

FITNESS TRADEOFFS CAN CONTRIBUTE TO THE MAINTENANCE OF VARIATION IN PERSONALITY TRAITS IN
LARGEMOUTH BASS (*MICROPTERUS SALMOIDES*)

By

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ABSTRACT

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Studies examining selection and fitness differences between phenotypes are essential for our understanding of evolutionary processes. Although many studies have examined fitness effects of morphological and life-history traits, studies of selection on personality traits are much less common. This has been due, in part, to the fact that personality is not easily characterized into phenotypes. In addition, personality has historically been viewed as highly plastic and therefore less likely to be under the direct influence of selection. However, recent studies suggest that personality is often consistent over biologically meaningful time periods. If personality traits are consistent across development, they have the potential to affect fitness through impacts on survival at the juvenile stage and reproductive success at the adult stage. Thus, personality traits may have a range of effects on fitness, some of which could result in tradeoffs. Further, personality likely determines an individual's vulnerability to human capture and harvest in a variety of contexts, which means human actions could alter the effects of personality on fitness. For example, a fish's personality may affect its vulnerability to capture by recreational angling, which could alter the relationships between personality and survival and reproductive success. Moreover, if personality traits are heritable, angling could result in the evolution of personality traits in angled populations, which could have ecological consequences. Consequently, studies to explain how personality is generated and maintained by evolution are greatly needed.

Here, I address the fitness consequences of multiple personality traits across life stages and their heritability in largemouth bass (*Micropterus salmoides*). Further, I address how angling could alter these fitness effects. To quantify personality and investigate its consistency, bass were observed in the laboratory under experimental behavioral contexts at age-1, age-3, age-4, and age-5. Bass behavior was

observed in four contexts: 1) a novel environment, 2) a familiar and safe environment, 3) a social environment (mirror-test), and 4) an environment in which both food and a predator were present. To quantify the fitness effects across life stages of the personality traits uncovered in the experimental behavioral assays, experiments were conducted in outdoor ponds on juvenile survivorship and on adult reproductive success. Further, bass were subjected to one of three angling contexts: 1) a mesocosm context, 2) an outdoor pond context, and 3) an outdoor pond context with casts made directly onto bass nests. Lastly, personality was quantified in two generations of bass to assess personality heritability.

The results showed that bass have context-specific personality traits that underlie the expression of behavior in each of the four contexts investigated and that the context-specific traits are sub-modules of a context-general trait, which was identified as boldness. The boldness trait, as well as some of the context-specific traits, were consistent across multiple years and developmental stages. Bolder juvenile bass had significantly lower survivorship than their conspecifics while adult bass that were larger and bolder had significantly higher reproductive success. Additionally, relationships were found between some of the context-specific traits and juvenile survival and reproductive success. Bolder bass were more vulnerable to angling in the mesocosm context and bolder nesting males were more vulnerable to nest angling. Additional relationships were found between some of the context-specific traits and angling vulnerability. Boldness was the only personality trait that was significantly heritable.

The results of this dissertation demonstrate for the first time that personality traits that are consistent across development can affect fitness in multiple ways over the course of an individual's lifetime. In some environments, these fitness effects can result in tradeoffs that could maintain within population variation in personality traits. Further, the results indicate that the selective capture of fish by angling can alter the selective landscape acting on personality traits, which could have significant evolutionary and ecological consequences and could affect the quality of fisheries.

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TABLE OF CONTENTS

LIST OF TABLES.....	ix
LIST OF FIGURES.....	xi
CHAPTER 1: Fish Behavioral Types and their Ecological Consequences.....	1
ABSTRACT.....	1
INTRODUCTION.....	2
Terminology and measurement.....	4
The evolution and maintenance of variation in behavioral traits.....	6
Fitness tradeoffs.....	6
Inter-individual differences in metabolism and state.....	7
ECOLOGICAL CONSEQUENCES OF BEHAVIORAL TYPES.....	9
Ecological consequences at the individual level.....	10
Growth and survival.....	10
Reproductive success.....	14
Habitat use and foraging specialization.....	15
Conclusions.....	17
Consequences at the population, community, and ecosystem level.....	18
MANAGEMENT IMPLICATIONS OF BEHAVIORAL TYPES.....	21
Fishing.....	22
Hatchery rearing.....	25
Effects of artificial selection on behavior.....	25
The effects of hatchery rearing environments on behavior.....	27
DISCUSSION.....	29
Examining behavioral type effects on growth and survival.....	29
Diet, habitat use, and ontogenetic niche shifts.....	30
Consistency in behavioral traits across life stages and fitness tradeoffs.....	31
Heritability of behavioral traits and consequences arising from the release of domesticated fish.....	33
SUMMARY.....	35
ACKNOWLEDGEMENTS.....	35
APPENDIX.....	37
LITERATURE CITED.....	49
CHAPTER 2: The Reliability and Accuracy of Four Behavioral Tests Frequently Used to Quantify Personality.....	61
ABSTRACT.....	61
INTRODUCTION.....	62
METHODS.....	64
Novel context.....	65
Familiar and safe context.....	66
Social context (mirror test)	66
Food and predator present context.....	67

Statistical analysis.....	67
RESULTS.....	69
DISCUSSION.....	70
ACKNOWLEDGEMENTS.....	73
APPENDIX.....	74
LITERATURE CITED.....	80
CHAPTER 3: The Consistency of Personality Traits Across a 4-Year Period in Largemouth Bass (<i>Micropterus Salmoides</i>).....	84
ABSTRACT.....	84
INTRDUCTION.....	85
METHODS.....	88
Study species and husbandry.....	88
Behavioral assay procedur.....	89
Statistical analysis.....	91
RESULTS.....	93
DISCUSSION.....	95
ACKNOWLEDGEMENTS.....	98
APPENDIX.....	99
LITERATURE CITED.....	108
CHAPTER 4: Fitness Tradeoffs Across Development Can Contribute to the Maintenance of Adaptive Personality Differences.....	112
ABSTRACT.....	112
INTRODUCTION.....	113
METHODS.....	115
Study population and husbandry.....	115
Behavioral assay procedure.....	116
Experiments.....	118
Experiment 1: Juvenile survivorship.....	118
Experiment 2: Adult reproductive success.....	118
Experiment 3: Personality heritability.....	120
Statistical analysis.....	121
RESULTS.....	123
Experiment 1: Juvenile survivorship.....	123
Experiment 2: Adult reproductive success.....	123
Personality heritability.....	124
DISCUSSION.....	124
ACKNOWLEDGEMENTS.....	127
APPENDIX.....	128
LITERATURE CITED.....	136
CHAPTER 5: Personality Affects Angling Vulnerability in Largemouth Bass (<i>Micropterus Salmoides</i>)...140	140
ABSTRACT.....	140
INTRODUCTION.....	141
METHODS.....	144
Study population and husbandry.....	144
Behavioral assay procedure.....	145

Angling experiments.....	147
Experiment 1: Mesocosm context.....	147
Experiment 2: Outdoor pond context.....	148
Experiment 3: Outdoor pond context with casts made directly onto bass nests.....	148
Statistical analysis.....	149
RESULTS.....	150
Angling experiment 1: Mesocosm context.....	150
Angling experiment 2: Outdoor pond context.....	150
Angling experiment 3: Outdoor pond context with casts made directly onto bass nests.....	151
DISCUSSION.....	151
ACKNOWLEDGEMENTS.....	154
APPENDIX.....	155
LITERATURE CITED.....	162

LIST OF TABLES

Table 1	Glossary of terms related to animal personality.....	38
Table 2	Summary of evidence for the ecological consequences of behavioral types in fishes at the individual level.....	39
Table 3	Summary of evidence for the ecological consequences of behavioral types in fishes at the population and community level.....	41
Table 4	Summary of the effects of angling and hatchery rearing on behavioral traits in fishes and their ecological consequences.....	42
Table 5	Definition of terms.....	75
Table 6	Behaviors measured in the four behavioral assays, the context for each measurement, common psychological trait(s) assumed to cause behavior, and other internal states that could affect each behavior.....	76
Table 7	Intra-class correlation coefficients (values in parenthesis indicate 95% confidence intervals) between standardized measurements in the four contexts as well the composite personality traits (boldness and energeticness) generated from a principal components analysis of the measurements in the four contexts.....	77
Table 8	Contributions (loadings) of the four context-specific measurements in trial periods 1 and 2 to principal component axis 1 and 2.....	78
Table 9	Behaviors measured in the four behavioral assays, the context for each assay, and the ages in which the assays were conducted.....	100
Table 10	Correlations between context-specific personality traits within each age. Values are intra-class correlation coefficients (95% confidence intervals in parenthesis) of the standardized measurements.....	101
Table 11	Principal components analysis of 3 context-specific traits (safe and familiar context, social context (mirror-test), and predator and food present context) at 12, 15, 36, 48, and 60 months of age. Only the loadings (first column for each age) and correlations (second column for each age) for axis 1 are shown.....	102
Table 12	Temporal consistency within each personality trait across varying time intervals and at different ages. Values are Pearson correlation coefficients (95% confidence intervals in parenthesis).....	103
Table 13	Regressions of personality trait temporal consistency (log-transformed) as a function of the time between measurements. Values were weighted by the sample size from each	

interval (e.g. N = 122 for the 3 month interval and N = 39 for the 48 month interval). $\text{Log}(y) = \text{intercept} + \text{slope}(x)$104

Table 14	Logistic regressions of the effect of length and personality on juvenile survivorship in two different experimental ponds. One pond was older and contained abundant macrophytes and invertebrates while the other was newly renovated and contained little vegetation and a less productive invertebrate community. Each model has 233 degrees of freedom. $\text{Survival (Yes/No)} = \text{Length} + \text{Personality} + \text{Pond} + \text{Length:Personality} + \text{Length:Pond} + \text{Personality:Pond}$. For comparison, the null model deviance was 329.89.....129
Table 15	Linear regressions of the effect of sex, length, and personality on adult bass reproductive success. $\text{Reproductive success} = \text{Sex} + \text{Length} + \text{Personality} + \text{Sex:Length} + \text{Sex:Personality} + \text{Length:Personality}$. Each model has 94 degrees of freedom.....130
Table 16	Linear regressions of the heritability of each personality trait. Each model has 5 degrees of freedom. $\text{Average offspring personality} = \text{Mid-parent personality}$. Regressions weighted by number of offspring in each family.....131
Table 17	Linear regressions of the effect of length and personality on angling vulnerability in angling experiment 1 (mesocosm). Each model has 30 degrees of freedom. $\text{Angling vulnerability} = \text{Length} + \text{Personality} + \text{Length:Personality}$156
Table 18	Logistic regressions of the effect of length and personality on angling vulnerability in angling experiment 2 (outdoor pond). Each model has 198 degrees of freedom. $\text{Vulnerable to Angling (Yes/No)} = \text{Length} + \text{Personality} + \text{Length:Personality}$. For comparison, the null model deviance was 253.80.....157
Table 19	Linear regressions of the effect of length, nest egg count, and personality on angling vulnerability in angling experiment 3 (nest guarding males). $\text{Angling vulnerability} = \text{Length} + \text{Nest Egg Count} + \text{Personality} + \text{Length:Personality} + \text{Egg Count:Personality}$. Each model has 30 degrees of freedom.....158

LIST OF FIGURES

Figure 1	The consequences of variation in fish behavioral types may be expressed at different levels of ecological organization (from individuals to ecosystems) and have implications for conservation and management, as well as basic biology.....44
Figure 2	Five scenarios (a-f), each depicting the behavior of four individuals (solid horizontal lines) in two different situations (S1 and S2). In scenario a, all individuals display the same phenotypes in both S1 and S2 and there is plasticity between situations. In scenario b, there is phenotypic variability in situations S1 and S2 (equal between situations), no plasticity between situations, and consistent inter-individual differences in phenotype between situations. In scenario c, there is phenotypic variability in situations S1 and S2 (equal between situations), plasticity between situations, and consistent inter-individual differences in behavior. In scenario d, there is unequal phenotypic variation between situations S1 and S2 (S2 has much more), inter-individual differences in plasticity between situations (the individual with the smallest phenotype has high individual plasticity while the individual with the second smallest phenotype demonstrates a lower level of plasticity), and consistent inter-individual differences in behavior (perfect consistency in rank order but less in the raw values). In scenario e, there is phenotypic variability in situations S1 and S2, plasticity between situations, but individuals do not show consistent differences in behavior across situations because of differential directionality in responses. Modified from Dingemanse et al. (2010).....45
Figure 3	A representation of different phenotypic traits along the pace-of-life continuum. Double arrows illustrate presumed continuous variation in a trait, with traits grouped under life-history strategies, behavior, and physiology, and distributed along a pace-of-life continuum from “slow” to “fast”. Modified from Réale et al. (2010).....46
Figure 4	Bluegill sunfish display two distinct behavioral types when foraging on open-water versus vegetation-dwelling prey in the laboratory. Graphed are the foraging behaviors (hover duration when searching) used by individual bluegill when searching for damselfly nymphs in the vegetation and when searching for zooplankton (<i>Daphnia</i>) in the open-water habitat of aquaria. Each point represents the mean hover time (+ 1 SE) of six feeding trials for a given fish in each habitat. The diagonal line represents equal hover duration in each habitat. From Ehlinger and Wilson (1988).....47
Figure 5	Length-frequency distribution of young-of-year largemouth bass collected from Paul Lake, Michigan in late August 1994. Fish were categorized by age (age determined using daily rings from otoliths). Age categories represent roughly the youngest 25%, the central 50%, and the oldest 25% of fish collected. Only fish >85 mm in length become piscivorous during their first summer of life. From Post (2003).....48
Figure 6	Plots a) and b) depict two possible outcomes for a test of the convergent validity of two measurements that may both be theorized to measure boldness. Plot a) would support the theory that the two measurements quantify the same property while plot b) would suggest that they do not. Plots c) and d) depict two possible outcomes for a test of the

discriminant validity of two measurements that may be theorized to measure two different personality traits. Plot c) would support the theory that the two measurements quantify two different traits while plot d) would not.....79

Figure 7 Four hierarchical models illustrating alternative hypotheses for the organization and structure of personality traits. Model (a) proposes a scenario where a general boldness trait underlies the expression of behavior in each context. Thus, repeated observations of inter-individual differences in behavior would yield roughly the same correlations between any two behaviors observed, regardless of whether the observations were made in the same or different contexts. Model (b) proposes a scenario where context-specific personality traits underlie the expression of behavior in each context. These context-specific traits are all sub-modules of the same general boldness trait. Thus, repeated observations of behavior in these contexts would all yield positive correlations. However, repeated observations from within contexts would yield higher correlations than those between contexts. Model (c) proposes a scenario where semi-general personality traits underlie the expression of behavior within functionally similar contexts (e.g. foraging and novelty). Thus, repeated observations of behavior would yield equivalent correlations regardless of whether the observations were made in the same or different contexts, as long as the contexts were functionally similar (e.g. involved novelty). Behaviors expressed in functionally different contexts (e.g. novelty and feeding) would not be correlated. Model (d) proposes a scenario where context-specific traits underlie behavior in each context and each of these context-specific traits are also sub-modules of semi-general traits that underlie behavior in functionally similar contexts (e.g. foraging and novelty). The semi-general traits are themselves sub-modules of a general boldness trait. Under this scenario, repeated observations of inter-individual differences in behavior from within specific contexts would yield the highest correlations, inter-individual differences in behavior from within functionally similar contexts would yield the next highest, and inter-individual differences in behavior across functionally similar contexts would yield the lowest (but still significant) correlations.....105

Figure 8 Model illustrating the organization and structure of personality traits based on the results of this study. A context-specific personality trait influenced behavior across all ages of development that were investigated in the novel environment context, in the foraging in the presence of an aerial predator context, and in the mirror-test context. A boldness personality trait generalized beyond specific functional contexts was found to underlie each of these context-specific traits. A personality trait also influenced adult (but not juvenile) behavior in the safe and familiar environment. This personality trait may have been a context-specific trait (indicated by the dashed line between behavior and the unidentified trait) or may have been the general boldness trait (indicated by a dashed line between boldness and the unidentified trait).....106

Figure 9 Regressions of personality trait temporal consistency (log-transformed) as a function of the time between measurements in the: a) mirror-test context-specific personality trait, b) food and predation threat context-specific personality trait, and c) boldness trait. Values were weighted by the sample size from each interval (e.g. N = 122 for the 3 month interval and N = 39 for the 48 month interval). $\text{Log}(y) = \text{intercept} + \text{slope}(x)$. Solid black regression lines are statistically significant while dashed grey lines are not.....107

Figure 10	Model illustrating the organization and structure of personality traits in this population of largemouth bass. A context-specific personality trait influenced behavior across all ages of development that were investigated in the novel environment context, in the foraging in the presence of an aerial predator context, and in the mirror-test context. A boldness personality trait generalized beyond specific functional contexts was found to underlie each of these context-specific traits. A personality trait also influenced adult (but not juvenile) behavior in the safe and familiar environment. This personality trait may have been a context-specific trait (indicated by the dashed line between behavior and the unidentified trait) or may have been the general boldness trait (indicated by a dashed line between boldness and the unidentified trait).....132
Figure 11	a) Average boldness and b) average initial length of bass that survived to the end of the experiment (grey circles) and bass that did not survive (black circles) in the high vegetation pond and in the low vegetation pond. Error bars indicate the standard error of the mean.....133
Figure 12	The effects of boldness, length, and the interaction between them on adult reproductive success. The light grey plane represents the relationships between the variables for males and the dark grey plane represents the relationships between the variables for females. The circles (light grey = males; dark grey = females) represent individual males and the lines from the circles to the planes represent residual values.....134
Figure 13	The heritability of boldness. Each circle represents the average boldness of offspring in a full-sib family. The numbers below the circles represent the number of offspring in each family. The trend line (black) is weighted by the number of offspring in each family....135
Figure 14	The effect of initial boldness, length, and the interaction between them on angling vulnerability in a mesocosm experiment. The circles represent individuals and the lines from the circles to the plane indicate individual residual values.....159
Figure 15	a) Average length, b) average mirror-test context trait, and c) average boldness of bass that were caught and those that were not caught in an outdoor pond. Error bars indicate the standard error of the mean.....160
Figure 16	Effects of a) length, b) nest egg count, c) the safe and familiar context trait, and d) boldness on angling vulnerability of nest guarding male bass in an outdoor pond. Solid black lines indicate significant relationships (b-d) while dashed lines do not.....161

Chapter 1: Fish Behavioral Types and their Ecological Consequences

ABSTRACT

Fish have proven to be model organisms for the study of animal personalities and a rich literature documents consistent inter-individual behavioral differences in a variety of species. However, relatively few studies have examined the ecological consequences of such consistent inter-individual differences in behaviors in fish or other organisms, especially under field conditions. In this review and perspective, we discuss the factors that may lead to the formation and maintenance of behavioral types in fish populations. We then examine what is known about the effects of personality variation on: individual growth and survival, breeding behaviors and reproductive success, habitat use, diet, and ontogenetic niche shifts, migration and dispersal, as well as potential consequences for species interactions and ecosystem functioning. We focus as much as possible on studies conducted under natural or semi-natural conditions, because such field studies are most relevant to elucidating the ecological consequences of behavioral variation. Finally, we discuss the potential importance of consistent individual differences in behaviors to fisheries management and conservation, specifically examining consequences for recreational and commercial fishing, hatchery rearing, and stock enhancement.

INTRODUCTION

Fish, like many other vertebrates, show consistent individual differences in behavior despite maintaining a high degree of behavioral plasticity. These consistent inter-individual differences in behavior have been variously termed: animal personalities (Dall et al. 2004), behavioral profiles (Groothuis and Trillmich 2011), temperaments (Réale et al. 2007), coping styles (Koolhaas et al. 1999), or behavioral syndromes (Sih et al. 2004a,b). Much of the large and rapidly expanding literature on animal personalities involves studies with fish (Stamps 2007), and it was early work by Huntingford (1976, 1982) with sticklebacks, and Ehlinger and Wilson (1988) and Wilson et al. (1993, 1994) with sunfish, that provided some of the first evidence that individuals may exhibit consistent differences in behavioral traits within a population (e.g., individuals may be relatively shy or bold, aggressive or timid). Wilson et al. (1993) suggested that such consistent behavioral differences between individuals represented more than random variation around an adaptive mean. Rather, “individual differences are interpreted not as the raw material on which natural selection acts but as the end product of natural selection” (Wilson et al. 1993: page 255). That is, variation in behavioral traits may be maintained within a population because such variation represents different adaptive solutions to a complex environment (e.g., Wolf and McNamara 2012).

Although studies of animal personalities initially struggled to gain traction against the idea that variation in phenotype is expected within a population and therefore does not require a special explanation (Wilson 1998), subsequent years have validated the early insights of Huntingford, Wilson, and their colleagues. Today the study of consistent individual differences in behavior enjoys a vigorous growth, as evidenced by the publication of a number of recent reviews; e.g., Sih et al. 2004a,b; Réale et al. 2007; Sih and Bell 2008; Stamps and Groothuis 2010; Wolf and Weissing 2012; including three reviews devoted specifically to fish (Toms et al. 2010; Budaev and Brown 2011; Conrad et al. 2011). As Wolf and McNamara (2012) note, three key features associated with personalities have been observed

in a variety of species: (1) **variation**: individuals differ in their behaviors, (2) **consistency**: individual differences in behaviors are stable over time, and (3) **correlations**: certain behavioral traits (e.g., boldness, aggression, exploration) tend to be correlated among individuals.

Although consistent individual differences in behavior are now well documented in fish and other organisms, for the most part these studies have been conducted in the laboratory under simplified and highly controlled conditions. Studies of behavioral trait variation under natural or semi-natural conditions are still quite rare (e.g., Fraser et al. 2001; Biro et al. 2007; Adriaenssens and Johnsson 2011a). While laboratory studies have opened the door to the rich array of behavioral diversity found in nature, a key question before us is what are the ecological consequences of consistent individual differences in behavior to organisms in the wild (Dingemanse and Réale 2005; Archard and Braithwaite 2010; Bolnick et al. 2011; Adriaenssens and Johnsson 2011a; Sih et al. 2012; Wolf and Weissing 2012). These ecological consequences include potential effects on an individual's survival and reproductive success, population dynamics (through influences on species' vital rates; e.g., growth, fecundity, and survival), community structure and species diversity (through influences on species interactions), and on the conservation and management of natural resources (Figure 1). To understand these consequences of animal personalities, we need to study organisms in the complex environments found in nature (Stamps and Groothuis 2010).

Our goal in this paper is to review what is known about the ecological consequences of behavioral trait variation in fishes at the individual, population and community levels, including the consequences of personality for the conservation and management of fishes. More than twenty years ago, Wilson et al. (1993) noted that the ecological consequences of such consistent individual differences had not been studied in a natural population of any species. Despite the explosion of research into animal personalities since Wilson et al.'s paper, the ecological and evolutionary consequences of consistent inter-individual differences in behavioral traits in natural populations are

only now coming into focus (Bolnick et al. 2011; Dall et al. 2012; Sih et al. 2012; Wolf and Weissing 2012). We begin our review with a short description of terminology and measurement issues in the study of animal personalities, followed by a discussion of the proximate and ultimate factors that may lead to consistent inter-individual differences in behavior. We then examine what is known about the ecological consequences of behavioral types in fishes, including effects at the individual, population, and community levels. We focus as much as possible on studies conducted under natural or semi-natural conditions, because such field studies are most relevant to elucidating the ecological consequences of behavioral variation. Finally, we discuss the potential importance of consistent individual differences in behavior to fisheries management and conservation, specifically examining consequences for recreational and commercial fishing, hatchery rearing, and stock enhancement.

Terminology and measurement

Multiple terms surround the discussion of animal personalities, which has led to considerable debate in the literature. Table 1 lists many of the terms used in the study of animal personalities and defines how we use these terms in the current paper. The terms “animal personality”, “temperament”, and “coping style” have been used more or less synonymously (Réale et al. 2007). These terms describe consistent differences between individuals in behaviors across contexts over some period of time and are most often used to refer to general behavioral patterns (e.g., individual differences in boldness, activity, and aggressiveness and the relationships between them). We use the term “behavioral type” to describe an individual’s phenotype (e.g., bold vs shy, aggressive vs timid) relative to other individuals in the population.

One of the challenges in assessing personality traits in fish and other species is the fact that behavior can be extremely plastic; individuals often respond to changes in their environment by adjusting their behaviors to meet current conditions. Further, individuals may differ in their degree of

behavioral plasticity, which at the individual level could affect the measurement of personality traits (Nussey et al. 2007; Dingemanse et al. 2010) and at the population level could affect stability and population persistence in response to environmental change (Dingemanse and Wolf 2013). A useful framework for examining personality traits in light of behavioral plasticity is the concept of behavioral reaction norms (Figure 2). The reaction norm framework illustrates how individual differences in personality traits can be assessed across multiple contexts to examine consistency of behavioral types and the extent of behavioral plasticity within and between individuals (Réale et al. 2007; Dingemanse et al. 2010). For example, Budaev and Brown (2011) provide a table of over a dozen measures that have been used to assess boldness in fish (e.g. predator inspection, foraging under predation risk, latency to emerge from cover, behavior in an open field, etc.). Measuring individuals in a number of these contexts would allow for the development of reaction norms that would more accurately characterize an individual's personality type.

The behavioral reaction norm approach also provides an opportunity to identify which measures actually quantify the same personality trait. The few studies that have investigated correlations among different personality measures that were thought to quantify the same trait have found some surprising results (Carter et al. 2013; Garamszegi et al. 2013). For example, two measures that are often assumed to quantify aggression were investigated in yellow-bellied marmots. While both measures were repeatable over time, they were independent from each other (Blumstein et al. 2012). A similar result was found when investigating two measures that are often assumed to quantify boldness (i.e., response to a novel object and response to a predator; Carter et al. 2012). These results show how different ways of measuring a personality trait may not be interchangeable, providing additional justification for taking a reaction norm approach.

The application of behavioral reaction norms is still relatively new and not yet widely applied. Never-the-less, numerous studies of behavioral types in fish and other organisms provide results that

allow us to explore the ecological consequences of personality variation, as long as we are careful in our interpretation and recognize that different ways of measuring a personality trait like “boldness” may in fact measure different things (Réale et al. 2007). Finally, while this review and prospectus focuses on personality variation in fish and its ecological consequences, we want to emphasize the wealth of studies that exist for other taxa. These studies provide a broader context in which to view the results from fishes and we refer readers to publications by Réale et al. (2000), Dall et al. (2004), and Dingemanse and Réale (2005), as well as the review papers cited in the Introduction, as an entry point to the literature on animal personalities in birds, mammals, and other groups.

The evolution and maintenance of variation in behavioral traits

Fitness tradeoffs

The fitness consequences of behavioral traits are often context-dependent. For example, bold behavioral types may be less fit than shy behavioral types in an environment with high levels of predation, while the opposite may be true in an environment without predators. Behavioral ecologists have focused on fitness tradeoffs as an important mechanism to explain the generation and maintenance of variation in behavioral traits within a population, both on ecological and evolutionary time scales. For example, consider the situation where individuals that are bolder are more likely to encounter predators, resulting in higher mortality rates. Now imagine that these bolder individuals are also more likely to encounter more prey per unit foraging time and therefore experience higher feeding rates, resulting in higher energy gain (Stamps 2007). As a result, under this hypothetical scenario, a potential tradeoff between energy gain/growth and survival would exist that could maintain variation in boldness.

Mangel and Stamps (2001) developed a simple model to show how tradeoffs between growth and survival can result in a range of individual growth rates that all yield equivalent fitness (as measured

by r in the Euler-Lotka equation), thus favoring the maintenance of multiple behavioral types within a population. Similarly, models for the evolution of inter-individual differences in dispersal rates have been developed under the premise that the expected fitness of “dispersers” equals the expected fitness of “stayers”, due to a growth-mortality tradeoff (Hamilton and May 1977; Frank 1986; Johst and Brandl 1999; Ronce et al. 2000).

