact that the likelihood of capture may depend on both intrinsic characteristics (e.g., metabolic phenotype) as well as chance encounter with the lure. By grouping all captured fish by session of capture, this issue is eliminated because, within each angling session, the entire pond was angled, and every fish likely was presented with a lure, especially given the relatively small size (0.04 ha) of the angling pond.

For all tests, homogeneity of variances on raw data were confirmed using Levene's Tests, and normality was assessed following visual inspection of residual q-q plots. All analyses were conducted in R 3.3.1 (R Core Team, Vienna, Austria), and the level of significance (α) used for all tests was 0.05.

Results

Summaries of all metabolic metrics and fish weight by capture status are given in Figure 3-1. Three principal components of metabolic phenotype with eigenvalues over 1 were extracted from these metabolic metrics (PCs 1-3). Maximum metabolic rate and AS loaded positively on PC1, T_s and EPOC loaded positively on PC2, and SMR/MMR loaded positively on PC3 (Table 3-1). Cumulatively, the three extracted components explained over 96% of the total variance in the data (Table 3-1). No relationship was present between fish weight and PC1, however weight was significantly and negatively associated with both PC2 ($t=-2.39$, $p = 0.02$) and PC3 ($t=-3.95$, $p < 0.001$). This indicates that larger fish had a shorter recovery time and smaller EPOC, as well as a lower SMR, than smaller fish.

Angling resulted in the capture of 34 of the available 115 fish (36 total capture events, including two recaptures). Twelve of the capture events occurred in session one, six in session two, seven in session three, and 11 in session four. No fish were captured during session five.

The subsample of fish used for respirometry paralleled the proportion of fish caught in each session overall, with nine fish captured in session one, three captured in session two, four captured in session three, and seven captured in session four. When a strike was detected, as evidenced by the bobber being pulled beneath the surface of the water, the landing success rate across both anglers was 51.4%. While this potentially leaves several fish that struck the bait classified as "uncaptured", this landing rate is comparable to previously reported landing rates for bluegill anglers (Cooke et al. 2005), making the angling regime used presently a realistic representation of angling selection on bluegill in the wild. Furthermore, the majority of "misses" were "nibbles", where fish likely did not completely ingest the hook. In my case, fish which fully struck the hook were classified as vulnerable, whereas "nibbles" were not considered indicative of a vulnerable fish. Of the total captures, 23 (64 %) were by one angler, with 13 fish captured by the second angler. While this difference in the proportion of captures by each angler was statistically significant (Fisher's Exact Test, p=0.03), no components of metabolic phenotype nor fish weight differed across anglers (t-tests, all p's > 0.3 for all extracted metabolic components and fish weight) or lure color (ANOVA, p > 0.17 for all components and fish weight). Therefore, all captures were pooled regardless of angler or lure color for the purpose of metabolic phenotype comparison between captured and uncaptured fish.

Neither the extracted metabolic components nor fish weight were a significant predictor of capture (Table 3-2). Among the captured fish however, PC2 was significantly associated with the session in which fish were captured, with those fish that were captured later tending to have a higher PC2 score (Figure 3-2)

Discussion

Metabolic phenotype did not influence whether or not an individual bluegill sunfish was captured during experimental angling. Metabolic rate describes the rate of energy consumption in organisms, and individuals that have high metabolic rates will need to have high rates of food consumption to meet their energetic demands (Biro and Stamps 2010). Metabolic phenotype is a heritable characteristic in organisms that has been found to correlate positively with several ecologically relevant behavioral characteristics including boldness, aggression, performance, and activity level (Biro and Stamps 2008, 2010; Reale et al. 2010b; Metcalfe et al. 2016). This positive relationship has also been found in bluegill sunfish, with bold individuals having higher aerobic scopes for activity (Binder et al. 2016). In turn, these behaviors can be drivers of fitness, and a frequent finding has been that bolder, more active, and/or aggressive individuals achieve higher fitness (Biro and Stamps 2008). This relationship however has not been universally demonstrated, and may be dependent on life stage (Ballew et al. 2017), or selective pressures that may lead to the decoupling of behavioral and metabolic characteristics (Houston 2010; Hille and Cooper 2015). While this is possible, I have no reason to suspect that the relationship between metabolic phenotype and boldness in bluegill, demonstrated by Binder et al. (2016) is any different for fish in this chapter. The bluegill used for this chapter are the products of natural reproduction in a lake featuring a full suite of native predators as well as typical forage and cover items. Therefore, the selective pressures on these bluegill were likely similar to those in any other natural environment, including the lake the bluegill described in Binder et al. (2016) were taken from. If I am to assume, therefore, the same link between metabolic phenotype and behavior is common for bluegill, angling-driven selection based on metabolic phenotype could drive evolutionary changes in the behavior of exploited populations (Arlinghaus et al. 2016). However, because the date from this chapter showed that metabolic phenotype did not impact whether or not an individual was captured, I would not expect anglers to impart selection on metabolic phenotypes for bluegill.

Previous work has examined the role of behavior (particularly boldness) in driving vulnerability to capture independent of metabolic phenotype, with some studies suggesting that bold individuals are more vulnerable and thus would be selected against in an envioronment exploited by anglers (Harkonen et al. 2014; Alós et al. 2016). Additionally, studies utilizing lines of largemouth bass artificially selected for differing vulnerability to angling found not only that the "high vulnerability" line exhibited higher metabolic rates relative to less vulnerable fish (Cooke et al. 2007; Redpath et al. 2010), but also that more aggressive nest defense behavior in highly vulnerable fish led to higher reproductive success (Sutter et al. 2012). Furthermore, Hessenauer et al. (2015) showed that largemouth bass from unfished reservoirs had higher standard metabolic rates relative to fish from reservoirs exploited by anglers, providing further evidence that angling-induced selection can influence metabolic rates. While it is tempting to then generalize these findings to all species, some evidence exists indicating that relationships among metabolic phenotype, behavior, and angling vulnerability may differ in bluegill sunfish compared to other species. While a prior study of bluegill sunfish showed that a positive relationship between metabolic rate and boldness is indeed present (Binder et al. 2016), another study that assessed the relationship between boldness and angling vulnerability found that individuals captured *via* angling were shyer than those captured *via* seining (Wilson et al. 2011). Under this combined framework where shyer individuals are more vulnerable to angling, it might therefore be expected that individuals with lower metabolic rates would actually be more likely to be caught, however the data in this chapter do not support this prediction. Perhaps the angling context (lure type, size of the pond, etc.) used for this chapter prevented the selective capture of certain metabolic phenotypes, or did not provide enough angling time to detect a significant effect of metabolism on angling vulnerability. Future work will be needed to determine if metabolic phenotype may indeed be under selection in bluegill sunfish, focusing on the role of metabolism in various contexts.

Among captured fish, individuals with longer recovery times and lower EPOC were more likely to be captured in later angling sessions. However, given the relatively low number of captured fish and the lack of relationship between session of capture and other aspects of metabolic phenotype, this finding is difficult to interpret. Prior to the outset of the study, I posited that capture order might be either positively or negatively associated with metabolic phenotype (particularly SMR and aerobic scope) even if overall mean metabolic rate was similar between captured and uncaptured fish, through several possible mechanisms. First, high metabolic rates are driven by relatively high allocation costs, with a greater amount of energy being routed towards active behavior, sexual development, digestion, and other needs (Enberg et al. 2012). This would lead fish to have to feed more frequently in order to satisfy those demands, in turn leading to a greater probability of striking a fishing bait. In a second connected mechanism, higher activity levels as a result of high metabolic rates could have led bluegill to be more likely to randomly encounter fishing gear (Stamps 2007). Finally, at least two studies (Metcalfe et al. 1995, Killen et al. 2014) have found a positive relationship between metabolic rate and aggression, which may facilitate dominance over the food resource (in this case, the bait), leading to more captures. Alternatively, if feeding motivation and behavior are not driving lure striking, then the phenotype of individuals captured early or late in the angling process could be driven by relative learning ability. It is well established that fish are able to learn to avoid lures following a period of angling pressure (Young and Hayes 2004; Lennox et al. 2016). The process of learning has been previously described as a type of behavioral flexibility (Stamps 2016), and high metabolic rates, while positively associated with boldness, have been negatively associated with behavioral flexibility (Koolhaas et al. 1999). With regards to capture order, it would then be possible that fish caught later in the angling process would have higher metabolic rates, as behaviorally flexible individuals with lower metabolic rates would have altered their behaviors to avoid striking the bait more successfully. However, neither of these possible mechanisms were supported by my data, which found no relationship between capture order and the aerobic components (SMR, MMR, AS) of metabolic phenotype. This finding presents another piece of evidence that, for bluegill sunfish, metabolic phenotype is not associated with angling vulnerability.

Vulnerability to angling for a fish is likely driven by a host of behavioral and state-driven factors (Lennox et al. 2017). While prior work has found metabolic phenotype to be altered in heavily angled populations (Redpath et al. 2010; Hessenauer et al. 2015), I propose four potential explanations for why metabolic phenotype did not predict capture for bluegill sunfish that could be explored in future work. First, metabolic phenotype may not be a major driver of capture in fish, at least over short periods of angling, but still may be altered over a longer period of time due to its covariance with other physiological or behavioral characteristics that are actually proximal drivers (Ketterson and Nolan, Jr. 1999). For example, a recent study found that, over a week of angling, individual largemouth bass that showed lower rises in cortisol concentration in plasma following a stressor were more likely to be captured (Chapter 2). While cortisol levels and metabolic rate were not correlated in that study, the fact that these physiological traits have been shown to be linked previously (Careau et al. 2008) could provide a route through which metabolic phenotype could evolve under the selective pressure of angling even if metabolic rate is not the proximal driver of vulnerability. A second alternative explanation could be that conditions present in the pond altered the selectivity of capture based on metabolic phenotype. The pond where angling took place featured a high density of forage between the stocked juvenile fathead minnows and natural aquatic invertebrates. Under these conditions, it is possible that all fish, regardless of their metabolic rate, were fed to satiation. As a result, the angled population may not have differed in feeding motivation, which could eliminate the role of metabolic rate in driving the response to fishing baits. A third potential explanation applies to the species used in this chapter. While many studies have quantified the relationship between boldness/activity and angling vulnerability, a notable exception to the general finding that boldness is positively correlated with vulnerability (Alós et al. 2012, 2016; Harkonen et al. 2014; Villegas-Rios et al. 2014) was found in bluegill sunfish, where individuals that were caught *via* angling were shyer than those captured from the same area *via* seining (Wilson et al. 2011). These results indicate that there is perhaps something specific and unknown about this species and its behavior that leads to individuals with the high boldness/high metabolic rate phenotype (Binder et al. 2016) to not be more vulnerable to angling as in other species. It should be noted however that, in the Wilson et al. (2011) study, when seined fish were subjected to angling in an artificial environment, it was the bolder fish that were found to be more vulnerable. This could indicate that vulnerability to angling is driven both by the fish's phenotype as well as the angling environment, which would lead to particular phenotypes being more vulnerable in some situations but not in others. Alternatively, the lack of a relationship between metabolic phenotype and capture likelihood may be related to the methodology of the study, specifically angling over a relatively short period of time (single captures over 3 angling sessions). This short period may not have allowed for angling in a wide variety of environmental contexts (different water temperatures, forage availability, photoperiod, etc.) that change seasonally, and metabolic phenotype may prove to be a driver of capture likelihood under alternative environmental conditions. Indeed, previous work that demonstrated an impact of angling on metabolic rate in largemouth bass occurred over several generations (Redpath et al. 2010; Hessenauer et al. 2015). Further work will therefore be necessary to determine if the findings of this chapter apply to all environental contexts in bluegill sunfish, and also to examine how environmental context may change patterns of angling-induced selection in other targeted species.

The selective capture of individuals with particular traits has the potential to evolutionarily alter exploited fish populations. This process of 'fisheries-induced evolution' has previously been quantified in commercially exploited marine fisheries, with studies demonstrating alterations in life history traits such as age-at-maturity and mean growth rate (Devine et al. 2012; Kuparinen and Hutchings 2012; Eikeset et al. 2013). The potential for fisheries-induced evolution to occur in recreationally-targeted fisheries has been demonstrated as well (Edeline et al. 2007; Philipp et al. 2009). For recreational stocks, this necessitates the determination of characteristics that may be drivers of angling vulnerability, and thus under selective pressure. Metabolic phenotype emerges as a primary variable of interest, due to its cascading impacts on the behavior and ecology of individuals (Metcalfe et al. 1995; Killen et al. 2012; Myles-Gonzalez et al. 2015) and the fact that prior studies have indicated that it may be under selective pressure in recreationally fished populations (Redpath et al. 2010; Hessenauer et al. 2015). I found no evidence that any measurement of metabolic phenotype is a determinant of angling vulnerability in bluegill sunfish in the context of acute, short term fishing pressure. This finding is a further demonstration of the fact that the drivers of angling vulnerability may not be simple, and that within different contexts (different times of year, gear types, targeted species), angling-induced selection may or may not cause evolution in particular traits. Because metabolic phenotype has been shown to be linked to boldness, and prior work has shown that bolder bluegill sunfish are not more vulnerable to capture (Wilson et al. 2011), a behavioral cascade leading to shyer average behavior as well as lowered metabolic rates in exploited populations (Arlinghaus et al. 2016) may therefore be unlikely to occur for this species. The lack of a metabolic influence on capture likelihood however does not preclude the possibility that bluegill sunfish populations have indeed been evolutionarily changed due to angling, with alternative characteristics driving angling vulnerability. Going forward, it will be incumbent on managers and researchers to continue to investigate these possible factors, with an eye towards accurate predictions of how various targeted species may evolutionarily respond to angling pressure.

TABLES AND FIGURES

Table 3-1: Factor Loadings of metabolic metrics across all bluegill sunfish *Lepomis macrochirus* derived from principal components analysis (PCA).

Factor	PC1 Loadings	PC2 Loadings	PC3 Loadings
SMR (mg O_2 kg^{-1} h^{-1})			0.989
MMR (mg O_2 kg^{-1} h^{-1})	0.815		0.575
AS (mg O_2 kg^{-1} h^{-1})	0.974		
EPOC (mg O_2 kg^{-1})	0.490	0.747	
T_s (h)		0.956	
Eigenvalue	1.96	1.77	1.03
% Variance Explained	39.22	35.41	21.46

Table 3-2: Output of binary logistic regression analysis examining relationships between principal components of metabolic phenotype and angling vulnerability in bluegill *Lepomis macrochirus* (N = 23 captured, 25 uncaptured).

Factor	Estimate	St. Error	Z	p
Intercept	1.06	2.05	0.52	0.60
Fish Weight	-0.01	0.02	-0.56	0.57
PC1	0.18	0.30	0.61	0.54
PC2	-0.03	0.32	-0.11	0.91
PC3	-0.23	0.35	-0.66	0.50

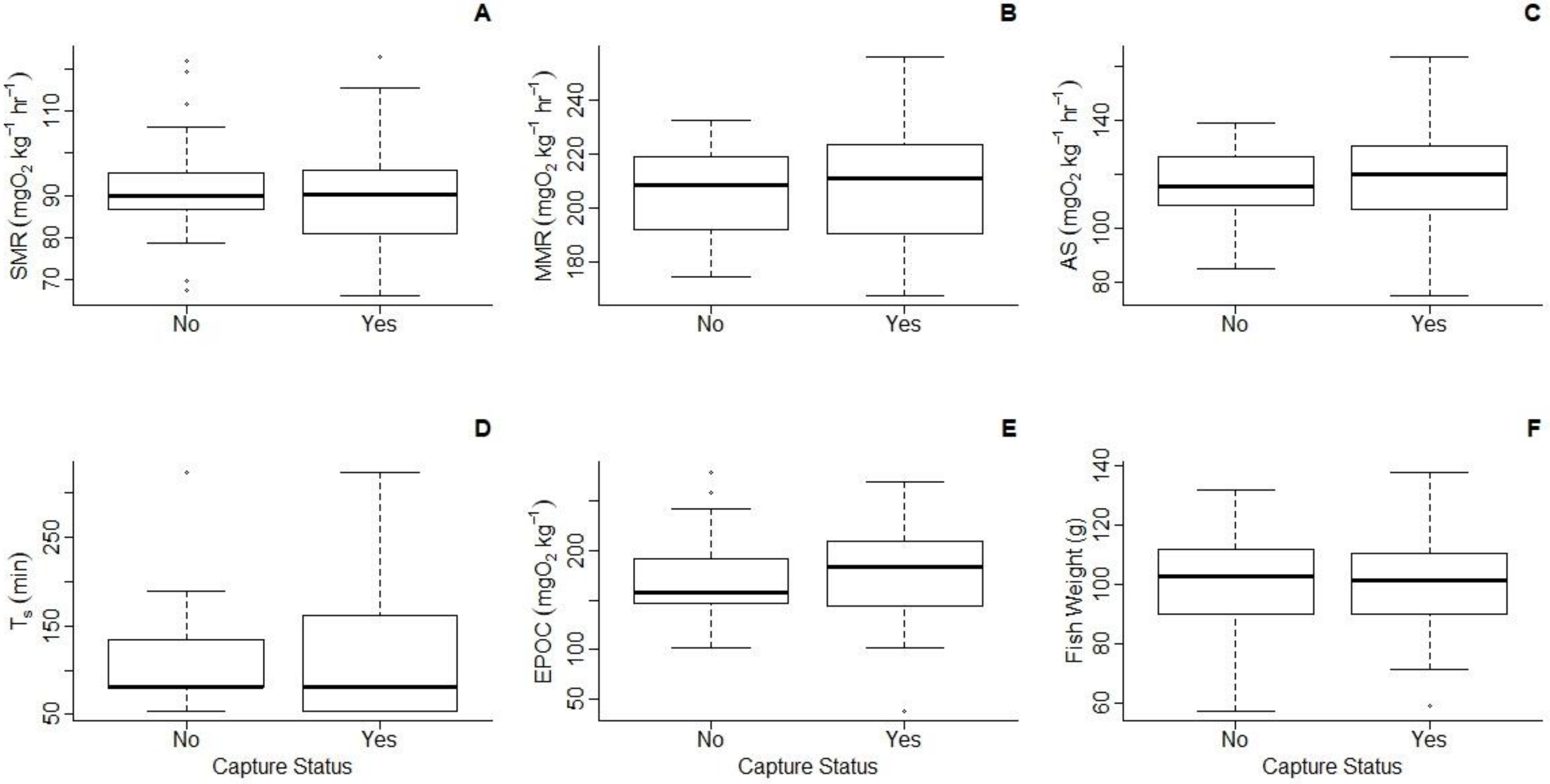

Figure 3-1: Boxplots describing A) Standard Metabolic Rate, B) Maximum Metabolic Rate, C) Aerobic Scope, D) Recovery Time, E) Exess Post-Exercise Oxygen Consumption, and F) Fish Weight for bluegill *Lepomis macrochirus* by capture status (N=23 yes, N = 25 no). No measure of metabolic phenotype differed between captured and uncaptured fish.

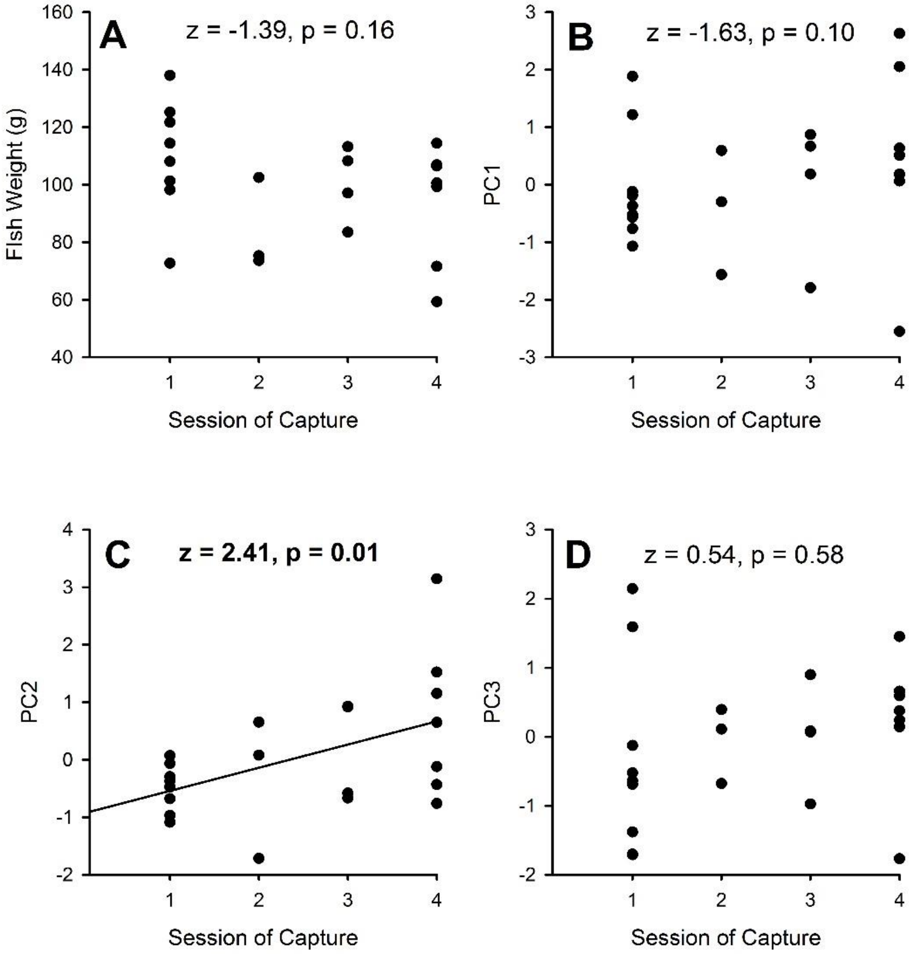

Figure 3-2: Relationships between extracted components of metabolic phenotype and the session in which bluegill sunfish *Lepomis macrochirus* (N = 23) were captured. Statistical outputs provided are derived from an ordinal regression analysis which included fish weight as independent variables, and the session in which the fish was captured as the dependent variable. The regression line on panel C indicates a significant relationship between PC2 and angling session, with higher scores associated with capture in later sessions.

CHAPTER 4: SOCIABLE BLUEGILL (*LEPOMIS MACROCHIRUS*) ARE SELECTIVELY CAPTURED VIA RECREATIONAL ANGLING

Introduction

Interactions among individuals within a population are often dictated by overarching social structure. Many species form herds, shoals, or loosely-tied aggregations that provide for mutual protection and the acquisition of crucial resources to group members (Krause et al. 2003; Dyer et al. 2009; Sih et al. 2009). Social groups are often hierarchical, and group members may adopt specific roles based on their size, age, experience, and behavioral tendencies (Croft et al. 2009; Modlmeier et al. 2014). The consistent behavioral tendencies of an individual are often collectively referred to as its “personality”, while the term “behavioral syndrome” refers to sets of traits that are correlated across a population of individuals (Bell 2007; Reale et al. 2010b). An individual’s sociability, defined as the tendency to associate with conspecifics, is considered a major axis of animal behavior and a significant determinant of social position within a hierarchy (Reale et al. 2007). Within these social groups, certain individuals may be critical to group cohesion, and the loss of such individuals can lead to a cascading loss of social function for the entire group (Modlmeier et al. 2014). These critical individuals may be leaders that obtain that position as a result of their behavioral dominance (Harcourt et al. 2009; Burns et al. 2012), individuals that have acquired important knowledge that is of benefit to other group-members (Franks and Marshall 2013; Jolles et al. 2014), or highly social individuals that quickly spread such information throughout an entire group (Vital and Martins 2013). Since individual behavioral characteristics (such as sociability and aggression) are likely to determine what role and individual occupies, understanding how these individual traits drive mortality risk is crucial in order to predict how group function may be impacted by the selective mortality of individuals with particular traits.

Selective mortality for social species can come in the form of harvest, where individual characteristics predispose game animals to greater risk. For instance, more active elk *Cervus canadensis* have been found to be more vulnerable to hunters (Ciuti et al. 2012), while it has been posited that highly social spiny lobsters *Panulirus argus* are more likely to form tight congregations in traps, leading to capture (Childress et al. 2015). Indeed, the propensity for individuals with particular behavioral traits to be more likely to be captured in traps or other gear has been demonstrated in reptiles (Michelangeli et al. 2016) as well as fish (Olsen et al. 2012; Pauli et al. 2015). Within the specific context of fishing, selective harvest of individuals with key behavioral, physiological, or life history characteristics has been shown to lead to evolutionary change in exploited marine (Kuparinen and Merila 2007; Eikeset et al. 2013) and freshwater (Philipp et al. 2009; Kendall and Quinn 2011) recreational systems, a process known as fisheries-induced evolution (Diaz Pauli and Sih 2017). Fisheries-induced evolutionary changes can lead to major impacts on the viability of exploited populations (Jorgensen et al. 2007). With regards to behavior, studies examining links between angling vulnerability and individual traits have largely focused on two behavioral axes (Reale et al. 2007) that may evolve in response to selective capture – individual boldness and exploratory tendency (Wilson et al. 2011; Harkonen et al. 2014; Alós et al. 2016), with a typical finding that bolder and/or more exploratory individuals are more likely to approach lures and strike, leading to capture (Klefoth et al. 2013, 2017). A third behavioral axis, sociability, has rarely been studied in this context (but see Mourier et al. 2017). Sociability is also often linked with aggression in individuals (Weeks et al. 2000; Overli et al. 2004), another understudied behavioral axis in the context of angling vulnerability (but see Sutter et al. 2012). In the case of aggression, it might be expected that individuals that are aggressive towards other individuals could also be more aggressive in striking lures (Sutter et al. 2012). With regards to sociability, prior work has shown that social tendencies impact various aspects of an individual's ecology, such as its habitat choice (Budaev 1997; Webster and Hart 2006), that may in turn lead fish to be more vulnerable by causing them to frequent areas targeted by anglers (Matthias et al. 2014; Monk and Arlinghaus 2018). Furthermore, intrinsic sociability may lead individuals to select differing social settings, for instance large groups where intense competition for food (Stoner and Ottmar 2004; Ward et al. 2006) may leave individuals more likely to strike a baited hook. Collectively, social behavior and/or aggression may well be linked to angling vulnerability, however work examining this potential relationship is currently scarce.