Fish often face situations in nature where there is a potential tradeoff between increased feeding rate and reduced survival (Lima 1998; Mangel and Stamps 2001). For example; 1) open-water (pelagic habitats) may contain richer food resources, but pose higher predation risk (e.g., Werner and Hall 1988; Gliwicz et al. 2006), 2) daytime foraging may yield a higher feeding rate but greater risk of predation than nocturnal foraging (e.g., Fraser and Metcalfe 1997; Metcalfe et al. 1999; Ryer and Hurst 2008), and 3) more active foragers may encounter more prey (or richer habitats) and grow faster, but suffer higher mortality rates (e.g., Werner and Anholt 1993; Fraser et al. 2001; Biro et al. 2004, 2006; Sundström et al. 2004). Fitness tradeoffs can also occur spatially (e.g. one area of a habitat favors one behavioral type while another area favors a different one), temporally within generations (e.g. across development or across genetically linked behavioral traits), and temporally between generations (e.g. frequency-dependent selection).

Inter-individual differences in metabolism and state

While fitness tradeoffs provide a powerful mechanism that may select for a variety of (equal fitness) behavioral types within a population, the maintenance of consistent behavioral types or personalities over time requires more than just a fitness tradeoff. To see this, consider the question: what prevents individuals from continually shifting back and forth between different behavioral types that have equivalent fitness? Or, stated in another way - why do we find differential consistency (as defined in Table 1) in behavioral types within a population (e.g., individuals that are consistently bolder

than others over time)? One possibility is that individuals differ in their relatively unchanging physiological traits (e.g., resting metabolic rate or the size of metabolically costly organs) and therefore the behavioral type that results in the optimal value of the growth-mortality tradeoff differs depending on physiological state. A number of authors (Stamps 2007; Biro and Stamps 2010; Houston 2010) have suggested that consistent individual differences in physiological state could be an important factor promoting the formation of individual differences in personality. The first step in examining this hypothesis is to determine whether individuals differ consistently in their physiological traits (e.g., resting metabolic rates or potential growth rate); the second step is to determine whether any such differences in physiological measures are correlated with behavioral traits (see Biro and Stamps (2010) for a review of the literature on resting metabolic rate and their relationship to behavioral traits).

Recently, it has been suggested that behavioral traits may covary with a whole suite of physiological and life-history traits, such that these covarying phenotypic traits can be effectively grouped under the umbrella of a “pace-of-life-syndrome” (Réale et al. 2010). Figure 3 illustrates the potential integration of life-history, behavioral, and physiological traits along a pace-of-life continuum from “slow” to “fast”. Evidence for a pace-of-life syndrome in fish or other organisms is still tentative (Adriaenssens and Johnsson 2009). However, Biro and Stamps (2008) show that behavioral traits are linked to life-history variation in a variety of organisms, including fish. For example, activity rates and boldness are positively related to growth rates in rainbow trout, *Oncorhynchus mykiss* (Biro et al. 2004, 2005, 2007), and boldness is positively related to growth, fecundity, and size at maturity in Atlantic silverside, *Menidia menidia* (Walsh et al. 2006). The pace-of-life syndrome provides a useful heuristic framework in which animal personality studies can be integrated to address how behavioral traits are maintained within populations, and how they may have ecological consequences affecting individual growth, survival, and reproductive success, as well as population dynamics and successful resource management. Moreover, viewing behavioral variation in the light of life-history traits and the pace-of-

life syndrome allows us to consider the impacts of behavioral trait variation at different life stages and to better understand when and why personality types may be maintained over ontogeny (e.g., Schürch and Heg 2010; Chervet et al. 2011), even potentially across metamorphosis (e.g., Wilson and Krause 2012a,b).

There are additional ways in which the “state” of an individual can affect the relative costs and benefits of different behavioral actions, leading to the generation and maintenance of adaptive behavioral trait variation within a population (Houston and McNamara 1999; Dingemanse and Wolf 2010; Luttbeg and Sih 2010; Wolf and Weissing 2010, Wolf and McNamara 2012). In the case of foraging boldness (where taking greater risk yields higher rewards), Luttbeg and Sih (2010) show how positive-feedback mechanisms can maintain differential consistency in behavioral traits. For example, if individuals having higher state (e.g., better condition, larger size, more energy reserves) are better at defending themselves or fleeing from predators, then animals with higher state will have lower predation risk while being bold and should be bolder than low state individuals (Luttbeg and Sih 2010). Thus, small differences in initial state between individuals (e.g., due to parental provisioning, carryover from larval to adult stages) can lead to a positive-feedback loop between assets and behaviors, such that “....individuals that already have high state (assets) would be bold, and thus gain more resources that maintain their high state” (Luttbeg and Sih 2010: 2979). In addition, positive feedbacks based on experience or learning can lead to differences in foraging efficiency in a habitat or on a particular prey type that can act to reinforce and maintain behavioral differences between individuals (Werner et al. 1981; Dingemanse and Wolf 2010).

ECOLOGICAL CONSEQUENCES OF BEHAVIORAL TYPES

“Surprisingly little attention has been paid to the ecological and evolutionary consequences of personality differences” (Wolf and Weissing 2012: page 452).

In the sections above, we examined the factors thought to drive the evolution and maintenance of animal personalities in fish and other organisms. These mostly theoretical studies seek to provide “ultimate” evolutionary explanations for the existence of consistent differences in behaviors between individuals. In the following sections, we focus on the ecological consequences of these behavioral differences. That is, given the presence of varying behavioral types within a population, how might this behavioral variation affect the ecology, management, and conservation of fishes. These ecological consequences may include effects on an individual’s survival and reproductive success, the dynamics of populations (through influences on species’ vital rates; e.g., growth, fecundity, and survival), effects on community structure and species diversity (through influences on species interactions), and impacts on the management and conservation of species and fish stocks (e.g., through hatchery rearing and supplemental stocking). We recognize that separating the factors thought to ultimately drive the evolution of behavioral types in fishes from the more proximate consequences of such behavioral types to the ecology of individuals and populations is a somewhat false dichotomy. Ecology and evolution go hand in hand. Still, this distinction is useful for highlighting how the existence of behavioral types within a population may impact various aspects of an individual’s ecology (e.g., growth, survival, diet, habitat use), as well as population dynamics and species interactions.

Ecological consequences at the individual level

Growth and survival

Personality traits have the potential to affect an individual at nearly every stage of development, from a juvenile’s chances of surviving to adulthood to an adult’s reproductive success. We summarize what is known about the ecological consequences of behavioral trait variation in fish at the individual level in Table 2. Table 2 includes both laboratory and field studies. However, in the discussion below we

focus on the results from natural and semi-natural environments because field studies provide the most direct tests of the ecological consequences of behavioral trait variation. Looking first at the impact of boldness, aggressiveness, and exploration on individual growth, dispersal, and survival, we find support for a hypothesized growth-mortality tradeoff, although the evidence from field studies is surprisingly limited.

Fraser et al. (2001) found that bolder individuals of the Trinidad killifish (*Rivulus hartti*) moved greater distances in the field. Moreover, movement distance was positively correlated with individual growth over a 19-month mark-recapture study in a section of river containing *Rivulus* predators. However, in a predator-absent zone, there was no correlation between movement and growth (Fraser et al. 2001). Our own studies with juvenile bluegill (*Lepomis macrochirus*) in ponds have shown a positive correlation between boldness measured in the laboratory and individual growth rates observed in the field over periods of 2-6 months (M. Kjelvik and G. Mittelbach, unpublished data). In studies comparing domestic and wild strains of salmon and trout, Sundström et al. (2004) and Biro et al. (2003a,b, 2004) examined the growth, survival and habitat use of fish in the presence and absence of predators. Sundström et al. (2004) found a trade-off between growth and survival for strains of coho salmon (*Oncorhynchus kisutch*) transgenic for growth-hormone (GH) relative to wild salmon. In seminatural stream channels, GH-transgenic coho fry grew faster than wild coho fry, but suffered higher mortality from predators (non-transgenic coho juveniles) (Sundström et al. 2004). Higher mortality on GH-transgenic fry was most pronounced under low food conditions. Other studies have documented increased risk-taking behavior in GH-transgenic salmon in the laboratory (Abrahams and Sutterlin 1999; Sundström et al. 2003), as well as increased movement by GH-enhanced trout in the wild (Sundt-Hansen et al. 2009). Thus, there appears to be an interaction between behavior, growth, and mortality when comparing salmon and trout strains modified with GH relative to wild populations (but see Johnsson and Björnsson 2001).

In a series of whole-lake experiments, Biro et al. (2003a,b, 2004, 2006) compared the growth, survival, and habitat use of domestic (hatchery stock) and wild strains of rainbow trout (*Oncorhynchus mykiss*). In the presence of avian predators (loons, *Gavia immer*), age-1 domestic trout gained 20% more mass than wild trout (Biro et al. 2004) and age-0 domestic trout gained 100% more mass than wild trout (Biro et al. 2006). However, domestic trout (age-0 and age-1) suffered 50- 60% greater mortality than wild trout when predators were present (Biro et al. 2004, 2006). Behavioral differences between domestic and wild strains in the field were not specifically quantified in these experiments. However, in a subsequent field experiment (Biro et al. 2007), the authors examined more directly the behaviors of domestic and wild rainbow trout strains released into lakes that differed in predation pressure from loons. They found that fish from the domestic strain responded less to the presence of predators, used riskier habitats, and had higher catch rates during the day than did fish from the wild strain. Thus, Biro et al. (2007: page 894) conclude that “greater overall activity and greater daytime use of deep and pelagic habitats by the domestic genotype should lead to greater growth (given sufficient food) but higher predation mortality”. These and other studies comparing the behaviors, growth, and survival of domestic versus wild stocks of salmonid fishes provide some of the clearest evidence for the ecological consequences of behavioral trait variation under a growth-mortality tradeoff.

Other studies in natural or semi-natural environments provide no support for the expected link between behavioral traits and a growth-mortality tradeoff. Adriaenssens and Johnsson (2011a) found that shy trout (individuals with low exploration tendency in the lab) actually grew faster than bold trout when released into a natural stream. In a subsequent study, they found no significant effects of activity or exploration measured in the laboratory on growth in the field, and if we can assume that recovery following release into the wild is an indication of survival, they found that more active individuals had higher survival (Adriaenssens and Johnsson 2011a). In both of the above studies, fish were collected

from the wild, assayed for behavioral traits in the laboratory, and then released back into the wild at a site near where they were collected.

Höjesjö et al. (2011) also found no association between boldness measured on juvenile brown trout (*Salmo trutta*) reared in the laboratory and their growth and survival when released into the river that was the source of the parental stock. However, only about 4% of the released fish were recovered, which raises the question of whether the missing fish died or simply moved away. The inability to distinguish mortality from disappearance in release/recovery experiments into the wild (especially when recovery rates are low) greatly hinders the ability to assess the impact of behavioral traits on fish survival (and growth). In Höjesjö et al.'s (2011) experiment, the authors note that juvenile brown trout in their study population are very stationary (seldom moving further than 200 m). Thus, recapture should provide a good estimate of survival in the wild.

Following the pace-of-life syndrome (Figure 3), we might expect individuals with bold, active, and asocial behavioral types to have a higher propensity to explore their environment and disperse greater distances, which could give them an advantage in terms of finding richer habitats. As stated earlier, Fraser et al. (2001) found that individual killifish that were bolder in the laboratory dispersed greater distances when released into the field, and that individuals that moved greater distances in the field had higher growth rates (in stream sections with predatory fish). Bolder individuals of European roach (*Rutilus rutilus*) also showed a greater propensity to migrate (lake to stream) than shy individuals (Chapman et al. 2011), more asocial mosquitofish (*Gambusia affinis*) moved further from their social conspecifics when simultaneously introduced to experimental streams (Cote et al. 2010), and dominant brown trout moved longer distances and had larger home ranges in a radio telemetry study (Höjesjö et al, 2007). An individual's dispersal tendency is likely related to the strength of its social network (the number of social interactions an individual has and the strength of those interactions), which itself has been shown to be affected by an individual's behavioral type. A study with guppies investigating the

relationship between boldness and social networks found a correlation between an individual's boldness (measured by predator inspection and shoaling tendency in the lab) and aspects of its social network in natural shoals in the field. Bolder individuals were found to have fewer total social connections and the average strength of the connections they had were weaker than those of shyer individuals (Croft et al. 2009). Again, following predictions of the pace-of-life syndrome, we might expect such traits of increased activity and dispersal to carry with them higher mortality costs, if migrating or dispersing greater distances increases exposure to predators. However, no studies that we are aware of have assessed these mortality costs in the field.

Reproductive success

Behavioral traits have the potential to affect the reproductive success of adults, with both intra- and intersexual selection likely to be influenced by inter-individual variation in behavioral traits (Schuett et al. 2010). Numerous laboratory studies with a variety of fish species document positive relationships between boldness, dominance, and reproductive success. For example, in zebrafish (*Danio rerio*) the boldest and most aggressive males fertilized more of a female's eggs than the shyer and less aggressive males (Ariyomo and Watt 2012) and in guppies, females (*Poecilia reticulata*) have been shown to prefer to mate with bolder males (boldness measured by predator-inspection behavior; Godin and Dugatkin 1996). However, field studies examining the relationship between behavioral traits and reproductive success are still quite rare. Our own studies with largemouth bass (*Micropterus salmoides*) demonstrate that boldness measured in the laboratory is positively correlated with nesting success in the field; i.e., bolder males were more successful at building nests and receiving eggs when stocked into ponds with females than less-bold males (N. Ballew and G. Mittelbach, unpublished data). These apparent fitness benefits of being bolder and more aggressive may be offset in other situations (see Discussion).

Behavioral traits also have the potential to affect offspring survival during periods of parental care. For example, in fish species that build and guard redds or nests (e.g., Salmonidae, Centrarchidae), bolder, more aggressive individuals are likely to outcompete conspecifics to secure better nesting sites, and bolder, more aggressive individuals may be better at guarding their nests from potential predators (McPhee and Quinn 1998). A series of studies by D.P. Philipp and colleagues, using largemouth bass lines that originated from a single wild population and were selected over multiple generations for increased or decreased vulnerability to recreational angling during the non-nesting season, show that the high angling vulnerability (HV) line and low angling vulnerability (LV) line differ in parental care behavior and reproductive success (Philipp et al. 2009). Male bass from the high vulnerability to angling line displayed increased parental care activity and higher reproductive success in ponds with nest predators (juvenile bluegill) compared to males from the low vulnerability line (Cooke et al. 2007; Sutter et al. 2012). It is difficult to say how the trait of angling vulnerability relates to more commonly studied behavioral traits such as boldness and aggression. However, our own studies with largemouth bass show that male bass assayed as more aggressive towards conspecifics in the laboratory are more diligent at defending their nests from potential brood predators (bluegill) in the field and have higher reproductive success (N. Ballew and G. Mittelbach, unpublished data).

Habitat use and foraging specialization

Behavioral traits related to boldness/aggression, foraging styles, or predator avoidance have the potential to affect habitat use and resource consumption. For example, a study with bullheads (*Cottus perifretum*) found that less aggressive individuals (as assayed in the laboratory) showed a greater propensity to use complex habitats (i.e., branch jams) in the field (Kobler et al. 2011). In the same study, there was no correlation between habitat use in the field and individual differences in activity level measured in the laboratory. Functional linkages may also exist between behavioral traits that confer

greater feeding efficiency in particular habitats and morphological traits, leading to complex polymorphisms (Wolf and Weissing 2012). In one of the first studies to look for an association between morphological and behavioral traits, Ehlinger and Wilson (1988) examined a foraging polymorphism in populations of bluegill sunfish. They found that bluegill collected from a small, Michigan lake clustered into two behavioral (foraging mode) types when allowed to feed on open-water prey (zooplankton) and benthic prey (damselfly nymphs) in the laboratory (Figure 4). These behavioral differences between individuals were stable across a 20 week testing period.

Differences in foraging behaviors (hover duration) between bluegill individuals corresponded to differences in feeding rate; fish exhibiting relatively short hover durations were more successful at capturing zooplankton whereas fish displaying longer hover durations were more successful at capturing damselfly nymphs. When Ehlinger and Wilson (1988) compared the morphologies of these two behavioral types, they found that morphology and behavior were tightly correlated. Fish classified as “vegetation” (benthic) morphological types exhibited long hover durations, whereas fish classified as “open-water” morphological types exhibited short hover durations. Subsequent morphological analyses of sunfish (bluegill and pumpkinseed, *Lepomis gibbosus*) collected from open-water and littoral habitats in lakes confirmed the subtle but repeatable morphological distinctions between phenotypes associated with pelagic and littoral habitats (Robinson et al. 1993; Robinson et al. 2000).

Selection on morphological and behavioral traits that increase feeding efficiency on certain prey types or within certain habitats is likely to go hand-in-hand. Therefore, an important question is how much does habitat/foraging specialization lead to the development of animal personalities and the generation of behavioral trait variation within a population? Further, might there be subtle differences in functional morphology between behavioral types within populations that have generally gone undetected? The morphological differences between bluegill behavioral types in the study of Ehlinger and Wilson (1988) were not visible to the naked eye, but were detectable with morphometric analyses

(e.g., Ehlinger and Wilson 1988; Robinson et al. 1993; Robinson and Wilson 1996). Other fish species (e.g., threespine stickleback) show distinct resource polymorphisms in morphology/behavior/resource use in some populations (McPhail 1993), but continuous variation in others (Robinson 2000). Thus, how much subtle variation in morphology and physiology is associated with inter-individual behavioral variation in populations is unknown. When viewed in the holistic framework of individual specialization (Bolnick et al. 2011), it is clear that inter-individual differences in behavioral types and personalities may be an expected outcome of natural selection acting on populations in a complex environment.

Conclusions

At the individual level, variation in boldness, activity, and dispersal is often hypothesized to result from a tradeoff between growth and mortality (i.e., bolder fish are more active and grow faster, but suffer higher mortality). Despite wide-spread acceptance of a growth-mortality tradeoff as a likely driver of behavioral variation in fish (Stamps 2007), to date there is little empirical evidence from field studies and the results are mixed (Table 2). Studies of other taxa (mammals, birds) also provide only mixed support for the hypothesis that bolder (more exploratory) individuals take more risks to gain food but may suffer higher mortality as a result (e.g., Réale and Festa-Bianchet 2003; Dingemanse et al. 2004; Réale et al. 2007; Quinn et al. 2012). The strongest support for a growth-mortality tradeoff associated with differences in boldness or aggression in fish comes from studies of wild versus domesticated strains of trout and salmon (e.g., Biro et al. 2003a,b, 2004; Sundström et al. 2004).

Boldness and dominance appear to be positively associated with increased mating success in the laboratory and in the field, and individuals more vulnerable to angling exhibit more persistent nest guarding behavior and greater reproductive success in pond studies with largemouth bass. Boldness and aggression during reproductive events are likely to have negative consequences for adult energetics, survival and future reproductive success, and there are many examples of the high cost of parental care

in fishes (e.g., Dufrense et al. 1990; Gillooly and Baylis 1999; Steinhart et al. 2005). To date, however, no field studies have examined the full set of correlations between boldness/aggression during the breeding season, offspring survival, and adult current and future reproductive success. In the Discussion section, we consider how the costs and benefits of various behavioral traits may differ at the adult and juvenile life stages. Such life-history asynchrony in the impact of behavioral traits may provide an additional mechanism for the maintenance of variation in behavioral traits within a population.

Field studies also suggest that habitat heterogeneity and habitat-specific foraging success may maintain phenotypic polymorphisms in fish populations that include both behavioral and morphological traits. For example, in sunfish and sticklebacks, behaviors associated with increased foraging success in limnetic versus benthic habitats are also associated with variation in morphological traits (fin placement, body shape), resulting in complex polyphenisms (e.g., Ehlinger and Wilson 1988; Robinson and Wilson 1996; Robinson 2000; Weese et al. 2012). Thus, there are many opportunities in nature for consistent individual differences in behavior to arise when individuals can exploit different habitats and resources. Ecologists, behaviorists, and evolutionary biologists have joined together to highlight the importance of studying how environmental heterogeneity and habitat selection may generate and maintain intraspecific variation in populations, including variation in behavioral traits (Adriaenssens and Johnsson 2011a; Araújo et al. 2011; Bolnick et al. 2011; Dall et al. 2012; Sih et al. 2012; Wolf and Weissing 2012).

Consequences at the population, community, and ecosystem level

Intraspecific variation in behavioral traits can have numerous effects at the population, community, and ecosystem levels. Recent reviews have highlighted the potential for behavioral traits to affect population dynamics, predator-prey interactions, species diversity, and ecosystem primary productivity (Sih et al. 2012; Wolf and Weissing 2012). However, when compared to consequences at the individual level, far fewer theoretical expectations have been proposed for population and

community level consequences of multiple behavioral types within traits. Similarly, few empirical studies have examined the population and community level consequences of behavioral trait variation, and (to our knowledge) no studies have been conducted in natural conditions. We summarize in Table 3 the limited number of laboratory and mesocosm studies on the topic, looking first at studies that have investigated ecological consequences of variation in behavioral traits at the population level, then moving to studies examining consequences to species interactions, and concluding with studies on consequences to ecosystem functioning.

Population level consequences of behavioral trait variation have been investigated in terms of group performance and population dynamics. For example, shoal composition for boldness affects foraging success in guppies. Fish from mixed shoals were found to feed more than fish from all bold or all shy shoals, indicating that shoals containing a mixture of boldness behavioral types may outperform all bold and all shy shoals (Dyer et al. 2009). In a study with shoaling European perch, the frequency of different risk-taking behavioral types within the shoal was shown to affect overall shoal risk-taking behavior and bold individuals had an especially large effect on shoal behavior (Magnhagen and Bunnefeld 2009). A study with threespine sticklebacks investigated the effect of a population's composition of bold and shy individuals on population social structure. Individuals were assayed for boldness in the laboratory (measured as hesitancy to feed after being startled) and then artificial populations were formed based on the boldness scores. Populations were composed of either all shy individuals, all bold individuals, or were a mix of bold and shy individuals. The all shy populations had stronger social structures (measured as the average number of interactions for all individuals in the population) than the all bold populations. Additionally, the all shy populations were more cliquish, meaning social subgroups appeared to form (Pike et al. 2008). A field study with roach, while not directly investigating population level consequences, found that bold roach had a higher propensity to migrate (lake to stream) than shy roach (Chapman et al. 2011). Roach practice partial migration (only a

fraction of the population migrates). Thus, it is easy to see how the frequency of bold behavioral types could impact the proportion of the population that migrates.

In terms of species interactions, the consequences of behavioral types to predator-prey interactions, inter-specific competition, and invasive ability have been investigated in a single study for each type of interaction. In threespine stickleback, boldness was found to affect prey risk, with bolder sticklebacks feeding more heavily on chironomid larvae in laboratory trials (Ioannou et al. 2008). In a study that investigated inter-specific competition between two species of sticklebacks (threespine and ninespine), bold behavioral types were found to consume more prey in heterospecific competitive foraging trials, regardless of species (Webster et al. 2009). The only study to date on behavioral traits and invasiveness found no relationship between the level of boldness and invasiveness for four *Gambusia* species (Rehage and Sih 2004).

A key (but unanswered) question in the study of the population-level consequences of animal personalities is whether the amount of variance in behavioral traits within a population matters. That is, if populations share the same mean value for a given behavioral trait but possess different mixtures of behavioral types, is there an effect on population dynamics? If behavioral types are non-randomly distributed in space, such that they select different foraging habitats (e.g., Wilson et al. 1993), occupy different positions within a shoal (e.g., Ward et al. 2004), or preferentially associate with like behavioral types, then the mixture of behavioral types in a population will matter.

No studies to our knowledge have directly measured the effects of individual variation in behavioral traits on ecosystem functioning. However, a few studies suggest the possibility of such a relationship. An outdoor mesocosm study using guppies taken from natural streams that differ in predation pressure found that mesocosms containing guppies from the high predation environment contained fewer benthic invertebrates and more algae after a 28 d period than mesocosms with guppies from the low predation pressure environment (Bassar et al. 2012). In total, 9 of 13 ecosystem variables

measured by Bassar et al. showed significant river-of-origin effects. The authors attributed these differential effects on ecosystem functioning, in part, to differences in foraging behavior by guppies adapted to the different stream environments. However, Bassar et al. (2012) measured only one behavioral variable directly in their experiment (pecking at the substrate) and this behavior did not differ in fish from high predation and low predation sites. Thus, it is possible that other phenotypic differences between the populations caused the observed ecosystem effects. Harmon et al. (2009) and Des Roches et al. (2013) conducted similar types of mesocosm studies comparing the ecosystem effects of two threespine stickleback morphotypes (benthic and limnetic; McPhail 1993; Schluter 2000) and found significant effects of stickleback type on a variety of ecosystem functions. Again, behavioral variation was not specifically measured in these ecosystem studies, but previous work on stickleback morphotypes has shown pronounced differences in foraging behaviors between benthic and limnetic forms (e.g., Schluter 1993). Thus, while no studies that we are aware of definitively link variation in behavioral traits to effects on ecosystem functioning, the potential for such effects clearly exists and there is abundant opportunity for both theoretical and empirical studies that specifically examine the consequences of inter-individual variation in behavioral types to communities and ecosystems.

MANAGEMENT IMPLICATIONS OF BEHAVIORAL TYPES

When considering the ecological consequences of behavioral trait variation at the individual and population level, it is important to remember that these consequences are dependent on environmental context. For example, bold behavioral types may be less fit than shy behavioral types in an environment with high levels of predation, while the opposite may be true in an environment without predators. Therefore, human impacts on the environment, such as recreational angling, commercial fishing, and hatchery-reared stocking programs, are likely to affect the ecological consequences of consistent inter-individual behavioral variation. For example, bolder individuals may be more vulnerable to angling,

which could decrease their fitness relative to more timid individuals and result in the population becoming less bold on average. In the same way, hatchery rearing programs may select for certain behavioral types, resulting in hatchery stocks that differ genetically from wild populations (Huntingford 2004; Fraser 2008). Additionally, the hatchery environment can cause differences in the way behavioral traits develop with ontogeny. We summarize in Table 4 what is known about the management implications of behavioral trait variation and discuss these implications in more detail below. We note that many of the studies summarized in Table 4 have compared behavioral traits of different groups of fish (high vs. low angling vulnerability; domestic vs. wild stock), as opposed to comparing behavioral differences among individuals within a population.

Fishing

It is increasingly recognized that fishing pressure (recreational angling and commercial fishing) may alter the individual-level consequences of behavioral types, which in turn could affect natural selection and the evolution of population characteristics (Uusi-Heikkilä et al. 2008; Philipp et al. in press). For example, in non-fished populations of species that build and guard nests or redds, aggressive individuals may defend their nests more vigilantly from potential predators, increasing egg and larval survivorship. However, the introduction of angling could turn high nest guarding aggressiveness into a detriment if aggressive nest guarding individuals are more likely to be caught than their less aggressive counterparts (e.g., as shown by Cooke et al. 2007). Removal of the nest-guarding parent (even short-term removal by catch-and-release angling), can greatly increase the probability of egg and larval mortality (Siepker et al. 2007). Personality traits also have the potential to affect angling vulnerability outside of the nesting season (though the traits may be different).

The hypothesis that recreational angling can affect the relationship between behavior and reproductive success is supported by the previously mentioned study on reproductive success and

parental care in two largemouth bass lines selected for different vulnerabilities to angling during the non-nesting season. Bass from the line selected for high vulnerability to angling showed increased levels of aggression towards potential nest predators and greater diligence of parental care compared to bass from the low vulnerability line. Importantly, the high vulnerability line was also found to have the highest reproductive potential (Sutter et al. 2012). Thus, angling can reduce reproductive success and lower total reproductive output not only in current generations but also impact selection for traits associated with nest guarding behavior, potentially leading to reduced reproductive success and lower total reproductive output in future generations as well. Furthermore, as angling almost certainly selects for traits that reduce angling vulnerability, high levels of recreational angling are likely to impact the ability of the population to provide recreational angling opportunities in the future. This result was recently documented in bass populations that have historically been exposed to different levels of angling intensity (Philipp et al. in press).

As discussed earlier, bolder individuals in some fish species have been found to forage more actively and grow faster than their shyer counterparts. Angling, however, could alter the ecological consequences of boldness, shifting the balance towards shyer foragers if bold fish are captured more frequently. A recent study by Nannini et al. (2011) compared the foraging behaviors of individual largemouth bass obtained from the two artificially selected high and low angling vulnerability lines previously described. Contrary to expectations, fish from the low vulnerability line actually captured more prey (and attempted to capture more prey) than fish from the high vulnerability line. The low vulnerability line also had higher prey rejection rates and was more efficient at converting consumed prey into growth than the high vulnerability line (Nannini et al. 2011). While this study clearly demonstrates the potential for angling during the non-nesting season to have a selective effect on foraging behavior, it also cautions against jumping to conclusions about what behavioral types are likely to be associated with increased angling vulnerability. Only one study that we are aware of has explicitly

tested the link between an individual's boldness and angling vulnerability during the non-nesting season. Wilson et al. (2011) found that more timid bluegill were more likely to be caught by angling than their bolder counterparts in a natural lake – again, a result opposite of expectations. These early studies highlight the need for more research on the link between fish behavioral traits and responses to angling during the nesting and non-nesting seasons at the individual and population levels. However, unlike the relatively recent focus on the evolutionary impacts of recreational angling, the impacts of commercial fishing on fish life histories, growth rates, and behaviors have been studied for a much longer time.

Several studies over the last two decades have documented that the selective harvest of large individuals by commercial fisheries leads to decreased growth rates in future generations, as well as a variety of other effects (e.g., Conover and Munch 2002; Hutchings 2004; Reznick and Ghalambor 2005; Walsh et al. 2006). More recently, it has been proposed that commercial harvest may also selectively target individuals based on their behavioral type and growth rate, irrespective of size. As Uusi-Heikkilä et al. (2008; page 419) note, “fishing-induced selection directly acting on behavioral rather than on life-history traits per se can be expected in all fisheries that operate with passive gears such as trapping, angling and gill-netting”. Biro and Post (2008) found exactly this result in an experimental study of rainbow trout in Canadian lakes, where faster-growing individuals were found to be more vulnerable to harvest by gill nets irrespective of their size. The authors attributed the greater vulnerability of faster-growing individuals to differences in their behaviors, as faster-growing fish were more active and bolder than their slower-growing, non-harvested counterparts (Biro and Post 2008). Even if commercial fishing does not select directly on behavioral traits, early findings from the pace-of-life syndrome suggest that direct selection on one trait, be it a behavioral trait like boldness or a life-history trait like growth rate, likely leads to indirect selection on a whole suite of correlated traits. These effects can have important impacts on species performance as well as community dynamics, making it essential that fisheries managers consider these effects when making management decisions.

Hatchery rearing

Hatchery rearing and fish stocking represent the opposite-side of the coin from fish harvest; i.e., they add rather than remove fish from a population. But, like selective harvest, hatchery programs designed to supplement the abundance of wild populations can impact behavioral variation and may have important ecological consequences. It is well known that fish raised in hatchery environments often perform poorly when stocked into the wild (Araki et al. 2008) and there is a long-standing debate on whether or not hatchery stocking demographically boosts wild populations. For this reason, there is a wealth of literature examining how hatchery selection, including both purposeful selection on desirable traits (such as increased growth rate) and unintentional selection resulting from rearing experiences, may affect fitness (see reviews by Huntingford 2004; Huntingford and Adams 2005; Araki et al. 2008; Fraser 2008). Changes in behavioral phenotypes due to domestication selection have been suggested to be a major factor contributing to the poor performance of hatchery-reared fish stocked into the wild (Fraser 2008).

Effects of artificial selection on behavior

Common garden studies demonstrate that offspring from hatchery-reared adults are often bolder and/or more aggressive than those from wild stocks (e.g. Berejikian 1995; Einum and Fleming 1997), and laboratory studies comparing the behaviors of domestic and wild strains have found that domestic strains tend to be bolder and more aggressive than their wild counterparts (Budaev and Brown 2011; Conrad et al. 2011). For example, fry from sea-ranched brown trout parents initiated feeding sooner and bit at a novel object more often than fry from wild brown trout parents (Sundström et al. 2004). Domesticated strains of fishes often undergo selection aimed at increasing production traits such as rapid growth (Huntingford 2004). However, selection for increased growth rate can have

unintentional consequences on behavioral trait variation, either by altering variation in the behavioral traits themselves (e.g., selecting for individuals that are more bold/aggressive/active in their feeding behaviors), or selecting on metabolic traits that may cause individuals to act more boldly to fulfill their metabolic needs (see prior discussion on this topic).

Behavioral traits that confer an advantage to individuals in a hatchery environment may carry a cost in nature. The most obvious examples involve feeding behaviors in the absence or presence of predators. The work by Biro and colleagues discussed earlier nicely documents how domesticated trout strains grow faster but suffer higher mortality than wild fish when stocked into natural lakes with predators (Biro et al. 2006, 2007). Looking at foraging behavior in a different context, Adriaenssens and Johnsson (2011b) assayed hatchery-reared and wild-origin brown trout for cognitive tasks such as cryptic prey discovery and maze solving. They found that hatchery-reared trout had higher feeding rates than wild fish, but they did so with less accuracy. In the wild, lowered accuracy in foraging may incur energetically costly errors such as prey misidentification, whereas higher foraging rates may be advantageous in hatchery settings with consistent food dispersal (Adriaenssens and Johnsson 2011b).

The behavioral syndromes approach has been applied to determine whether selection on behaviors in the hatchery environment (e.g., propensity to feed in a predator-free environment), may influence the distribution of behaviors expressed in other environments (e.g., aggressiveness, boldness under predation risk). For example, Lee and Berejikian (2008) found that juvenile rockfish (*Sebastes auriculatis*) that fed at high rates in the absence of a predator also tended to feed at higher rates when a model predator was present. However, they found the behaviors of individuals were inconsistent across two assay periods (8-12 days apart), suggesting plastic responses and behavioral flexibility. In contrast, a study using rainbow trout found that individuals were consistent in their behaviors over 2-3 days and across safe/unsafe contexts (Conrad and Sih 2009). Behavioral flexibility may be important when determining whether selection on fast growth rates has unintentional consequences on associated

behaviors. Selection may be limited if individuals are capable of changing behavior in response to their environment. Alternatively, if behaviors are tightly correlated and not plastic, selection for high growth rates is likely to also select for bold and aggressive individuals. Determining the degree to which individuals (or species) differ in their behavioral plasticity (e.g., Figure 2), and understanding how early development and rearing environment may affect levels of behavioral plasticity, are important areas for future research (Dingemanse et al. 2010; Dingemanse and Wolf 2013).

The effects of hatchery rearing environments on behavior

The process of raising juvenile fish in hatchery environments has been shown to affect the cognitive pathways that influence behavior (Huntingford and Adams 2005). Enrichment strategies, such as providing physical structure, decreasing fish densities, feeding with live prey, and introducing simulated predator attacks have been suggested to better prepare hatchery fish for stocking (Brown et al. 2003; Lee and Berejikian 2009; Brockmark and Johnsson 2010; Brockmark et al. 2010; see review in Huntingford 2004). All of these modifications to current hatchery conditions have been shown to benefit hatchery-reared fish in ways that could increase post-stocking survival. For example, brown trout assigned to “low” and “moderate” rearing density treatments showed superior skills when tested for their ability to locate food, identify novel prey as resources, and respond to predators (Brockmark et al. 2010). Additionally, when stocked into an experimental stream, fish that were reared in high densities showed decreased survival relative to individuals reared at low or medium density (Brockmark et al. 2010). Individuals that were reared with physical structure, fed natural prey, and subjected to simulated attacks showed decreased boldness relative to individuals raised under conventional hatchery conditions (Roberts et al. 2011). When comparing both the presence and stability of physical structure during rearing, Lee and Berejikian (2009) found that stable structures (the “unstable” treatment moved structure throughout the experiment) were important for individuals to assess current risk and display

behaviors accordingly. Individuals reared with stable structure were more explorative without predators, but showed reduced exploration under predation threat. Thus, there is accumulating evidence suggesting that the hatchery experience itself affects behaviors that can have important implications for fish stocked into the wild (e.g., impacts on habitat use, growth, and survival). Encouragingly, these studies demonstrate that carefully considering rearing experiences of hatchery fish and attempting to replicate natural environments could be a promising direction for hatcheries.

Although a number of studies have investigated individual behaviors of hatchery-reared fish in lab settings and others have compared how hatchery strains compare to wild strains, comparatively few studies have evaluated how the behaviors of hatchery-reared fish influence their fitness in natural environments. In one recent study, Moore et al. (2011) examined the field survival and migration rates of hatchery-reared steelhead trout compared to fish of wild origin across three years. As an additional component, the hatchery-reared fish were from two hatcheries that differed in rearing environment (stocking density and shape of tanks). Fish that were reared under lower densities and in circular tanks (thought to decrease effects of density), survived as well as wild steelhead. However, fish raised at higher densities and in rectangular raceways showed decreased survival relative to wild fish. Moore et al. (2011) also found that migration ranges for steelhead from both hatcheries were less than those of wild steelhead. This study suggests that changes in conventional hatchery rearing may facilitate behavioral flexibility and the development of cognitive skills fish need upon entering natural systems. However, to justify these changes, more field studies examining fitness of individuals subjected to various enrichment regimes are needed to understand how these changes affect survival in natural conditions.

DISCUSSION

Fish have proven to be excellent model organisms for the study of animal personalities, providing some of the earliest demonstrations of behavioral trait variation in any species (e.g., Huntingford 1976, 1982; Ehlinger and Wilson 1988) and continuing today as one of the most studied taxonomic groups (Stamps 2007; Toms et al. 2010; Budaev and Brown 2011; Conrad et al. 2011). Still, as Wolf and Weissing (2012) and others have noted, relatively little attention has been paid to the ecological consequences of varying behavioral types. This comment applies to all species, not just fish, and is especially true of studies conducted in natural or semi-natural environments. Our review has sought to summarize what ecologists, behaviorists, and managers know about the ecological consequences of behavioral types at the individual, population, and community/ecosystem levels, including implications for fisheries management and conservation. Important research foci in this area include the impacts of behavioral trait variation on: individual growth and survival, nesting behaviors and reproductive success, habitat use, diet, and ontogenetic niche shifts, migration and dispersal, commercial and recreational fishing, and hatchery rearing for supplemental stocking. We discuss these different research foci below and suggest avenues for future research.

Examining behavioral type effects on growth and survival

The concept of a growth-mortality tradeoff is firmly entrenched in the ecological literature (e.g., Werner and Anholt 1993; Lima 1998), and a growth-mortality tradeoff provides much of the theoretical underpinning for the maintenance of behavioral variation in boldness in fish and other organisms (e.g., Stamps 2007). Thus, it is surprising that evidence from natural or semi-natural environments documenting the effects of variation in boldness and/or aggression on fish growth or survival is limited and is almost entirely based on comparisons of wild and domesticated stocks (e.g., Biro et al. 2003a,b). This is not to question the reality of a growth-mortality tradeoff, or to doubt its relationship to fish

behavioral traits, but only to note that much more work is needed to examine how individual variation in boldness affects growth and survival. Archard and Braithwaite (2010) discuss some of the challenges involved in studying the consequences of behavioral traits in wild animals. They note that a particularly hard nut to crack is the effect of behavioral type on the survival of free-living individuals, because the recovery of marked individuals is often very low (see Höjesjö et al. 2011 for an example with fish). The low recovery of marked individuals leaves us wondering, are missing individuals dead? Or, have they simply dispersed from the study area? Studies conducted in closed, semi-natural environments (experimental ponds, outdoor raceways, or fenced reaches of streams), where all surviving individuals can be recovered post-stocking, can provide useful experimental systems for testing the growth-mortality tradeoff and its relationship to boldness variation in fishes.

Diet, habitat use, and ontogenetic niche shifts

Fish, like many other organisms, show pronounced changes in diet and habitat as they grow. For example, most piscivorous fish begin life feeding on zooplankton and benthic invertebrates before reaching a size where they can switch to feeding on other fish (Mittelbach and Persson 1998). Many other fishes occupy protective habitats (e.g., littoral zone vegetation) when small and vulnerable to predators, and then shift to feeding in more open and riskier habitats when they reach sizes that are less vulnerable to predation (Werner et al. 1983; Werner and Hall 1988). These ontogenetic niche shifts have important consequences for population dynamics and species interactions (de Roos and Persson 2013). However, a completely unexplored question is - what role does personality play in determining the timing and extent of ontogenetic niche shifts, in fish or other organisms?

Studies documenting ontogenetic niche shifts in diet and habitat invariably show considerable variation amongst individuals (e.g., Mittelbach 1981; Werner and Hall 1988; Hjelm et al. 2000). How much of this individual variation in the timing and extent of ontogenetic niche shifts is due to differences

in personality? Consider for example the study by Post (2003), who examined the factors contributing to the onset of piscivory in a cohort of young-of-year (YOY) largemouth bass. In bass and other piscivores, becoming piscivorous in the first summer of life greatly increases fitness by increasing the probability of surviving through the winter (Buijse and Hourthuijzen 1992; Post et al. 1998). Post (2003) found that only the largest individuals in the YOY bass cohort from Paul Lake, Michigan were able to successfully transition to feeding on YOY bluegill during their first summer. Further, all bass that grew large enough to become piscivorous in their first year were born early in the spring (Figure 5). Birth date, however, was by itself a poor predictor of either bass size in August or the propensity to shift to piscivory (i.e., many early-born bass didn't get large enough to become piscivorous; Figure 5). Why did some early-born bass grow quickly and become piscivorous in their first summer, whereas others did not? Chance could of course play a role; e.g., some individuals may have been lucky enough to find and consume a large number of energetically rewarding prey early in life and get a jump on their less-fortunate fellows. However, it's tempting to speculate that differences in personality may contribute as well. In this case, the hypothesis would be that those early-born bass growing large enough to become piscivorous are individuals that are relatively bold and take greater risks to increase their feeding rate, either by being more active or by using riskier habitats. No studies to date have examined the impact of behavioral types on the timing of ontogenetic niche shifts. This seems a particularly ripe area for future research.

Consistency in behavioral traits across life stages and fitness tradeoffs

Numerous studies have documented consistency in behavioral traits or behavioral syndromes in fish and other organisms over relatively short time periods of days and weeks (Bell et al. 2009; Conrad et al. 2011). However, much less is known about consistency in behaviors across longer time periods or across life stages. Wilson and Godin (2009) found that shy-bold behavioral types showed differential consistency in bluegill sunfish over a 1-3 month period (measured in the field). However, Bell and

Stamps (2004) and Edenbrow and Croft (2011) observed little differential consistency in individual behavioral types between life stages (e.g., juveniles to adults) in threespine sticklebacks and mangrove killifish (*Kryptolebias marmoratus*) respectively (measured in the lab). In a study of how behavioral consistency changed across ontogeny in an Africa cichlid (*Steatocranus casuarius*), Budaev et al. (1999) found that behaviors (response to a novel environment, a novel fish, and a mirror) were not consistent in juveniles (4 and 4.5 months of age), but were consistent in adults (12-13.5 months). Bell and Stamps (2004) measured three types of behavior (activity, aggression toward a conspecific, and boldness under predation risk) at three developmental stages (juvenile, subadult, and adult) and found that individual behavioral types were not stable over ontogeny. In one stickleback population, the boldness-aggression behavioral syndrome was stable over ontogeny (showed structural consistency), but in another population it was not. Edenbrow and Croft (2011) also found that behavioral types of boldness and exploration were highly plastic during ontogeny, but that correlations between these two behaviors (i.e., bold types were more exploratory) were maintained from juvenile to adulthood (structural consistency; see also Schürch and Heg 2010, Chervet et al. 2011).

Studies with aquatic organisms other than fish have observed differential consistency in activity traits across life stages: e.g., tadpole to adult frog (*Rana ridibunda*; Wilson and Krause 2012a), nymph to adult damselfly (*Lestes congener*; Brodin 2009). In general, however, we know very little about the differential consistency of behavioral traits across life stages (e.g., juvenile to adult) or in individuals undergoing ontogenetic niche shifts (e.g., freshwater to marine, benthic to pelagic, insectivorous to piscivorous). Clearly, such long-term differential consistency in behavioral traits has important implications for fitness and for the maintenance of variation in behavioral traits in populations.

If behavioral traits have differential consistency only over short-intervals, then the potential for fitness tradeoffs to contribute to the maintenance of variation in behavioral traits is rather limited. However, if behavioral traits are consistent across life stages or across ontogenetic niche shifts, then

there are many more opportunities for tradeoffs to occur. For example, it is commonly assumed that boldness may have a positive effect on individual fitness through increased energy gain and/or reproductive success, but a negative effect due to reduced survival (Stamps 2007; Smith and Blumstein 2008). If fish that are relatively bold as juveniles are also relatively bold as adults, then boldness could positively affect fitness at the juvenile stage through higher feeding rates/energy gains and at the adult stage through greater reproductive output (per breeding event), but negatively affect fitness at the juvenile stage due to decreased survival, and/or negatively affect reproductive success at the adult stage due to decreased survival during a reproductive event and/or reduced probability of surviving to reproduce again. Thus, there are multiple ways in which boldness effects on growth, fecundity, and survival could trade off to affect lifetime fitness.

To date, studies that have investigated the relationship between behavioral traits and fitness have generally focused on a single measure of fitness (such as survival) at a specific life stage (Dingemanse and Réale 2005; Smith and Blumstein 2008). However, fitness tradeoffs across life stages or between different components of selection (sexual and viability), provide a potentially powerful mechanism for the maintenance of adaptive variation in behavioral traits. Moreover, if behavioral traits are heritable, the fitness consequences of animal personalities can extend across generations.

Heritability of behavioral traits and consequences arising from the release of domesticated fish

Although there are relatively few estimates of the heritability of behavioral traits in fishes, the evidence suggests that many behavioral traits are heritable, with levels of heritability that are generally lower than those for morphological traits, but roughly comparable to those measured for life-history traits (Bakker 1986; Stirling et al. 2002; Bell 2005; Brown et al. 2007; Dingemanse et al. 2009; Chervet et al. 2011). Additionally, researchers have been able to artificially select stocks of largemouth bass to express high and low vulnerability to recreational angling (Sutter et al. 2012), demonstrating again a

strong genetic component to certain aspects of fish behavior. The heritability of behavioral traits has many important ecological implications, particularly with regard to the mixing of wild and domestic fish stocks.

Fisheries biologists have long been concerned with potential consequences of interbreeding between wild, hatchery-reared, or escaped farmed fish, particularly salmon, (e.g., Gross 1998). This concern has been largely focused on the detrimental effects of introducing non-adaptive life-history traits into wild stocks (causing, for example, a mismatch in the timing/orientation of migration and reproduction). However, interbreeding between wild and domestic stocks (e.g., farmed or hatchery-reared fish) could influence behavioral traits as well, with unknown consequences for wild fish. A number of studies comparing domestic and wild strains of salmon and trout show that hatchery-reared fish, or fish that have been genetically modified for faster growth, may be bolder, more aggressive, and/or more risk-prone in their habitat use, resulting in higher growth rates but reduced survival in nature (e.g., Abrahams and Sutterlin 1999; Sundström et al. 2003, 2004; Biro et al. 2003a,b, 2004, 2007; Sundt-Hansen et al. 2009). To the extent that behavioral traits are heritable and adaptive, the interbreeding of domestic and wild fish stocks has the clear potential to reduce the fitness of locally adapted stocks.

Commercial and recreational fishing may also select on heritable behavioral traits that have unanticipated evolutionary consequences. One possibility discussed earlier is the association between boldness/aggression in nest guarding behavior and angling vulnerability in largemouth bass. Male bass that are bolder and more aggressive are more diligent in guarding their young and have higher reproductive success (Cooke et al. 2007). However, bolder/more aggressive bass may also be more vulnerable to recreational angling (Suski and Philipp 2004). Thus, if boldness and aggression are heritable traits (see Bell 2005), then increased fishing pressure may lead to the evolution of reduced boldness/aggression in the population, a reduction in angling vulnerability, and the unwelcome

consequence of a reduction in average reproductive success (Sutter et al. 2012). Here again, an understanding of the correlations among behaviors, combined with a knowledge of their heritabilities, and their ecological consequences at different life stages, is an important avenue for future research for the effective management of fish stocks.

SUMMARY

Inter-individual variation in behavioral traits is now recognized to be an important feature of most animal populations, including fish. In this review, we have sought to highlight some of the mechanisms driving the evolution and maintenance of variation in behavioral traits within fish populations, as well as the ecological consequences of this variation. Field evidence for the ecological consequences of behavioral trait variation is still quite limited in any group of organisms. However, there is little doubt that behavioral trait variation plays an important role in the growth, survival, and reproductive success of individuals, as well as having potential impacts on species interactions and ecosystem functioning. It is also clear, however, that we must be careful not to jump to conclusions about the universality of the causes and consequences of behavioral trait variation (e.g., the growth-mortality tradeoff) without more evidence from nature. In fishes, behavioral trait variation has added implications for conservation, harvest, and resource management. Biologists and managers recognize the importance of environmental context to the evolution of behavioral traits and the role that behavioral variation among individuals and between populations (wild versus domestic stocks) may play in successful stocking and conservation. Again, more data from field studies, especially with tagged/marked individuals of known behavioral types, is crucial.

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APPENDIX

Table 1. Glossary of terms related to animal personality.

Term	Definition
Behavior/ behavioral response	An individual's action or response at a given time in a given context
Behavioral/personality trait	A behavioral pattern that characterizes consistent individual differences in behavior in a given type of situation. For example, boldness characterizes consistent individual differences in behavior in situations that involve risk.
Behavioral/personality type	An individual's consistent response over a given period of time relative to other individuals for one or more behavioral traits. For example, an individual could be relatively bold or shy in situations that involve risk-taking.
Animal personality	A behavioral pattern that can describe multiple behavioral traits and the relationship between those traits across time (Caspi et al. 2005; Réale et al. 2007; Stamps and Groothuis 2010).
Differential consistency	Consistency between individuals in a particular behavior (or behavioral trait) across time (Stamps and Groothuis 2010).
Contextual generality	Consistency between individuals in behaviors measured in different contexts (e.g. activity in a safe, familiar environment and activity in an unfamiliar environment).
Structural consistency	Consistency across time in the correlation between two behaviors in a group (Stamps and Groothuis 2010).
Behavioral syndrome	Correlated suites of behaviors. Such correlations may occur within an individual (i.e., an individual's tendency to behave in a certain way may be correlated across contexts or over time). In this sense, behavioral syndromes and animal personalities describe similar phenomena. A behavioral syndrome also may describe a correlation between two or more behavioral traits between individuals in a population (e.g., boldness and aggression are commonly correlated when examined in a group of individuals; Sih and Bell 2008).
Pace-of-life syndrome	A suite of covarying behavioral, physiological, and life-history phenotypic traits arrayed on a continuum from "slow" to "fast" life-styles.

Note: Definitions refer to how terms are used in the current text and are not meant to resolve disputes in meaning. See also: Stamps and Groothuis (2010); Wolf and Weissing (2012).

Table 2. Summary of evidence for the ecological consequences of behavioral types in fishes at the individual level.

Consequence	Trait(s)	Result	Study	Study Method
Dispersal	Boldness	Bolder fish had a higher propensity to disperse.	Fraser et al. 2001	Field
	Sociability	More asocial fish had a higher tendency to disperse.	Cote et al. 2010	Lab
Social network	Boldness	Bolder fish had fewer total social connections and the average strength of the connections were weaker.	Croft et al. 2009	Field
Growth	Exploration and Aggressiveness	Slow explorers grew faster. Aggressiveness was not related to growth.	Adriaenssens and Johnsson 2011a	Field
	Boldness	No correlation between boldness and growth.	Höjesjö et al. 2011	Field
	Boldness	Bolder fish grew faster.	Ward et al. 2004	Lab
Survival	Boldness	Bolder fish were preyed on more.	Dugatkin 1992	Lab
	Exploration and Aggressiveness	Neither exploration nor aggressiveness was related to survival.	Adriaenssens and Johnsson 2011a	Field
	Exploration	More exploratory individuals had higher survival.	Adriaenssens and Johnsson 2011a	Field
	Boldness	No correlation between boldness and survival.	Höjesjö et al. 2011	Field
	Activity, Boldness, and Exploration	More active, bold, and exploratory individuals survived longer with predators.	Smith and Blumstein 2010	Lab

Table 2 (cont'd).

Consequence	Trait(s)	Result	Study	Study Method
Social status	Boldness	Bolder fish were more dominant.	Dahlbom et al. 2011	Lab
	Aggressiveness, Boldness, and Activity	Males that were more aggressive, bolder, and more active had higher positions in the dominance hierarchy.	McGhee and Travis 2010, Colleter and Brown 2011	Lab Lab
Reproduction	Boldness	Females chose bolder males as mates.	Godin and Dugatkin 1996	Lab
	Aggressiveness	Females chose low or moderately aggressive males, whereas highly aggressive males were rarely chosen.	Ward and Fitzgerald, 1987	Lab
	Boldness and Activity	Assortative mating based on personality type.	Budaev et al. 1999	Lab
	Boldness and Aggressiveness	Bolder and more aggressive male zebrafish fertilized more eggs.	Ariyomo and Watt 2012	Lab
Survival of offspring during parental care	Aggressiveness	Females that were more aggressive in guarding their nests from threats were found to stay on their nests longer.	McPhee and Quinn 1998	Field
Habitat use	Aggressiveness, Boldness, and Activity	More aggressive individuals were found more frequently in open water whereas less aggressive individuals were found in or near structured refuge. No relationship between boldness and aggression was found.	Kobler et al. 2011	Field
Migration	Boldness	Bolder fish were found to have a higher propensity to migrate.	Chapman et al. 2011	Field

Table 3. Summary of evidence for the ecological consequences of behavioral types in fishes at the population and community level.

Consequence	Trait(s)	Result	Study	Study Method
Population performance	Boldness	Full bold and mixed shoals approached food more than full shy shoals. Mixed shoals fed most.	Dyer et al. 2009	Lab
	Boldness	Shoal group behavior was impacted by the frequency of boldness types within the shoal. Bold individuals especially impacted shoal behavior.	Magnhagen and Bunnefeld 2009	Lab
Social structure	Boldness	Populations of all shy fish had stronger social structures and were more cliquish than populations of all bold fish.	Pike et al. 2008	Lab
Predator-prey	Boldness	Prey where more heavily preyed upon by bolder fish.	Ioannou et al. 2008	Lab
Interspecific competition	Boldness	Bolder behavioral types were found to consume more prey regardless of species in heterospecific competitive foraging trials.	Webster et al. 2009	Lab
Invasiveness	Boldness	No relationship between boldness and invasiveness.	Rehage and Sih 2004	Lab

Table 4. Summary of the effects of angling and hatchery rearing on behavioral traits in fishes and their ecological consequences.

Comparison	Variables	Result	Study	Study Method
Between individuals	Angling vulnerability with reproductive success, anti-predator aggression, and parental care	Male bass that have a high vulnerability to angling demonstrated greater anti-predator aggression and parental care and have higher reproductive success.	Sutter et al. 2012	Field
Between individuals	Angling vulnerability and foraging behavior	Bass that have a low vulnerability to angling foraged more frequently and also had more successful foraging attempts.	Nannini et al. 2011	Field
Between individuals	Boldness, angling vulnerability	Bolder bluegill were found to be less vulnerable to angling than more timid bluegill.	Wilson et al. 2011	Lab and Field
Domestic, wild strains	Boldness, dominance	Domestic fish initiated feeding sooner, but no difference in latency to approach novel object. Domestic fish bit at novel object more. All bold fish, regardless of origin were socially dominant.	Sundström et al. 2004	Lab
Hatchery vs wild rearing, low vs. high density hatcheries	Survival, Migration	Hatchery-reared fish showed similar survival over three years, but only for fish reared in lower densities and circular tanks. Migration ranges smaller for hatchery fish.	Moore et al. 2011	Field

Table 4 (cont'd).