To better understand whether individuals that differ in their vulnerability to angling also differ in their sociability or aggression, I conducted a laboratory study utilizing bluegill, *Lepomis macrochirus.* Bluegill are a semi-gregarious freshwater fish species that form social hierarchies based on aggressive interactions (Lorenz et al. 2011; Gaeta et al. 2013) and are commonly targeted by anglers throughout much of North America. To define the relationship between angling vulnerability and social behaviors, a population of bluegill were first subjected to a series of angling trials in a natural pond environment. Next, a subset of captured and uncaptured bluegill were tested for sociability in a behavioral arena and aggression in a dyadic contest. This work is among the first to examine the role of social behavior broadly in driving angling vulnerability, a relationship that could have evolutionary significance if these characteristics are indeed subject to angling selection in exploited systems.

Methods

Study Site and Experimental Animals

All experiments took place at the Illinois Natural History Survey's Aquatic Research Facility using 151 adult bluegill acquired from Jake Wolf Fish Hatchery in Topeka IL on 4 June 2016. While bluegill were not aged over the course of this study, based on their lengths it is likely that all fish were at least 3 years old when they were acquired (Peterson et al. 2010). Mean total length among study fish was 16.7 cm (± 6.5 cm standard deviation), and mean weight was 80.4 g (± 11.2 g standard deviation).Bluegill acquired from the hatchery had been reared in a natural lake environment featuring natural forage and aquatic predators such as largemouth bass *Micropterus salmoides* and muskellunge *Esox masquinongy*. While bluegill in this environment had to evade predators, they had not been previously exposed to angling pressure. Upon arrival at the Aquatic Research Facility, all fish were first implanted with a Passive Integrated Transponder (PIT) tag for individual identification before being stocked into a single 0.04 ha experimental pond. The pond featured an earthen bottom and native macrophytes for cover, and fish were able to forage on stocked mosquitofish *Gambusia* spp. as well as naturally occurring macroinvertebrates.

Angling Trials

Angling sessions in the experimental pond took place over five days, on 13-15 and 20-21 June, and were conducted by two experienced anglers. Each day of angling consisted of one 90-minute session beginning at 7:00 AM, followed by a second 90-minute session beginning at 5:30 PM. Both the morning session and the evening session were divided into three 30-minute periods, and the shoreline of the angling pond was divided into two sections of equivalent length (approximately 40 m of shoreline). At the outset of the first period, an angler was randomly assigned to each of the two sections of the pond where they fished for 30 minutes, moving around the shoreline so as to target all possible areas of the pond within that section. After this period, the anglers switched sections and fished for a second 30-minute period, and the process was repeated a third time for the third period. Both anglers used light-action spinning rods spooled with 1.8 kg Berkley® Trilene monofilament fishing line for all sessions, as is typical for bluegill anglers. The lure presentation consisted of a size 12 Eagle Claw® J-Hook baited with Berkley® Crappie Nibbles in one of three colors (chartreuse, pink, or white). During each period, anglers used a different color bait as determined by random selection. Upon capture, the hook was immediately removed from the fish, the identity of the individual fish was determined via PIT tag, and the fish was returned to the pond no more than 1 minute after capture. All captured fish except one were hooked superficially in the mouth, allowing for easy dehooking, the one fish that was "deep-hooked" was removed from the study to avoid the complications of a more prolonged dehooking time on its subsequent behavior. A total of 40 fish were captured at least once, with only a single fish being captured twice.

Fish Holding

On 22 June, the pond was drained, 141 of the original 151 bluegill were recovered, and a subsample of 19 captured and 19 uncaptured fish were haphazardly selected to be assessed for sociability and dominance. The remaining fish were used to populate stimulus shoals during sociability trials (see below). Initially, 32 captured and uncaptured fish were selected for behavioral testing, however during the holding period abnormally warm ambient temperatures over a three-day period combined with an unexpected failure of the flow-through pump system led to the death of 19 of the 64 fish across a subset of the holding tanks. Following this event, the remaining fish in the impacted tanks were placed across the remaining holding tanks, in order to ensure that each experimental fish experienced a tank environment that included a similar density of conspecifics. In the immediate aftermath of this event, an additional two fish were removed from the experiments due to listless behavior in the tank and a lack of feeding motivation, indicating stress. An additional five fish showed no signs of stress, however, they could not be paired successfully with an “unfamiliar” fish during dyadic trials (see below), which began six days after the conclusion of the mortality event. Given that the remaining fish were feeding normally and displaying typical behavior, and because this time frame has been found to be sufficient to allow for recovery in bluegill previously (McConnachie et al. 2012), I did not expect that this event would have impacted the subsequent behavior of the fish. Holding tanks for bluegill consisted of one of several circular 1135 L outdoor holding tanks, where fish were fed daily with frozen bloodworms (Chironomidae). Holding tanks were equipped with a flow-through pump system that continuously circulated water from an adjacent pond into the holding tanks at a rate of approximately eight full water exchanges per tank per day. An equal number of captured and uncaptured fish were put into each holding tank prior to experimentation, in order to avoid any possible tank effects that might lead to systematic differences in behavior between captured and uncaptured fish. With regards to the possible impacts of angling stress on the captured fish, because fish typically recover from the stress of angling within 24 h (Cooke et al. 2003; Cooke and Schramm 2007), I did not anticipate any impact of the angling event on the subsequent behavior. Indeed previous studies have taken the approach of subjecting fish to angling prior to an assessment of individual behavior or physiology (Wilson et al. 2011; Harkonen et al. 2016; Chapter 2)

Shoaling Trials

The evening before shoaling trials were conducted, each focal fish was placed in a 27 L black plastic isolation box to prevent potentially confounding social interactions among trial subjects. Each isolation box was connected to a recirculation system that continuously provided oxygenated water from a common reservoir tank. Water temperature in the isolation tanks was maintained near 22ºC by a Teco® Heater-Chiller (Ravenna, Italy) that recirculated water within the reservoir tank. Shoaling trials were designed to assess the willingness of an individual to associate near conspecifics on the opposing side of a transparent barrier, based on methods described in previous studies (Ward et al. 2004; Cote et al. 2012; Jolles et al. 2014). Social behavior was assessed only in the 38 focal fish (i.e., 19 captured and 19 uncaptured), while the remaining fish that were recovered from the pond were used to populate shoals for the purpose of this test. Trials were conducted in one of two behavioral arenas consisting of 565 L (181 cm long × 65 cm wide) rectangular polyethylene stock tanks filled with water to a depth of 30 cm. Behavioral arenas were divided in half along their short axis by a clear plexiglass divider that was punctured by a series of holes that allowed the exchange of water between the sides of the arena (Figure 4-1). A single 15 cm long piece of 7.6 cm diameter PVC piping was placed on one side of the arena to serve as a shelter item for the focal fish. On the day of the trial, a shoal of 6 conspecifics were drawn from the population of fish in the angling trials that were not selected for behavioral assessments and placed in the side of the behavioral arena opposite of the focal fish. Over the course of the experiment, each non-focal fish was used multiple times to populate shoals. By using a reasonably large shoal of non-focal conspecifics, I increased the chances of having each shoal populated by a mix of behavioral types, preventing potential bias as a result of a focal fish desiring to interact more or less with shoals depending on the behavioral types present in the shoal (Harcourt et al. 2009b).

Each trial was filmed with a GoPro® Hero 3 camera positioned directly over a line marking 8 cm from the divider on the focal side of the arena. This area within 8 cm of the divider was referred to as the "social zone" for the purpose of the experiment. A second line was drawn 24 cm from the divider, the area from that line to the end of the arena away from the divider was designated as the anti-social zone, with the space in-between labeled the "neutral zone" (Figure 1). Each trial consisted of a 15-minute acclimation period followed by a 15-minute trial when behaviors were observed and recorded. During the trial, the total amount of time each focal fish spent in the social and anti-social zones was determined. Time spent in the social zone was considered a measure of sociability in that greater time spent in the social zone indicated a more social focal fish (Cote et al. 2012). Four days after the first trial, each focal fish was subjected to a second trial to assess the short-term repeatability of shoaling behavior. Following their second shoaling trial, each fish was returned to their original outdoor holding tank, where they were held until assessment for dominance in dyadic trials.

Dyadic Trials

To quantify social dominance and aggression as it relates to angling vulnerability, I subjected experimental fish to paired dyadic trials conducted in one of eight 37 L glass aquaria (50 cm long × 28 cm wide × 33 cm high) that were initially divided in half by a removable opaque plastic barrier. Three sides of the aquarium were blocked with opaque plastic sheeting to avoid startling of the fish by observers, and scoring of all trials was conducted by a single observer looking in through a small slit in an opaque plastic blind positioned in front of each aquarium. Trials began on 24 July and were conducted and scored based on previously described methods (DiBattista et al. 2005; Jeffrey et al. 2012). In each trial, two focal fish (one captured, one uncaptured) were size-matched within 5% total length and placed into opposing sides of the divided aquarium. Previous work on the closely related pumpkinseed sunfish *Lepomis gibbosus* has demonstrated that, while size is a major predictor of dominance, differences in size of the magnitude used for this chapter are unlikely to be determiners of dyadic outcomes (Beacham 1988). Each fish was given a differentiating caudal fin clip (a small clip to either the upper or lower lobe of the caudal fin) prior to loading to identify it during observations, however the observer was unaware of which fish was captured and uncaptured when making observations during the trial. Pairs of fish were selected for dyadic trials from different holding tanks to ensure each pair had no prior opportunity to interact with each other during holding. Upon being placed into the aquarium, both fish were immediately fed with bloodworms and allowed to acclimate to the aquaria overnight.

The following morning the divider was removed, and, after a 30-minute acclimation period, behavioral observations were initiated. The divider was not replaced over the two days of study, allowing the fish to continuously interact. The first behavioral observation for each pair took place between 8:30 and 10:00 AM, with the second observation taking place between 2:30 and 5:00 PM. This pattern of a morning and afternoon observation was repeated the following day for each pair, for a total of four behavioral observations over a period of two days. Categorical scores describing tank position, feeding, aggressive acts, and coloration were recorded during each observation using a scoring method developed based on pilot observations (Table 4-1). At the outset of the observation, the position of the fish in the tank was noted and categorized according to one of three possibilities: a “dominant” position where the fish was actively moving in the center of the tank, a “subordinate” position where the fish was found immobile in a corner facing one of the sides of the tank (i.e., skulking), and a “neutral” position where the fish was found near the bottom but was not in the corner and was still facing inwards, towards the center of the tank. Next, a small amount of frozen bloodworm was dropped into the tank, and the first fish to feed was noted. Over the next five minutes, aggressive interactions (chases, bites, gill flares, yawning displays) were counted for each fish, followed by a second assessment of tank position. Finally, at the conclusion of the observation the color of the fish was noted. Because brighter coloration in centrarchids is an indicator of high social status (Howard 1974), and because subordinate fish featured far darker coloration during the dyadic trial, the fish displaying brighter coloration (especially more prominent orange coloration on the breast and more vivid coloration on the rest of the body) compared to the opponent received one point. If no obvious difference in coloration was present, no points were awarded for either fish. It should be noted here as well that no differences in coloration were present between any paired fish prior to interactions, meaning differences in color almost certainly represented differences in social status and stress between the paired individuals. The overall social dominance score of the fish was determined by adding the scores from the four individual observations, with higher scores indicating more dominant individuals. Within this scoring system, position in the tank is weighted heavily, which reflects prior work that shows that commanding the center position of a tank is the best indicator of dominance (Sloman et al. 2000; Sloman et al. 2001). Following the conclusion of dyadic trials, the fish were removed from the tanks and returned to the outdoor holding tanks overnight before being stocked into an onsite pond.

Statistical Analysis

A chi-squared test was performed to determine if fish had any preference for the three zones in the shoaling assay and did not simply move about the tank at random, regardless of whether or not a fish was captured. This was done to validate the shoaling assay design, as it would be expected that fish on average would show a preference for the social zone, where they could associate with conspecifics. For this analysis, the null hypothesis of random movement was tested based on the expectation that the proportion of the trial time spent in each zone was proportional to the area of each zone within the arena, for each individual trial. Spearman Rank Correlations were used to determine the repeatability of times spent in each of the three zones between the first and second trials. This rank-based approach (Wilson and Godin 2009; McGhee and Travis 2010) was used to account for the fact that across all fish, time spent in the social zone was higher in the second trial compared to the first (Student T-test, $t = -2.81$, $df = 37$, $p = 0.007$). The difference in social behavior across trials was likely due to acclimation to the testing procedure (Dingemanse and Plas 2009), requiring that repeatability be evaluated based on an individual's zone occupancy across trials relative to other fish, independent of the change in mean level behavior among all fish across between trials (Bell et al. 2009).

Binary logistic regression was used to determine if dominance, social behavior and/or fish length predicted whether or not a fish was captured during angling trials. Because the three measures of social behavior taken from the shoaling assay (time spent in antisocial, social, and neutral zones) were compositional (i.e. not independent) and auto-correlated (i.e. a fish that spent more time in the social zone automatically spent less time in the antisocial zone), I included only time spent in the social zone as the predictor variable of interest. Effect sizes of dominance score, fish length, and time spent in the social zone were then tested for significance. Because each fish was assessed twice for sociability and only once for aggression/dominance, for the purpose of the model time spent in the social zone was summed between the two shoaling trials. Simple linear regression was used to determine if dominance score and the total time spent in the social zone over both shoaling trials were related to each other. All statistical analysis was performed in R 3.2.2 (R Core Team, Vienna, Austria) with alpha values for significance set at $p = 0.05$.

Results

Fish showed a disproportionate affinity for particular zones (Trial 1 $\chi^2 = 832.9$, df = 2, $p < 0.001$; Trial 2 $\chi^2 = 1712.6$, df = 2, $p < 0.001$) indicating fish position within the shoaling arena was not random. Specifically, fish spent significantly more time in the social zone than expected if distribution was random, and significantly less time in the anti-social zone, though as described above the time spent in each zone changed between trials 1 and 2 (Mean social, neutral, and antisocial zone time (in s) for trial 1 = 311.1, 234.6, 354.1; Mean social, neutral, and antisocial zone time for trial 2 = 427.1, 197.3, 275.6). Rank order of time spent in each of the three zones was significantly repeatable between trials (Social Zone Time $r_s = 0.38$, $p = 0.01$; Neutral Zone Time $r_s = 0.39$, $p = 0.01$; Antisocial Zone Time $r_s = 0.37$, $p = 0.01$).

Time spent by bluegills in the social zone of the behavioral arena emerged as a significant predictor of whether or not it was captured during angling. Captured fish spent, on average, 422 seconds in the social zone during shoaling trials, while uncaptured fish averaged 315 seconds in the social zone (Figures 4-2, 4-3). Although uncaptured fish emerged from dyadic trials with a higher dominance score in 12 of 19 trials, dominance in dyadic trials was not significantly associated with capture status (Table 4-2). Furthermore, no relationship was found between time spent in the social zone and dominance score (Linear Regression, $F_{1,36} = 0.1$, $p = 0.75$).

Discussion

Sociability is a critical factor in determining fitness for many species through its role in mate selection, predator avoidance, habitat selection, and knowledge transfer (Krause et al. 2003; Wilson et al. 2014). The results of this chapter indicate that increased sociability, one of five major axes of behavior (Reale et al. 2007), is associated with increased vulnerability to recreational angling in bluegill. In this chapter, bluegill that were captured by anglers spent 34% more time engaged with conspecifics on average when compared to fish that were not captured. Rank order of time spent in the three zones of the behavioral arena were repeatable across trials, indicating that experimental measures of sociability were indicative of social behavior tendencies that are intrinsic (van Oers et al. 2004; Bell et al. 2009). While tests assessing the role of sociability in driving angling vulnerability are scarce, Arlinghaus et al. (2016) argued that extensive angling selection on other behavioral axes (primarily boldness) can impact crucial social behaviors such shoal cohesiveness and nest defense. The results of this chapter, however, indicate that sociability itself as a behavioral axis may be under selective pressure, rather than being impacted *via* proxy through selection on other related behaviors. If selection favoring less social behavioral types is indeed occurring in the wild, there may be non-negligible ecological impacts. Cohesive social behavior is necessary for accomplishing crucial tasks such as foraging (Webster and Hart 2007; Morrell et al. 2008; Dyer et al. 2009) and avoiding predators (Croft et al. 2009; Lacasse and Aubin-Horth 2014). If fishing mortality rates of highly social individuals are high due to angler harvest, the ability of fish groups to perform functions that rely on highly social group members may indeed be reduced, however further work will be necessary to determine the extent of this selection in natural systems.

Along with sociability, aggression is another major axis of personality (Reale et al. 2007; Conrad et al. 2011) that has been posited to be a driver of angling vulnerability under the prediction that highly aggressive and dominant individuals would tend to aggressively strike fishing lures and baits (Suski and Philipp 2004; Sutter et al. 2012). In contrast to sociability, dominance was not associated with capture vulnerability in bluegill. Predictions regarding the ecological implications of fisheries selection on aggression have been studied largely within the context of changes in nest defense behavior following removal of especially aggressive individuals. For example, work on artificially selected lines of largemouth bass *Micropterus salmoides* demonstrated that 'low vulnerability' fish were less aggressive, albeit within the specific context of defending their nests against potential brood predators (Cooke et al. 2007; Sutter et al. 2012). The present results indicate that, outside the context of nest defense, intraspecific aggression is not associated with capture likelihood in bluegill. Based on data from this chapter and previous work, I postulate that for centrarchids, selective capture of aggressive individuals may primarily occur during the reproductive period when nest guarding males are angled off nests (Suski and Philipp 2004; Sutter et al. 2012). Alternatively, differences in selection may relate to the ecology of the individual species. Bluegill are known to be more socially gregarious than largemouth bass, and form social groups to facilitate foraging and predator avoidance (Savino and Stein 1982; McCartt et al. 1997). Perhaps social behaviors drive angling vulnerability only in species that are highly social, whereas in species where individuals are more solitary social behaviors are rendered irrelevant. If this is the case, we could expect that, in exploited populations, the impacts of fisheries selection on behavior may differ depending on the species in question. While conceptual models predicting increased timidity as a result of selective capture of bold/aggressive phenotypes have been put forward (Arlinghaus et al. 2016), the present results indicate that in bluegill increased timidity resulting from fisheries related selection is unlikely to occur, as elevated aggression and dominance were not associated with angling vulnerability.

In studies of selective harvest mortality, linkages between behaviors are of interest because selection based on one characteristic can also lead to evolutionary change in the linked characteristic. A behavioral syndrome describes a suite of behaviors that are linked together across individuals in a population (Bell 2007; Reale et al. 2010b). While it may be expected that sociability and aggression are correlated with each other within this framework, previous work examining the link between sociability and aggression has been met with mixed results. On one hand, a negative relationship between the two axes has been found whereby more social individuals were less aggressive in American eels *Anguilla anguilla* (Geffroy et al. 2014), as well as social spiders *Anelosimus studiosus* (Pruitt and Riechert 2011). By contrast, a positive relationship between sociability and aggression has been demonstrated in graylag geese *Anser anser* (Kralj-Fiser et al. 2010) and three-spine sticklebacks *Gasterosteus aculatus* (Laskowski and Bell 2014). In this chapter, dominance score was not a significant predictor of time spent in the social zone, indicating that a behavioral syndrome linking sociability and aggression (whether positively or negatively) either does not exist or is not especially strong in bluegill. If sociability and aggression are not linked in bluegill, this may allow for fisheries-induced selection to alter levels of sociability without changing aggression/dominance (Dochtermann and Roff 2010). If angling selection is indeed capturing bluegill based on the characteristics observed in this chapter, we should therefore expect a decline in social tendencies in bluegill from heavily fished systems, with no corresponding change in mean aggression levels.

Prior work on bluegill may provide clues as to why, in this species, I found that sociability, but not dominance, was associated with angling vulnerability. While sociability has not been heavily studied with respects to angling vulnerability (but see Mourier et al. 2017), many studies have found a positive relationship between boldness and angling vulnerability (Klefoth et al. 2013; Harkonen et al. 2014; Alós et al. 2016; Lennox et al. 2017), with an expectation that more aggressive individuals will be more vulnerable to capture as well (Wilson et al. 2011). Conversely, Wilson et al. (2011) found that for bluegill, shyer (i.e., less bold) individuals were more vulnerable to capture. Combining these results with those of this chapter, it appears that shy and social individuals are more likely to be captured. While there is currently little direct study as to the specific mechanisms that might underlie the connection between shyness/sociability and angling vulnerability, perhaps this finding is due to social individuals being among the first to explore novel food sources, leading to capture on baited hooks (Vital and Martins 2013; Modlmeier et al. 2014). Or, perhaps social bluegill tend to form more densely packed groups, leading to a density-driven increase in feeding motivation and competition when a baited hook is placed nearby a large group of social individuals (Stoner and Ottmar 2004). Regardless of the mechanism, the oft-reported connection between high boldness, aggression, and capture vulnerability does not appear to apply to bluegill, and, in fact, angling may be expected to selectively capture more social phenotypes in exploited populations.

Recreational angling is a popular activity throughout much of the world, having a massive cultural and economic impact (Post 2013). The maintenance of healthy recreational fisheries is the primary mission of fisheries managers, and research has examined the possibility of fisheries collapse as a result of recreational harvest (Post et al. 2002; Cooke and Cowx 2004; Post 2013). A relatively new emphasis has been placed on the role of individual behavior in driving vulnerability to capture, which could lead to evolutionary shifts in the behavioral characteristics of populations (Uusi-Heikkila et al. 2008; Ward et al. 2016; Diaz Pauli and Sih 2017). The negative impacts of such shifts are largely a matter of speculation, with a major concern being the disruption of social functioning in exploited populations (Arlinghaus et al. 2016). While other work has speculated on impacts on social behavior through other behavioral mechanisms, I show here that social behavior in and of itself may be under selection in recreational fisheries, with more social individuals being more vulnerable to capture. Given the relatively small sample size used for this chapter however, it is clear that more work will be required to determine if selection based on sociability is widespread in this species. Even if sociability is indeed a primary driver of angling vulnerability in bluegill, it remains possible that the selective capture of social phenotypes may apply only to the study species; currently very little additional work has examined the role of social behavior in driving vulnerability to capture (Mourier et al. 2017). Therefore, if we are to form more concrete conclusions about the impact of fishing on population functioning, more investigation will be required that examines the behaviors of interest more directly, both through laboratory as well as field-based observations of behavior.

TABLES AND FIGURES

Table 4-1: Summary of scoring system used for bluegill in dyadic trials for dominance. Trials consisted of four five-minute observations over a two-day period.

Tank Position[a]	**5 Points** – In the center of the tank, patrolling	**2.5 Points** – Near the bottom, but not in a corner	**0 Points** – "Skulking", in a corner of the tank facing outwards
Feeding	**1 Point** – First to feed	**0 Points** – Not first to feed	
Aggressive Acts	**2 Points** – Initiated 5 or more aggressive acts (bites, chases, gill flares, side displays)	**1 Point** – 1 to 4 aggressive acts	**0 Points** – Zero aggressive acts
Coloration	**1 Point** – Brighter overall coloration	**0 Points** – Darker overall coloration	

Table 4-2: Summary of a logistic regression model assessing the effects of fish length, dominance score, and time spent in the social zone on whether or not a bluegill was captured during angling trials. Because bluegill were assessed twice for time spent in the social zone, the total time spent in the social zone between both trials was used as the predictor variable. Significant main effects within any model are given in **bold**.

Factor	**Estimate**	**Std. Error**	**Z**	**p**
Fish Length (cm)	-0.02	0.07	-0.33	0.74
Dominance Score	-0.03	0.02	-1.58	0.11
Time Spent in Social Zone (s)	**0.002**	**0.001**	**1.97**	**0.04**

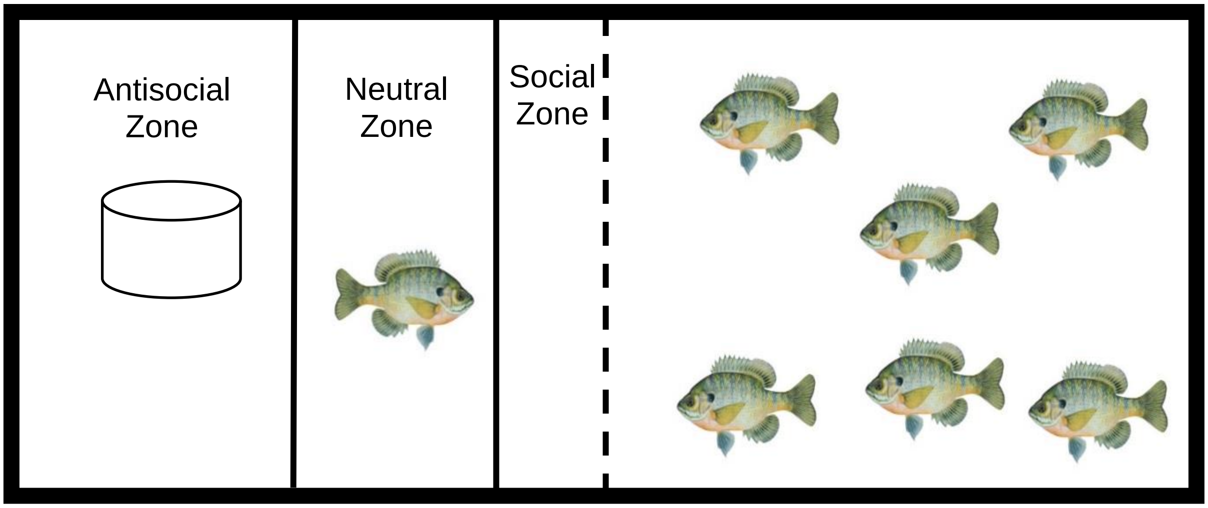

Figure 4-1: Diagram of the arena used in shoaling trials. The dashed line represents the transparent divider, and the cylinder of PVC piping used as a cover item for focal fish. One focal fish is shown on the left side of the arena, with six non-focal fish on the right side. The social zone consisted of the area within 8 cm of the divider on the focal side, the area more than 24 cm from the divider was the antisocial zone, and the area in between was the neutral zone. Time spent by the fish in the social, neutral, and antisocial zones were recorded from videos taken during each 15-minute trial.