Comparison	Variables	Result	Study	Study Method
Between individuals	Boldness	Behavioral syndromes found between behavior with and without predators, behaviors plastic during 16 weeks in hatchery environment.	Lee and Berejikian 2008	Lab
Rearing conditions with structure vs. without structure	Exploration	Individuals reared with stable structure increased exploration without predators, but no difference in structure treatments with predators.	Lee and Berejikian 2009	Lab
Conventional vs. enriched rearing	Boldness	Individuals subjected to simulated predator attacks, physical structure, and natural prey showed decreased boldness than conventional rearing.	Roberts et al. 2011	Lab
Low, medium, conventional rearing densities	Survival, Exploration, Boldness	Fish from lower densities consumed more prey, increased predator response, located food in a maze faster, and increased survival in field.	Brockmark et al. 2010	Lab and Field

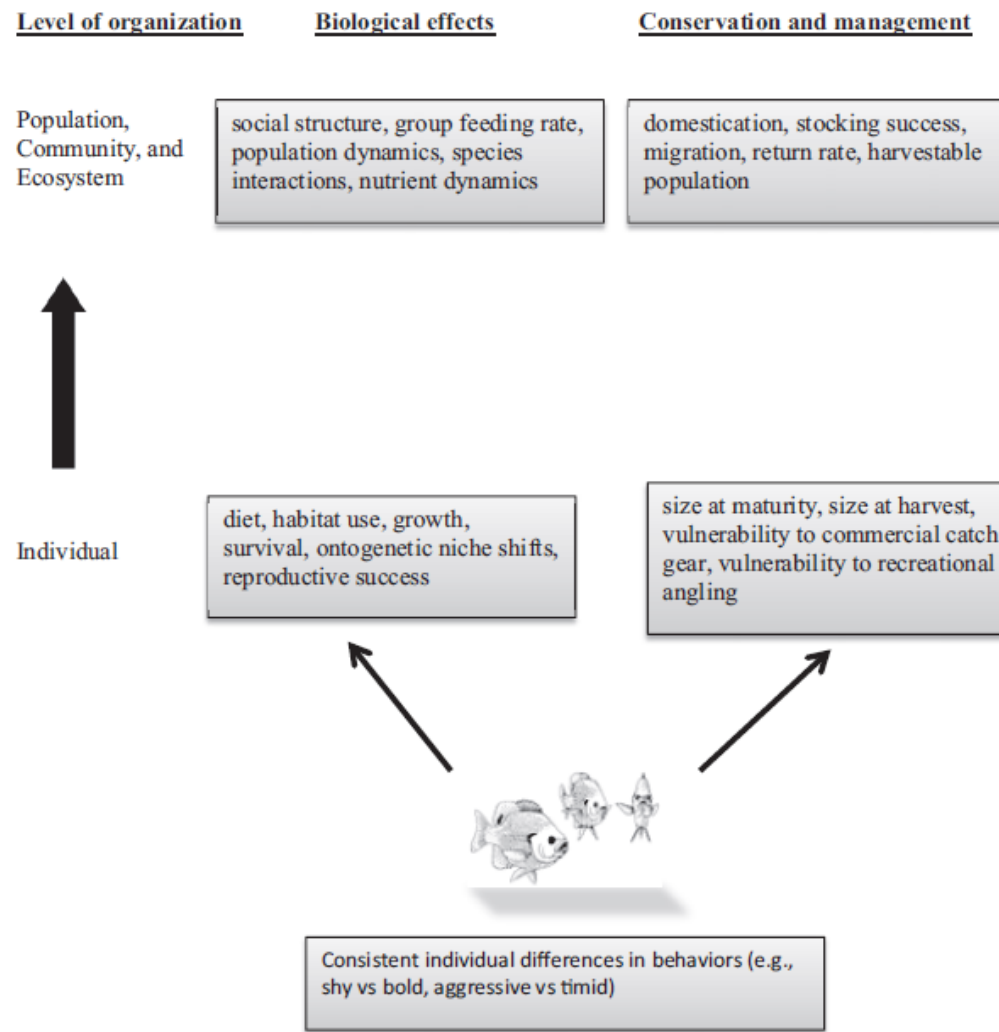


Figure 1. The consequences of variation in fish behavioral types may be expressed at different levels of ecological organization (from individuals to ecosystems) and have implications for conservation and management, as well as basic biology.

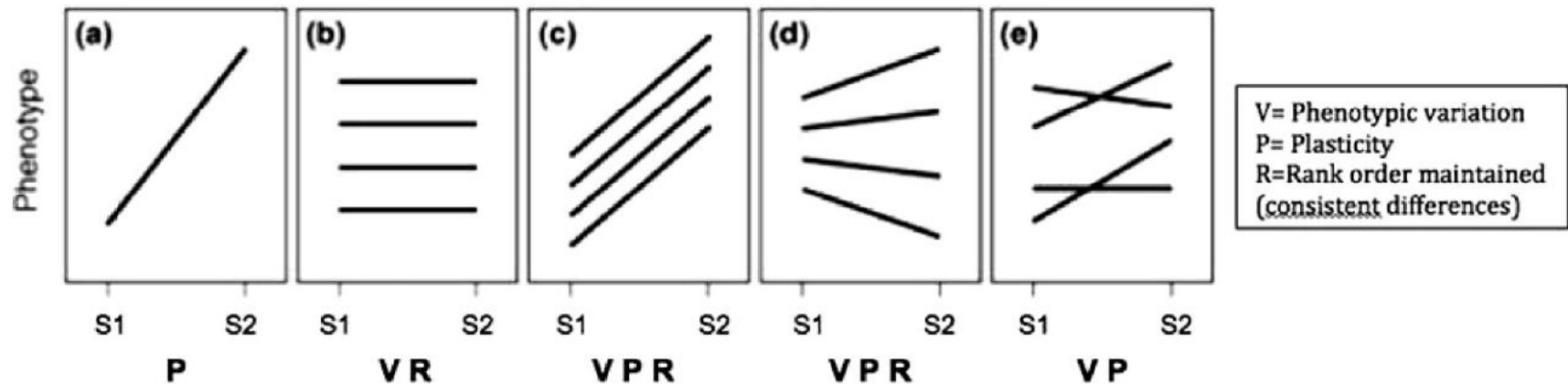


Figure 2. Five scenarios (a-f), each depicting the behavior of four individuals (solid horizontal lines) in two different situations (S1 and S2). In scenario a, all individuals display the same phenotypes in both S1 and S2 and there is plasticity between situations. In scenario b, there is phenotypic variability in situations S1 and S2 (equal between situations), no plasticity between situations, and consistent inter-individual differences in phenotype between situations. In scenario c, there is phenotypic variability in situations S1 and S2 (equal between situations), plasticity between situations, and consistent inter-individual differences in behavior. In scenario d, there is unequal phenotypic variation between situations S1 and S2 (S2 has much more), inter-individual differences in plasticity between situations (the individual with the smallest phenotype has high individual plasticity while the individual with the second smallest phenotype demonstrates a lower level of plasticity), and consistent inter-individual differences in behavior (perfect consistency in rank order but less in the raw values). In scenario e, there is phenotypic variability in situations S1 and S2, plasticity between situations, but individuals do not show consistent differences in behavior across situations because of differential directionality in responses. Modified from Dingemanse et al. (2010).

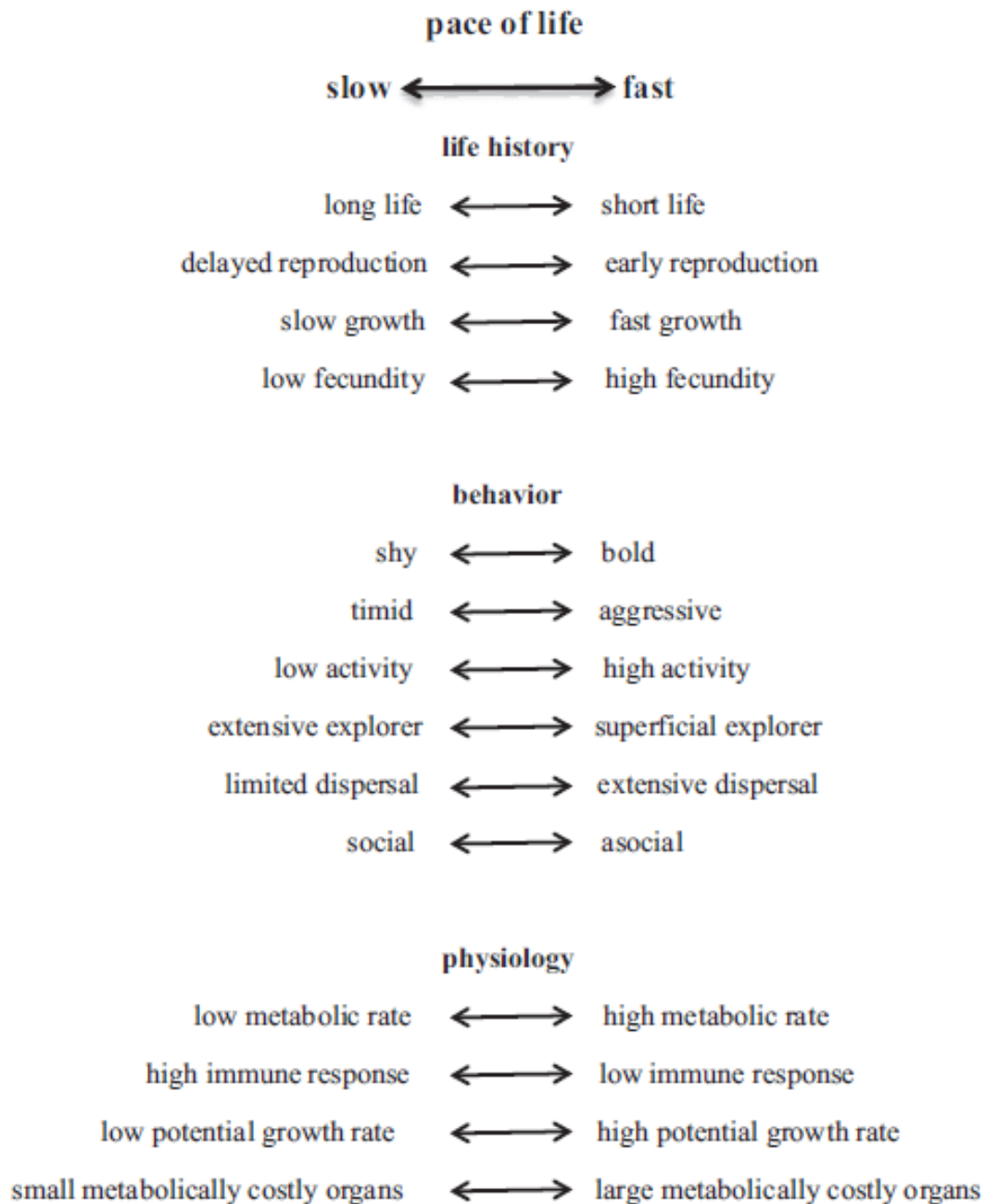


Figure 3. A representation of different phenotypic traits along the pace-of-life continuum. Double arrows illustrate presumed continuous variation in a trait, with traits grouped under life-history strategies, behavior, and physiology, and distributed along a pace-of-life continuum from “slow” to “fast”. Modified from Réale et al. (2010).

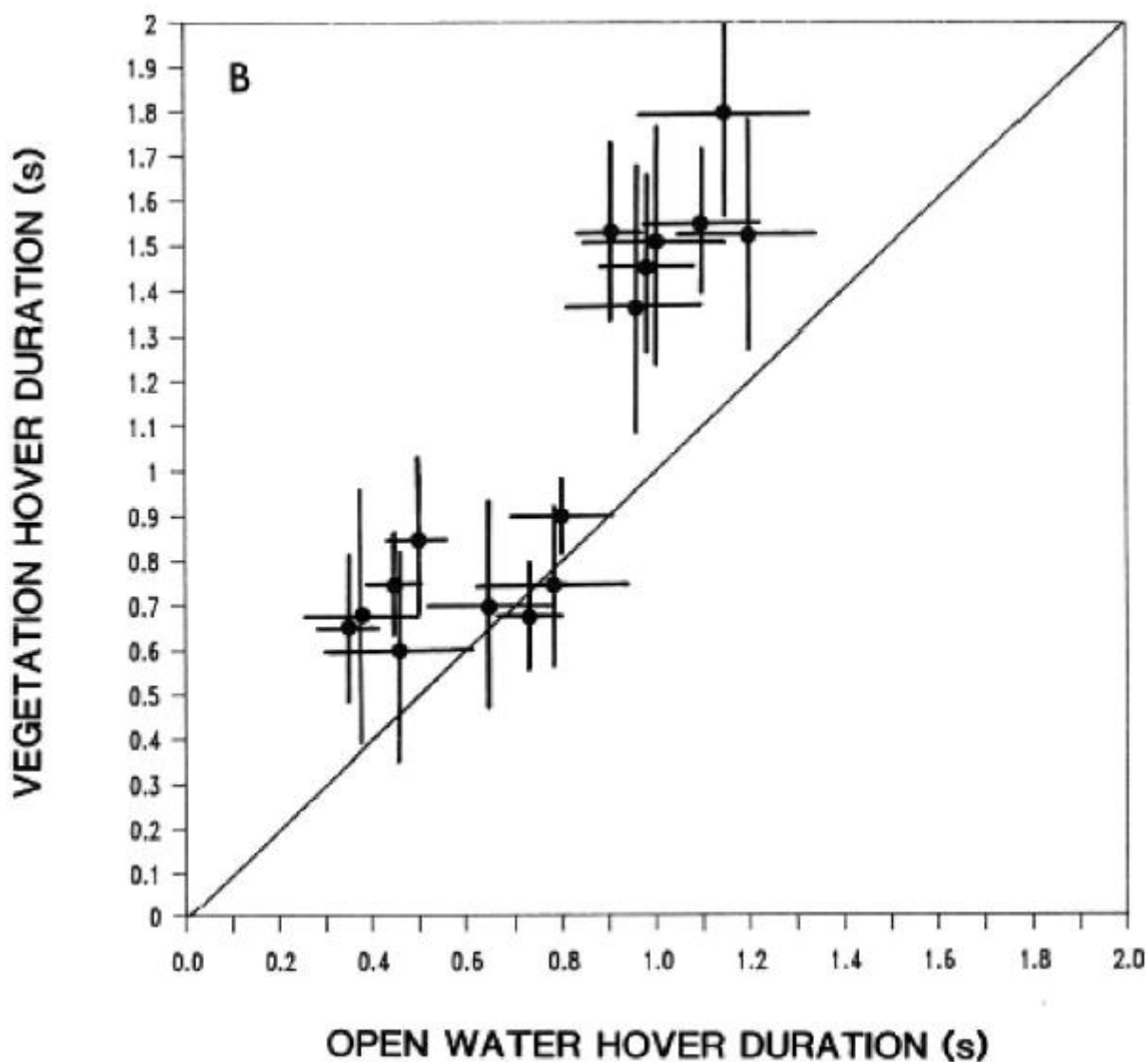


Figure 4. Bluegill sunfish display two distinct behavioral types when foraging on open-water versus vegetation-dwelling prey in the laboratory. Graphed are the foraging behaviors (hover duration when searching) used by individual bluegill when searching for damselfly nymphs in the vegetation and when searching for zooplankton (*Daphnia*) in the open-water habitat of aquaria. Each point represents the mean hover time (+ 1 SE) of six feeding trials for a given fish in each habitat. The diagonal line represents equal hover duration in each habitat. From Ehlinger and Wilson (1988).

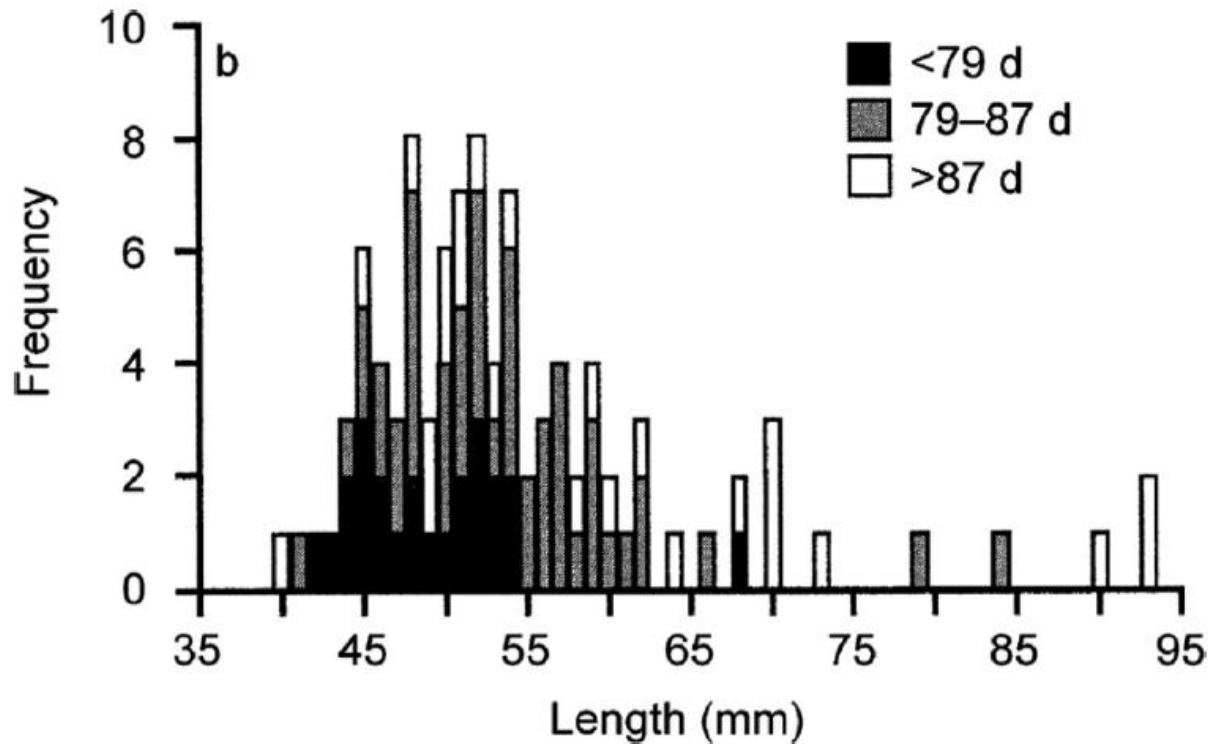


Figure 5. Length-frequency distribution of young-of-year largemouth bass collected from Paul Lake, Michigan in late August 1994. Fish were categorized by age (age determined using daily rings from otoliths). Age categories represent roughly the youngest 25%, the central 50%, and the oldest 25% of fish collected. Only fish >85 mm in length become piscivorous during their first summer of life. From Post (2003).

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CHAPTER 2: The Reliability and Accuracy of Four Behavioral Tests Frequently Used to Quantify Personality

ABSTRACT

Broad personality traits, such as boldness, entail individual differences in behavior that are consistent both across contexts and across time. However, broad personality traits are frequently quantified by measuring behavior in a singular context at a single point in time. For personality measurements obtained in this way to be valid, the behavioral tests used must yield highly repeatable and accurate measurements. Unfortunately, the repeatability and accuracy of behavioral tests are rarely verified. Using largemouth bass (*Micropterus salmoides*), I investigated the repeatability and accuracy of behavioral tests commonly employed in fish. I measured behavior in four contexts: 1) novel environment, 2) familiar and safe environment, 3) social context, and 4) a context with food and a model predator present. Measurements were repeated two days after initial measurements. Intraclass correlation coefficients were calculated within tests across trial periods to assess repeatability and between tests within trial periods to assess accuracy. The behavioral measure in a familiar and safe context lacked the repeatability necessary for a singular measurement to be used as a reliable personality trait measure. In contrast, single measures in the other three contexts could be used to reliably quantify personality. However, each of the three reliable measures contained a degree of context specificity, making them somewhat inaccurate measures of broad personality traits. When considering the four context-specific measures in combination, a principal components analysis revealed a component that was a reliable personality trait measure and that could be identified with a term independent of any specific context (i.e. boldness). *Key Words:* Personality traits, behavioral syndromes, boldness, measurement validity, repeatability, methodology.

INTRODUCTION

Consistent inter-individual differences in behavior are a common feature of many animal populations (Stamps and Groothuis 2010; Budaev and Brown 2011). Individuals may behave consistently across different environmental contexts at a single point in time (Garamszegi et al. 2013) and within contexts across time (Budaev et al. 1999; Bell et al. 2004; Carere et al. 2005). While less common, some studies have also shown that the relationship between behaviors measured in different contexts can be consistent across time (Brodin 2009). Thus, while behavior is produced as a stream of actions that can be adjusted almost instantaneously to match the context at hand, inter-individual consistency in repeated measures of behavior indicates that behavior is also the product of at least semi-stable traits (Chaplin et al. 1988). The traits responsible for producing consistency in repeated measures of behavior are variously termed “personality traits”, “temperament traits”, and “behavioral traits” (Réale et al. 2007).

The study of personality traits may provide answers to questions central to the study of behavioral ecology, such as, how apparently sub-optimal behaviors persist in populations (Dingemanse and Wolf 2010). Unfortunately, methodological challenges make the study of personality traits difficult. One major challenge in the study of personality traits is that it is rarely possible to identify the trait responsible for producing a behavior in terms of a concrete property, such as a specific gene, brain function, or physiological mechanism (but see Hariri 2009). As a result, researchers turn to more abstract psychological descriptions (e.g. boldness, aggressiveness, etc.) to categorize the personality traits of individuals. The apprehension to use such descriptions has led some researchers to abandon a trait-based categorical system of psychological descriptors all together and instead simply describe and catalog the contexts (e.g. predator present, novel environment, etc.) in which personality traits are observed (Table 5). The overall inability to identify the trait producing behavior is the basis of a recent perspective article aptly titled “Animal personality: what are behavioral ecologists measuring?” (Carter

et al. 2013). A related challenge is that even after deciding what trait is being measured, there is often no direct way to measure it. Researchers have little choice other than to measure personality traits indirectly through noisy indicator variables (Borsboom, 2008). Specifically, researchers use behavioral measures, which are thought to be the product of at least semi-stable traits acting in combination with additional factors, as proxy measures of personality to overcome the methodological challenges of measuring personality traits. While in general this approach to measuring personality traits is appropriate, the specific behavioral measures that are employed as proxy measures of personality traits must be individually validated (Burns 2008).

First, the reliability of a behavioral measurement to serve as a proxy measure of a personality trait must be investigated. Temporally repeated measures must be taken to verify that a measure is stable (test-retest reliability). If a behavioral measure lacks stability over repeated measures, it likely indicates that the behavioral measure is largely affected by unstable states (e.g. hunger level) and/or unstable contextual effects. Unfortunately, the reliability of behavioral measures is only investigated in roughly 25% of personality studies (Gosling 2001; Miller et al. 2005). Second, after determining that a measurement does reliably measure the same property when repeatedly used, the alignment between the measure and the interpretation made from it must be validated. To do so, the relationship between measures theorized to quantify the same trait (convergent validity) and measures theorized to quantify different traits (discriminant validity) must be assessed (Figure 6). Convergent and discriminant validity are very rarely investigated in personality studies and in the few studies in which they have been investigated, the specific measures investigated have often been found to be invalid (Miller et al. 2006; Burns 2008; Beckmann and Biro 2013). Thus, studies that investigate the reliability and accuracy of measures of personality are sorely needed.

In this study, I investigated the validity of four personality trait measures in largemouth bass (*Micropterus salmoides*), a fish species native to eastern North America. Behavior was observed in four

contexts to obtain proxy measures of personality traits: 1) behavior in a novel environmental context, 2) behavior in a familiar and safe environmental context, 3) behavior in a social context (mirror test), and 4) behavior in a context containing both food and a model predator (Table 6). The behavior of each bass was measured in each of the four experimental contexts twice, with a 2-day interval between measures in the same context. A 2-day interval between trials was chosen because it likely surpasses the stable period of most highly fluctuating internal states (e.g. hunger level) that could affect the measure, while at the same time minimizing the amount of plasticity experienced by more stable traits.

I investigated the reliability of each behavioral test by examining the repeatability between the values obtained from the first and second test in each context. I also assessed relationships between measurements that have been theorized to measure the same trait (convergent validity); e.g., the length of time to enter a novel environment and the length of time to approach food in the presence of a predator have both been interpreted as measures of boldness. Further, I performed a principal component analysis on the measurements from the four experimental contexts to organize them into components that may be more readily interpretable as context independent traits that can be described with common psychological terms. The results of this study help address whether a variety of measures commonly employed in the study of animal personalities do in fact quantify the personality traits intended (Carter et al. 2013).

METHODS

Sixty five largemouth bass were collected in June, 2011 from a pond located at the Kellogg Biological Station experimental pond facility in southwest Michigan. The 65 bass were bred on site from adult bass that were collected from nearby Wintergreen Lake. Bass ranged from 1 to 3 years of age and averaged 207.9 ± 67.4 mm in total length (± 1 standard deviation). Bass were individually marked with colored elastomer gel (a biocompatible pliable polymer; Northwest Marine Technology, Goldsmith et al.

2003) that was injected subcutaneously at two of seven possible locations. Bass were held in large (1000 liter) outdoor covered tanks for about 4 days. During this time, bass could feed on zooplankton ad libitum. The day before bass were to be tested, they were transferred to the laboratory and socially housed in 110 L aquaria (4 bass per aquarium) and again provided with an excess amount of zooplankton. On the testing day, bass were transferred from the indoor holding aquaria into their own 110 L aquarium. Over the next two days, bass underwent a series of behavioral assays (Table 6). Food was not available to bass during the two day testing period (except for the foraging trial). Following the completion of the series of behavioral assays, individuals were transferred back to the 110 L group holding tanks for one day. They were again provided with an excess amount of zooplankton while in the holding aquaria. The next day, the bass were returned to the testing aquaria and run through the same set of behavioral assays (again with no food available). The assays were run in the same order for both testing periods. Thus, all 65 bass were measured twice in each of the four contexts, with a 2 day-interval between measures in the same context.

Novel context

The 110 liter testing aquaria were divided into two sections by an opaque vertical partition with the smaller section making up about 10% of the total volume. Individual bass were transferred into the smaller section of a testing tank and then left for approximately 45 minutes to recover from handling and to acclimate to the new environment. After the 45 minute acclimation period, using a pulley system, the partition was raised approximately 10 centimeters above the floor of the aquarium, allowing the fish to swim from the smaller section into the larger section. For each trial, I measured the elapsed time from when the partition was raised until the fish swam into the larger area of the tank (up to 15 min). If after 15 minutes a fish had not moved to the larger section of the tank, I gently coaxed it out. Once a fish moved into the larger section of the tank, I lowered the partition so that it could not move back into

the smaller section. An individual's score in this context was calculated by subtracting the number of seconds that a fish waited before moving to the larger portion of the tank from 900 (the maximum trial length). Thus, individuals with higher scores moved more quickly to the larger section of the tank. Individuals that did not leave the small section during the trial received a score of 0. Following the trial, I placed a mirror on the wall in the smaller section of the tank (not visible to the fish). Fish were then left overnight in the larger section of the tank to acclimate to their new surroundings.

Familiar and safe context

The day after introducing a bass into a testing aquaria, I measured the amount of time the bass spent moving around the tank in the familiar environment (larger section of the tank). Fish were observed for 5 minutes and I summed the total time spent swimming (moving) to calculate the total number of seconds active per trial.