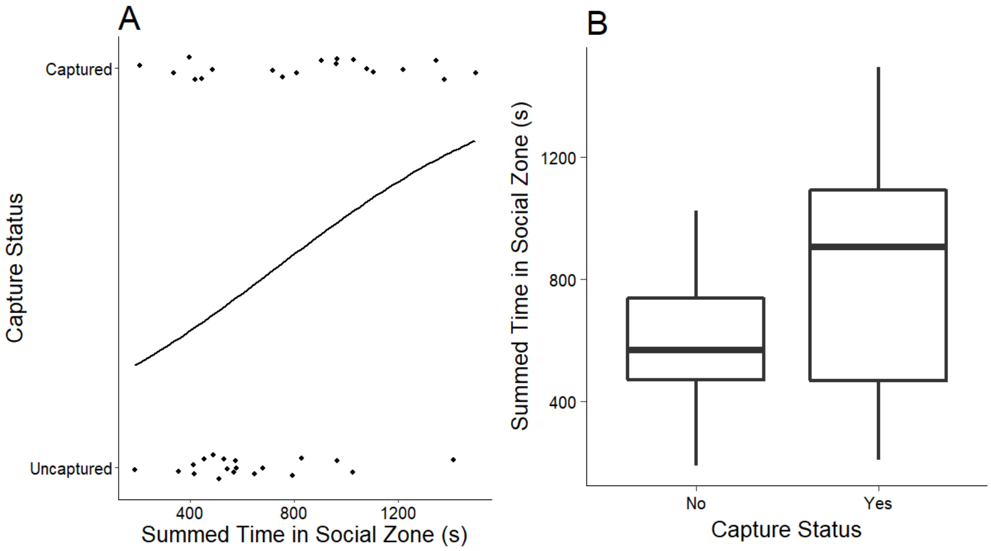

Figure 4-2: Summary of relationship between social behavior in a shoaling test and angling vulnerability in bluegill. A) Logistic regression line describing a significant effect of social time on capture status. Data points have been jittered to account for overlap. B) Boxplot showing time spent in the social zone during shoaling trials, for captured (N=19) and uncaptured (N=19) bluegill.

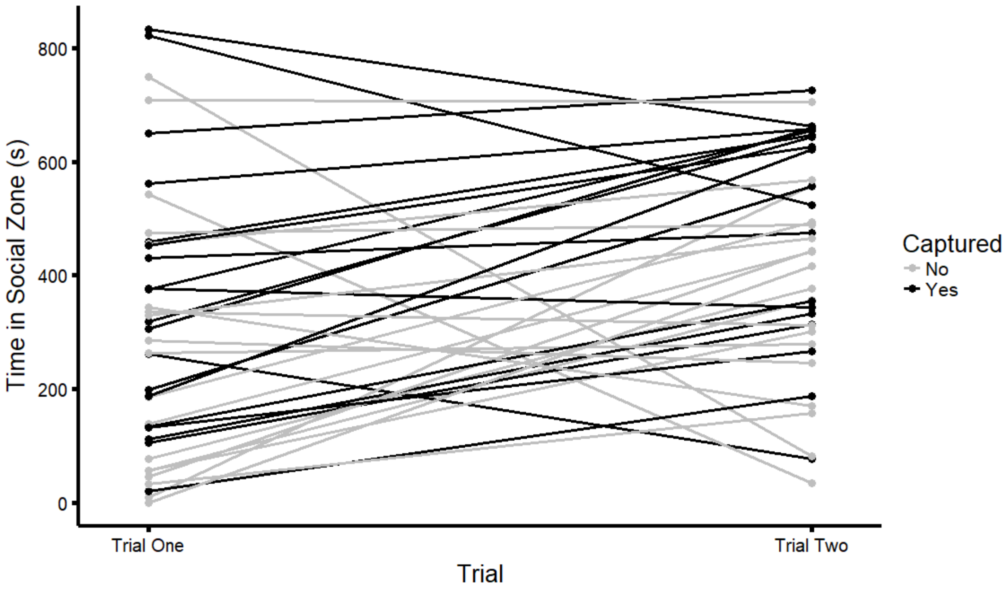

Figure 4-3: Time spent in the social zone by individual bluegill during each of the two shoaling trials. Black bars/dots represent captured fish, and gray bars/dots represent uncaptured fish. Overall, bluegill spent significantly more time in the social zone on the second trial compared to the first.

CHAPTER 5: FORTUNE FAVORS THE ANGRY: SOCIAL AND UNAGGRESSIVE BLUEGILL ARE CAPTURED EARLY AND OFTEN BY RECREATIONAL ANGLERS

Introduction

Within populations, individuals often show consistent differences in behavioral characteristics. These sets of behavioral traits, alternatively referred to as ‘behavioral syndromes’ (Sih et al. 2004b), ‘stress coping styles’ (Koolhaas et al. 1999), or ‘personalities’ (Biro and Stamps 2008) are marked by their consistency through time, and across different contexts. These behavioral syndromes are composed of individual components that may be correlated with each other (Bell 2007), and, indeed, prior work has identified five primary axes of animal behavior: boldness, exploratory tendency, activity, aggression, and sociability (Reale et al. 2007; Conrad et al. 2011). For species that live in groups, the aggression and sociability axes play a major part in defining the role of an individual within the group, and, in turn, its (Geffroy et al. 2014; Modlmeier et al. 2014). For instance, highly aggressive individuals may be likely to assume dominant positions within social groups (Winberg et al. 1991; Dugatkin and Wilson 1992), while less aggressive individuals may be forced into subordinate roles where access to resources may be limited (Overli et al. 1999; Webster et al. 2009). These less aggressive individuals may make up for this loss in fitness however by avoiding energetically costly confrontations with other individuals (Houston and McNamara 1988; Seebacher et al. 2013). In addition, non-aggressive individuals may also benefit by being more able to peacefully associate with conspecifics (i.e., by having higher sociability) and gaining advantages such as resource location and anti-predator vigilance provided by a group (Croft et al. 2003; Öst et al. 2015). The relative advantage of any of these social approaches is expected to vary depending on environmental conditions, including abiotic conditions, population density, predator abundance and food availability (Dingemanse and Wolf 2010; Sih et al. 2015). Understanding how these conditions may influence what behavioral characteristics are favored is therefore critical if we are to predict ecological and evolutionary responses to environmental change.

In many cases, inter-individual differences in behavior are associated with inter-individual differences in physiology as well. These behavior-physiology correlations have been heavily studied within the context of boldness behavior in that boldness has been often associated with high metabolic rate (Careau et al. 2008; Killen et al. 2012; Binder et al. 2016) as well as low glucocorticoid responsiveness to stress (Koolhaas et al. 1999; Archard et al. 2012). In addition to boldness, metabolic characteristics such as aerobic scope and standard metabolic rate have also been linked to aggression/dominance, whereas individuals possessing high metabolic rates were found to also be more dominant (Metcalfe et al. 1995, Killen et al. 2014). For fish, high metabolic rates are often linked with high capacity for swimming (Reidy et al. 2000), which can, in turn, be linked to social behavior and/or positioning within shoals (Killen et al. 2017; Seebacher and Krause 2017). If social behavior and performance are correlated within a species, any selective pressure favoring or disfavoring one trait will therefore lead to evolutionary change in the other (Dochtermann and Roff 2010; Wolf and Weissing 2012). As a result, it is a priority to determine the nature of these behavior-physiology correlations, and how these traits may interact with environmental conditions to drive fitness outcomes for individuals.

One notable situation where individual survival and fitness are linked with behavioral and/or physiological characteristics can be found in fish species targeted by recreational or commercial fishing. It is well documented that certain behavioral and physiological traits (particularly boldness and metabolism) can be drivers of vulnerability to capture (Cooke et al.

2007; Redpath et al. 2010; Lennox et al. 2017), leading to the evolution of those characteristics as a result of selective harvest (Uusi-Heikkila et al. 2008; Diaz Pauli and Sih 2017). The nature of this selection is context-dependent in that strength of selection will vary among species and be dependent on the method of harvest (Diaz Pauli et al. 2015). For instance, while individuals with high swimming performance (Killen et al. 2015a) or bold behavioral traits (Diaz Pauli et al. 2015) were better able to escape active netting, the reverse has been found for recreational angling as higher metabolic rates (Cooke et al. 2007; Hessenauer et al. 2015) and bold behavior (Klefoth et al. 2013, 2017) have been found to increase the likelihood of capture by anglers. While boldness and metabolic rate have indeed been extensively studied in the context of angling vulnerability, the influence of social behavior on vulnerability has been far less studied (but see Mourier et al. 2017). This gap in our knowledge is significant given the sweeping evolutionary changes that can occur if individuals with particular behavioral traits are more vulnerable to capture and harvest, as well as the over-arching importance of social behavior for many species (Krause et al. 2003; Uusi-Heikkila et al. 2008). In addition, the potential for angling to selectively capture individuals based on their swimming performance has never been assessed, even though fisheries-induced evolutionary changes in swimming performance could have major impacts on population fitness (Beecham et al. 2007; Mee et al. 2011). Exploring the relationships between these characteristics, and how they relate to angling vulnerability, will therefore provide significant insights into the potential evolutionary impacts of selective harvest.

In order to examine links between angling vulnerability, swimming performance, and social behavior, I conducted a study in bluegill, *Lepomis macrochirus*. This species was chosen because it is among the most popular targets of recreational anglers in North America (Gaeta et al. 2013), is a relatively social species that tends to congregate in groups (McCartt et al. 1997), and its relatively small size lends itself well to laboratory studies of behavior and physiology. In addition, results from Chapter 4 indicated that social behavior may be critical in driving angling vulnerability in this species. However, that chapter did not assess any potential physiological correlates of sociability, nor did it assess bluegill sociability and aggression in a group setting, which is more reflective of their generally gregarious behavior in the wild (McCartt et al. 1997). To evaluate these behavioral traits in bluegill, groups of focal individuals were loaded together into a behavioral arena, and their sociability and aggression was subsequently evaluated within the framework of Social Network Analysis (Krause et al. 2003; Croft et al. 2005; Wilson et al. 2014). Fish were also assessed for individual swimming performance in a Brett-style swim tunnel (Brett 1964) before being angled in a naturalistic pond setting. The goals of this chapter were threefold: 1) To examine relationships between sociability and aggression in bluegill, 2) To determine if swimming performance is linked with social behavior in this species, and 3) To identify whether any of these characteristics are associated with angling vulnerability. The findings from this chapter will advance our knowledge of how behavior and physiology drives capture vulnerability in sportfish, and allow for novel insights regarding the impacts of selective harvest on exploited populations.

Methods

Study Animals and Holding

On 5 April, 2017, 164 bluegill (total length range = 14.3 - 19.3 cm, mean total length ± standard error of the mean, S.E.M. = 16.6 ± 0.1 cm; weight range 57.5 – 152.6 g, mean weight ± S.E.M. = 93.3 ± 1.7 g) were delivered from Jake Wolf Fish Hatchery, Topeka, IL, USA to the Illinois Natural History Survey’s Aquatic Research Facility in Champaign, IL, USA. The facility consists of a wet laboratory, outdoor fish-holding tanks, as well as a series of 24 earthen bottom ponds ranging in total area from 0.04 – 0.12 ha. Upon arrival at the facility, bluegill were implanted with a 0.8 mm Passive Integrated Transponder tag (PIT, Biomark®, Boise, ID) for individual identification, and stocked into one of ten circular 1135 L plastic, holding tanks at a density of 15-17 bluegill per tank. Each holding tank was part of a flow-through system that continuously drew fresh water from an adjacent pond at a rate of ~8 full water exchanges per day, and water passively drained back to the pond. Every day during holding, fish were fed frozen bloodworms (Chironomidae) acquired from a local pet store, rationed to provide ~5% of the average fish's body weight per day.

Social Behavior Assay

Assessment of social behavior took place ~4 weeks after bluegill arrived at the facility, between 1 May, 2017 and continuing through 21 May, 2017. A total of 120 fish were assessed for social behavior. This assessment took place in one of five 565 L rectangular polyethylene stock tanks (hereafter 'arenas', 181 cm long × 65 cm wide) filled with pond water to a depth of 25 cm. Water temperatures were kept near 18º C for the duration of the experiment, with dissolved oxygen saturation maintained above 90% using a Pentair Sweetwater™ air compressor connected *via* tubing to an immersed air stone. A total of four sets of behavioral assays were conducted, with 5 groups of 6 fish (hereafter referred to as 'shoals') assayed within each set.

On the day before the first set of behavioral assessments, 30 fish were collected from the outdoor holding tanks and tagged for on-camera identification with two circular plastic buttons (1.4 cm diameter, 0.1 cm thickness) in one of six colors (black, green, red, orange, yellow, or white), attached to dorsal spines using 22 gauge art wire in a fashion similar to Wilson et al.

(2014). The buttons allowed for the differentiation of fish during subsequent behavioral scoring, and pilot trials conducted prior to experimentation demonstrated that the tags had minimal impact on swimming behavior. Following tagging, fish were loaded into behavioral arenas at a density of 6 fish per arena, with each fish within a shoal having a different colored button. Fish within each shoal were taken from separate holding tanks to prevent fish interactions from being impacted by familiarity (Keller et al. 2017; Trapp and Bell 2017). In addition, bluegill within each shoal were size matched such that the largest fish in each shoal was no more than 1 cm greater in total length than the smallest fish (approximately 7 % difference in size, depending on the mean size of fish in the shoal); previous research on the congeneric pumpkinseed *Lepomis gibbosus* demonstrated that differences in size of this degree are unlikely to impact the direction of aggressive interactions among fish (Beacham 1988). Following tagging, bluegill were allowed to acclimate overnight in the arena before the first social behavior observation took place the following morning (Jacoby et al. 2014).

Evaluation of social behavior consisted of once daily observations over the course of three consecutive days conducted between 8:30 and 11:30 AM. Immediately prior to the outset of observations, two GoPro^{TM} Hero 3 cameras were mounted over the arenas, and the air stone in the tank was removed to prevent bubbles from shielding fish from the view of the cameras. When videos were later scored for behavior, the first 30 min was discarded as an acclimation period, with behaviors scored during the following 30 min. This 30 min trial period has been shown previously to be a sufficient duration to quantify social behavior (Morrell et al. 2008; Dyer et al. 2009). At the conclusion of the 30-minute observation period on the first and second day, cameras were removed, the air stone was replaced, and fish were fed with bloodworms corresponding to ~5% body weight per fish. Following the third day of observations, bluegill were quickly netted from the arena, had their dorsal fin tags carefully removed, and were placed into one of two 1135 L indoor holding tanks featuring identical water conditions to the behavioral arenas prior to assessment of swimming performance (see below), at a density of 15 fish per tank. This entire process was repeated for three additional sets, until a total of 20 shoals (120 bluegill) were assayed for social behavior.

Scoring and Extraction of Individual Social Network Metrics

Scoring of behavioral trials took place after the conclusion of all aspects of the experiment and was performed only by myself to ensure consistency. Scoring consisted of the construction of both associative and aggression interaction matrices to quantify social behavior in each shoal, following previously established methods (Canon Jones et al. 2011). To compile these data, the location of each fish within the behavioral arena was noted at 1-minute intervals within the 30-minute observation, for a total of 30 observation points. If the end of the snout of one fish was within 1 body length of another fish, the two fish were considered to be interacting with each other (Keller et al. 2017). The standard of 1 body length was determined *a priori* based on observations from a series of pilot trials, where roughly 1 body length was a radius where fish either engaged in aggression, or continued to remain in proximity until disturbed by other fish. In the event of an interaction pattern featuring more than two fish (i.e. fish A associating with fish B, which was associating with fish C), all individuals were considered to be associating with each other for the purpose of scoring (Croft et al. 2011; Williams et al. 2017). A total of 90 observations were scored over the three days of trials for each shoal, with the final associative matrix for each shoal being pooled from all observation days (Büttner et al. 2015).

For the construction of aggression matrices to define dominant and submissive fish within each shoal, every aggressive act (bites, charges, chases) throughout the entire 30 min observation (not only at observation points) that forced the recipient fish to displace itself by at least 1 body length was tallied, as was the act's initiator and recipient (Cañon Jones et al. 2011). Following scoring of the three days of trials, aggression matrices, including the compiled number of aggressive acts from each fish towards each of the other 5 fish, were constructed for each shoal.

Analysis of all associative and aggression matrices was conducted using UCInet software, version 6.646 (Borgatti et al. 2002). An associative matrix for each shoal was weighted by the number of observation points in which each pair of individuals were found to be associating (Silk et al. 2015). These matrices were also used to determine each fish's "weighted degree" within a shoal, a measure of the overall sociability of each fish (Sih et al. 2009, Cañon Jones et al. 2011). For this metric, fish with a higher weighted degree had more total associations with a larger number of shoal mates, and were considered to be more social individuals, relative to individuals with a lower weighted degree. Aggression matrices, on the other hand, were directional, taking into account the initiator and recipient of each aggressive act. These matrices were used to compute "indegree centrality" and "outdegree centrality" for each fish. Briefly, out-degree centrality is a measure of aggression, whereby individuals with high outdegree centrality directed a large number of aggressive attacks towards shoalmates, while receiving relatively few. Inversely, high values of indegree centrality indicate being frequently attacked by shoalmates in combination with very few instances of initiating aggressive acts (Cañon Jones et al. 2010). Because measures of social behavior for each individual are not independent, and are impacted by the social behavior of the surrounding individuals in that shoal (Croft et al. 2011; Magnhagen 2012), I normalized weighted degree, indegree centrality, and outdegree centrality for each fish by dividing individual values by the mean value for that shoal, as shoals varied significantly in their cohesiveness and in frequency of aggressive interactions.

Assessment of Swimming Performance

Swimming performance of bluegill was conducted in the 2 days following the conclusion of the social behavior assay, using a Brett-style swim tunnel (Brett 1964, Reidy et al. 2000, Tierney 2011). Velocity in the swim tunnel could be adjusted with Food was withheld from fish for 2 days prior to the swim performance test to ensure that performance differences between fish were not impacted by differential energetic demands induced by the digestion of food (Pang et al. 2010; Rouleau et al. 2010). The chamber within the swim tunnel where fish were placed for assessment was 45 cm long, with a cross-sectional area of 209 cm^2. Water temperature was maintained between 17-18º C using a TK-500 Heater-Chiller (Teco®, Ravenna, Italy) and oxygen saturation was kept near 100% with an air compressor and air stone.

Swimming performance, defined as the fish's critical swimming speed, U_{crit}, was evaluated for 15 fish each day following behavioral trials for each set of fish, such that all evaluations for all 30 fish in each set were completed over two days. For each trial, a single fish was quickly netted from its holding tank, PIT-identified, measured for total length, and placed within the chamber of the swim tunnel where it was initially forced to swim at a speed equal to 1 body length per second for 5 minutes to acclimate (Plaut 2001), after which time water velocity within the tunnel was increased by 0.5 body lengths per second every 5 minutes (hereafter, referred to as steps) until the fish reached the failure threshold and could no longer sustain swimming (Castro-Santos 2011). While the length of time for each step before increasing the speed in the tunnel is shorter than in some prior studies of salmonids (Gregory and Wood 1998; Reidy et al. 2000), I argue that a shorter step time was more ecologically relevant given the fact that bluegill do not usually occupy areas such as fast-flowing streams, or engage in long distance swimming or migration that require long-term endurance (Jones et al. 2007). Each bluegill was considered to have reached the failure threshold when it was pushed by the current to the back of the chamber and its caudal fin was in contact with the rear grate of the chamber for a period of 4 s (Prenosil et al. 2016). When failure was reached before the end of a 5-minute step, U_{crit} was calculated according to the following equation (Brett 1964):

$$U_{crit} = u_1 + (t_1/t_2 \times u_2)$$

where u_1 is the highest speed (in cm/s) that a fish could sustain for the full 5-minute step, u_2 is the speed at which failure was reached, t_1 is the time swam within the step where failure was reached, and t_2 is the total time of each step (5 minutes). Upon failure, each bluegill was removed from the swim tunnel, weighed, and temporarily placed in a separate holding tank before being stocked into the 0.04 ha angling pond (see below). A total of 119 fish were stocked into the angling pond, with one fish dying in its holding tank prior to swim performance assessment.

Angling Trials

Angling trials were conducted in a single 0.04 ha angling pond and consisted of a series of nine angling sessions conducted over two weeks. The angling pond featured natural macrophyte cover and macroinvertebrate forage items and was also stocked with juvenile mosquitofish *Gambusia* spp. to serve as additional forage. Angling was conducted daily from 6

June to 10 June, and again from 12 June to 15 June, 2017. Each angling day included a single session that was conducted either in the morning (8:00 AM) midday (12:00 PM) or evening (4:00 PM) as determined by random selection. Each session was standardized to 45 total casts that, depending on the number of fish caught in the session, took between 45 min and 1 h to complete. All angling sessions were carried out by a single experienced angler who systematically moved around the entire perimeter of the pond during each session, and casted in a way to ensure that all areas of the pond were targeted. Gear consisted of a light-action spinning rod spooled with 1.8 kg test Berkely Trilene^{TM} monofilament fishing line, commonly used by bluegill anglers. The lure used was a simple size 8 Gamakatsu® J-hook baited with a live waxworm *Galleria* spp. suspended in the water 1-1.5 m below the surface with a stationary slip bobber. Strikes were detected by watching the slip bobber on the surface and setting the hook when the bobber was pulled beneath the surface by the fish, a common practice for capturing bluegill. If no strike was detected within 1 min of casting the bait into the water, the lure was retrieved and subsequently casted into another location in the pond. Upon capture, each fish was quickly identified using a hand-held PIT reader, and immediately released back into the pond to be potentially re-captured. Handling time for each captured fish was under 1 min, with no fish showing signs of bleeding or other disturbance upon release. The angling pond was drained approximately one month after the conclusion of angling trials on 17 July, and 107 bluegill were recovered.

Statistical Analysis

While normalized social network metrics were calculated for all 120 fish, analyses relevant to vulnerability to angling were performed only on the 107 fish recovered from the angling pond. To reduce the social network data to functional components and eliminate issues of multicollinearity (Scheiner and Gurevitch 2001; Graham 2003), principal components analysis (PCA), based on the correlation matrix, was performed on the three measures of social behavior (weighted degree, indegree centrality, outdegree centrality), following evaluation of the suitability of the data for factor analysis (Hair 2010) (Kaiser Meyer Olkin Test of Sampling Adequacy = 0.573, Bartlett's Test of Sphericity, $p < 0.001$). Varimax-rotated components with eigenvalues greater than 1 were retained based on the maximum likelihood solution (Kaiser 1960). Pearson Correlations were performed to determine if U_{crit} or fish length was associated with extracted social metrics.

Three separate models were used to assess links between social behavior, swimming performance, and three different aspects of angling vulnerability: (1) whether a fish was captured at least once during angling trials, (2) whether a fish was captured multiple times during angling trials, and (3) whether a fish was among the first to be captured. To assess vulnerability based on the first aspect, a binary logistic regression with capture status (yes or no) as the dependent variable and all extracted social PC's, fish length and U_{crit} as explanatory variables was performed. The same statistical approach was then repeated to evaluate vulnerability based on the second aspect using the same explanatory variables listed above, and whether a fish was captured more than once (yes or no) as the binary response variable. For the third aspect, a zero-truncated negative binomial regression model was constructed with the session in which a fish was first captured as a dependent count variable, and U_{crit}, fish length, and all extracted social PC's as explanatory variables. This modeling approach accounts for overdispersion of data, as well as the fact that there was no session 0 during which fish could be captured (Zuur et al. 2010). Only fish that were captured at least once were included in this third analysis, with uncaptured fish excluded. In addition to analyses examining individual characteristics, I also ran a separate zero-truncated negative binomial regression that included session number as the explanatory variable and the number of captured bluegill in each session as the dependent variable, to determine if catch rate changed over the course of the nine angling sessions.

All statistical analysis were performed using R Version 3.4.3, utilizing the packages ‘VGAM’ (Yee 2010), ‘Hmisc’ (Harrell et al. 2018), MASS (Venables and Ripley 2002), and ‘AER’ (Kleiber and Zeileis 2008). Thresholds for statistical significance in all cases were set at $\alpha \leq 0.05$ and all data are reported as means ± S.E.M. where appropriate.

Results

Bluegill shoals consisted of individuals with highly discrete social positioning, whereby certain individuals were highly aggressive, while others were submissive. On average, the two most aggressive fish within each shoal (as indicated by higher outdegree centrality) accounted for 68% of the total aggressive acts over the three days of trials, while the remaining four fish in a shoal combined for only 32% of aggressive acts. Following principal components analysis on the three behavioral metrics, only a single component (hereafter, the ‘social score’) was extracted. The social score was positively loaded for indegree centrality and weighted degree, and negatively loaded for outdegree centrality and accounted for 68.4% of the total behavioral data variance (Table 5-1). Individuals with high outdegree centrality had low indegree centrality and low weighted degree, indicating that more aggressive individuals received fewer attacks and spent less time associating with other individuals.

Among the 107 bluegill recovered from the angling pond, U_{crit} ranged from 33.8 - 79.3 cm s^{-1}, with a mean of 57.5 ± 0.9 cm s^{-1}. Neither social score ($r = -0.086$, $df = 105$, $p = 0.37$) nor fish length ($r = -0.084$, $df = 105$, $p = 0.38$) were related to U_{crit}, suggesting that swimming performance was likely not a driver of social rank in bluegill. Bluegill total length and social score were also not correlated with each other ($r = 0.025$, $df = 105$, $p = 0.79$), which was expected given that all social data were normalized to be relative to each individual's shoalmates, and members of each shoal were of similar length.