Social context (mirror test)

Immediately following the measurement in the familiar and safe environment trial, I raised the partition to reveal a mirror on the wall in the smaller section of the tank. Once the partition was raised the trial commenced. Trials lasted for 10 minutes. I measured the number of bites, tail swipes, and rams at the mirror. At the end of the trial, the partition was lowered so that the mirror was no longer viewable. As the partition was lowered, fish in the path of the partition consistently retreated to the larger section of the tank on their own. The number of bites, tail swipes, and rams were summed together to get an overall measure in this context. These behaviors were summed together because each was taken to be a specific form of agonistic behavior and other studies have shown that individuals often exhibit behavioral specificity so that they tend to primarily use their preferred method of a behavioral type (one individual may primarily use rams while another primarily uses bites; Uher 2011).

Food and predator present context

Approximately one hour after observing behavior in the presence of the mirror, a live earthworm tied to monofilament fishing line (no hook) was lowered into the tank near one end. When the bass approached the worm, a model bird suspended on a string and pulley system positioned directly above the worm was released to strike the surface of the water, simulating a predation attempt. The bird was then quickly lifted from the water, again using the string and pulley system. During this time, the fish most often retreated to a corner of the tank. Once the bird was appropriately positioned (10 centimeters above the water surface), the trial commenced. Trials lasted for 15 minutes. I recorded how many seconds it took the bass to re-approach the worm. An individual's score was calculated by subtracting the number of seconds that a fish waited before re-approaching the worm from 900 seconds (the maximum trial length). Thus, individuals with higher scores re-approached the worm faster. Individuals that did not re-approach the worm during the trial received a score of 0.

Statistical analysis

All statistical analyses were conducted using R version 2.13 (R Development Core Team 2008). First, each variable was standardized to a mean of 0 and a standard deviation of 1. Standardizing the measures removes contextual effects (be it due to the external context or habituation between trials 1 and 2) that may be responsible for producing variation in the behaviors. After standardization, the measures should only include behavioral variation that results from individual differences in states and traits (and experimental error that occurred in individual trials). To be appropriate proxies for measures of traits (as opposed to a state), the measures must exhibit minimal intra-individual variation over short intervals relative to the amount of inter-individual variation that exists in the measures.

To assess the appropriateness of the measures as indicator variables (i.e. measures of personality traits), an intra-class correlation analysis was conducted on the standardized values from the first and second time periods, within and between each context. Measures used for personality traits should be highly repeatable and have an intra-class correlation coefficient near 1 over short intervals. The further an intra-class correlation is from 1 for a measurement of a personality trait that is repeated over short intervals, the larger the amount of error contained in the measurement, be it due to experimental error or because the measure is affected by states that are unstable across measurements. Thus, it is the strength of the correlation that must be considered (including the 95% CI's), not merely the presence or absence of significance, when investigating the appropriateness of a measure to serve as a proxy of a trait.

To investigate the categorization of the measures as the same and as different traits (convergent and discriminate validity; see Figure 6), I performed a second round of intra-class correlation tests, this time looking at measures within the same assay trial period. I investigated the relationship between each of the context-specific measurements to assess if the context-specific measurements were measures of the same traits, of different traits, or something in between. Further, to determine whether the measurements in the four different contexts could be re-organized into components that were interpretable in terms of common psychological terms (e.g., boldness), I conducted a principal component analysis on the context-specific measurements. I then investigated the relationship between the component personality traits (more readily interpretable as psychological traits) and the context-specific traits to examine how closely the context-specific traits approximate the psychological traits that they are often said to describe.

RESULTS

Intra-class correlation coefficients (ICCs) were significant (all p. values were below 0.05) between trial periods 1 and 2 for each of the behaviors measured in the four experimental contexts (along top left to lower right diagonal in Table 7). However, when it comes to assessing the reliability of the measures, it is the magnitude of the correlations that are truly of interest. In this regard, three of the measurements showed moderately high ICCs (0.50-0.69) while the fourth (safe and familiar environment activity) was significantly lower (ICC = 0.30 with an upper 95% CI bound of 0.50). Significant ICC values were also obtained between the novel environment, mirror-test context, and food and predator present measurements taken within the same trial periods (Table 7; above the diagonal are ICCs between measurements in Trial 1 and below the diagonal are ICCs between measurements in Trial 2). However, it is again the magnitude of the correlations that is more relevant when investigating the convergent and discriminant validities of the measurements.

A principal component analysis revealed a similar pattern in the relationships between the context-specific measures. Principal component axis 1 explained 49.7% of the variation across the four experimental contexts in trial 1 and 46.2% of the variation in these measures in trial 2 (Table 8). Based on the loadings of the measurements from the four experimental contexts, PC axis 1 was interpreted as “boldness”. It affected behavior in the novel environment, in the mirror-test context, and when food and a predator were present. Each of these three behaviors contributed positively and to a similar extent to PC axis 1 in both trials 1 and 2 (Table 8). PC axis 2 explained 24.7% of the variation in trial 1 and 26.7% of the variation in trial 2. PC axis 2 was interpreted as an energeticness or activity personality trait. The measurement from the safe and familiar environment was essentially the sole contributor to PC axis 2 in trial 1 (84%) and trial 2 (89%), with a positive loading. PC axes 3 and 4 explained little of the variation (16.0% and 9.7% respectively during trial period 1 and 18% and 9.1% during trial period 2),

with little consistency in the loadings of the context measures onto these PC axes. Thus, further analyses are focused solely on PC axes 1 and 2.

The boldness component trait calculated from the principal components analysis had a higher intra-class coefficient between trials 1 and 2 than did the measurements from specific contexts that are also frequently interpreted as boldness (along the top left to lower right diagonal in Table 7). However, the ICC for the boldness component was not significantly higher than the ICC calculated from the measurement in the novel context (often also interpreted as boldness). A similar trend in ICCs was also displayed between the activity component trait and the measurement in the safe and familiar context. With regard to the suitability of measurements taken from singular contexts to serve as proxies of more context-general or context-independent traits, the measure taken in the presence of food and a predator most closely resembles the boldness component measurement (ICC of 0.803 between measures from Trial 1 and 0.812 between the measures from Trial 2.) However, the measurement taken when food and a predator were present was not always a significantly better measure of boldness than the measurement taken in a novel context (upper 95% CI bound of 0.86 in trial 2) or the measurement taken in the mirror-test context (upper 95% CI bound of 0.84 in trial 1).

DISCUSSION

Each of the four context-specific measurements in this study showed significant, positive correlations between trial periods 1 and 2. However, this says little about the reliability of the measurements and their appropriateness to serve as proxies for personality traits. Researchers must decide on the magnitude of a correlation under test-retest scenarios that is necessary to consider a behavioral measurement a suitable proxy measurement for a personality trait. For example, correlations between repeated behavioral measures of 0.5 (Cohen 1988) and 0.7 (Martin and Bateson 1993) have been proposed as the lower limit that indicates reliability in a measurement. In the current study, 3 of

the 4 context-specific measurements had ICCs high enough that they could pass a 0.5 magnitude correlation criterion and be considered appropriate personality trait measures (e.g. novel environment context measurement ICC 95% CI was 0.54 – 0.80). However, if a criterion of 0.7 was used, none of the four context-specific measurements would meet the criterion. Only the boldness component trait surpassed a 0.7 magnitude correlation.

When compared within each time period, significant ICCs between paired measurements involving the novel environment, the mirror-test, and/or the food and predator present context suggest that there is considerable overlap in the personality traits that affect behavior in these different contexts. If we assume that these context-specific measurements assess the same personality trait, then the ICCs between these measurements could be used to investigate the convergent validity of the measures. The ICCs (0.34 – 0.57) between these context-specific measures indicate that a theory treating each of these measures as the same thing would have a low to moderate degree of validity. Conversely, if these context-specific measurements were theorized to measure completely different personality traits (i.e. exploration, aggression, and boldness), the significant ICCs would cast doubt on the theory that the different measures actually measure different traits. In other words, the ICCs between these context-specific measurements suggest that the level of overlap in what they measure is too low to consider them measures of the same trait and too high to consider them measures of completely different traits. This conclusion is further supported by the result that, while the relationships between measurements in different contexts across the two time periods tend to have moderately high intra-class coefficients (e.g. novel environment measure and food and predator present measure ICC = 0.459), the relationships between measurements within a context (e.g. novel environment measure ICC = 0.690) tend to be significantly higher. Thus, the results of this study agree with others (Blumstein et al. 2012; Watanabe et al. 2012; Carter et al. 2012) that indicate that a psychological descriptor (i.e. boldness) is often a relatively inaccurate description of a personality trait

measured in any singular context. As a result, personality traits measured with a context-specific measure are likely most appropriately described in terms of the context in which the measure was taken, as opposed to a psychologically-based description.

Unfortunately, problems also arise from categorizing traits based solely on the contexts in which they are measured. The most obvious problem is that different studies may use a variety of different experimental contexts. Thus, the number of potential contexts used could be very large, making it difficult to compare results between studies. An option to address this issue is that the number of contexts could be condensed down to a few basic categories (such as the five contexts suggested by Réale et al. 2007). However, creating a context-based classification system for personality traits may give the false impression that traits in the same general category necessarily are the same biological trait while those in different categories are different traits. For example, measurements taken in a novel environment and those taken in foraging contexts may be classified into two different categories even though both measurements to a large degree measure boldness (propensity to take risks). Thus, given the issues involved in accurately describing and categorizing personality traits, I suggest that the most appropriate methodological approach is to take measurements in multiple contexts.

By taking measurements in multiple contexts, researchers can identify component traits that likely represent more accurate measures of psychological traits than any context-specific measurements. Additionally, researchers can employ a biologically-based categorization system and can ensure that their methods are valid. I used this approach in the current study and found that personality traits calculated by principal components analysis of multiple context-specific measurements were more repeatable than measurements in a single context. Additionally, based on the loadings of each context-specific measure onto each component, component 1 likely represents the quality of boldness (willingness to expose oneself to risk) better than any of the context-specific measures. Although measuring behaviors in multiple experimental contexts involves more time and effort than

assessing personality traits in a single experimental context, the results of this study show that a multiple context approach yields more fruitful results.

With the use of appropriate methods, researchers can move beyond the identification and description of traits to begin to understand the causes and consequences of personality traits. For example, further investigation into the boldness trait revealed in the current study could help researchers learn if boldness is explained by differences in sex, size, stage of development, and/or some other quality of an individual, such as metabolic rate or organ size. Furthermore, the current study indicates that singular traits (i.e. boldness) may be responsible for producing the behavioral syndromes often observed between contexts (see also Bell 2005, Dingemanse et al. 2007). If an individual's phenotype is relatively stable across relatively long time periods (Sinn 2008; Chervet et al. 2011; Wilson and Krause 2012), the resulting behavioral syndrome(s) could have important ecological consequences (Sih et al. 2004; Smith and Blumstein 2008; Conrad et al. 2011; Sih et al. 2012). Further, if the behavioral syndrome(s) result from a heritable personality trait (Van Oers et al. 2004; Sinn et al. 2006; Norton et al. 2011), the trait could function as an evolutionary constraint preventing individuals from exhibiting optimal behaviors at different life stages and could contribute to the maintenance of multiple personality types within a population (Mittelbach et al. 2014).

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APPENDIX

Table 5. Definitions of terms.

Term	Definition
Personality trait	Characteristic of an individual that is stable over some time period and is responsible for contributing to the production of behavior.
Internal state	Characteristic of an individual that can fluctuate greatly over relatively short time periods (mood, hunger level, etc.)
Psychologically-based classification system	The use of abstract psychological (e.g. bold, aggressive, etc.) descriptions in the categorization of personality traits of individuals.
Context-based trait classification system	The use of contextual information (e.g. predator present, novel environment, etc.) in the description of personality traits of individuals.
Convergent validity	An assessment of the degree to which a test actually measures what it purports to measure by investigating the relationships between measures that are theorized to be measurements of the same trait.
Discriminant validity	An assessment of the degree to which a test actually measures what it purports to measure by investigating the relationships between measures that are theorized to be measurements of different traits.

Table 6. Behaviors measured in the four behavioral assays, the context for each measurement, common psychological trait(s) assumed to cause behavior, and other internal states that could affect each behavior.

Behavior	Context for behavior	Psychological trait(s) theorized to produce behavior	Other temporary states that could affect behavior
Length of time to enter new habitat	Opportunity to move into novel environment	Boldness, Exploration	Restlessness
Amount of time moving	Familiar and safe open-field environment	Energeticness,	Restlessness, Tiredness
Bites and rams at mirror	Mirror added to open-field environment	Aggressiveness, Boldness	Irritableness
Length of time to approach food	Model bird predator strikes water above food	Boldness	Hunger level

Note: A more in depth discussion of this issue as it specifically relates to boldness can be found in Budaev and Brown, 2011.

Table 7. Intra-class correlation coefficients (values in parenthesis indicate 95% confidence intervals) between standardized measurements in the four contexts as well the composite personality traits (boldness and energeticness) generated from a principal components analysis of the measurements in the four contexts.

Measurement	Novel environment context	Safe and familiar context	Mirror-test context	Food and predator present context	Energeticness*	Boldness*
Novel environment context	0.690 (0.54 – 0.80)	0.081 (-0.163 – 0.317)	0.336 (0.10 – 0.53)	0.517 (0.32 – 0.67)	-0.303 (-0.51 - -0.07)	0.775 (0.66 – 0.86)
Safe and familiar context	-0.106 (-0.34 – 0.14)	0.300 (0.06 – 0.50)	0.058 (-0.19 – 0.30)	0.194 (-0.05 – 0.42)	0.972 (0.96 – 0.98)	0.008 (-0.23 – 0.25)
Mirror-test context	0.334 (0.10 – 0.53)	0.241 (0 – 0.46)	0.598 (0.42 – 0.73)	0.555 (0.36 – 0.70)	0.136 (-0.11 – 0.37)	0.648 (0.48 – 0.77)
Food and predator present context	0.571 (0.38 – 0.71)	0.107 (-0.14 – 0.34)	0.363 (0.13 – 0.56)	0.505 (0.30 – 0.67)	-0.198 (-0.42 – 0.05)	0.812 (0.71 – 0.88)
Energeticness*	-0.305 (-0.051 - -0.07)	0.913 (0.86 – 0.95)	0.021 (-0.22 – 0.26)	0.159 (-0.09 – 0.39)	0.336 (0.10 – 0.53)	0.121 (-0.12 – 0.35)
Boldness*	0.689 (0.54 – 0.80)	0.315 (0.08 – 0.52)	0.750 (0.62 – 0.84)	0.803 (0.70 – 0.88)	0.008 (-0.23 – 0.25)	0.734 (0.60 – 0.83)

Note: Coefficients between measurements across trial periods 1 and 2 within the same parameter are along the top-left to lower-right diagonal. Coefficients between measurements taken in the first trial period are above the diagonal and those below the diagonal are from the second trial period. Parameters denoted with an asterisk were obtained from a PCA of the four context specific parameters. Sample size = 65.

Table 8: Contributions (loadings) of the four context-specific measurements in trial periods 1 and 2 to principal component axis 1 and 2.

Behavior	Context for behavior	Contribution of context specific personality traits to general personality traits			
		PC axis 1 (Boldness) Trial 1	PC axis 1 (Boldness) Trial 2	PC axis 2 (Energeticness) Trial 1	PC axis 2 (Energeticness) Trial 2
Length of time to enter new habitat	Opportunity to move into new environment	26.6%	35.6%	9.7%	9.1%
Amount of time moving	Familiar and safe open-field environment	5.4%	0.8%	84.3%	88.7%
Bites and rams at mirror	Mirror added to open-field environment	31.6%	24.7%	1.6%	0.02%
Length of time to approach food	Model bird predator strikes water above food	36.4%	39.0%	4.2%	2.2%

Note: PC axis 1 explains 49.7% of the variation in trial 1 and 46.2 % of the variation in trial 2. PC axis 2 explains 24.6% of the variation in trial 1 and 26.7% of the variation in trial 2.

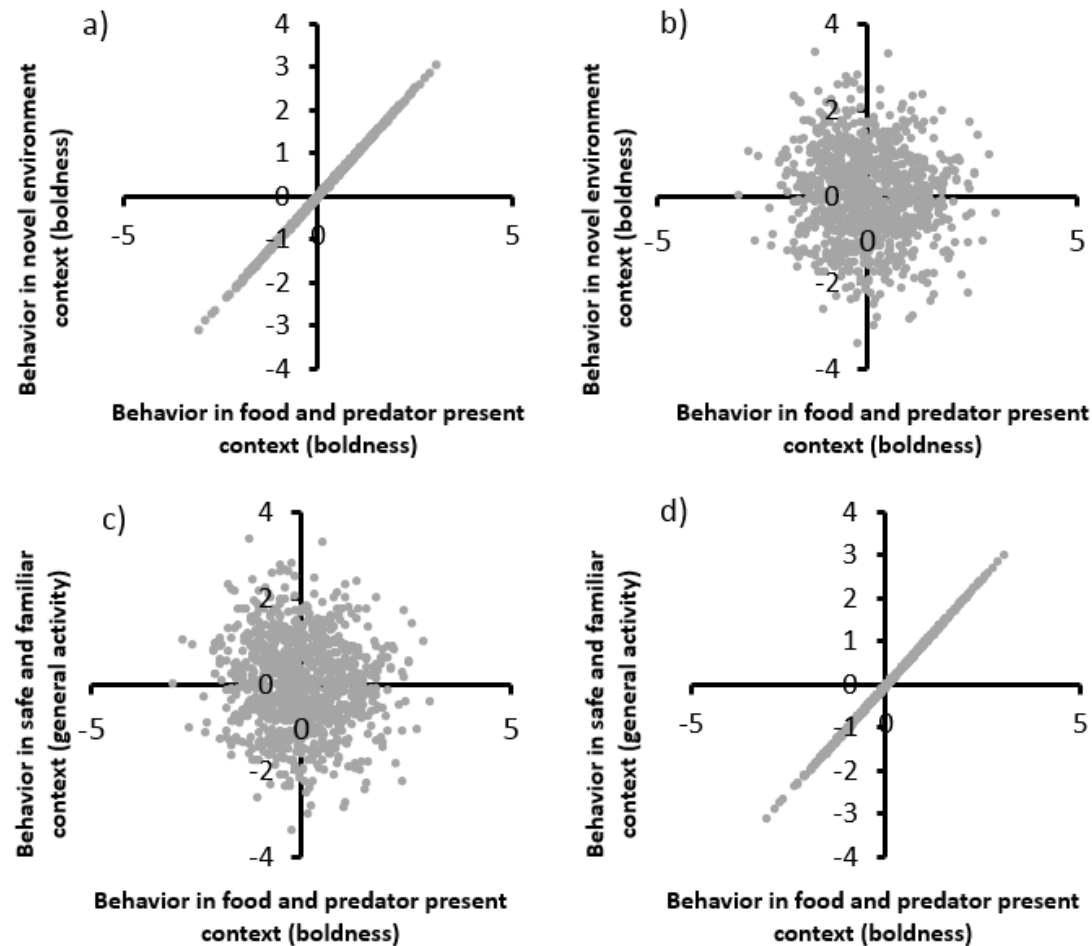


Figure 6. Plots a) and b) depict two possible outcomes for a test of the convergent validity of two measurements that may both be theorized to measure boldness. Plot a) would support the theory that the two measurements quantify the same property while plot b) would suggest that they do not. Plots c) and d) depict two possible outcomes for a test of the discriminant validity of two measurements that may be theorized to measure two different personality traits. Plot c) would support the theory that the two measurements quantify two different traits while plot d) would not.

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CHAPTER 3: The Consistency of Personality Traits Across a 4-Year Period in Largemouth Bass (*Micropterus Salmoides*)

ABSTRACT

Most studies that have investigated the temporal consistency of personality traits have been conducted in the laboratory, with very few studies conducted under natural or semi-natural conditions. Consequently, little is known about the consistency of personality traits in nature and the potential for natural selection to act on these traits. Here, I address this question by using a combination of laboratory and field approaches to obtain estimates of consistency in personality over a 4-year period as it develops naturally in a free ranging population of largemouth bass (*Micropterus salmoides*). In the laboratory, behavior was assayed under four experimental conditions: a novel environment context, a familiar environment context, a social context, and a feeding under predation risk context. These assays were conducted on fish at 12, 15, 36, 48, and 60 months of age. Between testing periods, fish lived freely in large outdoor ponds, where they were exposed to natural conditions of weather, food, social interactions, and potential predators. The correlational structure between the behavioral measurements indicated that there were context-specific personality traits underlying behavior in each context and that the context-specific traits were likely sub-modules of a more general personality trait. A principal components analysis conducted within each age on the context-specific traits revealed a context-general trait that was interpreted as boldness. Each of the personality traits displayed temporal consistency for a period of at least 24 months and the boldness trait was consistent across all four years of testing. These results indicate that personality traits can be temporally consistent across a significant portion of an individual's life history and therefore subject to natural selection.

INTRODUCTION

Individuals from the same population and at the same developmental stage often display consistent differences in behavior over time and across contexts (Gosling 2001; Réale et al. 2007; Bell et al. 2009). This consistent inter-individual variation in behavior is widely accepted as evidence of phenotypes that underlie the expression of behavior (Araya-Ajoy and Dingemanse 2014; Budaev and Brown 2013). Though a consensus is yet to be reached on what term best describes these phenotypes (i.e. behavioral, personality, temperament), several studies have demonstrated that they affect various components of fitness (Smith and Blumstein 2008; Kontiainen et al. 2009; Ariyomo and Watt 2012). Further, there is mounting evidence that personality types have a heritable component (Chervet et al. 2011; Ariyomo et al. 2013; Kortet et al. 2014). These results indicate that personality variation within populations may well be the adaptive outcome of natural selection. However, the potential for personality to affect lifetime fitness and be a target of natural selection remains unknown, due in large part to questions surrounding the temporal consistency of personality (Mittelbach et al. 2014).

Temporal consistency in personality is crucial for selection to act on personality types. If personality types have narrow temporal windows of inter-individual consistency then even if the fitness effects of personality types are large, temporal flip-flopping of personalities between individuals could remove the opportunity for selection to act on personality. Conversely, if personality types are temporally consistent between individuals across an entire lifetime, selection could easily take place (Stamps and Groothuis 2010; Wolf and Weissing 2010). Numerous studies have documented consistency in personality traits over relatively short time periods of days and weeks (Conrad et al. 2011). However, a meta-analysis that compared the average consistency observed in personality studies conducted over a period of less than one year to those conducted over a period greater than one year found that there was less consistency in periods over one year (Bell et al. 2009). Thus, lifetime consistency cannot be safely inferred from evidence of short-term consistency (Boulton et al. 2014). As a

result, there is a critical need for studies that describe the consistency of personality over long time periods. The number of studies conducted over timeframes that may be considered more representative of natural life spans is growing (Sinn et al. 2008; Chervet et al. 2011). However, nearly all of these studies have been carried out in the laboratory and thus may not reflect the level of consistency that exists in personality under natural conditions (Dingemanse et al 2002; Carere et al. 2005; Wilson and Krause 2012). This is an important point as it is the temporal consistency of personality under natural conditions that is relevant for the evolution of personality.

Investigating the temporal consistency of personality traits necessitates measuring the same trait or traits repeatedly across development. Unfortunately, this task is complicated by the fact that it is difficult to define and classify the personality traits that will be investigated *a priori*. This difficulty arises because the structure and organization of personality traits (and how it may change across development) is itself an open question (Carter et al. 2013; Garamszegi et al. 2013). For example, the expression of behavior within a given context may be dictated by a personality trait that applies only to the given context, by a personality trait that applies to contexts of some narrow category, or by a personality trait that applies to contexts of some very general category (Figure 7). Further, personality traits may exist at a combination of different levels, so that quasi-independent personality traits that apply at one level are sub-modules of more general traits that exist at another level. Additionally, traits that are defined *a priori* may not exist at all (or any) stages of development. For example, boldness is frequently defined as the propensity to take risks. Under this definition, boldness would underlie the expression of behavior in a range of contexts that involve risk (Figure 7A). However, it is quite possible that a general boldness trait that underlies behavior in most risky contexts exists at only certain life stages or does not exist at all. Instead, there may be more specific boldness traits that apply to certain functional risky contexts (Figure 7C). Thus, an exploratory approach into the structure and temporal consistency of personality traits is becoming widely accepted as an effective way to avoid difficulties

that can arise from *a priori* classifying traits and identifying the behavioral expressions that they trigger (Budeav 1997; Blumstein et al. 2012; Boulton et al. 2014).

Here, I address the question of temporal personality consistency by using a novel combination of laboratory and field approaches to obtain accurate estimates of personality traits over a 4-year period as it develops naturally in a free-living population of largemouth bass (*Micropterus salmoides*). I examined individual behaviors in the laboratory at 12, 15, 36, 48, and 60 months of age in four contexts: 1) a novel environment, 2) a familiar and safe environment, 3) a social environment (mirror test), and 4) an environment where both food and predation risk were present (Table 9). A previous study (Ballew submitted) revealed that personality underlies largemouth bass behavior in these specific contexts. Moderate to high correlations were found between measurements of behavior within the same contexts that were repeated over short time periods and low to moderate correlations were found between measurements of behaviors across most of the different contexts. This correlational pattern between measurements of behavioral observations within versus across contexts indicates that context-specific personality traits underlie behavior in these contexts and that these context-specific traits may well be sub-modules of a more general trait akin to boldness. However, in the previous study, the personality traits underlying behavior in these 4 contexts were only investigated at a single point in time. As a result, the personality traits underlying behavior in each of these contexts at each stage of development is unknown. Thus, in this study, I employ an exploratory approach to determine the temporal consistency of the personality traits underlying behavior in these four contexts at each stage of development.

In this study, I quantified behavior in four contexts over a four year period in a free-living population of largemouth bass (*Micropterus salmoides*) to address three main questions. 1) Which personality trait or traits underlie behavior in each of the four contexts investigated at each stage of development? 2) What level of temporal consistency (in both magnitude and temporal duration) exists

in each personality trait? 3) Is the temporal consistency in each of the personality traits dependent on the temporal duration between measurements? Answers to these questions, especially in populations exposed to natural conditions, will help address whether personality traits can be temporally consistent across a significant portion of an individual's life history and therefore subject to natural selection.

METHODS

Study species and husbandry

Three hundred yearling bass were collected in 2009 from a pond located at the Kellogg Biological Station experimental pond facility in southwest Michigan. These bass were bred on site from adult bass collected from nearby Wintergreen Lake. The yearling bass were transferred to the laboratory facility and were individually marked with colored elastomer gel (a biocompatible pliable polymer; Northwest Marine Technology, Goldsmith et al. 2003) that was injected subcutaneously at two of seven possible locations. Random samples from the 300 marked bass were subjected to a behavioral assay procedure over the course of their development. Bass were behaviorally assayed at approximately 12, 15, 36, 48, and 60 months of age, resulting in the following time intervals between measurements: 3 months, 1 year, 2 years, 3 years, and 4 years. Between assay periods, the bass were kept in an outdoor pond (30 m dia; 2 m deep) at the Kellogg Biological Station, where they were free-living, could feed on natural prey, and undergo normal developmental processes. Largemouth bass develop from vulnerable prey as juveniles to reproductively mature adults at age 3 that exhibit complex breeding behaviors and show extensive parental care. In most habitats (as in the case of this study population), bass assume the role of apex predator soon after reaching maturity.

Leading up to each round of behavioral assays, bass were transported to the laboratory area and kept in large (1000 liter) outdoor covered tanks. During this time, bass could feed on zooplankton (*Daphnia*) *ad libitum*. Bass were transferred to the laboratory the day before they were tested. In the

laboratory, each bass was identified based on its marks and measured for length. If the marks were no longer visible, bass were re-marked with a new unique combination of colors and locations not previously used in the population. Bass were socially housed in 110 L aquaria (four bass per aquarium) and provided with an excess amount of zooplankton. On the testing day, bass were transferred from the indoor holding aquaria into their own aquaria where they underwent a series of behavioral assays (Table 9). Upon completion of the assay procedure, the bass were returned to the pond until the next assay period, then they were re-collected to undergo another round of tests.

Over the 4-year testing period, I repeatedly observed bass behaviors in the laboratory under four experimental contexts: 1) a novel environment, 2) a familiar and safe environment, 3) a social environment (mirror-test), and 4) an environment where food and predators were present. Three of these environmental contexts (numbers 2, 3, and 4) were included in each assay testing period, whereas the novel environment (number 1) was not employed in the first two rounds of behavioral assays (conducted at 12 and 15 months of age). An additional alteration to the assay procedure was that different sized aquaria were used to observe behavior as the bass grew (40 liter aquaria when the bass were yearlings and 110 liter aquaria once the bass had reached an age of 36 months).

Behavioral assay procedure

The testing aquaria were divided into two sections by an opaque vertical partition with the smaller section making up about 10% of the total volume. Individual bass were transferred into the smaller section of a testing tank and then left for approximately 45 minutes to recover from handling and to acclimate to the new environment. After the 45 minute acclimation period, novel context trials were initiated. The partition was raised approximately 10 centimeters above the floor of the aquarium using a pulley system, allowing the fish to swim from the smaller section into the larger section. For each trial, I measured the elapsed time from when the partition was raised until the fish swam into the larger

area of the tank (up to 45 minutes). If after 45 minutes a fish had not moved to the larger section of the tank, I gently coaxed it out. Once a fish moved into the larger section of the tank, I lowered the partition so that it could not move back into the smaller section. An individual's score was calculated by subtracting the number of seconds that it waited before moving to the larger portion of the tank from 2700 (the maximum trial length). Thus, individuals with higher scores moved more quickly to the larger section of the tank. Individuals that did not leave the small section during the trial received a score of 0. Following the completion of the novelty trial, I placed a mirror on the wall in the smaller section of the tank (not visible to the fish). Fish were then left overnight in the larger section of the tank to acclimate to their new surroundings. The yearling fish were not subjected to the novel environment trial. Instead of placing them in the smaller section of the tank, yearling bass were simply placed in the larger section of the tank and left overnight to acclimate to their new surroundings.

The day after introducing a bass into a testing aquarium, I assayed its behavior in a familiar and safe context. I measured the amount of time the bass spent moving around the tank in the familiar environment (larger section of the tank). Fish were observed for 5 minutes and I summed the total time spent swimming (moving) to calculate the total number of seconds active per trial.

Immediately following the measurements taken in the familiar and safe environment trial, I conducted the social context (mirror-test) trial. I raised the partition to reveal a mirror on the wall in the smaller section of the tank. Once the partition was raised the trial commenced. Trials lasted for 10 minutes. I measured the number of bites, tail swipes, and rams at the mirror. At the end of the trial, the partition was lowered so that the mirror was no longer viewable. As the partition was lowered, fish in the path of the partition consistently retreated to the larger section of the tank. The number of bites, tail swipes, and rams were summed together to get an overall measure in this context. These behaviors were summed together because each was taken to be a specific form of agonistic behavior and other studies have shown that individuals often exhibit behavioral specificity so that they tend to primarily use

their preferred method of a behavioral type (one individual may primarily use rams while another primarily uses bites; Uher 2011).

Approximately one hour after observing behavior in the presence of the mirror, the feeding in the presence of a predator trial was conducted. A live earthworm tied to monofilament fishing line (no hook) was lowered into the tank near one end. When the bass approached the worm, a model bird suspended on a string and pulley system positioned directly above the worm was released to strike the surface of the water, simulating a predation attempt. The bird was then quickly lifted from the water, again using the string and pulley system. During this time, the fish most often retreated to a corner of the tank. Once the bird was appropriately positioned (10 centimeters above the water surface), the trial commenced. I recorded how many seconds it took the bass to re-approach the worm. An individual's score was calculated by subtracting the number of seconds that a fish waited before re-approaching the worm from the maximum trial length. Thus, individuals with higher scores re-approached the worm faster. Individuals that did not re-approach the worm during the trial received a score of 0. The maximum trial length was extended from 600 seconds in assays with yearlings to 1800 seconds with bass 36 months of age and older. This was done in an attempt to reduce the number of non-responders so that the total behavioral variation could be more fully represented.

Statistical analysis

All statistical analyses were conducted using R version 2.13 (R Development Core Team 2008). All scores were standardized (mean of 0 and standard deviation of 1) to control for context effects of the measures (slight differences between rounds of assays in the same trial type, major differences between trials of different types, habituation resulting in changes to how an individual perceives an environment, etc.). After removing context effects, the measures represent the traits responsible for producing behavior (in addition to any error). Standardizing the measurements also removes differences across

assays conducted at different ages that may be due to stereotypical developmental changes. For example, yearling bass tended to approach food with a predator present more quickly than older bass. This observed difference was potentially a developmental one and not due to context effects (Groothuis and Trillmich 2011). However, measurement standardization does not impact investigations into inter-individual consistency across temporal intervals, which is the interest of the current study.

Previous studies on this population of largemouth bass indicate that context-specific traits may underlie the expression of behavior in each of these contexts during at least some stages of development (Ballew submitted). Further, these context-specific personality traits may be sub-modules of a context-general trait akin to boldness. I investigated the correlational structure between behavioral measures within each age to determine which personality traits were present at each age (question 1). To do so, I calculated intra-class correlation coefficients, which partition variation into within and between individual components. The higher the correlation, the greater the proportion of variation that is due to inter-individual differences. Further, I conducted a principal component analysis on the context-specific traits at each age to identify context-general traits. As the novel environment measure was not conducted during every run, it was excluded from the principal component analysis conducted at each age.

To investigate the temporal consistency within each personality trait, I calculated Pearson correlation coefficients across several different time intervals (question 2). There were a total of seven time intervals; 3 months (sample size = 122), 12 months (from 36 to 48 months old; sample size = 93), 12 months (from 48 to 60 months old; sample size = 71), 24 months (from 12 to 36 months old; sample size = 52), 24 months (from 36 to 60 months old; sample size = 71), 36 months (from 12 to 48 months old; sample size = 52), and 48 months (from 12 to 60 months old; sample size = 39). To investigate the effect of interval duration on the temporal consistency of the personality traits (question 3), I performed regressions of personality trait temporal consistency (log-transformed) as a function of the time

between measurements. Values of temporal consistency were weighted by the sample size from each interval (e.g. $N = 122$ for the 3 month interval and $N = 39$ for the 48 month interval).

RESULTS

I examined the magnitude and 95% confidence intervals of the intra-class correlation coefficients (ICCs) within each time period (fish age) and found that ICCs were significant between several of the context-specific measures within each age, with magnitudes usually falling between 0.25 and 0.5 (Table 10; comparison of correlations within each column). A principal component analysis of the measures conducted within each age revealed a similar pattern in the relationships between the context-specific measures (Table 11; within each column). Based on the loadings of the measurements from the three experimental contexts used in the principal components analysis, PC axis 1, which explained between 40% - 55% of the variation within each age, was interpreted as a measure of “boldness”. Thus, taken together, with the exception of the measurement in the safe and familiar context, it appears that context-specific traits underlie behavior in each of these contexts at each age and that they are sub-modules of a general boldness trait (Figure 8).

The structure of the context-specific and context-general personality traits were fairly consistent across ages. For example, all five of the comparisons between the mirror-test context and the predator and food present context yielded ICCs between 0.26 and 0.36 (Table 10; bottom row). In addition, the mirror-test context measurement and the food and predator present context measurement were consistently highly correlated with PC axis 1 (Table 11; correlation coefficients were all between 0.65 and 0.83). Interestingly, the safe and familiar context measurement had more variability in its relationship with the boldness component (PC axis 1). In the two runs with yearlings, the safe and familiar context measurement was weakly correlated with boldness (0.01 and 0.46), whereas in all trials

with adults (age 36 months and above), it was moderately to highly correlated with boldness (0.52 – 0.73).

Pearson correlation coefficients were calculated to assess the consistency of each personality trait across a range of time intervals from 12 to 48 months (Table 12). Pearson correlation coefficients ranged from 0.27 – 0.53 for each of the three time intervals investigated for the novel context personality trait (Table 12). Correlation coefficients ranged from 0.08 – 0.51 for each of the seven time intervals investigated for the mirror-test context personality trait, and from 0.15 – 0.61 for each of the seven time intervals investigated for the food and predator present context personality trait (Table 12). The boldness personality trait (PC axis 1) had the highest magnitude and most consistent correlation coefficients through time. Correlation coefficients for boldness ranged from 0.26 – 0.68 for each of the seven time intervals and were significantly different from zero in all time intervals except 48 months, which had a sample size of only 39 fish (Table 12). Correlation coefficients ranged from 0.07 – 0.42 for each of the seven time intervals investigated for the safe and familiar context measurement.

Regressions (weighted by sample size for each interval) of personality trait temporal consistency (log-transformed) as a function of the time between measurements were run for the personality traits to investigate the effect of the temporal interval between measures on trait consistency (Table 13). A regression was not conducted with the context-specific trait observed in the novel environment as it was missing several data points. Similarly, a regression was not performed on the measurement in the safe and familiar context as previous analyses suggested that the trait underlying behavior in this context may have changed across development. In general, the consistency observed in the personality traits decreased with an increasing time interval between measures (Figure 9). However, the temporal decline in consistency was significant only for the mirror-test context personality trait. Boldness (PC axis 1), showed relatively little change in the strength of the correlation between the intervals from 3 months to four years (Figure 9C).

DISCUSSION

The results of this study show that context-specific personality traits typically underlie behavior in each context and that the context-specific traits are sub-modules of a general personality trait akin to boldness. Moreover, the results show that moderate levels of consistency are maintained over several years in most of the personality traits. With regard to whether or not the consistency of personality decreases over long time intervals, the results of this study are mixed. The consistency of personality decreased significantly over longer time periods for some traits but not others. Taken together, these results show that personality traits are sufficiently consistent across time to be molded by natural selection. To my knowledge, the current study represents the longest testing period (4 years) of any free ranging, non-primate species. Further, the current study provides a comprehensive investigation into the temporal consistency of several context-specific personality traits, as well as a more general trait (akin to boldness) that underlies the context-specific traits.

With the exception of the measurement in the safe and familiar context, it appears that context-specific traits underlie behavior in each of the investigated contexts at each age and that they are sub-modules of a general boldness trait (Figure 8). Temporal consistency in the relationships between the context-specific personality traits across developmental stages provides further support for this idea. In regards to the measurement in the safe and familiar, a less clear pattern emerged. The relationships between the measurement in the safe and familiar context and each of the other three context-specific traits varied considerably across ages. This may have been due to slight differences in the methodology across runs of the behavioral assays (e.g. there was a fourth context added at the adult stage and the tank size was increased). Alternatively, the fact that the measurement in the safe and familiar context became more highly correlated with the other context-specific traits as the bass became older may indicate that the bass perceived the safe and familiar context differently as they aged. Specifically, it

appears that while the context itself was safe and familiar, bass may have instead perceived it as risky as they grew older and, as a result, the personality trait underlying the expression of behavior in this context may have changed accordingly. This idea is further supported by the results of the principal components analysis conducted at each age. The change in the correlation between component 1 from the PCA (interpreted as boldness) and the measure in the safe and familiar context from the juvenile to the adult stage indicates that the context may have been perceived as risky by adults but not juveniles.

To address the magnitude of consistency maintained across time in each of the personality traits, I calculated Pearson correlation coefficients across time periods ranging from 3 months to 4 years. The novel context personality trait demonstrated temporal consistency over the 24 month testing period that it was observed and the mirror-test context personality trait also demonstrated consistency up to a 24 month period. The trait observed in the food and predator present context and the boldness personality trait both demonstrated significant consistency across a 36 month period that crossed from the juvenile to the adult stage. In terms of the magnitude of consistency, the personality traits tended to have low to moderate levels of consistency. This result is in line with other studies that have investigated personality consistency (Bell and Stamps 2004; Sinn et al. 2008). However, it is important to take the precision of personality trait measurements into consideration when interpreting these results (Burns 2008).

If measures of personality were precise, one would expect to observe intra-class correlation coefficients very close to 1 over very short intervals. I investigated the precision of each of these personality measures over very short intervals and obtained an intra-class correlation coefficient of 0.69 for the novel context personality trait, 0.30 for the safe and familiar context trait, 0.60 for the mirror-test trait, 0.51 for the food and predator context trait, and 0.61 for boldness (Ballew submitted). These relatively low levels of precision aren't surprising given that behavioral measures are used as proxies to quantify personality. Low levels of precision such as this are likely to bias personality consistency

estimates downwards. For example, even if boldness was perfectly consistent over the 48 month testing period, the amount of imprecision in its measurement would make it unlikely to observe levels of consistency above 0.6. Thus, the estimates for personality consistency presented in this study should be considered conservative estimates because each measure is lacking in precision (especially the safe and familiar context measure).

I conducted logarithmic regressions (weighted by sample size) to determine if the temporal consistency in each of the personality traits is dependent on the temporal duration between measurements. Except for the mirror-test context personality trait, the magnitude of consistency in the personality traits did not significantly decrease over longer time intervals. One explanation for this result is that the sample size (7 for most traits) was too low to comprehensively assess the effect of time on personality trait consistency. This result is supported by the relatively high R^2 values for the effect of time on the food and predator present context-specific trait (0.40) and the mirror-test context-specific trait (0.59). However, the R^2 value for the boldness trait was only 0.11. This could potentially indicate that general personality traits such as boldness are more consistent than context-specific traits over long time periods. To thoroughly address this hypotheses, much more data is needed than this study can provide.

If personality has evolved, there are both evolutionary and ecological consequences that must be considered (Wolf and Weissing 2012; Mittelbach et al. 2014). Answers must be sought to explain the maintenance of adaptive personality differences within populations (Dingemanse and Wolf 2010; Wolf and McNamara 2012). Additionally, the effects of personality on populations, communities and even ecosystems must be addressed (Mittelbach et al. 2014). However, before moving on to these larger issues, it is critical to comprehensively address the potential for selection to act on personality traits and cause evolution, which is dependent, in part, on the consistency of personality. Very few studies have investigated the issue of personality trait consistency over long time periods and none of these have

been conducted under situations where personality could develop naturally. To my knowledge, the current study is the first to provide such information and it does so by presenting a comprehensive view of personality. When all results are taken together, they support the notion that personality traits are consistent enough across time to allow selection to take place. However, it is important to note that these results come from a single population with a given evolutionary background that has experienced a given set of environmental conditions. It is difficult to say how personality consistency may be impacted in populations that experience different conditions or unstable conditions (e.g. different or changing predator regimes) over a lifetime. Additionally, different species may exhibit different levels of consistency. Thus, it is of paramount importance to continue to document the temporal consistency of personality traits in other species under various environmental scenarios over biologically relevant durations.

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APPENDIX

Table 9. Behaviors measured in the four behavioral assays, the context for each assay, and the ages in which the assays were conducted.

Behavior	Context	Age observations were made (months)
Length of time to enter new habitat	Opportunity to move into novel environment	36, 48, 60
Amount of time moving	Familiar and safe open-field environment	12, 15, 36, 48, 60
Bites and rams at mirror	Mirror added to open-field environment	12, 15, 36, 48, 60
Length of time to approach food	Model bird predator strikes water above food	12, 15, 36, 48, 60

Table 10. Correlations between context-specific personality traits within each age. Values are intra-class correlation coefficients (95% confidence intervals in parenthesis) of the standardized measurements.

Contexts	Age: 12 months	Age: 15 months	Age: 36 months	Age: 48 months	Age: 60 months
NEC and SFC	NA	NA	0.039 (-0.16, 0.23)	0.275 (0.07, 0.45)	0.243 (0.01, 0.45)
NEC and MTC	NA	NA	0.380 (0.20, 0.54)	0.183 (-0.02, 0.37)	0.297 (0.07, 0.49)
NEC and FPC	NA	NA	0.300 (0.11, 0.467)	0.392 (0.21, 0.55)	0.377 (0.16, 0.56)
SFC and MTC	0.004 (-0.17, 0.18)	-0.019 (-0.20, 0.16)	0.087 (-0.11, 0.28)	0.289 (0.09, 0.46)	0.348 (0.13, 0.54)
SFC and FPC	0.007 (-0.17, 0.18)	0.204 (0.03, 0.37)	0.201 (0.01, 0.38)	0.311 (0.12, 0.48)	0.279 (0.05, 0.48)
MTC and FPC	0.259 (0.09, 0.42)	0.273 (0.10, 0.43)	0.356 (0.17, 0.52)	0.357 (0.17, 0.52)	0.329 (0.11, 0.52)

Note: NEC = Novel environmental context. SFC = Safe and familiar context. MTC = Mirror-test context. FPC = Food and predator present context. Sample sizes; 12 months = 122, 15 months = 122, 36 months = 101, 48 months = 93, 60 months = 71.

Table 11. Principal components analysis of 3 context-specific traits (safe and familiar context, social context (mirror-test), and predator and food present context) at 12, 15, 36, 48, and 60 months of age. Only the loadings (first column for each age) and correlations (second column for each age) for axis 1 are shown.

Loadings (first column) and correlations (second column) to axis 1 at each age											
Behavior	Context for behavior	12 months		15 months		36 months		48 months		60 months	
Amount of time moving	Familiar and safe open-field environment	0.01	0.01	16.24	0.46	26.93	0.62	30.54	0.71	32.71	0.73
Bites and rams at mirror	Mirror added to open-field environment	49.99	0.79	32.15	0.65	31.14	0.67	33.98	0.74	36.07	0.77
Length of time to approach food	Model bird predator strikes water above food	50.00	0.79	51.61	0.83	41.92	0.78	35.48	0.76	31.22	0.71

Note: Axis 1 explained 41.8% of the variation at 12 months, 44.1% of the variation at 15 months, 48.1% of the variation at 36 months, 54.3% of the variation at 48 months, and 54.2% of the variation at 60 months.

Table 12. Temporal consistency within each personality trait across varying time intervals and at different ages. Values are Pearson correlation coefficients (95% confidence intervals in parenthesis).

Interval between measurements	Sample size	NEC	SFC	MTC	FPC	Boldness*
Interval = 3 months (12 – 15 months old)	122	NA	0.095 (-0.09, 0.27)	0.328 (0.16, 0.48)	0.372 (0.21, 0.52)	0.328 (0.16, 0.48)
Interval = 12 months (36 – 48 months old)	93	0.269 (0.07, 0.45)	0.21 (0.01, 0.40)	0.334 (0.14, 0.50)	0.338 (0.14, 0.51)	0.43 (0.25, 0.59)
Interval = 12 months (48 – 60 months old)	71	0.525 (0.33, 0.68)	0.422 (0.21, 0.60)	0.511 (0.32, 0.67)	0.610 (0.44, 0.74)	0.68 (0.52, 0.78)
Interval = 24 months (36 – 60 months old)	71	0.367 (0.15, 0.55)	0.068 (-0.17, 0.30)	0.369 (0.15, 0.56)	0.419 (0.21, 0.59)	0.37 (0.15, 0.55)
Interval = 24 months (12 – 36 months old)	52	NA	0.093 (-0.19, 0.36)	0.250 (-0.03, 0.49)	0.311 (0.04, 0.54)	0.32 (0.05, 0.54)
Interval = 36 months (12 – 48 months old)	52	NA	0.314 (0.05, 0.54)	0.194 (-0.08, 0.44)	0.295 (0.02, 0.53)	0.36 (0.09, 0.57)
Interval = 48 months (12 – 60 months old)	39	NA	0.074 (-0.25, 0.38)	0.076 (-0.25, 0.38)	0.150 (-0.17, 0.44)	0.26 (-0.07, 0.53)

Note: NEC = Novel environmental context. SFC = Safe and familiar context. MTC = Mirror-test context. FPC = Food and predator present context.

*Boldness represents axis one from a principal components analysis performed on the SFC, MTC, and FPC measurements from each age.

Table 13. Regressions of personality trait temporal consistency (log-transformed) as a function of the time between measurements. Values were weighted by the sample size from each interval (e.g. N = 122 for the 3 month interval and N = 39 for the 48 month interval). $\text{Log}(y) = \text{intercept} + \text{slope}(x)$.

Personality Trait	DoF	Intercept Coefficient	Intercept P. value	Slope Coefficient	Slope P. value	R-squared
Trait exhibited in mirror-test context	5	-0.751	0.016	-0.025	0.045	0.586
Trait exhibited with food and a predator in environment	5	-0.743	0.010	-0.015	0.126	0.402
Boldness	5	-0.825	0.007	-0.007	0.460	0.113

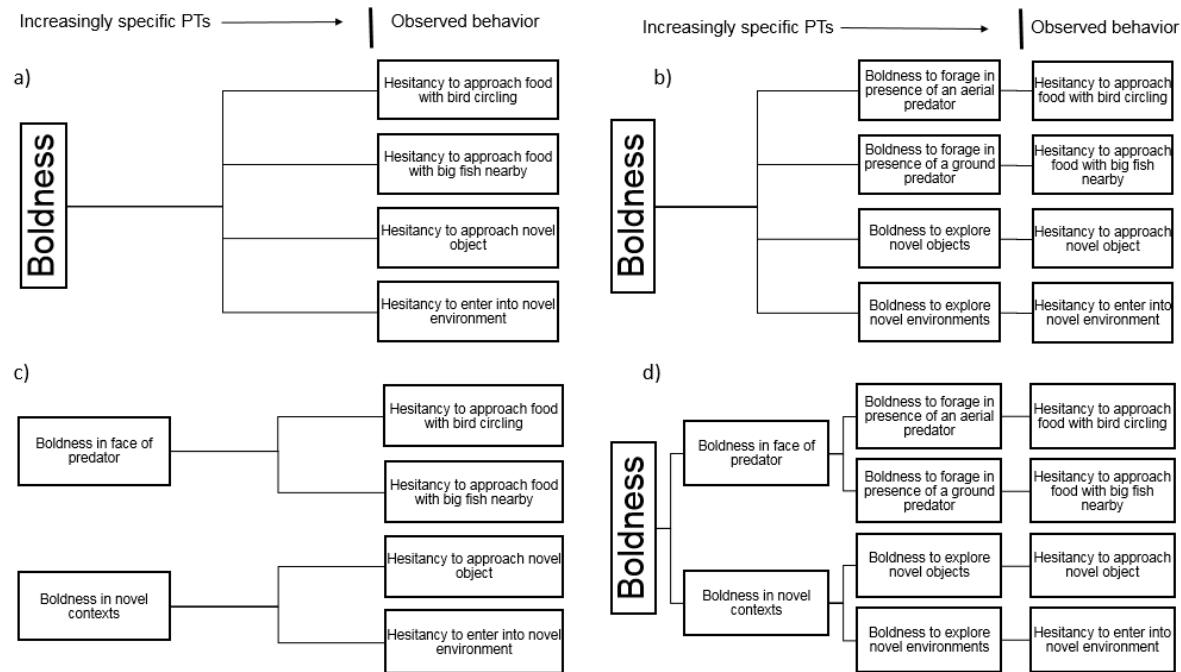


Figure 7. Four hierarchical models illustrating alternative hypotheses for the organization and structure of personality traits. Model (a) proposes a scenario where a general boldness trait underlies the expression of behavior in each context. Thus, repeated observations of inter-individual differences in behavior would yield roughly the same correlations between any two behaviors observed, regardless of whether the observations were made in the same or different contexts. Model (b) proposes a scenario where context-specific personality traits underlie the expression of behavior in each context. These context-specific traits are all sub-modules of the same general boldness trait. Thus, repeated observations of behavior in these contexts would all yield positive correlations. However, repeated observations from within contexts would yield higher correlations than those between contexts. Model (c) proposes a scenario where semi-general personality traits underlie the expression of behavior within functionally similar contexts (e.g. foraging and novelty). Thus, repeated observations of behavior would yield equivalent correlations regardless of whether the observations were made in the same or different contexts, as long as the contexts were functionally similar (e.g. involved novelty). Behaviors expressed in functionally different contexts (e.g. novelty and feeding) would not be correlated. Model (d) proposes a scenario where context-specific traits underlie behavior in each context and each of these context-specific traits are also sub-modules of semi-general traits that underlie behavior in functionally similar contexts (e.g. foraging and novelty). The semi-general traits are themselves sub-modules of a general boldness trait. Under this scenario, repeated observations of inter-individual differences in behavior from within specific contexts would yield the highest correlations, inter-individual differences in behavior from within functionally similar contexts would yield the next highest, and inter-individual differences in behavior across functionally similar contexts would yield the lowest (but still significant) correlations.

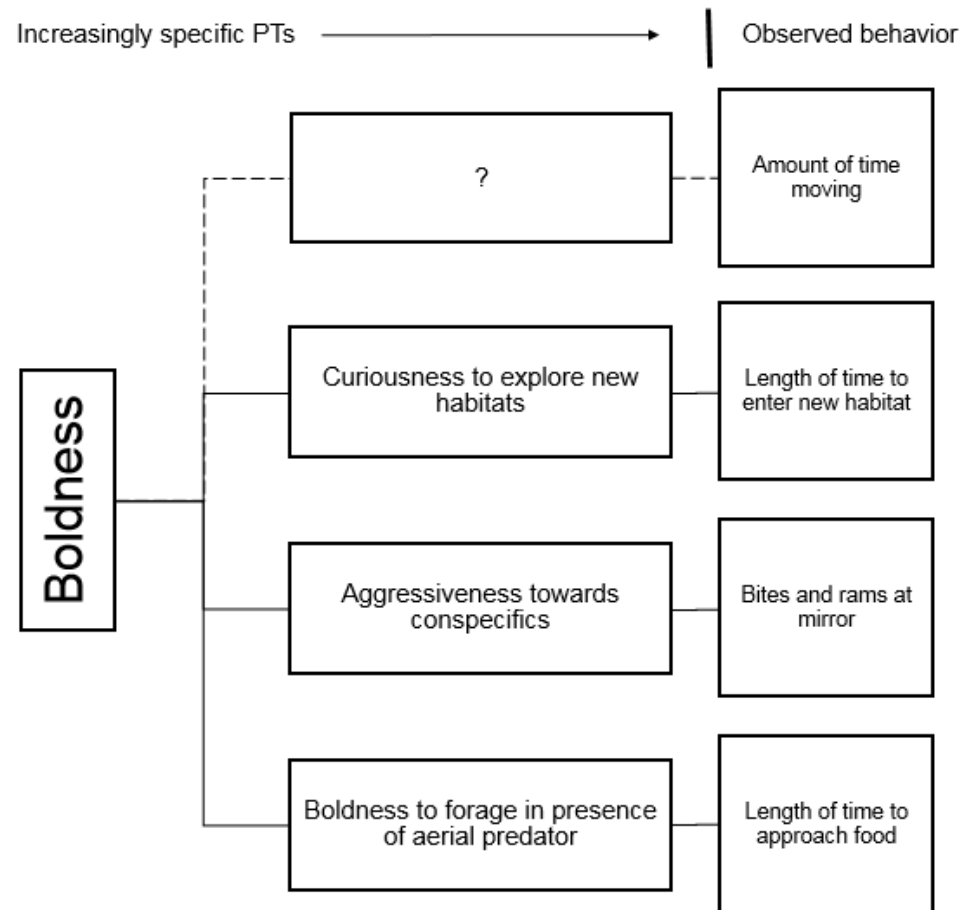


Figure 8. Model illustrating the organization and structure of personality traits based on the results of this study. A context-specific personality trait influenced behavior across all ages of development that were investigated in the novel environment context, in the foraging in the presence of an aerial predator context, and in the mirror-test context. A boldness personality trait generalized beyond specific functional contexts was found to underlie each of these context-specific traits. A personality trait also influenced adult (but not juvenile) behavior in the safe and familiar environment. This personality trait may have been a context-specific trait (indicated by the dashed line between behavior and the unidentified trait) or may have been the general boldness trait (indicated by a dashed line between boldness and the unidentified trait).