Nine angling sessions resulted in a total of 90 capture events. Twenty-six bluegill were captured during session one (Figure 5-1) and capture rate declined with each subsequent session ($z = -3.56$, $p < 0.001$) indicating lure avoidance learning. Of the 107 bluegill recovered following angling, 28 fish were uncaptured, 68 fish were captured once, and 11 fish were captured twice. The first recapture of a fish occurred during session 3, and no more than 1 recapture occurred in any subsequent session with the exception of session 7, when 7 out of the 14 captures were recaptures of previously captured fish.

Fish total length was the primary predictor of whether a fish was captured across all angling sessions (Table 5-2), with captured fish being larger than uncaptured fish. The difference in size between captured and uncaptured fish was small, with the captured fish being approximately 0.5 cm longer than the average uncaptured fish (Figure 5-2). Neither social score nor U_{crit} were significant predictors of whether a fish was captured at least once (Table 5-2). With regards to whether a fish was captured more than once, both body size and social behavior emerged as significant predictors (Table 5-3). Once again, larger fish were more likely to be captured twice (Figure 5-3A). In addition, fish with a higher social score (meaning fish that were more social and submissive, and less aggressive) were also more likely to be captured twice (Figure 5-3B).

Social behavior also predicted vulnerability to angling as defined as being captured earlier relative to other fish. The negative binomial regression that related social score, U_{crit}, and fish length to the session when a fish was captured found social score to be a significant predictor of the session in which a fish was first captured, with higher scores linked to being captured in earlier angling sessions (Table 5-4). Among the 79 fish that were captured at least once, social and submissive bluegill were likely to be captured in earlier angling sessions compared to asocial and aggressive bluegill (Figure 5-4). While U_{crit} was not a significant predictor of capture order, its effect was only marginally non-significant ($p = 0.051$) with a trend towards fish with high U_{crit} being captured in earlier sessions.

Discussion

In the present study described in this chapter, individual sociability drove vulnerability to angling in bluegill. Fish with higher sociability and lower aggressiveness were more likely to be captured multiple times, and were more likely to be caught within the first few angling sessions. Animal behavior can broadly be defined across 5 behavioral axes, including boldness, exploratory tendency, activity, aggression, and sociability (Reale et al. 2007; Conrad et al. 2011). While other behavioral axes (i.e. boldness and activity) have been heavily studied in the context of vulnerability to fisheries capture (Olsen et al. 2012; Harkonen et al. 2014; Klefoth et al. 2017), studies examining links between social behavior and angling vulnerability have been scarce. Indeed, to my knowledge the only published study to quantify the impacts of sociability on vulnerability to capture in fish found that social network position did not predict angling vulnerability in blacktip sharks *Carcharhinus melanopterus* (Mourier et al. 2017). For bluegill on the other hand, individuals that were more social were the most vulnerable to capture. With regards to aggression, the present results show that lower aggression is associated with high vulnerability in bluegill, a result that runs contrary to previous work in other fish species (e.g., largemouth bass, *Micropterus salmoides*) where results have shown that aggressive and (presumably) bold phenotypes are the most vulnerable (Sutter et al. 2012; Arlinghaus et al. 2016; Twardek et al. 2017). The mechanism driving the relationship between angling vulnerability and sociability may related to the fact that social individuals are more likely to congregate in large groups within their environment, which likely impacts their interaction with angling lures (Jacoby et al. 2014; Öst et al. 2015). While forming groups increases foraging success for individuals within the group (Pitcher et al. 1982), it also increases competition for food among group members (Kent et al. 2006; Ward et al. 2006) requiring individuals to make faster decisions regarding whether to feed on an available prey item (Stoner and Ottmar 2004). This process may extend to fishing lures as well, causing group-living individuals to be quicker to strike baited hooks and lures. Indeed, increases in fish density within small ponds have been shown to cause greater than expected increases in catch rates for angled fish, indicating that each individual fish becomes more vulnerable as density increases, possibly as a result of this competition (Harkonen et al. 2014). As a result, highly social bluegill that reside in larger groups may be less discerning when evaluating fishing lures as a potential prey item in a highly competitive social context, leading to greater vulnerability. Furthermore, because fish are aware of the foraging activity of fellow group members (Pitcher et al. 1982), any lure or bait that lands near any of the members in a group is likely to elicit a response from nearby group members, effectively increasing the “strike radius” for a fish in a group relative to a solitary fish.

Regardless of the mechanism however, the present results show that greater sociability, and lower aggression, is linked with greater angling vulnerability in bluegill.

Bluegill size was a predictor of angling vulnerability, with larger individuals being more likely to be captured. In addition, larger fish were more likely to be captured multiple times. While size was indeed a significant predictor of vulnerability, it should be noted that the difference in total length between captured and uncaptured bluegill was rather small, with ~3% difference in total length on average between captured and uncaptured fish. Several prior studies in fish have documented intraspecific size-selective harvest where larger fish are more vulnerable to capture by anglers in both marine (Olsen and Moland 2011; Enberg et al. 2012; Kokkonen et al. 2015) and freshwater (Vainikka et al. 2016; Arlinghaus et al. 2017) systems again with larger fish captured preferentially by anglers. In addition, intrinsic growth rate (independent of absolute fish size at capture) has also been linked with increased capture vulnerability previously (Biro and Post 2008; Saura et al. 2010). It is possible that the greater vulnerability of larger bluegill in this chapter could indeed be related to growth rate, where faster growers have higher feeding rates (Stamps 2007) and, as a result, are more likely to prey upon a baited hook. Because the bluegill in this chapter were not aged however, and were raised in a natural environment where they were not separated by spawning cohort, this possibility cannot be proven as the larger fish could have simply been older, and not necessarily faster growers *per se*. Alternatively, selective capture of larger bluegill in this chapter could be a product of gape size, where larger individuals with increased gape size are better able ingest lures, facilitating capture, while smaller fish may be more likely to “nibble” the bait rather than ingesting it completely (Alós et al. 2014). Given the fact that total length ranges of uncaptured fish overlapped with those of captured fish (i.e. there didn’t appear to be a cutoff where all fish below a certain total length were not captured), this appears to be an unlikely explanation for the present results. Finally, because larger fish within centrarchid groups tend to assume dominance (Beacham 1988; Dugatkin and Ohlsen 1990), it is possible that larger bluegill were simply able to dominate areas of foraging space and force smaller fish to more peripheral habitats, and in turn were more likely to encounter baited hooks. This behavioral explanation also seems unlikely though, given the fact that it was the most social and submissive, rather than the most aggressive, individuals that proved to be most vulnerable to angling, and also that efforts were made to cast lures to all areas of the pond to eliminate habitat-bias in capture. Within this experimental construct, it was found that larger bluegill were more vulnerable to angling, albeit within a relatively narrow size range.

Swimming performance, as measured by an individual's critical swimming speed, was not associated with social dominance and was also not a significant predictor of angling vulnerability. I had predicted that swimming performance would be associated with vulnerability and/or social behavior given that swimming performance can be a major determinant of social status in many species (Killen et al. 2017). No study has investigated a direct association between swimming performance and angling vulnerability, but higher swimming performance has been linked to the ability to avoid capture *via* trawl netting (Killen et al. 2015a). Swimming performance has been linked to angling vulnerability indirectly in that physiological and behavioral characteristics in fish, including aerobic scope (Reidy et al. 2000) and boldness (Kern et al. 2016) have been linked separately to both swimming performance and angling vulnerability (Redpath et al. 2010; Klefoth et al. 2017). While these links were not found in this chapter, this lack of a relationship could be related to the biology of bluegill. While bluegill form large aggregations around available resources, they do not typically form highly structured schools that travel for long distances (McCartt et al. 1997), which would necessitate social structuring based on individual performance (Killen et al. 2017). In addition, Neither boldness (Wilson et al. 2011) nor aerobic scope/metabolic rate (Chapter 2), two characteristics that have been linked with swimming per have been found to be drivers of angling vulnerability in bluegill, as they have for other species (Redpath et al. 2010; Klefoth et al. 2017). In light of this prior work on bluegill, the present results indicating no relationship between swimming performance and angling vulnerability or social behavior become more understandable for this species. This finding however does not preclude swimming performance as a driver (either in and of itself or *via* proxy through its correlation with another characteristic driving vulnerability) of angling vulnerability in other species, especially those species that form cohesive shoals where position is related to individual performance.

Results from this chapter show clear evidence for a behavioral syndrome in bluegill, whereby fish that spent more time associating with conspecifics were also likely to initiate fewer aggressive acts, while being the recipient of more aggressive acts. This was indicated by the fact that all social metrics (indegree centrality, outdegree centrality, and weighted degree) loaded onto a single principal component describing social behavior. A behavioral syndrome describes a set of behavioral tendencies that are correlated with each other across members of a population (Bell 2007). While a behavioral syndrome linking sociability and aggression are often predicted, it should be noted that prior studies have differed as to whether this relationship is positive or negative. While some work has shown that more social individuals tend to be less aggressive (Pruitt and Riechert 2011; Geffroy et al. 2014), the opposite result has also been found whereby more social individuals were more aggressive (Kralj-Fiser et al. 2010; Laskowski and Bell 2014). Even within bluegill, prior work found no correlation between sociability and aggression

(Chapter 4), a finding that runs in contrast to the present results, but this discrepancy could simply be the result of differences in experimental design. More specifically, in Chapter 4 bluegill were assessed for sociability based on their willingness to associate with a shoal of conspecifics across a transparent divider, and dominance/aggression in a dyadic trial. Because of that, it is possible that individuals that were aggressive intrinsically may have been scored as submissive if they happened to be paired with another more aggressive individual (Beacham 1988; Vindas et al. 2014), which would have skewed measurement of aggression and in turn the relationship between aggression and sociability. This was done intentionally in chapter 4, in order to evaluate social interactions without the confounding influence of additional fish. In this chapter, groups of six bluegills were allowed to interact with each other, and establish social dominance in a hierarchical fashion, which better reflects the nature of centrarchid social relationships in the wild (Howard 1974; Dugatkin and Wilson 1992). In this chapter a behavioral syndrome negatively linking aggression and sociability was found with some individuals occupying positions close to other fish, while more aggressive individuals remained solitary and attacked conspecifics that approached.

In many studies of links between behavior and angling vulnerability, a prediction is made that angling will select against bold and aggressive individuals, leading to an evolutionary shift towards timidity. For instance, it has often been found that bolder (Klefoth et al. 2013, 2017; Harkonen et al. 2014; Alós et al. 2016) and/or more aggressive (Cooke et al. 2007; Sutter et al. 2012) individuals are more likely to strike lures and be captured. This has led to the prediction that a population-level “timidity syndrome” will be the result of extensive fishing efforts, with shyer (i.e. less bold) phenotypes that can better avoid capture predominating (Arlinghaus et al. 2016). In contrast to this prediction, the present results show that, for bluegill, it is the less aggressive/more social individuals that are more vulnerable to angling. This finding is consistent with previous results in bluegill (Chapter 2), further demonstrating the importance of individual sociability in driving angling vulnerability for this species. Furthermore, Wilson et al. (2011) found that angled bluegill were shyer than those seined from the same location, indicating that bold and aggressive individuals are not more vulnerable to angling. In light of these results, I question whether a "timidity syndrome" will be the outcome of angling selection across all species and situations. For some species, boldness and aggression may indeed drive angling vulnerability, while for others (such as bluegill) these traits may be negatively associated with vulnerability.

Results from this chapter have important implications with regards to how angling can evolutionarily impact fish populations. The present results show that both sociability and size, two heritable characteristics in animals (Charmantier et al. 2007; Biro and Post 2008; Wark et al. 2011), may be under selective pressure in angled bluegill populations. With regards to size, an abundance of prior work has examined the evolutionary downsizing of fish populations due to selective harvest (Edeline et al. 2007; Nussle et al. 2009; Kuparinen and Festa-Bianchet 2016). This process can lead to a host of ecological and economic impacts as fisheries yields decrease and food webs/trophic dynamics are altered by downsizing of exploited species (Jorgensen et al. 2007). Independent of size, the selective harvest of individuals with particular behavioral traits also has the potential to drastically alter the ecology of exploited species (Uusi-Heikkila et al. 2008; Diaz Pauli and Sih 2017). For bluegill, sociability was found to be positively associated with higher angling vulnerability, and as a result the mean level of sociability in exploited populations could decrease, while mean aggression could increase. This increase could, in turn, be associated with changes in additional linked behavioral and physiological characteristics

(Metcalfe et al. 1995, Wolf and Weissing 2012). While it is possible that fish could plastically respond to this selection, with remaining individuals becoming more social to replace harvested individuals (Magnhagen 2012), previous work has also shown that type of response is not guaranteed, and that removal of these social phenotypes can have major cascading impacts on group function (Vital and Martins 2011, 2013). For example, because shoaling behavior is critical to predator avoidance at early life stages (McCartt et al. 1997), the reduction of bluegill sociability would lead to reduced shoaling and would, therefore, increase mortality rates through predation. It should be noted here, however, that while studies of FIE tend to focus on the negative fitness outcomes of selection, not all impacts may be negative. For instance, angling selection in bluegill is expected to favor more aggressive phenotypes, which may be more effective at defending territory and access to resources (Colgan and Brown 1988; Rodgers et al. 2013). Given that the fitness advantages of particular behavioral types are largely determined by the environment (Dingemanse et al. 2004; Brown et al. 2005), the determination of "net" fitness outcomes for less social and more aggressive bluegill populations as a result of intensive angling may therefore be dependent on a complex set of environmental characteristics, with different outcomes under different circumstances.

TABLES AND FIGURES

Table 5-1: Factor Loadings derived from principal components analysis (PCA) on the three social network metrics extracted from sociability trials in bluegill. Only a single component was extracted that included significant loadings for all three metrics, this component is hereafter referred to as the "social score".

Factor	PC1 Loading
Indegree Centrality	0.917
Outdegree Centrality	-0.806
Weighted Degree	0.749
Eigenvalue	2.052
% Variance Explained	68.4%

Table 5-2: Output from binary logistic regression assessing whether social score, fish total length, or swimming performance (as defined by the critical swimming speed, U_{crit}) predicted whether or not a bluegill was captured over nine days of angling trials. Significant main effect is given in **bold**.

Factor	Estimate	Std. Error	Z Value	p
Intercept	10.89	4.76	2.28	0.02
Social Score	0.02	0.23	0.12	0.90
Fish Total Length (cm)	**-0.57**	**0.25**	**-2.25**	**0.02**
U_{crit} (cm s^{-1})	0.03	0.02	1.57	0.11

Table 5-3: Output from binary logistic regression model assessing whether social score, fish length, or swimming performance (as defined by the critical swimming speed, U_{crit}) predicted whether or not a bluegill was captured multiple times over nine days of angling trials. Significant main effects are given in **bold**.

Factor	Estimate	Std. Error	Z Value	p
Intercept	-21.75	7.93	-2.70	0.006
Social Score	**0.86**	**0.40**	**2.16**	**0.03**
Fish Total Length (cm)	**0.88**	**0.39**	**2.24**	**0.02**
U_{crit} (cm s^{-1})	0.06	0.04	1.67	0.09

Table 5-4: Main effects output from zero-truncated, negative binomial regression assessing the effects of social behavior, size (total length), and swimming performance on which of the 9 angling sessions saw a bluegill captured by a recreational angler. Data are only included from the N=79 fish that were captured at least once. The significant main effect from the model is given in **bold**.

Factor	Estimate	Std. Error	Z Value	p
Social Score	**0.02**	**0.09**	**2.24**	**0.02**
Total Length (cm)	-0.06	0.10	-0.61	0.49
U_{crit} (cm s^{-1})	-0.02	0.01	-1.931	0.051

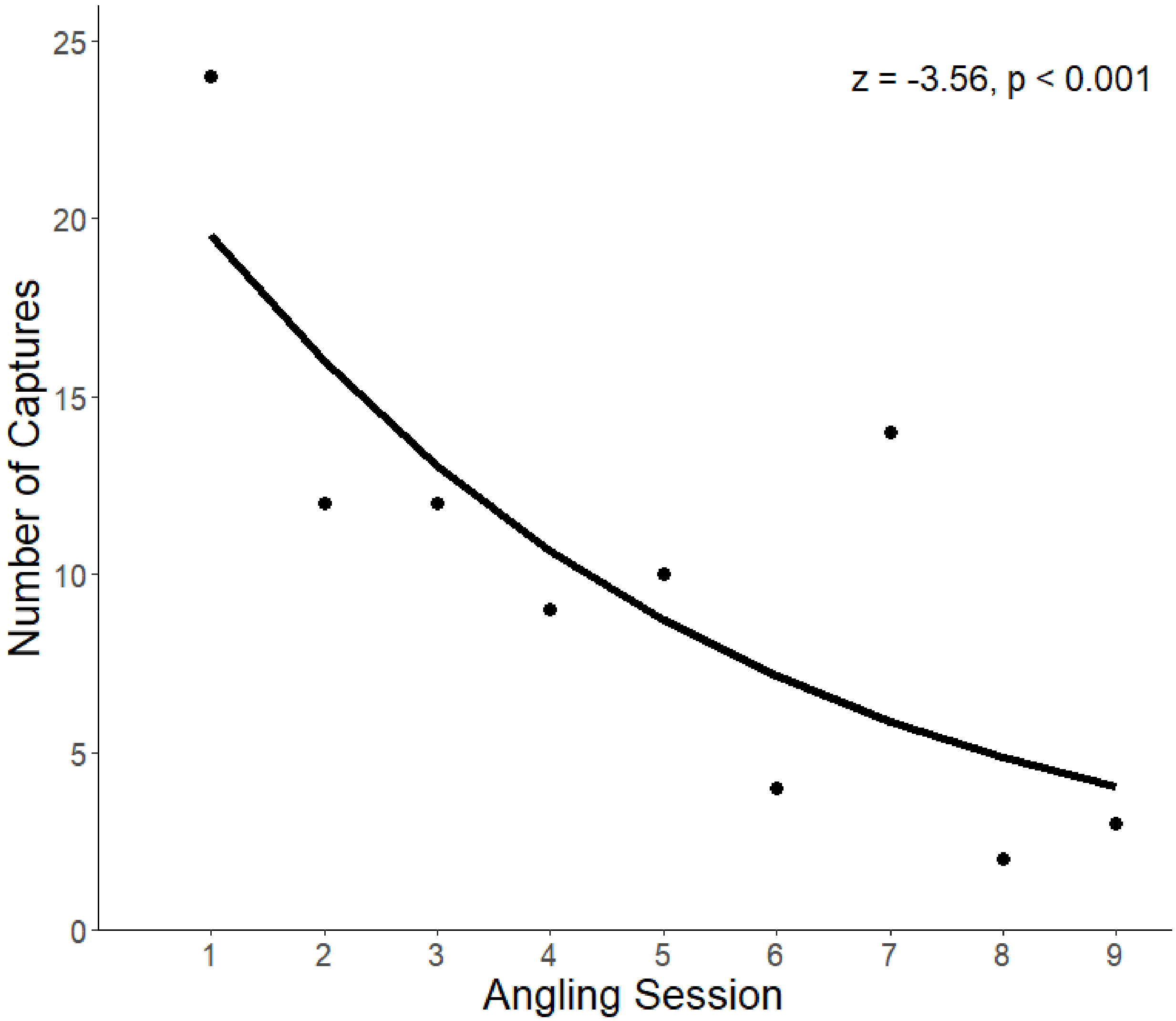

Figure 5-1: Number of bluegill captured by a recreation angler across 9 angling sessions. Total captures for each session includes captures of fish for the first time, as well as recaptures (1 recapture in sessions 3, 4, 5, and 9, 7 recaptures in session 7). The number of fish captured declined significantly over the course of the sessions, as determined by a zero-truncated negative binomial regression.

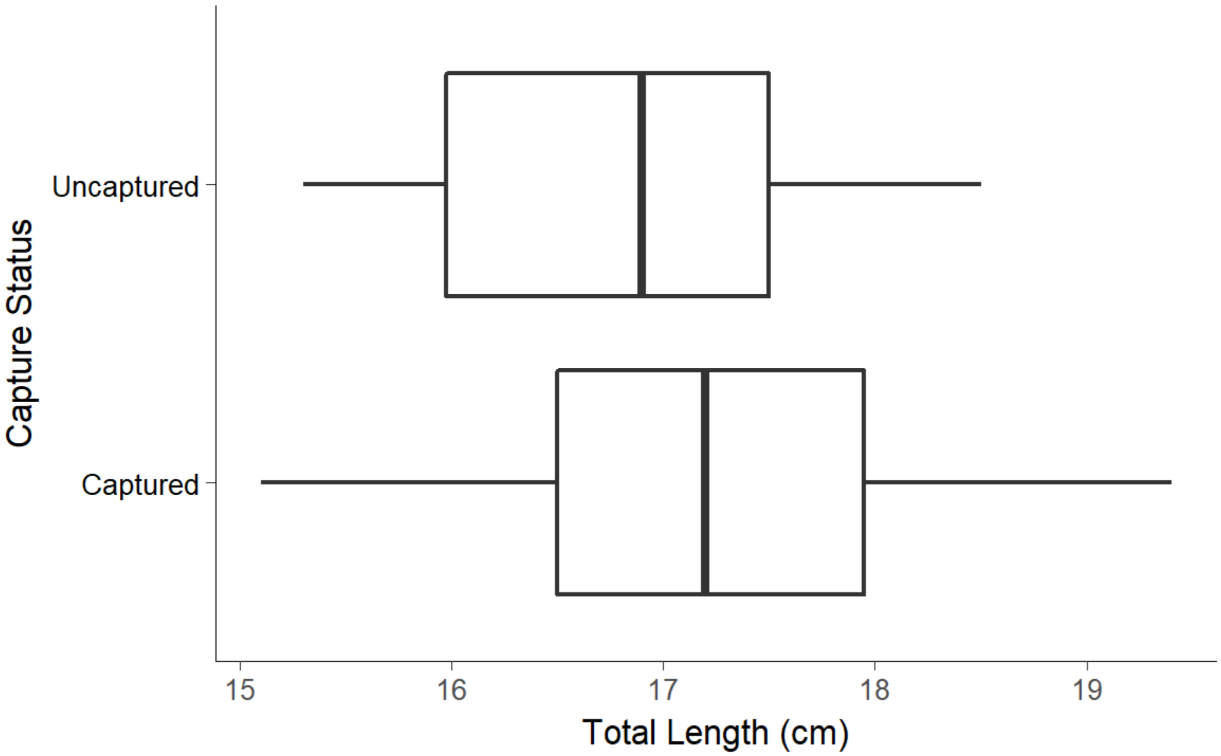

Figure 5-2: Total Length (in cm) of bluegill for fish that were captured (N = 79) and were not captured (N = 28) during angling trials. Bluegill total length was a significant predictor of whether or not a fish was captured, as determined by binary linear regression (Table 2).

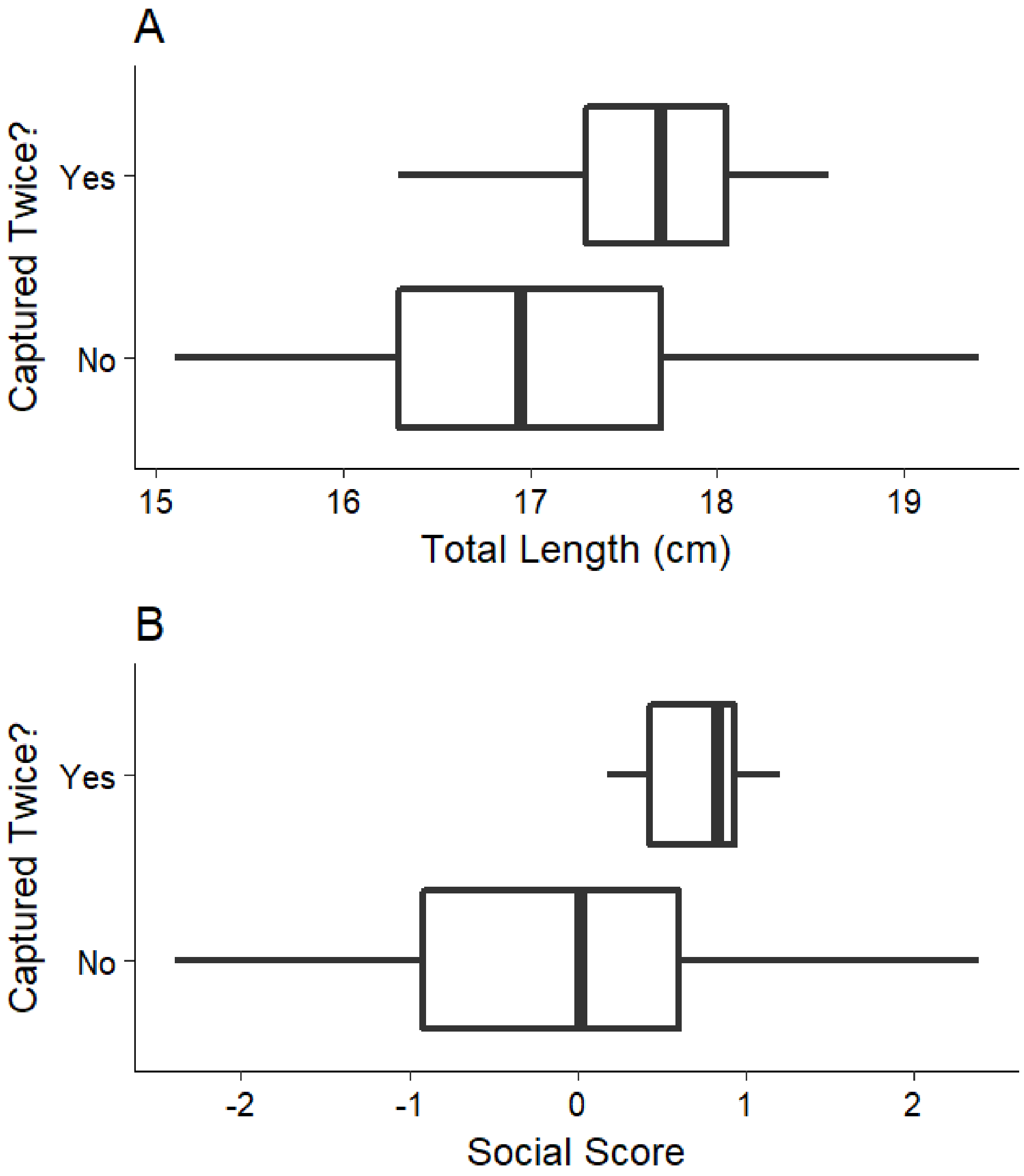

Figure 5-3: A) Total length (in cm) and B) Social score for N = 107 bluegill that were captured twice (N= 11) or once (N= 96) during angling trials. Both fish total length and social score (higher sociability and lower aggression) were significant predictors of if a bluegill was captured twice, as determined by binary logistic regression.