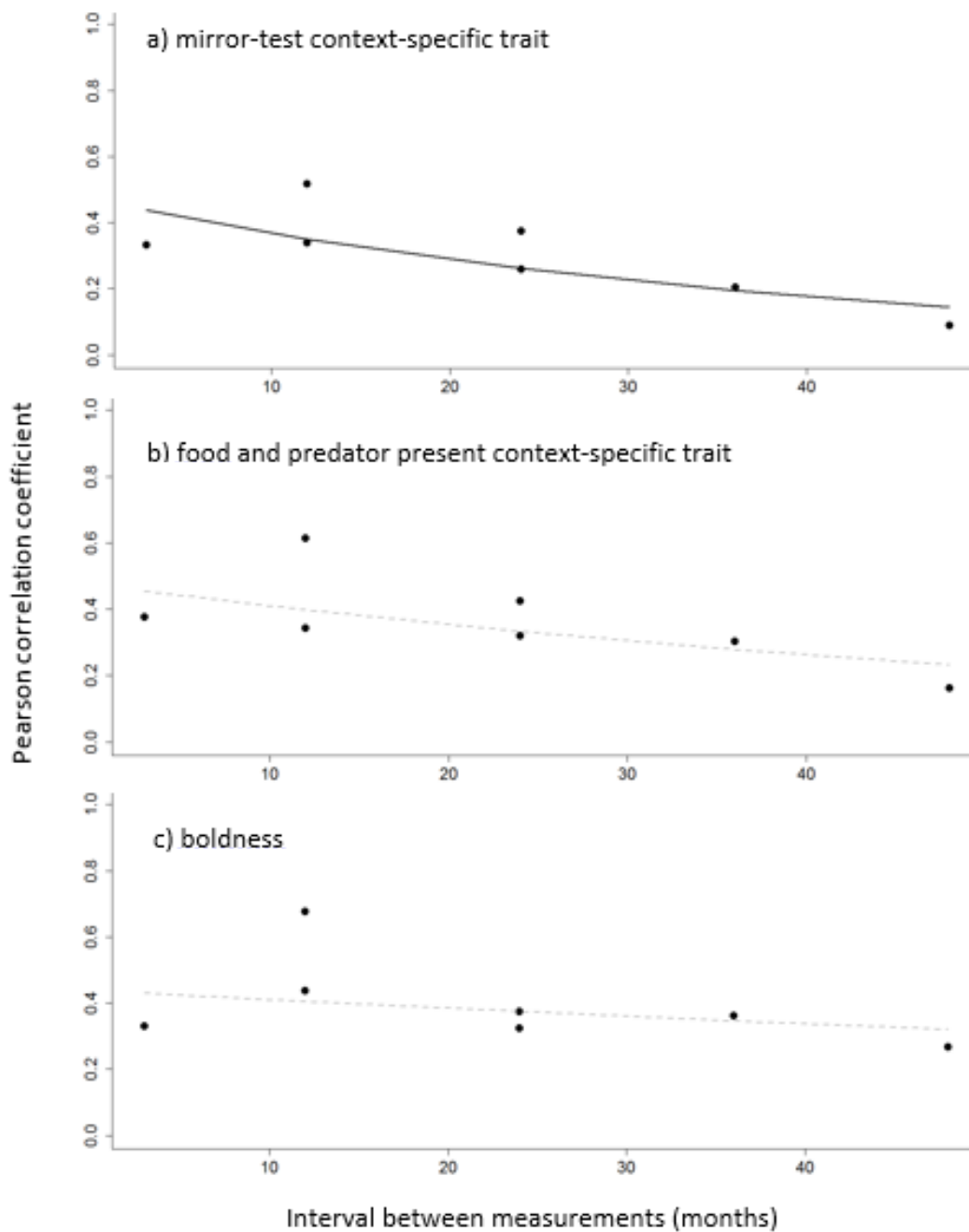


Figure 9. Regressions of personality trait temporal consistency (log-transformed) as a function of the time between measurements in the: a) mirror-test context-specific personality trait, b) food and predation threat context-specific personality trait, and c) boldness trait. Values were weighted by the sample size from each interval (e.g. $N = 122$ for the 3 month interval and $N = 39$ for the 48 month interval). $\text{Log}(y) = \text{intercept} + \text{slope}(x)$. Solid black regression lines are statistically significant while dashed grey lines are not.

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CHAPTER 4: Fitness Tradeoffs Across Development Can Contribute to the Maintenance of Adaptive Personality Differences

ABSTRACT

The maintenance of inter-individual differences in animal personality is often attributed to fitness tradeoffs between phenotypes across spatially or temporally heterogeneous environments. Few studies, however, have examined the potential for fitness tradeoffs across life stages to maintain different animal personality types. Here, we address the fitness consequences of multiple personality traits across life stages and their heritability in largemouth bass (*Micropterus salmoides*). We show that context-specific personality traits underlie the expression of behavior in: 1) a novel environment, 2) a familiar and safe environment, 3) a social environment (mirror-test), and 4) an environment in which both food and predators were present. Further, we show that each of the context-specific traits are sub-modules of a context-general trait identified as boldness (from principal components analysis). Juvenile bass that scored higher in the novel environment context, that were more willing to forage in the predation risk context, and bass that were bolder in general all had significantly lower survivorship than their conspecifics. In contrast, adult bass that were larger and had higher boldness scores had significantly higher reproductive success, as did bass that were more active in the familiar environment. Lastly, the general trait of boldness, but not any of the context-specific personality traits, was heritable at nearly a statistically significant level. The results of this study demonstrate for the first time that individual personality traits can affect fitness in multiple ways over the course of an individual's lifetime. In this case, boldness decreased survival in juveniles but increased reproductive success in adults. A previous study with this population of largemouth bass indicated that boldness is consistent across multiple years and developmental stages. Thus, the fitness tradeoffs across juvenile survival and reproductive success can contribute to the maintenance of adaptive personality differences in boldness.

INTRODUCTION

Studies examining selection and fitness differences between phenotypes are essential for our understanding of evolutionary processes (Pigliucci and Kaplan 2000). Although many studies have examined fitness effects of morphological and life-history traits, studies of selection on personality traits are much less common (Kingsolver et al. 2001; Smith and Blumstein 2008). This paucity in studies has been due, in part, to the fact that personality is not easily characterized into phenotypes that signify 1) a set of inter-related mechanisms that are involved in a character's expression, and 2) a functional significance (Aray-Ajoy and Dingemanse 2014). In addition, personality has historically been viewed as highly plastic and therefore less likely to be under the direct influence of selection (West-Eberhard 1989). However, recent methodological advances have made it possible to apply the traditional phenotypic framework to personality (Dall and Griffith 2014; Ballew in review). Further, two separate meta-analyses have shown that personality can be consistent over biologically meaningful time periods (Bell et al. 2009; Garamszegi et al. 2013; see also Ballew submitted). Thus, studies to explain how personality is generated and maintained by evolution are not only appropriate, they are very much needed (Sih et al. 2004; Réale et al. 2007; Dingemanse & Wolf 2010).

Personality traits have the potential to affect fitness at nearly every stage of development, from a juvenile's chances of surviving to adulthood to an adult's reproductive success (Mitellbach et al. 2014). If personality is consistent across life stages, personality traits may result in fitness tradeoffs across life stages or possibly between different components of selection (e.g. sexual and viability). Moreover, if personality traits are heritable, as has been found in several studies, the fitness consequences of animal personalities could extend across generations (Bell 2005; Brown et al. 2007; Dingemanse et al. 2009; Chervet et al. 2011). Under such circumstances, fitness tradeoffs could be a potentially powerful mechanism for the maintenance of adaptive variation in personality traits. However, to date, studies that have investigated the relationship between personality traits and fitness have generally focused on

a single measure of fitness (such as survival) at a specific life stage (Dingemanse and Réale 2005; Smith and Blumstein 2008). Here, we address the fitness consequences of multiple personality traits across life stages and their heritability in largemouth bass (*Micropterus salmoides*).

To quantify personality, bass were observed in the laboratory under four experimental behavioral contexts: 1) a novel environment, 2) a familiar and safe environment, 3) a social environment (mirror-test), and 4) an environment in which both food and predators were present. Previous studies on this population of largemouth bass indicate that context-specific personality traits underlie the expression of behavior in each of these contexts and that the context-specific traits are sub-modules of a context-general trait identified as boldness (Figure 10) (Ballew in review). Further, the boldness trait, as well as some of the context-specific traits, are consistent across multiple years and life stages (Ballew submitted). To quantify the fitness effects of these personality traits across life stages (and different components of selection), field experiments were conducted on juvenile survivorship and on adult reproductive success. Further, personality was assayed in two generations of bass to assess personality heritability.

In nature, largemouth bass develop from small juveniles that are very vulnerable to piscivorous predators, into large adults that are apex predators in their own right. During the early spring, reproductively mature male bass build nests (shallow depressions in the substrate) in the near-shore areas of lakes (Heidigner 1975; Philipp et al. 1997). Females are courted by nest-guarding males and lay their eggs in one or more nests, which are then fertilized by nest-guarding males (or by cuckolding males). Nesting males then provide sole parental care by guarding nests from potential egg and larval predators (Ridgway 1988; Philipp et al. 1997). Male bass guard their offspring for 2 weeks or more after the offspring leave the nest and begin exogenous feeding as a tightly organized school of fry. Thus, bass have a complex life-history that provides ample opportunities for personality to affect fitness. For example, boldness could positively affect fitness at the juvenile stage through higher feeding

rates/energy gains, which could allow juveniles to outgrow predation threats. Boldness also could positively affect fitness at the adult stage if bolder males have an advantage in intra-sexual competitive encounters and if bolder bass display more intense courting behaviors. However, boldness could negatively affect fitness at the juvenile stage if it increases vulnerability to predators. Further, boldness could negatively affect total reproductive output if bolder bass have shorter lifespans and thus have fewer reproductive opportunities. Environmental factors such as predator density, refuge availability, and adult population density likely play a role in determining the effects that boldness has on fitness at each stage of development. Thus, depending on the environment, the fitness effects of boldness could compound and make boldness very beneficial, very detrimental, or selectively neutral. We investigated the fitness effects of personality on juvenile survivorship in two outdoor pond treatments that varied in refuge availability and its fitness effects on reproductive success in a single treatment that spanned multiple reproductive seasons.

METHODS

Study population and husbandry

The largemouth bass used in each experiment described below were collected from ponds located at the Kellogg Biological Station experimental pond facility in southwest Michigan. These bass were bred on site from adult bass collected from nearby Wintergreen Lake. Bass were transferred to the laboratory facility and were individually marked with colored elastomer gel (a biocompatible pliable polymer; Northwest Marine Technology, Goldsmith et al. 2003) that was injected subcutaneously at two of seven possible locations. The bass were socially housed in aquaria (4 bass per aquarium) and provided with an excess amount of zooplankton. Bass were measured for length and a tissue sample was taken for DNA analysis. Bass were then transferred from the holding aquariums into their own testing aquaria to undergo a series of behavioral assays.

In the spring of 2011, 101 mature, age-3 bass were run through the behavioral assay procedure just prior to the reproductive season. All surviving adults were re-assayed in the spring at age-4 (n=93) and age-5 (n=71). 240 offspring produced from the age-4 bass were collected and they too were run through the behavioral assay procedure. The 240 offspring were used in an experiment to determine the effect of personality on juvenile survivorship. Adult bass were used in an experiment to determine the effect of personality on reproductive success. Further, the adult behavioral assay scores and a subset of the offspring scores were used to determine the heritability of each personality trait. The details of the behavioral assay procedure and experiments are provided below.

Behavioral assay procedure

Behavioral assays followed a similar procedure as outlined in previous studies with this population of largemouth bass (Ballew in review). The testing aquaria were divided into two sections by an opaque vertical partition with the smaller section making up about 10% of the total volume. Individual bass were transferred into the smaller section of a testing tank and then left for approximately 45 minutes to recover from handling and to acclimate to the new environment. After the 45 minute acclimation period, novel context trials were initiated. The partition was raised approximately 10 centimeters above the floor of the aquarium using a pulley system, allowing the fish to swim from the smaller section into the larger section. For each sample, we measured the elapsed time from when the partition was raised until the fish swam into the larger area of the tank. Once a fish moved into the larger section of the tank, we lowered the partition so that it could not move back into the smaller section. An individual's score was calculated by subtracting the number of seconds that it waited before moving to the larger portion of the tank from 2700 (the maximum trial length). Thus, individuals with higher scores moved more quickly to the larger section of the tank. Individuals that did not leave the small section during the trial received a score of 0. Following the completion of the novelty trial, we

placed a mirror on the wall in the smaller section of the tank (not visible to the fish). Fish were then left overnight in the larger section of the tank to acclimate to their new surroundings.

The day after introducing a bass into a testing aquarium, we assayed its behavior in a familiar and safe context. We measured the amount of time the bass spent moving around the tank in the familiar environment (larger section of the tank). Fish were observed for 5 minutes and we summed the total time spent swimming (moving) to calculate the total number of seconds active per trial.

Immediately following the measurements taken in the familiar and safe environment trial, we conducted the social context (mirror-test) trial. We raised the partition to reveal a mirror on the wall in the smaller section of the tank. Once the partition was raised the trial commenced. Trials lasted for 10 minutes. We measured the number of bites, tail swipes, and rams at the mirror. At the end of the trial, the partition was lowered so that the mirror was no longer viewable. The number of bites, tail swipes, and rams were summed together to get an overall measure in this context. These behaviors were summed together because each was taken to be a specific form of agonistic behavior and other studies have shown that individuals often exhibit behavioral specificity so that they tend to primarily use their preferred method of a behavioral type (one individual may primarily use rams while another primarily uses bites; Uher 2011).

Approximately one hour after observing behavior in the presence of the mirror, the feeding in the presence of a predator trial was conducted. A live earthworm tied to monofilament fishing line (no hook) was lowered into the tank near one end. When the bass approached the worm, a model bird suspended on a string and pulley system positioned directly above the worm was released to strike the surface of the water, simulating a predation attempt. The bird was then quickly lifted from the water, again using the string and pulley system. During this time, the fish most often retreated to a corner of the tank. Once the bird was appropriately positioned (10 centimeters above the water surface), the trial commenced. We recorded how many seconds it took the bass to re-approach the worm. An individual's

score was calculated by subtracting the number of seconds that a fish waited before re-approaching the worm from the maximum trial length. Thus, individuals with higher scores re-approached the worm faster. Individuals that did not re-approach the worm during the trial received a score of 0.

Experiments

Experiment 1: Juvenile survivorship

In the late summer of 2012, 240 young-of-year bass were individually marked, measured for size, assayed in the behavioral trials, and then randomly distributed between two experimental ponds (120 bass per pond). Each pond was approximately 30m in diameter and 2m deep. One pond was about 20 years old, contained well-developed aquatic vegetation, and a productive invertebrate community. The other pond was newer (renovated 2 years prior to experiment), was mostly free of aquatic vegetation, and had a less productive invertebrate community base. Three adult largemouth bass (average total length = 283mm) collected from a nearby lake were stocked into each pond to serve as potential predators on the juvenile bass. In the summer of 2013, both ponds were drained and all surviving bass were collected and measured for size. 66 juveniles survived in the vegetated pond and 67 survived in the pond mostly free of vegetation. All adult bass survived in each pond.

Experiment 2: Adult reproductive success

101 age-3, reproductively mature bass were assayed in the behavioral trials in the spring of 2011 and then sexed using methods previously developed by Benz and Jacobs (1986). Bass were randomly distributed among three experimental ponds (34 bass in two ponds and 33 in one, with a sex ratio of 18-19 males to 15 females). Once the reproductive season commenced, ponds were snorkeled daily by an observer to locate all male nests. When nests were found, an attempt was made to identify the nest guarding male. Photographs of nests were taken to quantify the number of eggs in each nest.

Additionally, a sample of approximately 20 eggs was collected from each nest and hatched in the laboratory. Laboratory hatched larvae were euthanized with MS-222 and then stored in ethanol for later DNA analysis. This experimental design was continued the following two years (2012 and 2013). In the spring, the ponds were drained and all surviving adults were collected and identified (age-4 n=93; age-5 n=71). The adults were then taken to the laboratory for approximately 1 week to run them through the behavioral assays and re-measure them for size. Adults were then placed back into the experimental ponds to observe the reproductive success. 35 nests with eggs were located over the 3 year study period (12 age-3 nests, 15 age-4 nests, and 8 age-5 nests).

We extracted DNA from all 101 adults and from up to 5 larvae from each nest (from the subset of 20 eggs that were collected from each nest and hatched in the laboratory) by using the QIAGEN DNeasy extraction kit in accordance with the manufacturer's specifications. We diluted DNA samples to 20 ng/ μ L and then genotyped them at 10 microsatellite loci; Lma21 (Colbourne et al. 1995), Msaf14, Msaf17 (Seyoum et al. 2013), MiSaTPW011, MiSaTPW012, MiSaTPW038, MiSaTPW068, MiSaTPW076, MiSaTPW107, and MiSaTPW173 (Lutz-Carrillo et al. 2008). Amplification was performed using polymerase chain reaction (PCR) and alleles were separated using gel electrophoresis on a 6% polyacrylamide gel. Products were visualized using an FMBIOII scanner (Hitachi Inc., Tokyo, Japan). All gels were independently scored by two experienced laboratory personnel. To estimate genotyping error, 10% of adults were randomly selected and re-genotyped for all loci. Estimates of expected heterozygosity, number of alleles, and tests for Hardy-Weinberg Equilibrium were performed using the program CERVUS 3.0.3 (Kalinowski et al. 2007).

To determine parentage for each nest and ultimately reproductive success for each adult at each age, a multi-step approach was employed. Firstly, we conducted a preliminary parentage analysis with unknown parents using the program CERVUS 3.0.3 (Kalinowski et al. 2007). The preliminary parentage analysis allowed for the successful identification of the sire (or sires) for 25 of the 35 nests. A

male was visually identified on 23 of those 25 nests. In those 23 cases, the paternal parent assigned to the nest based on the parentage analysis matched the male identified on the nest 22 times. Thus, the paternal parent was assumed to be known in all cases in which a male was identified on a nest (31 of the 35 nests). A second parentage analysis was then conducted using CERVUS 3.0.3 with the paternal parent/s assumed as known for 33 of the nests (31 from visual identification and 2 from the preliminary parentage analysis) to assign the maternal parent/s for each nest. Ultimately, of the 35 total nests, 34 had 1 or more male assigned at least partial parentage and 27 had 1 or more female assigned at least partial parentage. The egg score for each nest (calculated from photographs) was then used to determine the number of fertilized eggs produced by each adult during each reproductive season. In cases in which a nest had multiple paternity or multiple maternity (based on parentage analysis), the egg scores were distributed accordingly. For example, if 4 of the 5 larvae in a nest were assigned to male 1 and 1 of the 5 were assigned to male 2, male 1 would be given a reproductive success score = 80% of the nest egg score while male 2 would be given a reproductive success score = 20% of the nest egg score. If fertilized eggs from multiple nests were assigned to an adult, the egg scores from each nest were summed to calculate the adult's reproductive success. Thus, each adult had a reproductive success score at age-3, age-4, and age-5.

Experiment 3: Personality heritability

The 240 young-of-year offspring used in the juvenile survival experiment were produced by the age-4 adult bass used in the reproductive success experiment. Thus, we had personality data for 240 offspring and their 93 potential parents. 159 of the 240 offspring were randomly selected for DNA analysis. DNA was extracted, amplified, and visualized at 10 microsatellite loci following the methods described above in the reproductive success experiment. To determine parentage for these 159 samples, we conducted a parentage analysis with unknown parents (the genotypes for the 93 potential

parents were obtained during the reproductive success experiment) using the program CERVUS 3.0.3 (Kalinowski et al. 2007). After taking into account what was already known about the reproductive history of this population at 4 years of age (knowledge of the nests that were produced and parentage for each nest), the results of the parentage analysis allowed for the assignment of 39 of the 159 offspring to parent pairs.

Statistical analysis

All statistical analyses were conducted using R version 2.13 (R Development Core Team 2008). Previous studies on this population of largemouth bass indicate that context-specific personality traits underlie the expression of behavior in each of the contexts observed and that correlations exist between most of the context-specific traits (Ballew in review). To determine if the context-specific traits are sub-modules of a context-general trait (like boldness), we conducted a principal components analysis of the four context-specific personality traits. Separate principal components analyses were conducted for the 240 juvenile bass (which included the 39 used in the heritability study), and for the adult context-specific personality traits at age-3, age-4, and age-5. The principal components analyses revealed a general personality trait interpreted as boldness in the juveniles and at each age in the adults. This result is in line with other studies on this bass population (Ballew in review). Thus, in addition to the fitness effects of the context-specific traits, the fitness effects of the boldness trait (from the PCA) were also investigated.

To investigate the effect of personality traits on juvenile survivorship in experiment 1, we first standardized (mean = 0 and standard deviation = 1) the scores for initial and final length and for each personality trait. We then performed separate logistic regressions for each personality trait. We included initial length and pond as covariates; $\text{Survival (Yes/No)} = \text{Length} + \text{Personality} + \text{Pond} + \text{Length:Personality} + \text{Length:Pond} + \text{Personality:Pond}$.

To investigate the effect of personality on adult reproductive success in experiment 2, we first summed the reproductive success values from age-3, age-4, and age-5 to calculate a cumulative reproductive success score for each adult, which was then standardized to a mean of 0 and a standard deviation of 1. We standardized the personality and size scores for the adult context-specific personality traits at age-3, age-4, and age-5. We then calculated average personality scores for each personality trait within each individual and average size for each individual. If an adult survived over all three years, their average personality and average size scores were calculated based on their scores at age-3, age-4, and age-5. For those individuals who did not survive through age-5, the averages were calculated based on the years in which they were measured. Calculating an average score for each personality trait is warranted based on the consistency observed in these traits over this time period (Ballew submitted). We performed separate linear regressions for each personality trait (with the average scores) and included sex and average length as covariates; Cumulative reproductive success = Sex + Length + Personality + Sex:Length + Sex:Personality + Length:Personality.

To investigate the heritability of each personality trait in experiment 3, we used the standardized personality scores for the adults when they produced the offspring (age-4) and the standardized personality scores for the offspring (from the total 240 offspring) when they were young-of-year. The 39 offspring that had parentage assigned were produced by 7 families, with a range of 1 to 17 offspring per family. The average offspring personality score for each family was calculated for each personality trait. We then performed separate linear regressions for each personality trait; Average offspring personality for the family = Mid-parent personality. The regressions were weighted by number of offspring in each family. Separate regressions were conducted on each context-specific personality trait and on the general boldness trait.

RESULTS

Experiment 1: Juvenile survivorship

A general personality trait interpreted as boldness was uncovered from the principal components analysis on the four context-specific personality traits. Bolder individuals (higher scores on axis 1) were significantly less hesitant to enter a novel environment, were more active in the safe and familiar context, were more aggressive in the mirror-test context, and were less hesitant to approach the food in the food and predator present context. Overall, boldness explained 48% of the variation observed in the four context-specific traits.

Logistic regressions of the effect of initial length and personality on juvenile survivorship in two different pond environments (highly vegetated and not vegetated) revealed that larger juvenile bass had significantly higher survivorship (Table 14). Further, there was an interaction between pond environment and length. Initial length had a significantly greater positive effect on survivorship in the vegetated pond than in the non-vegetated pond (Figure 11b). Additionally, bass that scored higher in the novel environment context, bass that were more willing to forage in the predation risk context, and bass that were bolder in general (Axis 1 from PCA) all had significantly lower survivorship than their conspecifics. Each of these three traits also had a significant interaction with the pond environment. Bass that were bolder, more exploratory, and more willing to forage had much lower survivorship when compared to conspecifics in the vegetated pond but not in the non-vegetated pond (Figure 11a).

Experiment 2: Adult reproductive success

A boldness trait similar to the one found in the sample population used in experiment 1 was uncovered in the sample population used in experiment 2 (Boldness = Axis 1 from PCA and explains 43% of the variation at age-3, 47% of the variation at age-4, and 48% of the variation at age-5). Linear regressions of the effect of sex, average length, and average personality on reproductive success

revealed that bass that were more active in the familiar environment had a significantly higher reproductive success (Table 15). Additionally, length and personality interacted to effect reproductive success. Large, bold (Axis 1 from PCA) bass had significantly higher reproductive success than bold, small bass and large, timid bass and this effect was due primarily to males (Figure 12). Similar interactions were found between length and exploration in the novel environment and length and aggressiveness in the mirror context.

Experiment 3: Personality heritability

Small sample size (n=39) made it difficult to assess the heritability of the personality traits via parent-offspring regressions with a high degree of accuracy. Nonetheless, we found that the general boldness trait (Axis 1 from the PCA) had a nearly statistically significant heritability of 0.527 (Figure 13; Table 16 95% confidence interval = -0.031 – 1.084). While none of the context-specific personality traits were heritable at the statistically significant $p < 0.05$ level, both the novel environment context trait and the food and predator present context trait displayed moderate levels of heritability in this study population. Thus, further analysis into the heritability of these traits, as well as the other context-specific personality traits, is warranted.

DISCUSSION

The results of this study demonstrate for the first time that individual personality traits can affect fitness in multiple ways over the course of an individual's lifetime. Under semi-natural conditions (outdoor ponds), larger and bolder adult bass had higher reproductive success over a 3-year period. Bolder juveniles spawned by these adults, however, had significantly lower survivorship. Thus, boldness impacted fitness differently in the adult and juvenile stages. As a result, there may be a fitness tradeoff between juvenile survivorship and adult reproductive success. As boldness was significantly heritable, it

appears that in at least some environments, alternative boldness phenotypes may yield similar fitness, which could maintain variation in boldness within populations. This latter result is in line with a model that was developed to explain sexual cannibalism in the fishing spider *Dolomedes fimbriatus* (Arnqvist and Henriksson 1997). In this study, selection was modeled to favor high levels of aggression in juvenile females, as it increased growth rate and adult fecundity, but low levels of aggression in adulthood, as it led to maladaptive pre-copulatory sexual cannibalism. Further, aggression was modeled to be consistent from the juvenile to the adult stage. As a result, trade-offs across contexts were found that could lead to a population of individuals that varies dramatically in aggression levels.

While boldness did negatively impact juvenile survivorship, this effect was not observed in both pond environments. In the pond with dense vegetation, bold juveniles had significantly lower survival than their more timid conspecifics, but boldness did not significantly affect survivorship in the newly renovated pond with sparse vegetation. This interaction between boldness and pond type on juvenile survival could have been due to the fact that in the high vegetation pond in which boldness negatively affected juvenile survival, vegetation may have served as refuge from predation for juvenile bass that wished to use it. Shyer bass would likely be more apt to avoid predators when possible, and as a result, would likely be the ones that would take advantage of the refuge. In contrast, in the pond with low levels of vegetation, shy individuals had no opportunity to seek refuge from predation. Thus, the juvenile survivorship in this pond was unaffected by boldness. This result suggests that, in addition to fitness tradeoffs across development, tradeoffs across fluctuating selection pressures could further act to maintain variation in personality.

The “trade-off” hypothesis posits that individual fitness varies depending on environmental context and that contexts fluctuate frequently, resulting in the maintenance of variation (Sih et al. 2004). Studies have demonstrated that fitness consequences for personality traits can vary according to shifting environmental conditions such as predation pressure (Réale and Festa-Bianchet 2003), food

availability (Dingemanse et al. 2004), and social condition (Both et al. 2005). However, studies have yet to demonstrate how common it is for these environmental conditions to shift enough in nature to significantly reduce (or reverse) the direction of selection. A related idea is that frequency dependent selection may also operate on personality traits to maintain variation (Sih et al. 2004; Dingemanse and Réale 2005; Wolf and McNamara 2012).