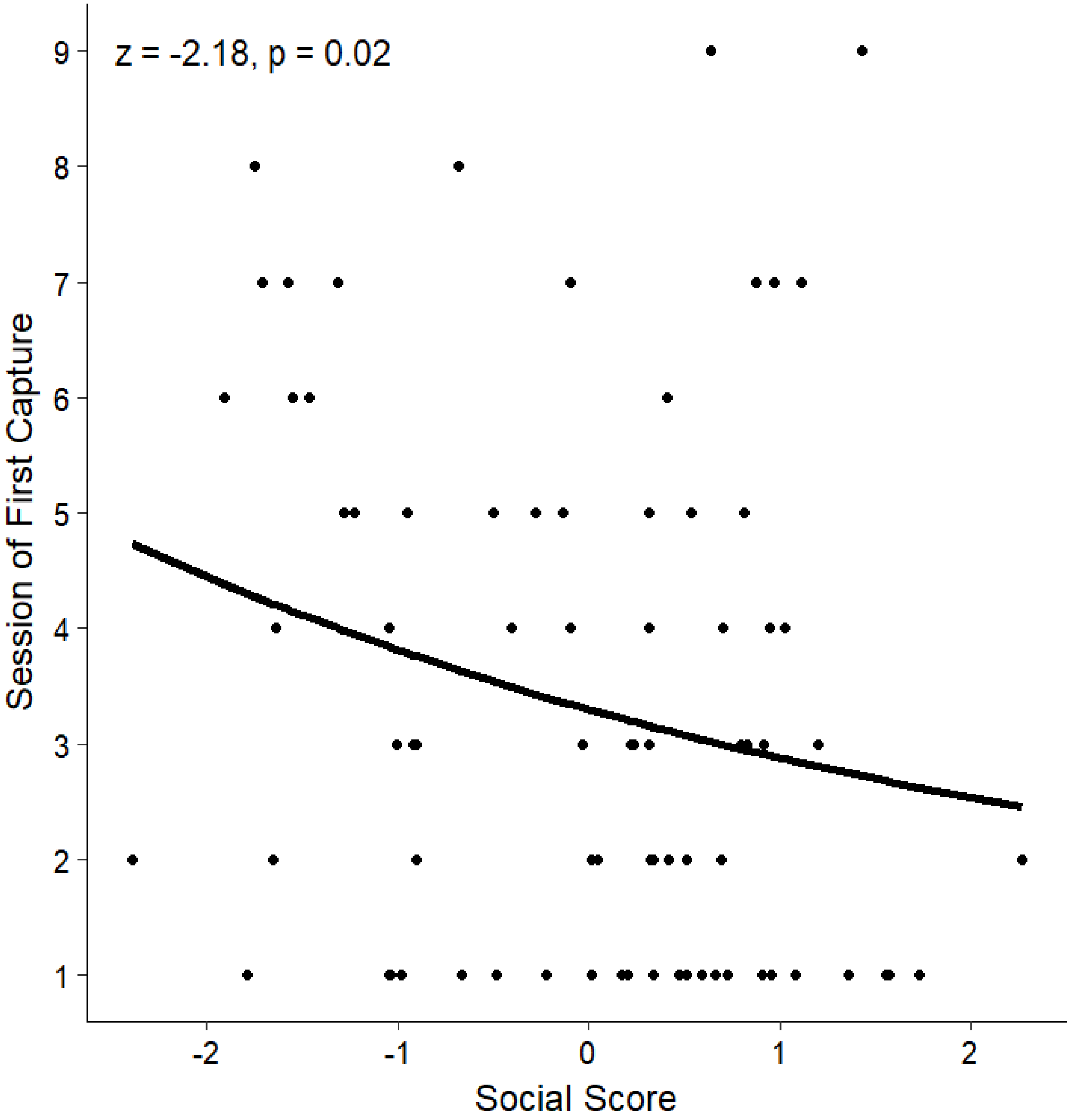

Figure 5-4: Relationship social score (see Table 1 for detailed explanation of how social score was derived) and the session in which a bluegill was captured (N=79 bluegill). Individuals with a high social score were highly social and unaggressive, while individuals with low social scores were asocial and aggressive. Each dot represents an individual fish. For fish captured multiple times, only the session of first capture is shown. Individuals with a high social score were likely to be captured in earlier angling sessions, as determined by zero-truncated negative binomial regression.

CHAPTER 6: QUICK LEARNING, QUICK CAPTURE: LARGEMOUTH BASS THAT RAPIDLY LEARN AN ASSOCIATION TASK ARE MORE LIKELY TO BE CAPTURED BY RECREATIONAL ANGLERS.

Introduction

Within species, individuals often show consistent differences in their behavioral responses to the environment. These suites of individual characteristics, which are often referred to as “behavioral types” (Bell 2007), “personalities” (Duckworth 2010), or “coping styles” (Koolhaas et al. 1999, 2007), are often presented as a continuum of behavioral responses to environmental stimuli. Some individuals are described as “proactive” because they exhibit bold and aggressive behavior in response to a stimulus, while others are described as “reactive” individuals because they are shyer and more passive (Benus et al. 1991; Overli et al. 2004). These coping styles are often associated with differences in key life history characteristics, whereby proactive individuals often feature faster growth and greater fecundity (Stamps 2007, Biro and Stamps 2008). Individual differences in behavior are often revealed when an individual faces a threatening situation, whereby proactive individuals tend towards a “fight or flight” response, while reactive individuals are more likely to freeze and remain immobile until the threat passes (Koolhaas et al. 1999, 2007). An individual’s coping style has a major impact on how it responds to environmental change, with reactive individuals typically being more flexible in their behavioral response to environmental shifts (de Lourdes Ruiz-Gomez et al. 2011; Stamps 2016). Particular coping styles, therefore, can be expected to be favored depending on environmental conditions, and, indeed, environmental diversity has been posited as a key factor maintaining a diversity of coping styles within populations (Reale et al. 2010a; Wolf and Weissing 2010).

In addition to differing in their behavioral traits, individuals also may differ in cognitive characteristics related to learning and problem solving. Variation in a generalized intelligence factor among individuals have been long described in humans (Deary and Caryl 1997; Duncan et al. 2000), though exactly how to measure intelligence and cognitive performance has long been controversial (Sternberg 2000). In non-human animals, generalized differences in cognitive performance have also been shown, where certain individuals consistently perform better on a variety of tasks related to problem solving and learning (Anderson 1993; Matzel and Kolata 2010; Shaw et al. 2015). In recent years however, a new framework has been posited where performance on cognitive tasks is not based on general intelligence, but rather based on alternative approaches to the solving of novel problems. These alternative approaches, termed ‘cognitive syndromes’, are often related within individuals to their coping style (Sih and Del Giudice 2012). Within this framework, “fast” individuals are likely to be proactive behaviorally and are expected to fearlessly approach novel problems and identify solutions quickly. “Slow” individuals, on the other hand, are slower to explore the novel situation, and as such do not arrive at a solution as rapidly. Alternative cognitive syndromes have associated tradeoffs: while fast individuals find solutions to novel tasks quickly, they are more prone to mistakes, less able to commit their experiences to long term memory, and show a low capacity for changing their behavior based on new information after the initial task has been learned (Sih and Del Giudice 2012). Indeed, the relationship between coping style (i.e., proactive vs. reactive) and cognitive syndrome (i.e., fast vs. slow) has been demonstrated in several animal taxa, including fish (Pintor et al. 2014; Mesquita et al. 2016; Bensky et al. 2017), insects (Udino et al. 2016), birds (Guillette et al. 2009, 2011), and mammals (Guenther et al. 2014; Guenther and Brust 2017). Depending on the environment, these cognitive differences have the potential to greatly impact an individual's fitness.

Inter-individual differences in behavior and cognition are especially relevant to fitness in environments altered by human activity. Adequately responding to human-induced threats, whether they be the introduction of invasive species (Mooney and Cleland 2001; Blake and Gabor 2016), harvest (Kuparinen and Merila 2007; Ciuti et al. 2012), or habitat loss (Sih et al. 2016) is essential if individuals are to survive and successfully produce offspring. It is theorized that cognition plays a major role in determining survival in these habitats, with superior cognition being linked to the ability to adjust behavior to both avoid human threats and take advantage of newly presented opportunities (Dridi and Lehmann 2016; Griffin et al. 2017). Independent of cognitive ability, an individual's cognitive syndrome can lead to a tradeoff that influences survival in the face of human activity. On one hand, bold behavior and a fast cognitive strategy may allow individuals to quickly explore human-impacted environments and take advantage of new resources (Miranda et al. 2013; Sol et al. 2013). Conversely, this type of behavior may leave individuals more at risk of mortality as a result of human harvest (Ciuti et al. 2012) or predation by introduced species (Sih et al. 2011). Given that selective mortality of individuals with particular cognitive traits is expected to lead to the evolution of those traits in a population (Sih et al. 2011; Dridi and Lehmann 2016), furthering our understanding of how cognitive characteristics impacts survivorship in human-dominated landscapes is essential if we are to make accurate predictions regarding the response of species to environmental change.

A specific example in which cognitive syndromes and learning performance is linked with survival can be found in the case of sportfish targeted by recreational and commercial fishing. The capacity for learning is well documented in fish, especially with regards to avoiding predators (Chivers and Smith 1995; Manassa and McCormick 2012, 2013) and identifying profitable foraging patches (Franks and Marshall 2013; Trapp and Bell 2017). This learning ability also extends to learned avoidance of fishing gears, including nets (Brown and Laland 2002) as well as recreational fishing lures (Askey et al. 2006; Lennox et al. 2016). It is also known that individual fish of the same species differ significantly in their capacity for learning (Budaev and Zhuikov 1998), which may lead to differences in overall fitness (Shohet and Watt 2009). In recreationally fished systems, fitness is likely linked to the ability to successfully avoid striking fishing lures and in turn avoid harvest or incidental mortality from hooking injury. While individual vulnerability to angling has been linked previously to metabolic phenotype (Redpath et al. 2010; Hessenauer et al. 2015), hormonal physiology (Chapter 2), and behavioral type/coping style (Sutter et al. 2012; Harkonen et al. 2014; Klefoth et al. 2017), the relationship between cognitive ability and angling vulnerability has never been examined. This is despite the fact that cognitive ability and individual cognitive syndromes could well be linked to the ability to discern potential danger posed by fishing lures, which would lead to successful lure avoidance. If selective capture of individual fish with certain cognitive characteristics is occurring, it would be expected that exploited populations would then evolve in response away from the traits associated with elevated vulnerability (Arlinghaus et al. 2016; Lennox et al. 2017), leading to cascading effects on the behavior and ecology of these populations (Uusi-Heikkila et al. 2008).

To address this gap in how cognitive characteristics are linked with vulnerability to capture by anglers, I conducted a study assessing learning performance, proactivity, growth, and angling vulnerability in largemouth bass *Micropterus salmoides*. Largemouth bass are an ideal species for addressing this question, as they are among most popular sportfish species in North

America, have been stocked extensively to support recreational fisheries, and have also been a frequent subject for studies examining inter-individual differences in angling vulnerability (Philipp et al. 2002; Gaeta et al. 2013). For this chapter, all fish were first subjected to an active-avoidance protocol (Yue et al. 2004; Morin et al. 2013) to define learning performance, then tested in an out-of-water restraint test intended to quantify each fish's proactivity. Finally, all fish were stocked into a single naturalistic pond and angled over the course of 10 days, allowing learning performance and proactivity scores to be related to angling capture. I anticipated two alternative outcomes regarding learning performance and angling vulnerability. On one hand, high performance on the learning task would reflect a high level of generalized cognitive ability (Matzel and Kolata 2010; Shaw et al. 2015) that would allow individuals to avoid capture. Alternatively, high performance on the learning task would be indicative of a fast cognitive syndrome that would be linked to a higher propensity to be captured (Sih and Del Giudice 2012; Guenther and Brust 2017). Under this construct, rapid learning might also be associated with higher levels of proactivity, as assessed in this chapter by the restraint test (Hau et al. 2015; Bensky et al. 2017). Regardless of the outcome, the data provided in this chapter is the first to quantify how cognitive performance specifically relates to vulnerability to capture in recreational angling and will allow for novel conclusions with regards to the evolution of behavior as a result of selective harvest.

Methods

Study Fish and Holding

Largemouth bass used in this chapter were acquired from Keystone Fish Hatchery in Richmond, IL on 10 May, 2017, and transported to the Illinois Natural History Survey's (INHS)

Aquatic Research Facility in Champaign, Illinois. The INHS facility consists of a wet laboratory as well as a series of naturalistic ponds ranging from 0.04-0.12 ha in area, each containing natural macrophyte cover items as well as stocked fathead minnows *Pimphales promelas* that serve as forage for fish. All largemouth bass were just over 1-year old at the time of transport, were members of the same cohort, and were of similar size (N = 60, mean length ± standard error of the mean (S.E.M.) = 181.7 ± 1.5 cm, range = 16 - 21 cm). Prior to stocking into one of the 0.12 ha holding ponds, all fish were tagged for individual identification with a 0.8 mm Passive Integrated Transponder tag (PIT; Biomark®, Boise, ID). On 30 May, the holding pond was drained, and the largemouth bass used in this chapter were retrieved and placed into a series of 1135 L circular outdoor holding tanks at a density of 20 fish per tank. Holding tanks at the facility were designed with continuous flow-through recirculation system that brought a continuous supply of fresh water from a nearby pond into the tanks at a rate of approximately 8 full water exchanges per day. During this period, fish were fed daily with commercial pelleted food obtained from Keystone Hatchery, at a daily ration amounting to ~3% of the average fish's body weight. Fish were held in this manner until 10 July, when the first learning assessments took place.

Active-Avoidance Learning Assessment

To assess learning performance in largemouth bass, an active-avoidance protocol was developed that was modified from previously described methods (Budaev and Zhuikov 1998; Yue et al. 2004; Morin et al. 2013). All fish were tested in one of ten 117 L (81 cm long × 40 cm wide × 36 cm high) acrylic aquaria (hereafter, 'arenas'), that were all connected to a recirculating system that drew water from a common reservoir tank. A TK-500 Heater-Chiller (Teco ®, Ravenna, Italy) and a Sweetwater^{TM} air compressor (Pentair, Florida, USA) cycled water within the reservoir tank, and kept water temperatures at 24ºC and dissolved oxygen saturation above 90% in the arenas. Each arena was divided in half along its short axis by an opaque polyethylene sheet that included a 10 cm diameter circular opening in its center, which allowed for shuttling between the sides of the arena by the fish. Opaque plastic blinds were attached to all sides of the tank to prevent disturbance of the fish by the activity of the observers, however a small slit was cut into the blinds to allow the observer to determine the location of the fish prior to learning trials.

Successful learning of a task required fish to form an association between a conditioned stimulus and an unconditioned aversive stimulus, in a manner similar to previous assessments (Yue et al. 2004; Morin et al. 2013). To establish this association, at the outset of each trial, an observer identified which side of the tank the fish was occupying, and proceeded to shine a light over that side of the tank using a Mag-Lite ® LED flashlight for a period of 45 s. The light was then turned off for a period of 15 s, after which the observer manually chased the fish using an aquarium net (15 cm^2 cross-sectional area) for a maximum period of 60 s. Chasing of the fish was haphazard in nature in that the net was moved quickly around the half of the arena occupied by the fish in a way that wasn't necessarily directed at the fish, and also never restricted the movement of the fish by pinning it against a wall of the arena. Chasing ceased when the fish shuttled through the opening in the divider to the other half of the arena or when 60 s had elapsed. For trials in which shuttling did not occur within 60 s the observer manually pushed the fish through the opening using the aquarium net. For each trial, three possible outcomes were defined. A trial was considered a 'success' when the fish responded to the conditioned stimulus by shuttling through the opening to the other side of the arena prior to the onset of chasing with the net. The trial result was defined as an ‘escape’ when the fish did not shuttle prior to the onset of chasing with the net but did shuttle before the end of the 60 s chasing period. Finally, the trial was considered a ‘failure’ when the fish failed to shuttle before the end of the chasing period and had to be manually forced through the opening.

Each fish was assessed using this methodology 10 times a day, with 5-10 min between trials, over the course of three days for a total of 30 learning trials. The following nine metrics describing learning performance for each individual largemouth bass were then extracted from the outcome data: (1) the total number of successes, (2) the total number of failures, (3) the number of trials until the first escape, (4) the number of trials until the last failure, (5) the number of trials until the first success, (6) the number of trials until the fish succeeded twice consecutively, (7) the number of trials until the fish succeeded three times consecutively, (8) the maximum number of successes within a single day, and (9) the maximum streak of successful trials (including overlaps between testing days). All 60 largemouth bass received learning assessment trials between 10 July and 28 July, and were returned to their outdoor holding tank at the conclusion of the learning assessment.

Restraint test

Following the assessment of learning performance, all largemouth bass were assessed for proactivity using a single out-of-water restraint test, performed in congruence with prior work (Mota Silva et al. 2010; Castanheira et al. 2013). Twenty largemouth bass were tested each day over three testing days, beginning on 31 July and ending on 2 August. On the day before each proactivity assessment, twenty fish were each isolated in one half of the behavioral arenas described above, which were modified so that the divider between the halves of the arena included no openings for shuttling. For the trial, each largemouth bass was first quickly netted from its holding tank and held out of water in a 30 L plastic container lined with wet towels, where it remained for a period of 3 minutes. Three metrics describing the fish's behavior during the test were then described: (1) the total number of jumps, defined as the fish fully displacing its body above the bottom of the container; (2) the time elapsed prior to the fish jumping for the first time, and (3) the time elapsed prior to the fish jumped for the last time. This assessment was used as a test of each fish's proactivity where more proactive fish would be expected to begin jumping earlier, more frequently and for a longer period of time (Mota Silva et al. 2010; Castanheira et al. 2013). Following the conclusion of the test, each fish was returned to an outdoor holding tank.

Angling Trials

On 5 August, all largemouth bass were stocked into a single 0.04 ha angling pond, which contained natural cover and stocked forage items as described above. Angling trials consisted of a series of nine daily angling sessions over the course of 10 days, starting on 14 August and ending on 24 August (no angling was performed on 17 August). Each session was 45 min in length, and during that time a single angler moved around the perimeter of the pond so as to make casts targeting all areas of the pond. Angling gear consisted of a medium-action spinning rod spooled with 2.7 kg Berkely Trilene^{TM} monofilament fishing line. Three different lures were used for this chapter: a size 0 Mepps ® Agila in-line spinnerbait, a Gary Yamamoto® 7.6 cm cream-white plastic worm rigged "wacky style" on a Gamakatsu® Size 6 circle hook, and a third plastic worm setup identical to the previous except that the worm was watermelon green in coloration. Only a single lure was used within each angling session. For the first six sessions the spinnerbait and white plastic worm were alternated such that the spinnerbait was fished in the first, third and fifth sessions and the white plastic worm in the second, fourth and sixth. After these six sessions ended with relatively few captures, the final three sessions were fished with the green plastic worm. Upon capture, each largemouth bass was dehooked, quickly identified using a hand-held PIT reader, and returned to the pond within 1 min to be potentially re-captured. No largemouth bass were "deep-hooked" in the gills or gullet during the study, and all fish swam away vigorously upon release. Angling trials ended on 23 August, and all 60 fish were recovered when the pond was subsequently drained on 24 August.

Statistical Analysis

After determination that the data were suitable (Kaiser-Meyer-Olkin Test Score = 0.767; Bartlett's Test of Sphericity, $p < 0.001$), Principal Components Analysis (PCA) based on the correlation matrix was performed to reduce all nine metrics from the active-avoidance learning assessment and proactivity assessment to relevant components. Following this analysis, varimax-rotated components with eigenvalues over one were extracted, based on the maximum likelihood solution (Kaiser 1960). Within each component, metrics with factor loadings ≥ 0.4 were considered significant drivers of that component (Kaiser 1960; King et al. 2016).

Following extraction of learning and proactivity components, I was then interested in whether growth rate was associated with learning performance and/or proactivity. To examine this, separate linear regressions were performed to determine if fish length was associated with any extracted components from the learning and restraint assessments. Because all fish used in this chapter were from the same spawning cohort and identical in age (Keystone Fish Hatchery personnel, personal communication), I considered the length of each fish to be a direct reflection of that fish’s growth rate, similar to previous work examining links between behavior and angling vulnerability in hatchery fish (Klefoth et al. 2017).

To determine the relationship between extracted learning and proactivity components and angling vulnerability, binary logistic regression was used. Because total length correlated positively with one extracted component (see results below), to avoid multicollinearity, total length was not included in this model. All extracted components were included as independent variables, with capture status as the dependent variable in the model. All means are shown ± S.E. where appropriate, and the level of significance (α) for all tests was 0.05. All analysis were performed in R, version 3.4.3 (R Core Team, Vienna, Austria) utilizing the ‘psych’ package (Revelle 2017).

Results

Means for all active-avoidance and restraint test metrics for captured and uncaptured fish are provided in Table 6-1. Three extracted principal components describing behavior in the active-avoidance and restraint assessments collectively accounted for 73% of the total variation in the data. The first principal component featured significant negative loadings for the total number of successes, the maximum number of successes within a day, and the maximum streak of successes (Table 6-2). Significant positive loadings for this component included the number of trials until the first success, the number of trials until two consecutive successes, and the number of trials until three consecutive successes (Table 6-2). Because more negative scores for this component represented higher levels of success, to facilitate easier interpretation the final ‘success score’ was calculated by multiplying PC 1 scores by -1 so that highly positive success scores would represent highly successful learners on the active-avoidance task. The second principal component featured significant positive loadings for the total number of failures, the number of trials until the first escape, and the number of trials until the last failure (Table 6-2). This second principal component was interpreted as the ‘failure score’, with higher component scores representing individuals that failed more frequently and took more trials before successfully escaping. The third principal component featured significant positive loadings for the total number of jumps and the time until the last jump was performed, and a significant negative loading for the time taken before the first jump was performed (Table 6-2). Scores for third principal component were interpreted as the ‘restraint score’ whereby individuals that began jumping sooner, jumped more often and longer through the trial received a higher restraint score. The fact that failure-related and success-related metrics were strongly segregated in their loadings among components demonstrates that these two aspects of behavior were not related (i.e. fish with more successes did not necessarily have fewer failures). Furthermore, the segregation of loadings for restraint test metrics on the third principle component shows that proactivity on this test was not related to learning performance.

Fish total length was significantly related to success score (Linear Regression, $t = -2.14$, $p = 0.03$), whereby larger fish succeeded on more trials, took fewer trials to achieve success, and accumulated longer streaks of successful trials in the active avoidance assessment (Figure 6-1A). Failure score ($t = 1.18$, $p = 0.24$) and restraint score ($t = 0.9$, $p = 0.37$) were not associated with the total length of largemouth bass (Figure 6-1B and C).

Angling trials resulted in the capture of 21 of the 60 fish in the angling pond. Of these 21 fish, 4 were captured multiple times for a total of 25 total capture events. Of the three lures used, the green plastic worm proved to be the most effective, accounting for 17 of the 25 capture events, while the spinnerbait and white plastic worm accounted for 4 capture events each.

Higher success scores in the active avoidance assessment were significantly associated with whether or not a fish was captured (Table 6-3), with captured fish having a significantly higher score (Student's T-test, df = 58, $p = 0.02$; Figure 6-2A). The number of trials in which a fish failed on the avoidance assessment, as well as the fish's behavior during the restraint test, were not associated with capture (Figure 6-2B and C, Table 6-3). The pooling of fish that were caught multiple times with fish caught only once was appropriate, given that largemouth bass that were captured multiple times did not differ from singly-captured fish for any component score or total length (Student's t-test, $p > 0.1$ in all cases).

Discussion

The results of this chapter demonstrate a link between learning performance and angling vulnerability in a highly sought-after sportfish species, as fast-learning largemouth bass were more likely to be captured during experimental angling trials. The success score PC was loaded on most heavily by the number of successful trials in the active-avoidance protocol, and captured fish, on average, successfully shuttled in response to the light on 5.7 trials out of 30, as opposed to uncaptured fish that successfully shuttled in 3.2 trials on average. In addition to achieving more successes, captured fish on average required approximately 6 fewer trials to achieve their first success than uncaptured fish. While the fact that faster learners were less adept at avoiding fishing lures may seem counterintuitive, this result is consistent with the predictions drawn from research examining cognitive syndromes. Within this framework, it has been found that individuals that employ a fast learning strategy are quicker to initially learn a task (especially tasks based on movement and activity), while those employing a slow strategy may take longer to initially learn a task, but are superior at retaining that information and adapting to new information and environmental cues (Guillette et al. 2011; Sih and Del Giudice 2012; Guenther et al. 2014). Fast learning has also been linked to an individual's behavioral characteristics, with proactive and bold behavior linked to initial learning speed in several animal taxa, including birds (Guillette et al. 2009), mammals (Guenther et al. 2014; Guenther and Brust 2017), and fish (DePasquale et al. 2014; Mesquita et al. 2016; Bensky et al. 2017). This rapid learning and bold behavior comes at a potential cost, as individuals with these traits have been found to be more mistake prone (Sih and Del Giudice 2012), and also more vulnerable to predation while actively foraging (Sih et al. 2003, 2004a; Stamps 2007). Recreational harvest of fish species represents a major predation risk, and, indeed, several studies have shown that individuals that are bolder, more active, and/or more exploratory are more vulnerable to hook-and-line angling (Harkonen et al. 2014; Alós et al. 2016; Klefoth et al. 2017), though this finding has not been unanimous (Wilson et al. 2011; Chapter 2). This chapter shows that in addition to behavioral phenotype, cognitive learning style is highly relevant to explaining angling vulnerability in that a fast cognitive phenotype is more likely to investigate and strike a novel fishing lure.

In addition to being linked with vulnerability to angling, learning performance was also associated with fish size. Success score was significantly and positively related to fish length, while failure score and restraint score were not. Because all largemouth bass in this chapter were acquired from a hatchery, were from the same age cohort, larger fish were almost certainly faster growers within the cohort, meaning that a positive relationship between learning performance and growth rate can therefore be inferred. Faster growth has been shown to be correlated with fast and proactive behavioral and physiological characteristics (Stamps 2007; Biro and Stamps 2008, 2010). This fast "pace of life" (Reale et al. 2010b) has recently been linked to fast cognitive syndromes and rapid initial learning (Sih and Del Giudice 2012). These characteristics are associated with a tradeoff that incurs higher mortality risk (Stamps 2007), a relationship that holds in this chapter where fast-learning/fast-growing largemouth bass were more vulnerable to angling. Indeed, selection based on correlated growth and behavioral characteristics has been described previously in both fish (Biro and Post 2008) and commercially harvested crustaceans (Biro and Sampson 2015). From a mechanistic standpoint, either behavior or growth rate could be the primary driver of vulnerability in fish. On one hand, fish that make rapid decisions and exhibit bold behavior may be more likely to approach and strike a fishing lure (Klefoth et al. 2013). Alternatively, vulnerability could be driven by growth rate *via* gape limitation, with larger-mouthed fish being better able to take the lure into their mouth while smaller fish fail to fully take in the lure, increasing the chances of successful hooking and landing by the angler (Alós et al. 2014; Klefoth et al. 2017). The relationship between growth rate and angling vulnerability may also relate to metabolism and feeding, where faster growers have higher metabolic rates, and as such need to feed more often to fulfill their metabolic needs (Careau et al. 2008; Biro and Stamps 2010), though this mechanism has yet to be fully studied. These potential mechanisms are of course not mutually exclusive, and it is possible that both interact to increase the likelihood of a fish being captured. As a result, it can be expected that fisheries selection in heavily fished ecosystems will affect both cognitive behavior and growth rate simultaneously.

In contrast to learning performance, behavior in a restraint test was not associated with angling vulnerability in largemouth bass. In addition, measures of behavior derived from the restraint test (number of jumps, the time until the first and last jump) did not load on either of the learning performance components, indicating that learning and “proactivity” as defined in this assessment are likely not related. This finding contrasts with previous studies demonstrating links between proactive behavioral traits and a fast cognitive syndrome (Sih and Del Giudice

2012). In addition, several proactive behavioral and physiological traits have been found to be positively linked with angling vulnerability in fish. These include low cortisol responsiveness to stress (Chapter 2), high metabolic rates (Redpath et al. 2010), and boldness in a behavioral assay (Harkonen et al. 2014; Klefoth et al. 2017). While the present results would suggest that proactivity is not linked to angling vulnerability, it should be noted the restraint test used for this chapter is only one measurement of proactivity and that different assessments for proactivity do not always align with each other (Backstrom et al. 2014; Boulton et al. 2015). For example, Koolhaas et al. (2007) described the behavioral response to environmental stimuli in terms of both 'proactivity' and 'emotionality', which describe both the approach an individual takes to a stimulus as well as the magnitude of the behavioral response, respectively. In this chapter, largemouth bass differed in their behavioral responses during the restraint test, however these differences do not necessarily align with other measures typically used to measure proactivity, such as boldness and cortisol responsiveness, which may reflect other components of the individual's coping style (Koolhaas et al. 2007). Indeed, while Chapter 2 found that fish that showed a low cortisol response to air exposure were more likely to be captured, boldness in a behavioral assay was not related to angling vulnerability, indicating that these two components typically associated with proactivity are not linked. Collectively, this means that a fish's response during a restraint test may not be reflective of other aspects of proactivity, and that additional proactive behavioral characteristics (such as cortisol responsiveness or behavior under risk) are better linked with learning performance or angling vulnerability.

The potential selective capture of individual fish based on their cognitive, behavioral, or physiological characteristics is of interest to behavioral scientists and fisheries researchers alike, due to the possible evolutionary consequences of such selection. This process, known as fisheries-induced evolution, has been predicted by numerous modelling approaches (Kuparinen and Hutchings 2012; Eikeset et al. 2013; Dunlop et al. 2015), and empirically demonstrated in both marine (Conover et al. 2009; Hidalgo et al. 2014) and freshwater (Consuegra et al. 2005; Edeline et al. 2007; Philipp et al. 2009) fish species. While life-history characteristics relevant to commercial harvest have been oft-studied (Jorgensen et al. 2007; Kuparinen and Merila 2007; Enberg et al. 2010), the potential for selection based on individual behavioral phenotype to evolutionarily disrupt fish behavior has been quantified as well (Sutter et al. 2012; Harkonen et al. 2014; Arlinghaus et al. 2016). Cognitive abilities have been demonstrated to be heritable in fish (Smith et al. 2015) and based on the results of this chapter, cognitive learning characteristics may be under selective pressure in exploited populations, with slow learners having an evolutionary advantage through reduced capture. We would expect, therefore, a population-level reduction in the speed of learning, which in turn would impact behaviors such as foraging and habitat selection that require associative learning. However, given the current lack of empirical findings examining the role of cognitive traits in driving angling vulnerability in wild populations, relating these findings to wild populations are somewhat tenuous. Selection favoring a slow cognitive strategy may be beneficial, whereby slow individuals initially take longer to learn a task/behavior, but are also more thorough learners with a greater ability to form stable memories and avoid costly mistakes (Sih and Del Giudice 2012). This is especially relevant in rapidly changing environments where slow explorers/learners have been shown to be more flexible when environmental change occurs (Benus and Koolhaas 1987; Ruiz-Gomez et al. 2011). Indeed, while this chapter is related specifically to angling vulnerability in fish, human-caused selective mortality favoring flexible phenotypes has been predicted to be beneficial in a variety of additional contexts, such as in the face of habitat destruction or the introduction of predatory invasive species (Sih et al. 2013). This means that, for taxa where human activity leads to selective mortality, we would expect that individuals with flexible behavior and a “slow” cognitive syndrome would be evolutionarily favored.

Recent work has demonstrated the existence of cognitive syndromes, whereby individuals consistently differ in their learning performance and approach to novel problems (Sih and Del Giudice 2012; Guenther and Brust 2017). These differences are often described in terms of a continuum, where fast individuals show greater speed in initially learning activity-based tasks, while slow individuals show greater flexibility and investigate new tasks with a higher degree of thoroughness. In this chapter, “fast” individuals that learned an avoidance task more quickly were also more likely to be captured by anglers. This finding is, to my knowledge, the first to demonstrate that cognitive characteristics in fish may be under selective pressure due to human activity, specifically intensive fishing pressure. In environments altered by humans, it has been suggested that individuals that show greater flexibility and lower activity may have an advantage in terms of avoiding conflict with people (Ciuti et al. 2012; Sih 2013). Because these traits are often associated with a slow cognitive approach, the present results re-enforce this concept as slow-learning largemouth bass were better able to avoid capture. Whether human-induced selection based on this characteristic is widespread in nature, or applies to multiple targeted species, is still unknown. Additional research involving multiple taxa impacted by human activity will be needed to determine how cognitive characteristics impart fitness advantages or disadvantages in disturbed environments.

TABLES AND FIGURES

Table 6-1: Summary of means (± S.E.M.) of all response variables generated following active-avoidance learning and restraint tests on largemouth bass that were captured or uncaptured during experimental angling trials.

Response variable	Captured (N = 21)	Uncaptured (N = 39)
Total Failures	2.0 (0.4)	2.5 (0.3)
Total Successes	5.7 (0.8)	3.2 (0.6)
Number of Trials Until First Escape	1.9 (0.3)	2.3 (0.2)
Trials Until First Success	12.6 (1.9)	18.3 (1.7)
Trials Until Last Failure	3.4 (0.7)	4.3 (0.6)
Number of Trials Until Two Consecutive Successes	22.8 (1.7)	26.6 (1.0)
Number of Trials Until Three Consecutive Successes	27.5 (0.9)	28.0 (0.8)
Maximum Number of Successes Within a Day	3.5 (0.9)	2.1 (0.4)
Maximum Streak of Successes	2.4 (0.4)	1.5 (0.3)
Time Until First Jump (s)	10.7 (8.5)	2.8 (1.4)
Total Number of Jumps	37.4 (3.4)	38.8 (1.9)
Time Until the Last Jump (s)	126.6 (10.2)	149.6 (3.9)

Table 6-2: Principal Component Loadings for all metrics derived from assessments for learning and restraint test performance in largemouth bass. All learning metrics are based on the outcome (success, escape, or failure) of 30 active-avoidance trials for each individual fish. Restraint test performance was based on how often and for how long a fish continued to “jump” while being held in a container out of water over three minutes. Three principal components were extracted, and subsequently named based on the factors which loaded most heavily on each component (significant loadings ≥ 0.4 are given in **bold**).

Response Variable	PC1 (success score)	PC2 (failure score)	PC3 (restraint score)
Total Successes	**-0.96**	-0.14	0.00
First Success	**0.71**	0.30	0.17
Number of Trials Until Two Consecutive Successes	**0.85**	0.06	0.11
Number of Trials Until Three Consecutive Successes	**0.83**	-0.10	0.01
Maximum Number of Successes Within a Day	**-0.96**	-0.04	0.01
Maximum Streak of Successes	**-0.90**	-0.01	0.02
Total Failures	0.08	**0.95**	0.07
Number of Trials Until First Escape	-0.04	**0.68**	-0.18
Last Failure	0.16	**0.81**	0.18
Time Until First Jump	0.14	0.08	**-0.79**
Total Number of Jumps	0.14	0.07	**0.76**
Time Until the Last Jump	0.11	0.05	**0.81**
Total Variance Explained	39%	18%	16%
Eigenvalue	4.8	2.1	1.8

Table 6-3: Output from binary logistic regression model analyzing the relationship between extracted components following a learning trial and a restraint test (success score, failure score and restraint score) and angling capture in largemouth bass. Significant effects are given in bold.

Term	Estimate	Std. Error	Z Score	p
Intercept	**-0.69**	**0.29**	**-2.36**	**0.01**
Success Score	**-0.29**	**0.13**	**-2.15**	**0.03**
Failure Score	-0.25	0.20	-1.22	0.22
Restraint Score	0.15	0.22	0.72	0.47

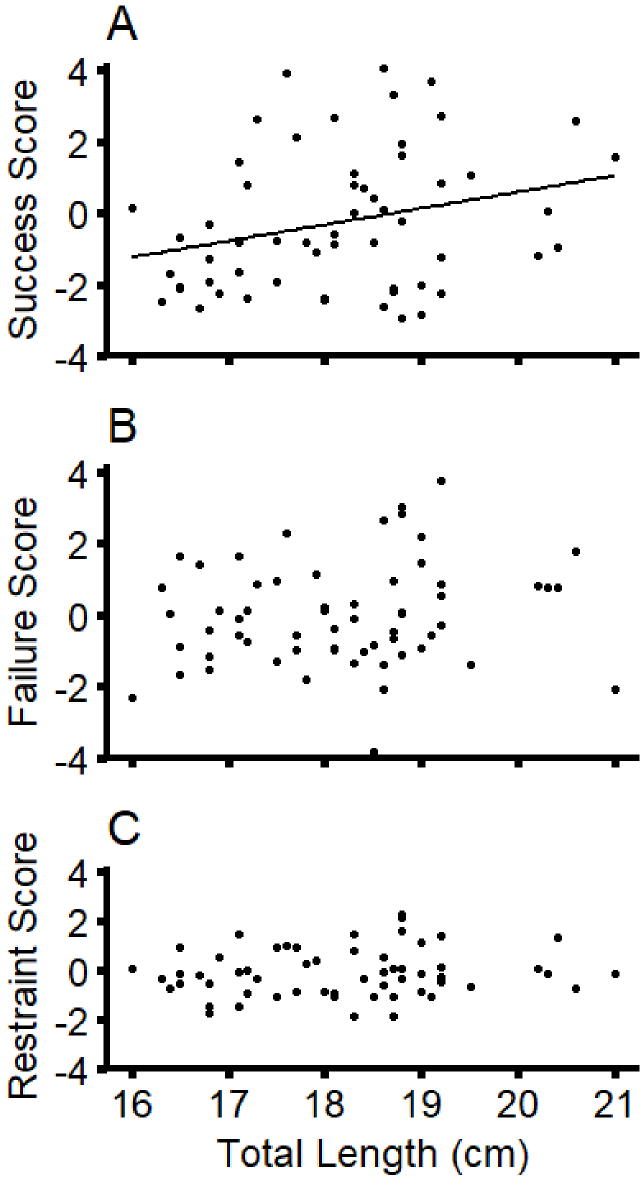

Figure 6-1: Relationships between total length (in cm) and A) success score, B) failure score, and C) restraint score across largemouth bass assessed for learning performance in an active-avoidance learning test and proactivity in a restraint test (N=60). Analyses performed to generate the three different response variables are outlined in Table 6-2. The regression line in panel A indicates a significant positive relationship between largemouth bass length and success score, as determined by simple linear regression. Relationships between total length and both failure score and restraint score were not significant.

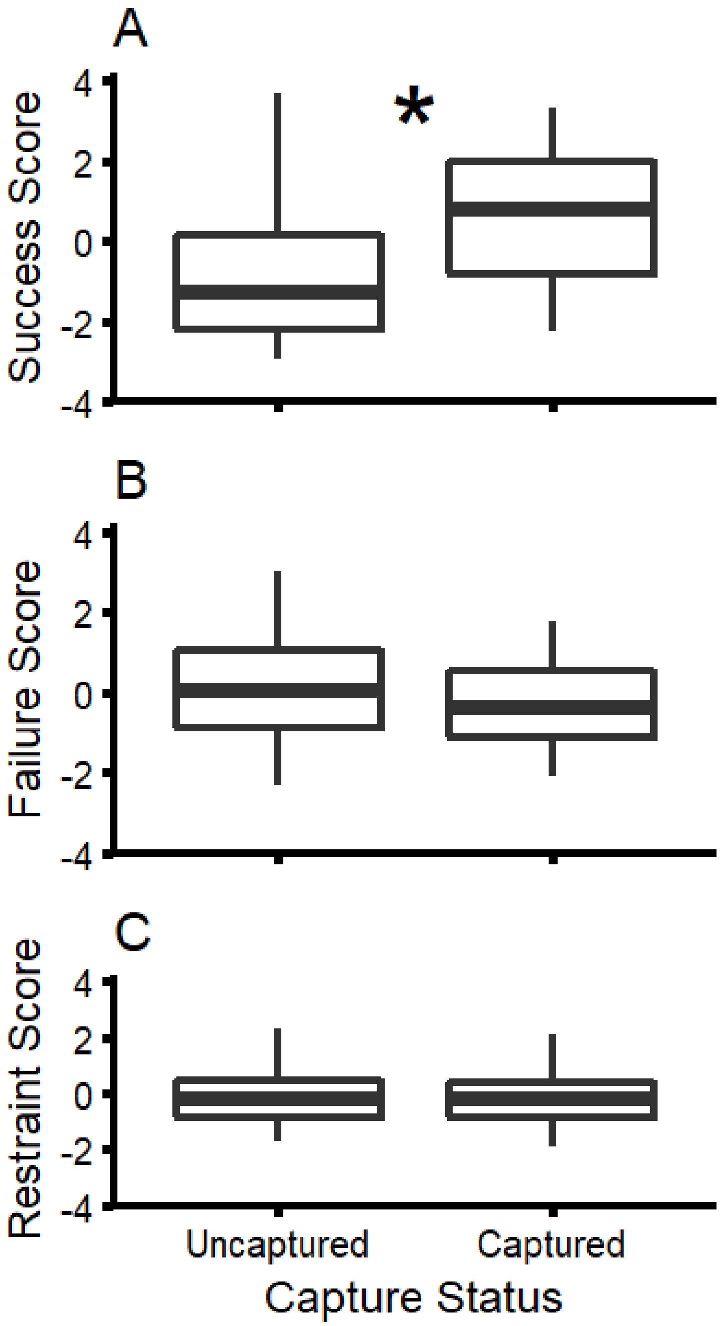

Figure 6-2: Boxplots showing comparisons between largemouth bass that were either captured or not captured during experimental angling trials and A) success score, B) failure score, and C) proactivity score. Analyses performed to generate the three different response variables are outlined in Table 6-2. The asterisk (*) in panel A indicates a significant difference between captured and uncaptured fish for success score, as determined by binary logistic regression.

CHAPTER 7: SUMMARY AND CONCLUSIONS

The research contained in this dissertation collectively shows that individual behavior and physiology can be associated with vulnerability to angling in popular recreational sportfish species. Indeed, this work has identified several novel characteristics that may be under selection in angled populations: Stress physiology (Chapter 2), sociability (Chapters 4 and 5), aggression (Chapter 5), and learning performance (Chapter 6). Metabolic phenotype on the other hand was not found to be a driver of angling vulnerability (Chapters 2 and 3). While boldness and exploratory behavior have been commonly hypothesized as the primary drivers of angling vulnerability (Harkonen et al. 2014; Klefoth et al. 2017), this research demonstrates that numerous additional behavioral and physiological characteristics may be targets of selection.

The identification of stress responsiveness as a major driver of angling vulnerability introduces not only the possibility that angling may select based on physiological traits (Cooke et al. 2007; Hollins et al. 2018), but that additional behavioral traits that covary with this characteristic may be under selective pressure as well (Dochtermann and Roff 2010). High cortisol responsiveness is linked with numerous behavioral characteristics, including generally timid behavior as well as a tendency to “freeze” in response to a threat (Koolhaas et al. 1999; Overli et al. 2005). Within the context of angling, it is fairly easy to speculate that this freezing behavior may be particularly important, as individuals that freeze when a lure drops in nearby would be expected to be less likely to be captured. Given that I did not evaluate freezing behavior specifically however, this hypothesis remains somewhat speculative. Regardless, it stands to reason that the increased vulnerability to angling seen in low stress responders is driven by a corresponding behavioral tendency, one that may have been found by conducting additional behavioral assays. Future work should consider all of the specific behaviors that are associated with angling vulnerability, taking a diverse approach to identifying the traits that are targets of angling selection.

Metabolic rate has previously been put forward as a likely driver of angling selection. This hypothesis is driven by the prediction that individuals with high metabolic rates will have to feed more often to meet those metabolic demands (Biro and Stamps 2008), leading to a greater likelihood of striking a fishing lure or bait. This hypothesis has been supported by empirical studies that demonstrate that artificially selected lines of largemouth bass has found more vulnerable fish to have higher aerobic scopes and maximum metabolic rates (Redpath et al. 2010). Furthermore, studies of largemouth bass in fished and unfished reservoirs has found that fish from fished reservoirs have lower standard metabolic rates, possibly due to angling selection removing individuals with higher metabolism (Hessenauer et al. 2015). Metabolic rates were addressed in chapters 2 and 3 of this dissertation however, with no difference between captured and uncaptured fish for any aspect of metabolic phenotype. While these results call into question the presumption that high metabolic rates lead to higher angling vulnerability, it is possible that the findings in this dissertation are the result of the experimental designs. In each case, angling was performed only over a short period of time at a time of year (summer) when metabolic rates in fish are at their highest due to high water temperatures. It is possible that selective capture of individuals with high metabolic rates only occurs at particular times of the year, perhaps in cooler conditions when high-metabolism individuals may continue feeding while others slow their feeding rates. This could explain why previous work in fished and unfished reservoirs (Hessenauer et al. 2015), as well as with lines artificially selected for differing angling vulnerability (Cooke et al. 2007; Redpath et al. 2010), found differences in metabolic rate while my work found no selection on this, as perhaps metabolic traits are selected on under circumstances different from the conditions described in my studies. To address this, future research should examine angling vulnerability across all contexts, keeping in mind the conditions at the time of angling, the species in question, and the duration of possible selective capture on the exploited population, as these factors may impact the nature of angling selection.

In both chapters 4 and 5, individual sociability was found to be a significant driver of angling vulnerability. Chapter 5 found a significant negative relationship between aggression and vulnerability as well, while this relationship was a non-significant trend in chapter 4. Within the context of FIE as a result of recreational angling, it is often presumed that more aggressive individuals will automatically be more vulnerable to capture by hook and line, as these individuals are expected to also “aggressively” strike fishing lures (Sutter et al. 2012). This, combined with the typical finding that bolder fish are more vulnerable (Klefoth et al. 2013, 2017), has led to the prediction that heavily fished populations will evolutionarily shift towards shy and submissive behavior, a so-called “timidity syndrome” (Arlinghaus et al. 2016). While this may indeed be the case for many targeted species, my results combined with previous work on bluegill (Wilson et al. 2011) suggest that the opposite selection that evolutionarily favors aggressive and antisocial phenotypes may occur. In light of these findings, I suggest that researchers take into account the ecology of the species in question when making predictions about the outcome of fisheries selection. Because bluegill are a socially gregarious species (McCartt et al. 1997), it stands to reason that social behavior may be involved in their vulnerability to angling capture, as it underpins virtually all other aspects of their behavior and ecology. Future work should take these between-species differences into account, and make predictions based not in an over-arching framework that predicts vulnerability across all targeted species, but rather specifically on the ecology and behavioral characteristics of the species in question.

It is well-documented that fish learn to avoid being caught by anglers over time, as their experience with lures increases (Askey et al. 2006; Hessenauer et al. 2016; Lennox et al. 2016). Given this, it might also be expected that individuals that are especially good at learning would be the least vulnerable, however my results in chapter 6 found the opposite, with “fast” learners being more likely to be captured. As discussed in chapter 6, it is likely that this result is related to the “cognitive syndrome” of individuals (Sih and Del Giudice 2012), with the individuals that were fast to learn the avoidance task also being fast to investigate and strike fishing lures. Indeed, these results in combination with the results of chapter 2 allow for the construction of a hypothetical framework where a proactive approach to challenges (low stress responsiveness and rapid learning) is positively linked with angling vulnerability in largemouth bass. Interestingly though, in both chapters 2 and 6 the behavioral test intended to assess those proactive traits (emergence from a refuge and vigor in a restraint test, respectively) were found to be unrelated to angling vulnerability. This of course could reflect the fact that “coping styles” are complex, composed of multiple facets that are difficult to encompass within a small set of behavioral experiments (Koolhaas et al. 2007; Boulton et al. 2015). Regardless, my research has shown that at least some components of coping styles/cognitive syndromes are linked to angling vulnerability in largemouth bass. This creates an impetus to further explore these characteristics, with an eye towards identifying additional behavioral characteristics that predispose individuals to angling capture.

In conclusion, my research indicates that the behavioral and physiological drivers of angling vulnerability are complex. Regardless of which traits are targets of angling selection, the question remains whether FIE due to angling actually has an impact on the health of freshwater fisheries broadly. While declines in stock productivity and population resilience have been documented heavily in commercial fisheries (Jorgensen et al. 2007; Kuparinen and Hutchings 2012; Audzijonyte et al. 2013), the question of whether FIE is actually modifying behavior (and in turn fitness) in exploited populations largely remains unanswered. Therefore, I conclude that future research in this area include investigations into three aspects of this question: 1) Which additional traits may be under selective pressure, 2) How does context (time of year, species, lure type) influence which phenotypes are most vulnerable to angling, and 3) Has the behavior and physiology of exploited populations actually changed as a result of extensive harvest. By answering these three questions, researchers and managers will be able to accurately evaluate whether FIE in freshwater systems is actually occurring, and at what pace. More importantly, evaluations of fisheries health can incorporate actual data on the impacts of FIE, with an overall goal of devising management solutions that mitigate any negative consequences of this phenomenon.

REFERENCES

Allendorf F.W., O. Berry, and N. Ryman. 2014. So long to genetic diversity, and thanks for all the fish. Mol Ecol 23:23–25.

Alós J., M. Palmer, and R. Arlinghaus. 2012. Consistent selection towards low activity phenotypes when catchability depends on encounters among human predators and fish. PLoS One 7:e48030.

Alós J., M. Palmer, M. Linde-Medina, and R. Arlinghaus. 2014. Consistent size-independent harvest selection on fish body shape in two recreationally exploited marine species. Ecol Evol 4: 2154-2164

Alós J., M. Palmer, R. Rosselló, and R. Arlinghaus. 2016. Fast and behavior-selective exploitation of a marine fish targeted by anglers. Sci Rep 6:38093.

Anderson B. 1993. Evidence from the rat for a general factor that underlies cognitive performance and that relates to brain size: intelligence? Neurosci Lett 153:98–102.

Anscombe F. and J. Tukey. 1963. The examination and analysis of residuals. Technometrics 5: 141-160

Archard G.A., R.L. Earley, A.F. Hanninen, and V.A. Braithwaite. 2012. Correlated behaviour and stress physiology in fish exposed to different levels of predation pressure. Funct Ecol 26:637–645.

Arlinghaus R., J. Alós, T. Pieterek, and T. Klefoth. 2017. Determinants of angling catch of northern pike (*Esox lucius*) as revealed by a controlled whole-lake catch-and-release angling experiment—The role of abiotic and biotic factors, spatial encounters and lure type. Fish Res 186:648–657.

Arlinghaus R., K.L. Laskowski, J. Alós, T. Klefoth, C.T. Monk, S. Nakayama, and A. Schröder. 2016. Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. Fish Fish 18:360-373.

Arnold T.W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. J Wildl Manage 74:1175–1178.

Askey P.J., S.A. Richards, J.R. Post, and E.A. Parkinson. 2006. Linking angling catch rates and fish learning under catch-and-release regulations. North Am J Fish Manag 26:1020–1029.

Audzijonyte A., A. Kuparinen, R. Gorton, and E.A. Fulton. 2013. Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. Biol Lett 9:20121103.

Backstrom T., E. Brannas, J. Nilsson, and C. Magnhagen. 2014. Behaviour, physiology and carotenoid pigmentation in Arctic charr Salvelinus alpinus. J Fish Biol 84:1–9.

Ballew N.G., G.G. Mittelbach, and K.T. Scribner. 2017. Fitness Consequences of Boldness in Juvenile and Adult Largemouth Bass. Am Nat 189:396–406.

Beacham J.L. 1988. The Relative Importance of Body Size and Aggressive Experience as Determinants of Dominance in Pumpkinseed Sunfish, Lepomis-Gibbosus. Anim Behav 36:621–623.

Beckmann C. and P.A. Biro. 2013. On the Validity of a Single (Boldness) Assay in Personality Research. Ethology 119:937–947.

Beecham R.V., C.D. Minchew, and G.R. Parsons. 2007. Comparative Swimming Performance of Juvenile Pond-Cultured and Wild-Caught Channel Catfish. North Am J Fish Manag 27:729–734.

Bell A.M. 2007. Future directions in behavioural syndromes research. Proc R Soc B-Biological

Sci 274:755–761.

Bell A.M., S.J. Hankison, and K.L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis. Anim Behav 77:771–783.

Bell A.M. and A. Sih. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). Ecol Lett 10:828–834.

Bensky M.K., R. Paitz, L. Pereira, and A.M. Bell. 2017. Testing the predictions of coping styles theory in threespined sticklebacks. Behav Processes 136:1–10.

Benus R. and J. Koolhaas. 1987. Individual differences in behavioural reaction to a changing environment in mice and rats. Behaviour 100: 105-122

Benus R.F., B. Bohus, J.M. Koolhaas, and G.A. van Oortmerssen. 1991. Heritable variation for aggression as a reflection of individual coping strategies. Experientia 47:1008–1019.

Berthon K. 2015. How do native species respond to invaders? Mechanistic and trait-based perspectives. Biol Invasions 17:2199–2211.

Binder T.R., M.A. Nannini, D.H. Wahl, R. Arlinghaus, T. Klefoth, D.P. Philipp, and S.J. Cooke. 2012. Largemouth Bass Selected for Differential Vulnerability to Angling Exhibit Similar Routine Locomotory Activity in Experimental Ponds. Trans Am Fish Soc 141:1252–1259.

Binder T.R., A.D.M. Wilson, S.M. Wilson, C.D. Suski, J.-G.J. Godin, and S.J. Cooke. 2016. Is there a pace-of-life syndrome linking boldness and metabolic capacity for locomotion in bluegill sunfish? Anim Behav 121:175–183.

Biro P.A. and J.R. Post. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proc Natl Acad Sci U S A 105:2919–2922.

Biro P.A. and P. Sampson. 2015. Fishing directly selects on growth rate via behaviour:

implications of growth-selection that is independent of size. ProceedingsBiological Sci / R Soc 282.

Biro P.A. and J.A. Stamps. 2008. Are animal personality traits linked to life-history productivity? Trends Ecol Evol 23:361–368.

Biro P.A. and J.A. Stamps. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends Ecol Evol 25:653–659.

Biswas A.K. and T. Takeuchi. 2002. Effect of different photoperiod cycles on metabolic rate and energy loss of fed and unfed adult tilapia *Oreochromis niloticus*: Part II. Fish Sci 68:543–553.

Blake C.A. and C.R. Gabor. 2016. Exploratory behaviour and novel predator recognition: behavioural correlations across contexts. J Fish Biol 89:1178–1189.

Bonga S.E.W. 1997. The stress response in fish. Physiol Rev 77:591–625.

Boulton K., E. Couto, A.J. Grimmer, R.L. Earley, A.V.M. Canario, A.J. Wilson, and C.A. Walling. 2015. How integrated are behavioral and endocrine stress response traits? A repeated measures approach to testing the stress-coping style model. Ecol Evol 5:618–633.

Brett J. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J Fish Board Canada 21:1183-1226

Brown C., F. Jones, and V. Braithwaite. 2005. In situ examination of boldness-shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. Anim Behav 70:1003–1009.

Brown C. and K.N. Laland. 2002. Social learning of a novel avoidance task in the guppy: conformity and social release. Anim Behav 64:41–47.

Brydges N.M. and V.A. Braithwaite. 2009. Does environmental enrichment affect the behaviour of fish commonly used in laboratory work? Appl Anim Behav Sci 118:137–143.

Budaev S. V. 1997. Alternative styles in the European wrasse, Symphodus ocellatus: boldness-related schooling tendency. Environ Biol Fishes 49:71–78.

Budaev S. V. and A.Y. Zhuikov. 1998. Avoidance learning and "personality" in the guppy (*Poecilia reticulata*). J Comp Psychol 112:92–94.

Burns A.L.J., J.E. Herbert-Read, L.J. Morrell, and A.J.W. Ward. 2012. Consistency of Leadership in Shoals of Mosquitofish (*Gambusia holbrooki*) in Novel and in Familiar Environments. PLoS One 7:e36567–e36567.

Büttner K., K. Scheffler, I. Czycholl, and J. Krieter. 2015. Social network analysis - centrality parameters and individual network positions of agonistic behavior in pigs over three different age levels. Springerplus 4:185.

Cañon Jones H.A., L.A. Hansen, C. Noble, B. Damsgård, D.M. Broom, and G.P. Pearce. 2010. Social network analysis of behavioural interactions influencing fin damage development in Atlantic salmon (*Salmo salar*) during feed-restriction. Appl Anim Behav Sci 127:139–151.

Cañon Jones H.A., C. Noble, B. Damsgard, and G.P. Pearce. 2011. Social network analysis of the behavioural interactions that influence the development of fin damage in Atlantic salmon parr (*Salmo salar*) held at different stocking densities. Appl Anim Behav Sci 133:117–126.

Careau V., D. Thomas, M.M. Humphries, and D. Reale. 2008. Energy metabolism and animal personality. Oikos 117:641–653.

Castanheira M.F., M. Herrera, B. Costas, L.E.C. Conceicao, and C.I.M. Martins. 2013. Linking cortisol responsiveness and aggressive behaviour in gilthead seabream Sparus aurata: Indication of divergent coping styles. Appl Anim Behav Sci 143:75–81.

Castro-Santos T. 2011. Swimming and Other Activities | Applied Aspects of Fish Swimming

Performance. pp. 1652–1663 in Encycl Fish Physiol. Elsevier.

Charmantier A., A.J. Keyser, and D.E.. Promislow. 2007. First evidence for heritable variation in cooperative breeding behaviour. Proc R Soc B Biol Sci 274:1757–1761.

Childress M.J., K.A. Heldt, and S.D. Miller. 2015. Are juvenile Caribbean spiny lobsters (*Panulirus argus*) becoming less social? ICES J Mar Sci J du Cons 72:i170–i176.

Chivers D.P. and R.J.F. Smith. 1995. Free-living fathead minnows rapidly learn to recognize pike as predators. J Fish Biol 46:949–954.

Ciuti S., T.B. Muhly, D.G. Paton, A.D. McDevitt, M. Musiani, and M.S. Boyce. 2012. Human selection of elk behavioural traits in a landscape of fear. Proc R Soc London B Biol Sci 279:4407-4416.

Colgan P.W. and J.A. Brown. 1988. Dynamics of nest defense by male centrarchid fish. Behav Processes 17:17–26.

Coltman D.W., P. O’Donoghue, J.T. Jorgenson, J.T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. Nature 426:655–658.

Conover D.O., S.B. Munch, and S.A. Arnott. 2009. Reversal of evolutionary downsizing caused by selective harvest of large fish. Proc R Soc B-Biological Sci 276:2015–2020.

Conrad J.L., K.L. Weinersmith, T. Brodin, J.B. Saltz, and A. Sih. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. J Fish Biol 78:395–435.

Consuegra S., C.G. De Leaniz, A. Serdio, and E. Verspoor. 2005. Selective exploitation of early running fish may induce genetic and phenotypic changes in Atlantic salmon. J Fish Biol 67:129–145.

Cook K. V, C.M. O’Connor, K.M. Gilmour, and S.J. Cooke. 2011. The glucocorticoid stress response is repeatable between years in a wild teleost fish. J Comp Physiol A-Neuroethology Sens Neural Behav Physiol 197:1189–1196.

Cooke S.J., B.L. Barthel, C.D. Suski, M.J. Siepker, and D.P. Philipp. 2005. Influence of Circle Hook Size on Hooking Efficiency, Injury, and Size Selectivity of Bluegill with Comments on Circle Hook Conservation Benefits in Recreational Fisheries. North Am J Fish Manag 25:211–219.

Cooke S.J. and I.G. Cowx. 2004. The role of recreational fishing in global fish crises. Bioscience 54:857–859.

Cooke S.J., M.R. Donaldson, S.G. Hinch, G.T. Crossin, D.A. Patterson, K.C. Hanson, K.K. English, et al. 2009. Is fishing selective for physiological and energetic characteristics in migratory adult sockeye salmon? Evol Appl 2:299–311.

Cooke S.J., K.G. Ostrand, C.M. Bunt, J.F. Schreer, D.H. Wahl, and D.P. Philipp. 2003. Cardiovascular Responses of Largemouth Bass to Exhaustive Exercise and Brief Air Exposure over a Range of Water Temperatures. Trans Am Fish Soc 132:1154–1165.

Cooke S.J. and H.L. Schramm. 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. Fish Manag Ecol 14:73–79.

Cooke S.J., C.D. Suski, K.G. Ostrand, D.H. Wahl, and D.P. Philipp. 2007. Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. Physiol Biochem Zool 80:480–490.

Cote J., S. Fogarty, and A. Sih. 2012. Individual sociability and choosiness between shoal types. Anim Behav 83:1469–1476.

Croft D.P., S.K. Darden, and G.D. Ruxton. 2009a. Predation risk as a driving force for phenotypic assortment: a cross-population comparison. Proceedings Biol Sci 276:1899–904.

Croft D.P., R. James, A.J.W. Ward, M.S. Botham, D. Mawdsley, and J. Krause. 2005. Assortative interactions and social networks in fish. Oecologia 143:211–219.

Croft D.P., J. Krause, I.D. Couzin, and T.J. Pitcher. 2003. When fish shoals meet: outcomes for evolution and fisheries. Fish Fish 4:138–146.

Croft D.P., J. Krause, S.K. Darden, I.W. Ramnarine, J.J. Faria, and R. James. 2009b. Behavioural trait assortment in a social network: patterns and implications. Behav Ecol Sociobiol 63:1495–1503.

Croft D.P., J.R. Madden, D.W. Franks, and R. James. 2011. Hypothesis testing in animal social networks. Trends Ecol Evol 26:502–507.

Deary I.J. and P.G. Caryl. 1997. Neuroscience and human intelligence differences. Trends Neurosci 20:365–371.

DePasquale C., T. Wagner, G.A. Archard, B. Ferguson, and V.A. Braithwaite. 2014. Learning rate and temperament in a high predation risk environment. Oecologia 176:661–667.

Devine J.A., P.J. Wright, H.E. Pardoe, and M. Heino. 2012. Comparing rates of contemporary evolution in life-history traits for exploited fish stocks. Can J Fish Aquat Sci 69:1105–1120.

Diaz Pauli B. and A. Sih. 2017. Behavioural responses to human-induced change: Why fishing should not be ignored. Evol Appl 10:231–240.

DiBattista J.D., H. Anisman, M. Whitehead, and K.M. Gilmour. 2005. The effects of cortisol administration on social status and brain monoaminergic activity in rainbow trout *Oncorhynchus mykiss*. J Exp Biol 208:2707–2718.

Dingemanse N. and F. Van der Plas. 2009. Individual experience and evolutionary history of predation affect expression of heritable variation in fish personality and morphology. R ….

Dingemanse N.J., I. Barber, J. Wright, and J.E. Brommer. 2012. Quantitative genetics of behavioural reaction norms: genetic correlations between personality and behavioural plasticity vary across stickleback populations. J Evol Biol 25:485–496.

Dingemanse N.J., C. Both, P.J. Drent, and J.M. Tinbergen. 2004. Fitness consequences of avian personalities in a fluctuating environment. Proc R Soc B Biol Sci 271:847–852.

Dingemanse N.J. and M. Wolf. 2010. Recent models for adaptive personality differences: a review. Philos Trans R Soc B Biol Sci 365:3947–3958.

Dochtermann N.A. and D.A. Roff. 2010. Applying a quantitative genetics framework to behavioural syndrome research. Philos Trans R Soc B Biol Sci 365:4013–4020.

Dridi S. and L. Lehmann. 2016. Environmental complexity favors the evolution of learning. Behav Ecol 27:842–850.

Duckworth R. 2010. Evolution of personality: developmental constraints on behavioral flexibility. Auk.

Dugatkin L.A. and S.R. Ohlsen. 1990. Contrasting Asymmetries in Value Expectation and Resource Holding Power - Effects on Attack Behavior and Dominance in the Pumpkinseed Sunfish, Lepomis-Gibbosus. Anim Behav 39:802–804.

Dugatkin L.A. and D.S. Wilson. 1992. The Prerequisites for Strategic Behavior in Bluegill Sunfish, Lepomis-Macrochirus. Anim Behav 44:223–230.

Duncan J., R.J. Seitz, J. Kolodny, D. Bor, H. Herzog, A. Ahmed, F.N. Newell, et al. 2000. A neural basis for general intelligence. Science 289:457–60.

Dunlop E.S., A.M. Eikeset, and N.C. Stenseth. 2015. From genes to populations: how fisheries-induced evolution alters stock productivity. Ecol Appl 25:1860–1868.

Dyer J.R.G., D.P. Croft, L.J. Morrell, and J. Krause. 2009. Shoal composition determines foraging success in the guppy. Behav Ecol 20:165–171.

Edeline E., S.M. Carlson, L.C. Stige, I.J. Winfield, J.M. Fletcher, J.B. James, T.O. Haugen, et al. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. Proc Natl Acad Sci 104:15799–15804.

Eikeset A.M., A. Richter, E.S. Dunlop, U. Dieckmann, and N.C. Stenseth. 2013. Economic repercussions of fisheries-induced evolution. Proc Natl Acad Sci U S A 110:12259–12264.

Enberg K., C. Jørgensen, E.S. Dunlop, Ø. Varpe, D.S. Boukal, L. Baulier, S. Eliassen, et al. 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Mar Ecol 33:1–25.

Enberg K., C. Jorgensen, and M. Mangel. 2010. Fishing-induced evolution and changing reproductive ecology of fish: the evolution of steepness. Can J Fish Aquat Sci 67:1708–1719.

Evans D.O. Temperature Independence of the Annual Cycle of Standard Metabolism in the Pumpkinseed 113:494–512.

Feiner Z.S., S.C. Chong, C.T. Knight, T.E. Lauer, M. V. Thomas, J.T. Tyson, and T.O. Höök. 2015. Rapidly shifting maturation schedules following reduced commercial harvest in a freshwater fish. Evol Appl 8:724–737.

Franks V.R. and R.C. Marshall. 2013. Mechanisms and extent of information transfer in socially foraging guppies, *Poecilia reticulata*. Anim Behav 85:103–108.

Gaeta J.W., B. Beardmore, A.W. Latzka, B. Provencher, and S.R. Carpenter. 2013. Catch-and-Release Rates of Sport Fishes in Northern Wisconsin from an Angler Diary Survey. North Am J Fish Manag 33:606–614.

Geffroy B., N. Bru, S. Dossou-Gbete, C. Tentelier, and A. Bardonnet. 2014. The link between social network density and rank-order consistency of aggressiveness in juvenile eels. Behav

Ecol Sociobiol 68:1073–1083.

Graham M.H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84:2809–2815.

Gregory T.R. and C.M. Wood. 1998. Individual variation and interrelationships between swimming performance, growth rate, and feeding in juvenile rainbow trout (*Oncorhynchus mykiss*). Can J Fish Aquat Sci 55:1583–1590.

Griffin A.S., S. Tebbich, and T. Bugnyar. 2017. Animal cognition in a human-dominated world. Anim Cogn 20:1–6.

Groothuis T.G.G. and C. Carere. 2005. Avian personalities: characterization and epigenesis. Neurosci Biobehav Rev 29:137–150.

Guenther A. and V. Brust. 2017. Individual consistency in multiple cognitive performance: behavioural versus cognitive syndromes. Anim Behav 130:119–131.

Guenther A., V. Brust, M. Dersen, and F. Trillmich. 2014. Learning and personality types are related in cavies (Cavia aperea). J Comp Psychol 128:74–81.

Guillette L.M., A.R. Reddon, M. Hoeschele, and C.B. Sturdy. 2011. Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. Proc R Soc B Biol Sci 278:767–773.

Guillette L.M., A.R. Reddon, P.L. Hurd, and C.B. Sturdy. 2009. Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. Behav Processes 82:265–270.

Hair, J.F., Jr., W.C. Black, B.J. Babin, and R.E. Anderson. 2010. Multivariate data analysis. 7th ed. Prentice Hall, Upper Saddle River, NJ.

Harcourt J.L., T.Z. Ang, G. Sweetman, R.A. Johnstone, and A. Manica. 2009a. Social Feedback and the Emergence of Leaders and Followers. Curr Biol 19:248–252.

Harcourt J.L., G. Sweetman, R.A. Johnstone, and A. Manica. 2009b. Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks. Anim Behav 77:1501–1505.

Harkonen L., P. Hyvarinen, P.T. Niemela, and A. Vainikka. 2016. Behavioural variation in Eurasian perch populations with respect to relative catchability. Acta Ethol 19:21–31.

Harkonen L., P. Hyvarinen, J. Paappanen, and A. Vainikka. 2014. Explorative behavior increases vulnerability to angling in hatchery-reared brown trout (*Salmo trutta*). Can J Fish Aquat Sci 71:1900–1909.

Hau M., W. Goymann, D. Reale, S. Reader, D. Sol, P. McDougall, N. Dingemanse, et al. 2015. Endocrine mechanisms, behavioral phenotypes and plasticity: known relationships and open questions. Front Zool 12:S7.

Hedrick P.W. 2011. Rapid Decrease in Horn Size of Bighorn Sheep: Environmental Decline, Inbreeding Depression, or Evolutionary Response to Trophy Hunting? J Hered 102:770–781.

Hengeveld P.E. and M. Festa-Bianchet. 2011. Harvest regulations and artificial selection on horn size in male bighorn sheep. J Wildl Manage 75:189–197.

Herrera M., M. Filipa Castanheira, L.E.C. Conceicao, and C.I. Martins. 2014. Linking risk taking and the behavioral and metabolic responses to confinement stress in gilthead seabream *Sparus aurata*. Appl Anim Behav Sci 155:101–108.

Hessenauer J.-M., J. Vokoun, J. Davis, R. Jacobs, and E. O’Donnell. 2016. Loss of Naivety to Angling at Different Rates in Fished and Unfished Populations of Largemouth Bass. Trans Am Fish Soc 145:1068–1076.

Hessenauer J.M., J.C. Vokoun, C.D. Suski, J. Davis, R. Jacobs, and E. O’Donnell. 2015.

Differences in the Metabolic Rates of Exploited and Unexploited Fish Populations: A Signature of Recreational Fisheries Induced Evolution? PLoS One 10:e0128336–e0128336.

Hidalgo M., E.M. Olsen, J. Ohlberger, F. Saborido-Rey, H. Murua, C. Piñeiro, and N.C. Stenseth. 2014. Contrasting evolutionary demography induced by fishing: the role of adaptive phenotypic plasticity. Ecol Appl 24:1101–1114.

Hille S.M. and C.B. Cooper. 2015. Elevational trends in life histories: revising the pace-of-life framework. Biol Rev 90:204–213.

Hollins J., D. Thambithurai, B. Koeck, A. Crespel, D.M. Bailey, S.J. Cooke, J. Lindström, et al. 2018. A physiological perspective on fisheries-induced evolution. Evol Appl 11:561-576.

Houston A.I. 2010. Evolutionary models of metabolism, behaviour and personality. Philos Trans R Soc B-Biological Sci 365:3969–3975.

Houston A.I. and J.M. McNamara. 1988. Fighting for food: a dynamic version of the Hawk-Dove game. Evol Ecol 2:51–64.

Howard J.W. 1974. Dominance and Relation to Coloration in Green Sunfish, *Lepomis cyanellus*. Behav Biol 12:559–565.

Jacoby D.M.P., L.N. Fear, D.W. Sims, and D.P. Croft. 2014. Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. Behav Ecol Sociobiol 68:1995–2003.

Jeffrey J.D., A.J. Esbaugh, M.M. Vijayan, and K.M. Gilmour. 2012. Modulation of hypothalamic-pituitary-interrenal axis function by social status in rainbow trout. Gen Comp Endocrinol 176:201–210.

Jolles J.W., A. Fleetwood-Wilson, S. Nakayama, M.C. Stumpe, R.A. Johnstone, and A. Manica. 2014. The role of previous social experience on risk-taking and leadership in three-spined sticklebacks. Behav Ecol 25:1395–1401.

Jones E.A., K.S. Lucey, and D.J. Ellerby. 2007. Efficiency of labriform swimming in the bluegill sunfish (*Lepomis macrochirus*). J Exp Biol 210:3422–3429.

Jorgensen C., K. Enberg, E.S. Dunlop, R. Arlinghaus, D.S. Boukal, K. Brander, B. Ernande, et al. 2007. Ecology - Managing evolving fish stocks. Science (80-) 318:1247–1248.

Kaiser H.F. 1960. The Application of Electronic-Computers to Factor-Analysis. Educ Psychol Meas 20:141–151.

Kekalainen J., T. Podgorniak, T. Puolakka, P. Hyvarinen, and A. Vainikka. 2014. Individually assessed boldness predicts Perca fluviatilis behaviour in shoals, but is not associated with the capture order or angling method. J Fish Biol 85:1603–1616.

Keller B.A., J.-S. Finger, S.H. Gruber, D.C. Abel, and T.L. Guttridge. 2017. The effects of familiarity on the social interactions of juvenile lemon sharks, Negaprion brevirostris. J Exp Mar Bio Ecol 489:24–31.

Kendall N.W. and T.P. Quinn. 2011. Length and Age Trends of Chinook Salmon in the Nushagak River, Alaska, Related to Commercial and Recreational Fishery Selection and Exploitation. Trans Am Fish Soc 140:611–622.

Kent R., R. Holzman, and A. Genin. 2006. Preliminary evidence on group-size dependent feeding success in the damselfish Dascyllus marginatus. Mar Ecol Prog Ser 323:299–303.

Kern E.M.A., D. Robinson, E. Gass, J. Godwin, and R.B. Langerhans. 2016. Correlated evolution of personality, morphology and performance. Anim Behav 117:79–86.

Ketterson E.D. and V. Nolan, Jr. 1999. Adaptation, Exaptation, and Constraint: A Hormonal Perspective. Am Nat 154:S4–S25.

Killen S.S., S. Marras, L. Nadler, and P. Domenici. 2017. The role of physiological traits in assortment among and within fish shoals. Philos Trans R Soc London B Biol Sci 372.

Killen S.S., S. Marras, M.R. Ryan, P. Domenici, and D.J. McKenzie. 2012. A relationship between metabolic rate and risk-taking behaviour is revealed during hypoxia in juvenile European sea bass. Funct Ecol 26:134–143.

Killen S.S., M.D. Mitchell, J.L. Rummer, D.P. Chivers, M.C.O. Ferrari, M.G. Meekan, and M.I. McCormick. 2014. Aerobic scope predicts dominance during early life in a tropical damselfish. Funct Ecol 28:1367–1376.

Killen S.S., J.J.H. Nati, and C.D. Suski. 2015a. Vulnerability of individual fish to capture by trawling is influenced by capacity for anaerobic metabolism. ProceedingsBiological Sci / R Soc 282.

Killen S.S., D. Reid, S. Marras, and P. Domenici. 2015b. The interplay between aerobic metabolism and antipredator performance: vigilance is related to recovery rate after exercise. Front Physiol 6:111.

King G.D., J.M. Chapman, J.D. Midwood, S.J. Cooke, and C.D. Suski. 2016. Watershed-Scale Land Use Activities Influence the Physiological Condition of Stream Fish. Physiol Biochem Zool 89:10–25.

Klefoth T., T. Pieterek, and R. Arlinghaus. 2013. Impacts of domestication on angling vulnerability of common carp, Cyprinus carpio: the role of learning, foraging behaviour and food preferences. Fish Manag Ecol 20:174–186.

Klefoth T., C. Skov, A. Kuparinen, and R. Arlinghaus. 2017. Towards a mechanistic understanding of vulnerability to hook-and-line fishing: boldness as the basic target of angling-induced selection. Evol Appl.

Kokkonen E., A. Vainikka, and O. Heikinheimo. 2015. Probabilistic maturation reaction norm trends reveal decreased size and age at maturation in an intensively harvested stock of pikeperch Sander lucioperca. Fish Res 167:1–12.

Koolhaas J.M., S.F. de Boer, B. Buwalda, and K. van Reenen. 2007. Individual variation in coping with stress: A multidimensional approach of ultimate and proximate mechanisms. Brain Behav Evol 70:218–226.

Koolhaas J.M., S.M. Korte, S.F. De Boer, B.J. Van Der Vegt, C.G. Van Reenen, H. Hopster, I.C. De Jong, et al. 1999. Coping styles in animals: current status in behavior and stress-physiology. Neurosci Biobehav Rev 23:925–935.

Kortet R., A. Vainikka, M. Janhunen, J. Piironen, and P. Hyvarinen. 2014. Behavioral variation shows heritability in juvenile brown trout Salmo trutta. Behav Ecol Sociobiol 68:927–934.

Kralj-Fiser S., B.M. Weiss, and K. Kotrschal. 2010. Behavioural and physiological correlates of personality in greylag geese (*Anser anser*). J Ethol 28:363–370.

Krause J., D. Croft, and R. James. 2003. Social networks in fish. J Fish Biol 63:235.

Kuparinen A. and M. Festa-Bianchet. 2016. Harvest-induced evolution: insights from aquatic and terrestrial systems. Philos Trans R Soc B Biol Sci 372.

Kuparinen A. and J.A. Hutchings. 2012. Consequences of fisheries-induced evolution for population productivity and recovery potential. Proc R Soc B-Biological Sci 279:2571–2579.

Kuparinen A. and J. Merila. 2007. Detecting and managing fisheries-induced evolution. Trends Ecol Evol 22:652–659.

Lacasse J. and N. Aubin-Horth. 2014. Population-dependent conflict between individual sociability and aggressiveness. Anim Behav 87:53–57.

Laskowski K.L. and A.M. Bell. 2014. Strong personalities, not social niches, drive individual differences in social behaviours in sticklebacks. Anim Behav 90:287–295.

Lee J.S.F. and B.A. Berejikian. 2008. Effects of the rearing environment on average behaviour and behavioural variation in steelhead. J Fish Biol 72:1736–1749.

Lennox R.J., J. Alós, R. Arlinghaus, A. Horodysky, T. Klefoth, C.T. Monk, and S.J. Cooke. 2017. What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. Fish Fish 18: 986-1010.

Lennox R.J., O.H. Diserud, S.J. Cooke, E.B. Thorstad, F.G. Whoriskey, Ø. Solem, T.B. Havn, et al. 2016. Influence of gear switching on recapture of Atlantic salmon (*Salmo salar*) in catch-and-release fisheries. Ecol Freshw Fish 25:422–428.

Lorenz O.T., M.T. O’Connell, and P.J. Schofield. 2011. Aggressive interactions between the invasive Rio Grande cichlid (*Herichthys cyanoguttatus*) and native bluegill (*Lepomis macrochirus*), with notes on redspotted sunfish (*Lepomis miniatus*). J Ethol 29:39–46.

Luttbeg B. and A. Sih. 2010. Risk, resources and state-dependent adaptive behavioural syndromes. Philos Trans R Soc Lond B Biol Sci 365:3977–90.

Magnhagen C. 2012. Personalities in a crowd: What shapes the behaviour of Eurasian perch and other shoaling fishes? Curr Zool 58:35–44.

Manassa R.P. and M.I. McCormick. 2012. Social learning and acquired recognition of a predator by a marine fish. Anim Cogn 15:559–565.

Manassa R.P. and M.I. McCormick. 2013. Social learning improves survivorship at a life-history transition. Oecologia 171:845–852.

Matthias B.G., M.S. Allen, R.N.M. Ahrens, T.D. Beard Jr., and J.A. Kerns. 2014. Hide and Seek: Interplay of Fish and Anglers Influences Spatial Fisheries Management. Fisheries 39:261–269.

Matzel L.D. and S. Kolata. 2010. Selective attention, working memory, and animal intelligence. Neurosci Biobehav Rev 34:23–30.

Mazue G.P.F., F.-X. Dechaume-Moncharmont, and J.-G.J. Godin. 2015. Boldness-exploration behavioral syndrome: interfamily variability and repeatability of personality traits in the young of the convict cichlid (*Amatitlania siquia*). Behav Ecol 26:900–908.

McCartt A.L., W.E. Lynch Jr., and D.L. Johnson. 1997. How light, a predator, and experience influence bluegill use of shade and schooling. Environ Biol Fishes 49:79–87.

McConnachie S.H., C.M. O'Connor, K.M. Gilmour, G.K. Iwama, and S.J. Cooke. 2012. Supraphysiological Cortisol Elevation Alters the Response of Wild Bluegill Sunfish to Subsequent Stressors. J Exp Zool Part A Ecol Genet Physiol 317:321–332.

McGhee K.E. and J. Travis. 2010. Repeatable behavioural type and stable dominance rank in the bluefin killifish. Anim Behav 79:497–507.

Mee J.A., C.J. Brauner, and E.B. Taylor. 2011. Repeat Swimming Performance and Its Implications for Inferring the Relative Fitness of Asexual Hybrid Dace (Pisces: *Phoxinus*) and Their Sexually Reproducing Parental Species. Physiol Biochem Zool 84:306–315.

Mesquita F.O., I.F.A. Torres, and R.K. Luz. 2016. Behaviour of proactive and reactive tilapia Oreochromis niloticus in a T-maze. Appl Anim Behav Sci 181:200–204.

Metcalfe N.B., A.C. Taylor, and J.E. Thorpe. 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. Anim Behav 49:431–436.

Metcalfe N.B., T.E. Van Leeuwen, and S.S. Killen. 2016. Does individual variation in metabolic phenotype predict fish behaviour and performance? J Fish Biol 88:298–321.

Michelangeli M., B.B.M. Wong, and D.G. Chapple. 2016. It's a trap: sampling bias due to animal personality is not always inevitable. Behav Ecol 27:62–67.

Milligan C.L., G.B. Hooke, C. Johnson, L. Boesgaard, M.E. Nielsen, P. Rosenkilde, R.G. Boutilier, et al. 2000. Sustained swimming at low velocity following a bout of exhaustive exercise enhances metabolic recovery in rainbow trout. J Exp Biol 203:921–926.

Miranda A.C., H. Schielzeth, T. Sonntag, and J. Partecke. 2013. Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? Glob Chang Biol 19:2634–2644.

Mittelbach G.G., N.G. Ballew, and M.K. Kjelvik. 2014. Fish behavioral types and their ecological consequences. Can J Fish Aquat Sci 71:927–944.

Modlmeier A.P., C.N. Keiser, J. V Watters, A. Sih, and J.N. Pruitt. 2014. The keystone individual concept: an ecological and evolutionary overview. Anim Behav 89:53–62.

Monk C.T. and R. Arlinghaus. 2018. Eurasian perch, *Perca fluviatilis*, spatial behaviour determines vulnerability independent of angler skill in a whole-lake reality mining experiment. Can J Fish Aquat Sci 75:417–428.

Mooney H.A. and E.E. Cleland. 2001. The evolutionary impact of invasive species. Proc Natl Acad Sci U S A 98:5446–51.

Morin C., M.A. de Souza Silva, C.P. Müller, P. Hardigan, and R.E. Spieler. 2013. Active avoidance learning in zebrafish (*Danio rerio*) - The role of sensory modality and inter-stimulus interval. Behav Brain Res 248:141–143.

Morrell L.J., D.P. Croft, J.R.G. Dyer, B.B. Chapman, J.L. Kelley, K.N. Laland, and J. Krause. 2008. Association patterns and foraging behaviour in natural and artificial guppy shoals. Anim Behav 76:855–864.

Mota Silva P.I., C.I.M. Martins, S. Engrola, G. Marino, O. Overli, and L.E.C. Conceicao. 2010. Individual differences in cortisol levels and behaviour of Senegalese sole (*Solea* *senegalensis*) juveniles: Evidence for coping styles. Appl Anim Behav Sci 124:75–81.

Mourier J., C. Brown, and S. Planes. 2017. Learning and robustness to catch-and-release fishing in a shark social network. Biol Lett 13:20160824.

Myles-Gonzalez E., G. Burness, S. Yavno, A. Rooke, and M.G. Fox. 2015. To boldly go where no goby has gone before: boldness, dispersal tendency, and metabolism at the invasion front. Behav Ecol 26:1083–1090.

Nannini M.A., D.H. Wahl, D.P. Philipp, and S.J. Cooke. 2011. The influence of selection for vulnerability to angling on foraging ecology in largemouth bass Micropterus salmoides. J Fish Biol 79:1017–1028.

Näslund J. and J.I. Johnsson. 2016. State-dependent behavior and alternative behavioral strategies in brown trout (*Salmo trutta* L.) fry. Behav Ecol Sociobiol 70:2111–2125.

Nelson J.A. and D. Chabot. 2011. General Energy Metabolism. pp. 1566-1572 in Farrell eds. Encycl Fish Physiol from Genome to Environment. Academic Press, Cambridge, MA.

Norin T. and T.D. Clark. 2016. Measurement and relevance of maximum metabolic rate in fishes. J Fish Biol 88:122–151.

Nussle S., C.N. Bornand, and C. Wedekind. 2009. Fishery-induced selection on an Alpine whitefish: quantifying genetic and environmental effects on individual growth rate. Evol Appl 2:200–208.

Olsen E.M., M.R. Heupel, C.A. Simpfendorfer, and E. Moland. 2012. Harvest selection on Atlantic cod behavioral traits: implications for spatial management. Ecol Evol 2:1549–1562.

Olsen E.M. and E. Moland. 2011. Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. Evol Ecol 25:695–710.

Öst M., M.W. Seltmann, and K. Jaatinen. 2015. Personality, body condition and breeding experience drive sociality in a facultatively social bird. Anim Behav 100:166–173.

Overli O., C.A. Harris, and S. Winberg. 1999. Short-term effects of fights for social dominance and the establishment of dominant-subordinate relationships on brain monoamines and cortisol in rainbow trout. Brain Behav Evol 54:263–275.

Overli O., W.J. Korzan, E. Hoglund, S. Winberg, H. Bollig, M. Watt, G.L. Forster, et al. 2004. Stress coping style predicts aggression and social dominance in rainbow trout. Horm Behav 45:235–241.

Overli O., S. Winberg, and T.G. Pottinger. 2005. Behavioral and neuroendocrine correlates of selection for stress responsiveness in rainbow trout - a review. Integr Comp Biol 45:463–474.

Palkovacs E.P., M.T. Kinnison, C. Correa, C.M. Dalton, and A.P. Hendry. 2012. Fates beyond traits: ecological consequences of human-induced trait change. Evol Appl 5:183–191.

Pang X., Z.-D. Cao, J.-L. Peng, and S.-J. Fu. 2010. The effects of feeding on the swimming performance and metabolic response of juvenile southern catfish, Silurus meridionalis, acclimated at different temperatures. Comp Biochem Physiol Part A Mol Integr Physiol 155:253–258.

Pauli B.D., M. Wiech, M. Heino, and A.C. Utne-Palm. 2015. Opposite selection on behavioural types by active and passive fishing gears in a simulated guppy *Poecilia reticulata* fishery. J Fish Biol 86:1030–1045.

Peterson N.R., J.A. VanDeHey, and D.W. Willis. 2010. Size and Age at Maturity of Bluegill (*Lepomis macrochirus*) in Southeastern South Dakota Impoundments. J Freshw Ecol 25:303–312.

Philipp D.P., J.E. Claussen, T.W. Kassler, and J.M. Epifanio. 2002. Mixing, stocks of largemouth bass reduces fitness through outbreeding depression. Am Fish Soc Symp 31:349–363.

Philipp D.P., S.J. Cooke, J.E. Claussen, J.B. Koppelman, C.D. Suski, and D.P. Burkett. 2009. Selection for Vulnerability to Angling in Largemouth Bass. Trans Am Fish Soc 138:189–199.

Pintor L.M., K.E. McGhee, D.P. Roche, and A.M. Bell. 2014. Individual variation in foraging behavior reveals a trade-off between flexibility and performance of a top predator. Behav Ecol Sociobiol 68:1711–1722.

Pitcher T.J., A.E. Magurran, and I.J. Winfield. 1982. Fish in larger shoals find food faster. Behav Ecol Sociobiol 10:149–151.

Plaut I. 2001. Critical swimming speed: its ecological relevance. Comp Biochem Physiol Part A Mol Integr Physiol 131:41–50.

Post J.R. 2013. Resilient recreational fisheries or prone to collapse? A decade of research on the science and management of recreational fisheries. Fish Manag Ecol 20:99–110.

Post J.R., M. Sullivan, S. Cox, N.P. Lester, C.J. Walters, E.A. Parkinson, A.J. Paul, et al. 2002. Canada’s recreational fisheries: The invisible collapse? Fisheries 27:6–17.

Prenosil E., K. Koupal, J. Grauf, C. Schoenebeck, and W.W. Hoback. 2016. Swimming and jumping ability of 10 Great Plains fish species. J Freshw Ecol 31:123–130.

Pruitt J.N. and S.E. Riechert. 2011. How within-group behavioural variation and task efficiency enhance fitness in a social group. Proc R Soc B Biol Sci 278:1209–1215.

Reale D., N.J. Dingemanse, A.J.N. Kazem, and J. Wright. 2010a. Evolutionary and ecological approaches to the study of personality. Philos Trans R Soc B Biol Sci 365:3937–3946.

Reale D., D. Garant, M.M. Humphries, P. Bergeron, V. Careau, and P.O. Montiglio. 2010b.

Personality and the emergence of the pace-of-life syndrome concept at the population level. Philos Trans R Soc B Biol Sci 365:4051–4063.

Reale D., S.M. Reader, D. Sol, P.T. McDougall, and N.J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. Biol Rev 82:291–318.

Redpath T.D., S.J. Cooke, R. Arlinghaus, D.H. Wahl, and D.P. Philipp. 2009. Life-history traits and energetic status in relation to vulnerability to angling in an experimentally selected teleost fish. Evol Appl 2:312–323.

Redpath T.D., S.J. Cooke, C.D. Suski, R. Arlinghaus, P. Couture, D.H. Wahl, and D.P. Philipp. 2010. The metabolic and biochemical basis of vulnerability to recreational angling after three generations of angling-induced selection in a teleost fish. Can J Fish Aquat Sci 67:1983–1992.

Reidy S.P., S.R. Kerr, and J.A. Nelson. 2000. Aerobic and anaerobic swimming performance of individual Atlantic cod. J Exp Biol 203:347–57.

Riesch R., T. Easter, C.A. Layman, and R.B. Langerhans. 2015. Rapid human-induced divergence of life-history strategies in Bahamian livebearing fishes (family Poeciliidae). J Anim Ecol 84:1732–1743.

Rodgers C.M.C., B.D. Neff, and R. Knapp. 2013. Androgen-mediated nurturing and aggressive behaviors during paternal care in bluegill sunfish (Lepomis macrochirus). Horm Behav 63:454–461.

Rodgers G.G., P. Tenzing, and T.D. Clark. 2016. Experimental methods in aquatic respirometry: the importance of mixing devices and accounting for background respiration. J Fish Biol 88:65–80.

Rouleau S., H. Glémet, and P. Magnan. 2010. Effects of morphology on swimming performance in wild and laboratory crosses of brook trout ecotypes. Funct Ecol 24:310–321.

Ruiz-Gomez M., F.A. Huntingford, O. Overli, P.-O. Thornqvist, and E. Hoglund. 2011. Response to environmental change in rainbow trout selected for divergent stress coping styles. Physiol Behav 102:317–322.

Ruiz-Gomez M. de L., S. Kittilsen, E. Hoglund, F.A. Huntingford, C. Sorensen, T.G. Pottinger, M. Bakken, et al. 2008. Behavioral plasticity in rainbow trout (Oncorhynchus mykiss) with divergent coping styles: When doves become hawks. Horm Behav 54:534–538.

Sarrazin F. and J. Lecomte. 2016. Evolution in the Anthropocene. Science 351:922–3.

Saura M., P. Moran, S. Brotherstone, A. Caballero, J. Alvarez, and B. Villanueva. 2010. Predictions of response to selection caused by angling in a wild population of Atlantic salmon (*Salmo salar*). Freshw Biol 55:923–930.

Savino J.F. and R.A. Stein. 1982. Predator-Prey Interaction between Largemouth Bass and Bluegills as Influenced by Simulated, Submersed Vegetation. Trans Am Fish Soc 111:255–266.

Scheiner S.M. and J. Gurevitch. 2001. Design and analysis of ecological experiments. Oxford University Press, Oxford, UK.

Seebacher F. and J. Krause. 2017. Physiological mechanisms underlying animal social behaviour. Philos Trans R Soc B Biol Sci 372:20160231.

Seebacher F., A.J.W. Ward, and R.S. Wilson. 2013. Increased aggression during pregnancy comes at a higher metabolic cost. J Exp Biol 216:771–776.

Shaw R.C., N.J. Boogert, N.S. Clayton, and K.C. Burns. 2015. Wild psychometrics: evidence for “general” cognitive performance in wild New Zealand robins, *Petroica longipe*s. Anim Behav 109:101–111.

Shohet A.J. and P.J. Watt. 2009. Female guppies *Poecilia reticulata* prefer males that can learn fast. J Fish Biol 75:1323–1330.

Sih A. 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. Anim Behav 85:1077–1088.

Sih A., A. Bell, and J.C. Johnson. 2004a. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol 19:372–378.

Sih A., A.M. Bell, J.C. Johnson, and R.E. Ziemba. 2004b. Behavioral Syndromes: An Integrative Overview. Q Rev Biol 79:241–277.

Sih A. and M. Del Giudice. 2012. Linking behavioural syndromes and cognition: a behavioural ecology perspective. Philos Trans R Soc Lond B Biol Sci 367:2762–72.

Sih A., M.C.O. Ferrari, and D.J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evol Appl 4:367–387.

Sih A., S.F. Hanser, and K.A. McHugh. 2009. Social network theory: new insights and issues for behavioral ecologists. Behav Ecol Sociobiol 63:975–988.

Sih A., L.B. Kats, and E.F. Maurer. 2003. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. Anim Behav 65:29–44.

Sih A., K.J. Mathot, M. Moirón, P.-O. Montiglio, M. Wolf, and N.J. Dingemanse. 2015. Animal personality and state–behaviour feedbacks: a review and guide for empiricists. Trends Ecol Evol 30:50–60.

Sih A., P.C. Trimmer, and S.M. Ehlman. 2016. A conceptual framework for understanding behavioral responses to HIREC. Curr Opin Behav Sci 12:109–114.

Silk M.J., A.L. Jackson, D.P. Croft, K. Colhoun, and S. Bearhop. 2015. The consequences of unidentifiable individuals for the analysis of an animal social network. Anim Behav 104:1–

11.

Sink T.D., R.T. Lochmann, and K.A. Fecteau. 2008. Validation, use, and disadvantages of enzyme-linked immunosorbent assay kits for detection of cortisol in channel catfish, largemouth bass, red pacu, and golden shiners. Fish Physiol Biochem 34:95–101.

Smith C., A. Philips, and M. Reichard. 2015. Cognitive ability is heritable and predicts the success of an alternative mating tactic. Proc R Soc B Biol Sci 282:20151046.

Smith T.B., B. Mila, G.F. Grether, H. Slabbekoorn, I. Sepil, W. Buermann, S. Saatchi, et al. 2008. Evolutionary consequences of human disturbance in a rainforest bird species from Central Africa. Mol Ecol 17:58–71.

Sol D., O. Lapiedra, and C. González-Lagos. 2013. Behavioural adjustments for a life in the city. Anim Behav 85:1101–1112.

Stamps J.A. 2007. Growth-mortality tradeoffs and “personality traits” in animals. Ecol Lett 10:355–363.

Stamps J.A. 2016. Individual differences in behavioural plasticities. Biol Rev 91:534–567.

Sternberg R.J. 2000. Cognition. The holey grail of general intelligence. Science 289:399–401.

Stoner A.W. and M.L. Ottmar. 2004. Fish density and size alter Pacific halibut feeding: implications for stock assessment. J Fish Biol 64:1712–1724.

Suski C.D., S.J. Cooke, and B.L. Tufts. 2007. Failure of low-velocity swimming to enhance recovery from exhaustive exercise in largemouth bass (*Micropterus salmoides*). Physiol Biochem Zool 80:78–87.

Suski C.D. and D.P. Philipp. 2004. Factors affecting the vulnerability to angling of nesting male largemouth and smallmouth bass. Trans Am Fish Soc 133:1100–1106.

Sutter D.A.H., C.D. Suski, D.P. Philipp, T. Klefoth, D.H. Wahl, P. Kersten, S.J. Cooke, et al.

2012. Recreational fishing selectively captures individuals with the highest fitness potential. Proc Natl Acad Sci U S A 109:20960–20965.

Templeton A.R., R.J. Robertson, J. Brisson, and J. Strasburg. 2001. Disrupting evolutionary processes: The effect of habitat fragmentation on collared lizards in the Missouri Ozarks. Proc Natl Acad Sci U S A 98:5426–5432.

Tierney K.B. 2011. Swimming performance assessment in fishes. J Vis Exp 51: 2572.

Trapp R.M. and A.M. Bell. 2017. The Effect of Familiarity with Demonstrators on Social Learning in Three-Spined Sticklebacks (*Gasterosteus aculeatus*). Ethology 123:213–220.

Twardek W.M., C.K. Elvidge, A.D.M. Wilson, D.A. Algera, A.J. Zolderdo, S.C. Lougheed, and S.J. Cooke. 2017. Do protected areas mitigate the effects of fisheries-induced evolution on parental care behaviour of a teleost fish? Aquat Conserv Mar Freshw Ecosyst 27:789–796.

Udino E., M. Perez, C. Carere, and P. d'Ettorre. 2016. Active explorers show low learning performance in a social insect. Curr Zool 63:zow101.

Uusi-Heikkila S., C. Wolter, T. Klefoth, and R. Arlinghaus. 2008. A behavioral perspective on fishing-induced evolution. Trends Ecol Evol 23:419–421.

Uusi-Heikkilae S., A.R. Whiteley, A. Kuparinen, S. Matsumura, P.A. Venturelli, C. Wolter, J. Slate, et al. 2015. The evolutionary legacy of size-selective harvesting extends from genes to populations. Evol Appl 8:597–620.

Vainikka A., I. Tammela, and P. Hyvarinen. 2016. Does boldness explain vulnerability to angling in Eurasian perch Perca fluviatilis? Curr Zool 62:109–115.

van Oers K., P.J. Drent, P. de Goede, and A.J. van Noordwijk. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. Proc R Soc B Biol Sci 271:65–73.

Villegas-Rios D., J. Alos, M. Palmer, S.K. Lowerre-Barbieri, R. Banon, A. Alonso-Fernandez, and F. Saborido-Rey. 2014. Life-history and activity shape catchability in a sedentary fish. Mar Ecol Prog Ser 515:239–250.

Vindas M.A., I.B. Johansen, S. Vela-Avitua, K.S. Norstrud, M. Aalgaard, B.O. Braastad, E. Hoglund, et al. 2014. Frustrative reward omission increases aggressive behaviour of inferior fighters. Proc R Soc B-Biological Sci 281:20140300.

Vital C. and E. Martins. 2013. Socially-central zebrafish influence group behavior more than those on the social periphery. PLoS One e55503.

Vital C. and E.P. Martins. 2011. Strain Differences in Zebrafish (*Danio rerio*) Social Roles and Their Impact on Group Task Performance. J Comp Psychol 125:278–285.

Ward A.J.W., P. Thomas, P.J.B. Hart, and J. Krause. 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). Behav Ecol Sociobiol 55:561–568.

Ward A.J.W., M.M. Webster, and P.J.B. Hart. 2006. Intraspecific food competition in fishes. Fish Fish 7:231–261.

Ward T.D., D.A. Algera, A.J. Gallagher, E. Hawkins, A. Horodysky, C. Jørgensen, S.S. Killen, et al. 2016. Understanding the individual to implement the ecosystem approach to fisheries management. Conserv Physiol 4:cow005.

Wark A.R., A.K. Greenwood, E.M. Taylor, K. Yoshida, and C.L. Peichel. 2011. Heritable Differences in Schooling Behavior among Threespine Stickleback Populations Revealed by a Novel Assay. PLoS One 6:e18316.

Webster M.M. and P.J.B. Hart. 2006. Subhabitat selection by foraging threespine stickleback (*Gasterosteus aculeatus*): previous experience and social conformity. Behav Ecol Sociobiol 60:77–86.

Webster M.M. and P.J.B. Hart. 2007. Prior association reduces kleptoparasitic prey competition in shoals of three-spined sticklebacks. Anim Behav 74:253–258.

Webster M.M., A.J.W. Ward, and P.J.B. Hart. 2009. Individual boldness affects interspecific interactions in sticklebacks. Behav Ecol Sociobiol 63:511–520.

Weeks J.W., S.L. Crowell-Davis, A.B. Caudle, and G.L. Heusner. 2000. Aggression and social spacing in light horse (*Equus caballus*) mares and foals. Appl Anim Behav Sci 68:319–337.

Williams A.E., K.E.L. Worsley-Tonks, and V.O. Ezenwa. 2017. Drivers and consequences of variation in individual social connectivity. Anim Behav 133:1–9.

Wilson A.D.M., T.R. Binder, K.P. McGrath, S.J. Cooke, and J.-G.J. Godin. 2011. Capture technique and fish personality: angling targets timid bluegill sunfish, *Lepomis macrochirus*. Can J Fish Aquat Sci 68:749–757.

Wilson A.D.M., J.W. Brownscombe, B. Sullivan, S. Jain-Schlaepfer, and S.J. Cooke. 2015. Does Angling Technique Selectively Target Fishes Based on Their Behavioural Type? PLoS One 10:1–14.

Wilson A.D.M., D.P. Croft, and J. Krause. 2014. Social networks in elasmobranchs and teleost fishes. Fish Fish 15:676–689.

Wilson A.D.M. and J.-G.J. Godin. 2009. Boldness and behavioral syndromes in the bluegill sunfish, Lepomis macrochirus. Behav Ecol 20:231–237.

Winberg S., G.E. Nilsson, and K.H. Olsen. 1991. Social Rank and Brain Levels of Monoamines and Monoamine Metabolites in Arctic-Charr, *Salvelinus alpinus* (L). J Comp Physiol A-Sensory Neural Behav Physiol 168:241–246.

Wolf M. and F.J. Weissing. 2010. An explanatory framework for adaptive personality differences. Philos Trans R Soc B Biol Sci 365:3959–3968.

Wolf M. and F.J. Weissing. 2012. Animal personalities: consequences for ecology and evolution. Trends Ecol Evol 27:452–461.

Young R.G. and J.W. Hayes. 2004. Angling pressure and trout catchability: Behavioral observations of brown trout in two New Zealand backcountry rivers. North Am J Fish Manag 24:1203–1213.

Yue S., R.. Moccia, and I.J.. Duncan. 2004. Investigating fear in domestic rainbow trout, Oncorhynchus mykiss, using an avoidance learning task. Appl Anim Behav Sci 87:343–354.

Zuur A.F., E.N. Ieno, and C.S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14.