Larger juveniles survived better in the densely vegetated pond but size did not affect juvenile survivorship in the sparsely vegetated pond. Further, juveniles in the more densely vegetated pond grew much faster than in the sparsely vegetated pond, likely due to a higher density of invertebrates. Thus, the largest juveniles in the densely vegetated pond may have grown fast enough to reach sizes that allowed them to escape the threat of predation during the course of the experiment. In contrast, in the sparsely vegetated pond, the largest individuals likely did not grow enough to reach sizes large enough to escape predation. This differences in growth rate in the two ponds could explain the interaction effect between length and pond environment on juvenile survival. In addition, past studies have shown that bolder juveniles grow faster (Ballew submitted). Thus, in the densely vegetated pond, boldness may have directly negatively affected juvenile survivorship and indirectly positively affected juvenile survivorship (through faster juvenile growth). This explanation would be consistent with the growth-mortality hypothesis that boldness results in reduced survivorship at the early juvenile stage but higher growth, which could result in increased survivorship at the later juvenile stage and also in increased reproductive success at the adult stage (Mittelbach et al. 2014).

The results of the current study suggest that selective forces on personality traits in nature can be substantial and may shape personality variation within the time frame of a single generation. It should be noted, however, that not all observed variation is attributable to heritable differences. For example, while each of the context-specific traits investigated in this study had a significant effect on fitness during at least one life stage, none of the context-specific personality traits were heritable at a

statistically significant level. This may be in part due to the low power of the parent-offspring test of heritability conducted in this study. However, other studies have also reported low, and in some cases, non-significant levels of heritability in personality traits (Bell 2005; Dingemanse et al. 2009; Kortet et al. 2014; reviewed for fish in Mittelbach et al. 2014). Thus, early experience, maternal effects, and paternal effects are also likely to have relatively large effects on an individual's personality type (Dingemanse et al. 2009; Stamps & Groothuis 2010).

Our results demonstrate for the first time that trade-offs across components of fitness, as well as fluctuating environmental conditions, have the potential to maintain variation in boldness within populations. Our results also caution against drawing conclusions regarding the overall fitness consequences of a personality trait from studies conducted on a single component of fitness at a given stage of development (Smith and Blumstein 2008). To adequately address the fitness consequences of personality in a species of interest, it is necessary to fully consider the ecology and evolutionary context of the species, properly characterize personality phenotypes, and assess their level of consistency (Dall and Griffith 2014; Aray-Ajoy and Dingemanse 2014). Comprehensive studies that investigate the fitness consequences of personality over its entire length of consistency are needed in order to fully understand the mechanisms that most commonly shape and maintain personality variation within populations.

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APPENDIX

Table 14. Logistic regressions of the effect of length and personality on juvenile survivorship in two different experimental ponds. One pond was older and contained abundant macrophytes and invertebrates while the other was newly renovated and contained little vegetation and a less productive invertebrate community. Each model has 233 degrees of freedom. Survival (Yes/No) = Length + Personality + Pond + Length:Personality + Length:Pond + Personality:Pond. For comparison, the null model deviance was 329.89.

Personality Trait	Intercept	Length Coefficient	Personality Coefficient	Pond Coefficient	Length:PT Coefficient	Length:Pond Coefficient	PT:Pond Coefficient	Residual Deviance from model
NECT	0.122	0.667**	-0.519*	0.106	0.169	-0.699*	0.553*	311.66
SFCT	0.196	0.604**	-0.295	0.031	0.051	-0.631*	0.231	317.23
MTCT	0.188	0.613**	-0.084	0.065	0.043	-0.682*	-0.075	318.95
FPCT	0.120	0.693**	-0.693**	0.114	0.121	-0.733*	0.732*	309.64
Boldness	0.108	0.671**	-0.657**	0.131	0.155	-0.716*	0.636*	309.48

Note: NECT = Novel environment context trait, SFCT = Safe and familiar context trait, MTCT = mirror-test context trait, FPCT = food and predator present context trait. * = $P \leq 0.05$; ** = $P \leq 0.005$.

Table 15. Linear regressions of the effect of sex, length, and personality on adult bass reproductive success. Reproductive success = Sex + Length + Personality + Sex:Length + Sex:Personality + Length:Personality. Each model has 94 degrees of freedom.

Personality Trait	Intercept	Sex Coefficient	Length Coefficient	Personality Coefficient	Sex:Length Coefficient	Sex:PT Coefficient	Length:PT Coefficient	R-squared
NECT	0.011	-0.077	0.013	0.028	0.253	0.270	0.218*	0.149
SFCT	0.076	-0.072	-0.063	0.334*	0.401	-0.202	-0.013	0.130
MTCT	0.067	-0.111	0.165	0.190	0.188	-0.051	0.421**	0.238
FPCT	0.009	-0.038	-0.015	-0.046	0.289	0.204	0.099	0.100
Boldness	0.045	-0.138	0.061	0.100	0.169	0.180	0.219*	0.169

Note: NECT = novel environment context trait, SFCT = Safe and familiar context trait, MTCT = mirror-test context trait, FPCT = food and predator present context trait. * = $P \leq 0.05$, ** = $P \leq 0.005$.

Table 16. Linear regressions of the heritability of each personality trait. Each model has 5 degrees of freedom. Average offspring personality = Mid-parent personality. Regressions weighted by number of offspring in each family.

Personality Trait	Heritability	95% Confidence Intervals
NECT	0.153	-0.392 – 0.697
SFCT	-0.233	-0.604 – 0.139
MTCT	-0.111	-0.745 – 0.523
FPCT	0.270	-0.228 – 0.769
Boldness	0.527	-0.031 – 1.084

Note: NECT = novel environment context trait, SFCT = Safe and familiar context trait, MTCT = mirror-test context trait, FPCT = food and predator present context trait.

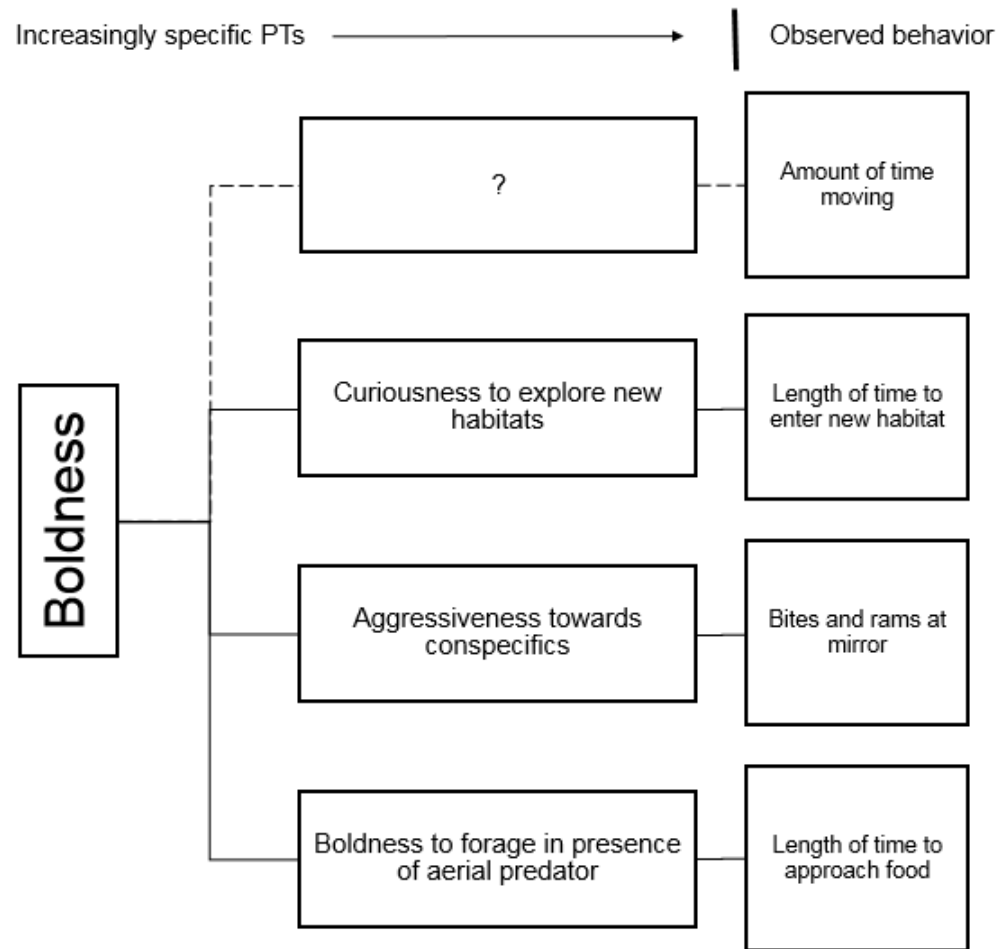


Figure 10. Model illustrating the organization and structure of personality traits in this population of largemouth bass. A context-specific personality trait influenced behavior across all ages of development that were investigated in the novel environment context, in the foraging in the presence of an aerial predator context, and in the mirror-test context. A boldness personality trait generalized beyond specific functional contexts was found to underlie each of these context-specific traits. A personality trait also influenced adult (but not juvenile) behavior in the safe and familiar environment. This personality trait may have been a context-specific trait (indicated by the dashed line between behavior and the unidentified trait) or may have been the general boldness trait (indicated by a dashed line between boldness and the unidentified trait).

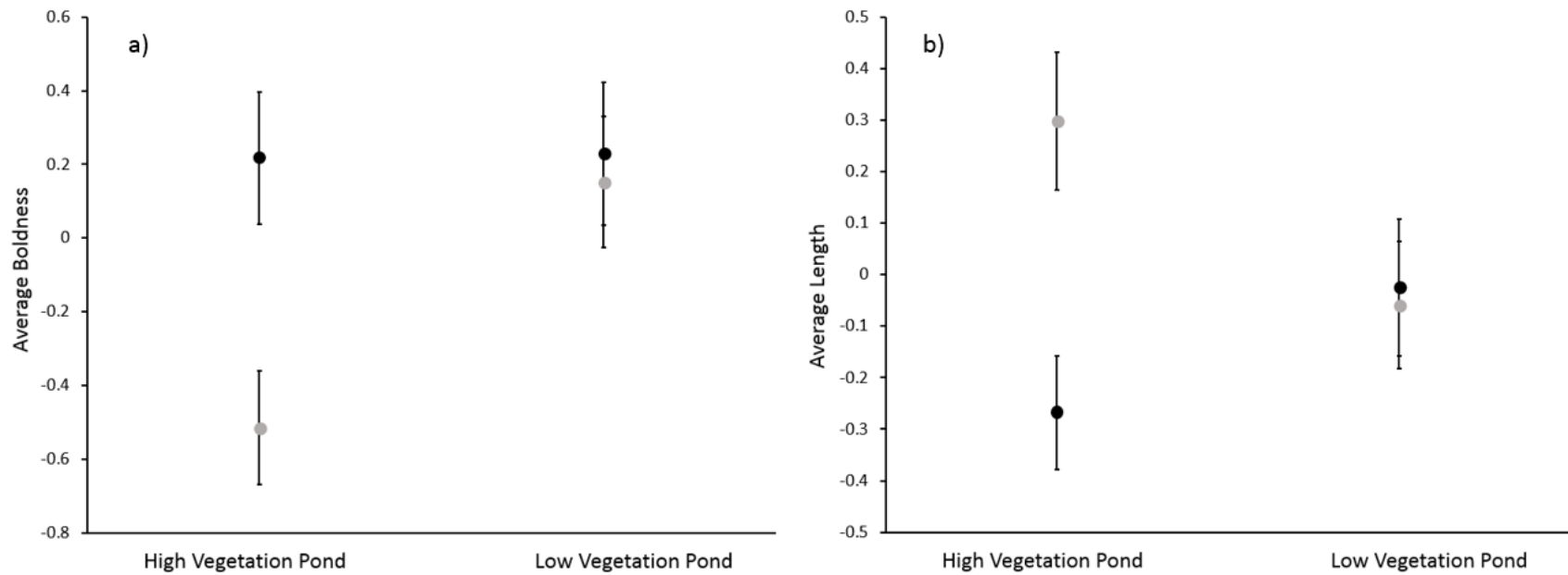


Figure 11. a) Average boldness and b) average initial length of bass that survived to the end of the experiment (grey circles) and bass that did not survive (black circles) in the high vegetation pond and in the low vegetation pond. Error bars indicate the standard error of the mean.

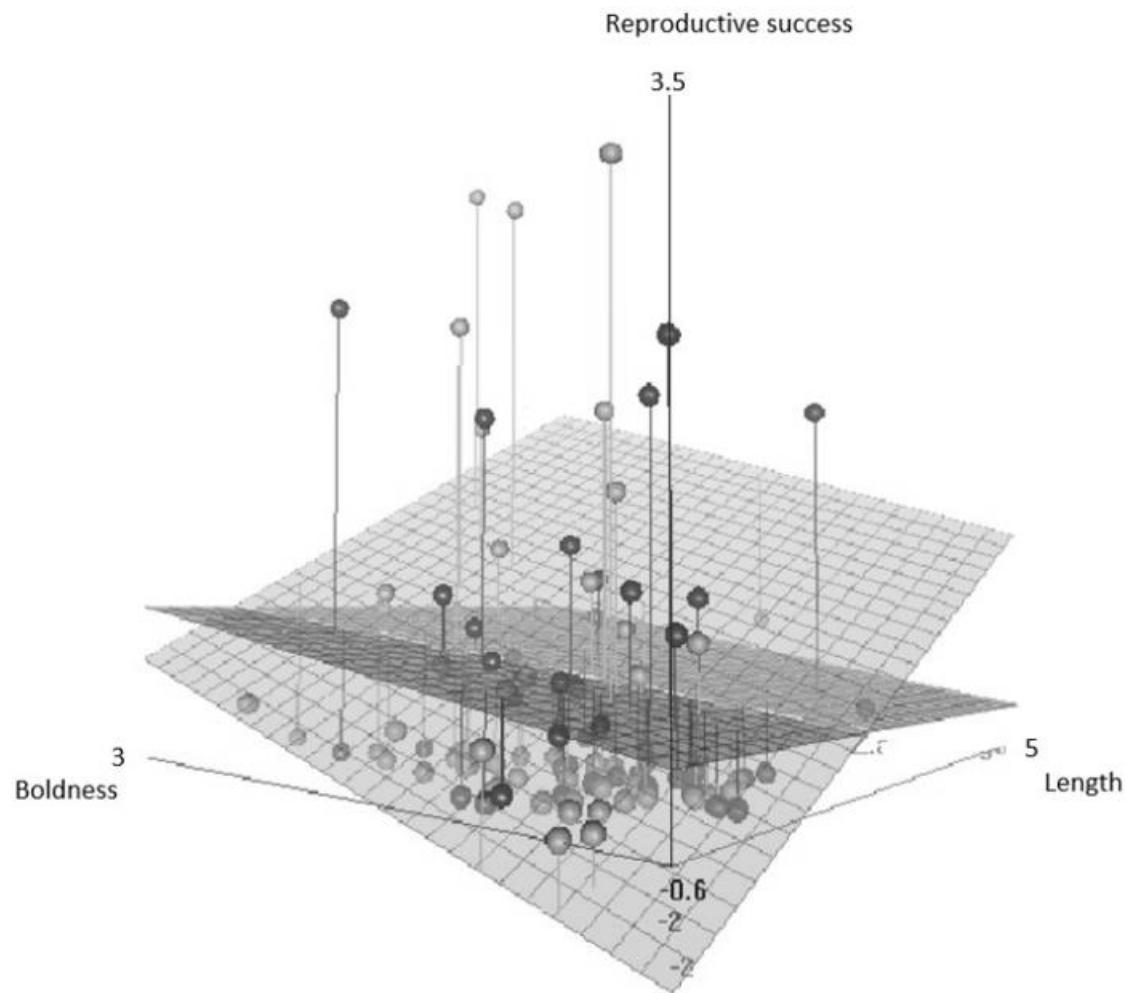


Figure 12. The effects of boldness, length, and the interaction between them on adult reproductive success. The light grey plane represents the relationships between the variables for males and the dark grey plane represents the relationships between the variables for females. The circles (light grey = males; dark grey = females) represent individual males and the lines from the circles to the planes represent residual values.

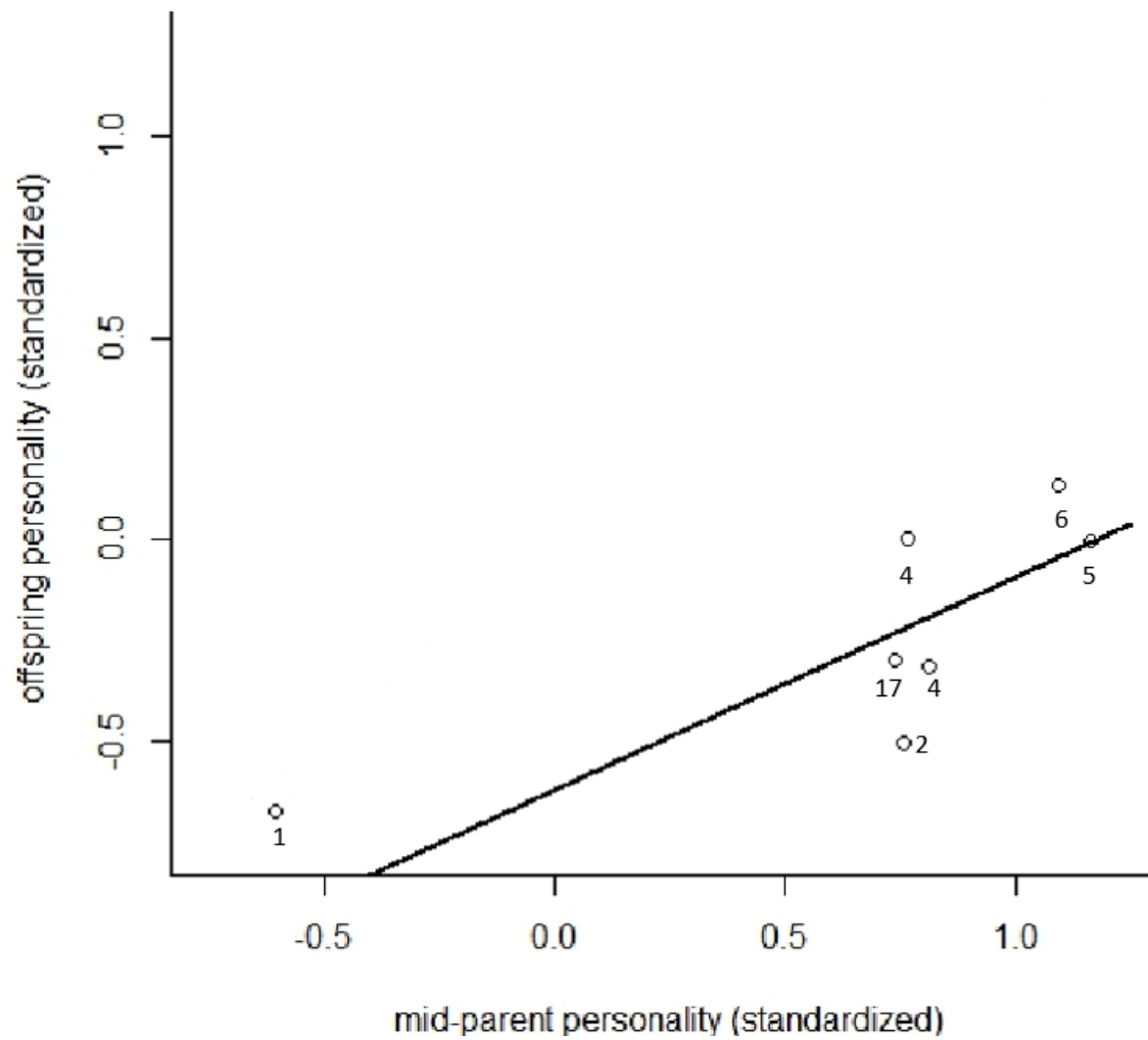


Figure 13. The heritability of boldness. Each circle represents the average boldness of offspring in a full-sib family. The numbers below the circles represent the number of offspring in each family. The trend line (black) is weighted by the number of offspring in each family.

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CHAPTER 5: Personality Affects Angling Vulnerability in Largemouth Bass (*Micropterus Salmoides*)

ABSTRACT

Commercial and recreational fishing can be a strong selective force, however, studies of the effects of personality on vulnerability to angling are scarce. Here, I investigated if personality traits affect vulnerability to angling in largemouth bass (*Micropterus salmoides*) in three different angling contexts. To quantify personality, behavior was assayed in the laboratory under four experimental conditions: a novel environment context, a familiar environment context, a social context, and a feeding under predation risk context. After quantifying personality, fish were subjected to one of three angling contexts: 1) a mesocosm context, 2) an outdoor pond, and 3) an outdoor pond with casts made directly onto bass nests. When angling was conducted in a mesocosm, which was likely perceived to contain a high level of risk, bass that were more risky foragers with predators present in the laboratory were more vulnerable to angling. Additionally, bass that were bolder in general (boldness obtained from a principal components analysis of the context-specific behavioral measurements) were also more vulnerable to angling in the mesocosm context. When angling was conducted in an outdoor pond, which was likely perceived to contain a low level of risk, bass that were more aggressive in the laboratory were more vulnerable to angling. Lastly, nest guarding males that were more active in the safe and familiar environment and were bolder in general were more vulnerable to angling. The results of this study aid in our understanding of the selective capture of fish by recreational angling, which may have significant evolutionary and ecological consequences and may affect the quality of fisheries.

INTRODUCTION

Individuals from the same population and at the same developmental stage often display consistent differences in behavior over time and across contexts (Gosling 2001; Réale et al. 2007; Bell et al. 2009). This consistent inter-individual variation in behavior is widely accepted as evidence of personality types that underlie the expression of behavior (Budaev and Brown 2011; Araya-Ajoy and Dingemanse 2014). Several studies have demonstrated that personality can affect various components of fitness (Smith and Blumstein 2008; Kontiainen et al. 2009; Ariyomo and Watt 2012). Further, there is mounting evidence that personality types have a heritable component (Chervet et al. 2011; Ariyomo et al. 2013; Kortet et al. 2014; Ballew et al. in prep). These results indicate that personality variation within populations may well be the adaptive outcome of natural selection (Mittelbach et al. 2014). A study that compared levels of activity, aggression, and boldness in populations of threespined stickleback supports this idea (Bell 2005). Stickleback populations differed significantly in mean levels of boldness and aggressiveness, likely due to differences in predator regime. The idea that personality may be the adaptive outcome of natural selection has also been recently applied to fisheries research to develop hypotheses regarding the potential evolutionary consequences of recreational fishing (angling).

A fish's personality may determine its vulnerability to capture by recreational angling and thus its survival and fitness (Uusi-Heikkilä et al. 2008; Mittelbach et al. 2014). However, studies of the effects of personality on angling vulnerability are scarce (Biro and Post 2008; Wilson et al. 2011; Binder et al. 2012; Klefoth et al. 2013). Previous empirical studies on vulnerability to angling have mainly compared personalities between groups selected for high or low vulnerability to angling (Redpath et al. 2009; Binder et al. 2012) or groups differing in domestication history (Biro and Post 2008; Klefoth et al. 2013). For example, artificial selection for vulnerability to angling has been shown to affect foraging behavior in largemouth bass (Nannini et al. 2011). To date, the relationship between personality and angling vulnerability has only been investigated at the individual level in one study with bluegill sunfish (Wilson

et al. 2011), which surprisingly showed that timid fish may be more vulnerable to angling. Thus, there is great need for more studies that directly investigate the selection pathways that may lead to fisheries-induced evolution (Uusi-Heikkilä et al. 2008).

Boldness and aggressiveness, in particular, are frequently hypothesized to affect angling vulnerability (Cooke et al. 2007; Biro and Post 2008; Klefoth et al. 2013). Boldness has been shown to underlie behaviors such as general activity, space use, foraging behavior, and exploration (Wilson and McLaughlin 2007; Farwell and McLaughlin 2009; Wilson and Godin 2009). Thus, if a bait or a lure is perceived by a fish as a risky foraging opportunity, it is easy to see how boldness would affect an individual's propensity to strike. Conversely, if striking a bait or a lure represents an aggressive act (as opposed to a foraging one), then an individual's angling vulnerability would be more affected by its level of aggressiveness. However, it is important to note that aggressive behavior, such as biting at conspecifics, has also been hypothesized to be influenced by boldness, as agonistic interactions carry a significant level of risk in their own right (Budaev and Brown 2011). Additionally, all angling scenarios may not be perceived in the same manner and as a result, different scenarios may result in different selection pathways. For example, lures cast into cover (logs, under docks, etc) may be perceived by fish as non-risky foraging opportunities while lures cast into open water may be perceived as more risky. In the same way, in species that build nests or redds and provide parental care, a lure cast onto the nest of a guarding parent may be perceived very differently than one cast into open water. As such, the personality traits that affect angling vulnerability in each of these situations may be very different.

Here, I use largemouth bass (*Micropterus salmoides*) to address if personality traits affect angling vulnerability. Largemouth bass are particularly amenable to this type of study as they are abundant in many freshwater systems and are known to exhibit consistent inter-individual differences in personality across life stages (Philipp et al. 2014; Ballew submitted). In most habitats, largemouth bass develop from small juvenile fish that are vulnerable to predation into large adults that are apex

predators in their own right. During the spring, reproductively mature male bass build highly visible nests in the shallow littoral areas of lakes (Heidigner 1975; Philipp et al. 1997). Females lay eggs in the nests and then leave the males, who provide sole parental care by guarding the nests from potential egg and larval predators (Ridgway 1988; Philipp et al. 1997). Bass are a popular target of recreational fisherman and results from an artificial selection experiment show that largemouth bass have the potential to adapt to recreational angling (Philipp et al. 2009). Further, angling during the bass reproductive season is especially popular among a segment of bass anglers.

I investigated the relationship between personality and angling vulnerability in three different angling contexts. To quantify personality, fish were observed in the laboratory under four experimental behavioral contexts: 1) a novel environment, 2) a familiar and safe environment, 3) a social environment (mirror-test), and 4) an environment where food and predators were present. Previous studies on this population of largemouth bass indicate that context-specific personality traits underlie the expression of behavior in each of these contexts and that the context-specific traits are sub-modules of a context-general trait identified as boldness (Ballew submitted). After quantifying personality, fish were subjected to angling in one of three contexts: 1) a mesocosm, 2) a semi-natural outdoor pond, 3) a semi-natural outdoor pond where casts were made directly onto bass nests.

I predicted that in the mesocosm angling context, bass that hesitate less before approaching food in the food and predator present context would be caught more frequently than their conspecifics. In the mesocosm context, I assumed that bass would be aware of the angler overhead and also be witness to their conspecifics being caught. Thus, I assumed that bass would perceive the mesocosm as a risky context. I predicted that in the outdoor pond angling context, bass would perceive it to be a relatively non-risky context and as a result, more aggressive bass in the mirror-test context would be more vulnerable to angling. Further, I predicted that in the outdoor pond angling context where casts were made directly onto bass nests, more aggressive males in the mirror-test context would be more

vulnerable to angling. The rationale behind this prediction is that nest guarding males strike lures to protect their nests and more aggressive males are expected to be more protective. Lastly, I predicted that bolder (the context-general personality trait obtained from a principal components analysis of the context-specific traits) bass would be more vulnerable to angling in all three contexts. Boldness was predicted to affect angling vulnerability in all three contexts, as opposed to just in the mesocosm, because even though only the mesocosm context is expected to be perceived as overtly risky, striking at the lures themselves in the outdoor ponds is may still be perceived to carry a low level of risk. In other words, the mesocosm context is predicted to be risky in and of itself whereas in the outdoor ponds, it is direct engagement with the lures that may be perceived as risky. The results of this study will aid in our understanding of the selective capture of fish by recreational angling, which may have significant evolutionary and ecological consequences for the affected populations and the quality of the fisheries (Sutter et al. 2012; Philipp et al. 2014; Mittelbach et al. 2014).

METHODS

Study population and husbandry

The largemouth bass used in each experiment described below were collected from a pond located at the Kellogg Biological Station experimental pond facility in southwest Michigan. These bass were bred on site from adult bass collected from nearby Wintergreen Lake. Randomly selected individuals were transferred to the laboratory facility and were individually marked with colored elastomer gel (a biocompatible pliable polymer; Northwest Marine Technology, Goldsmith et al. 2003) that was injected subcutaneously at two of seven possible locations. The bass were socially housed in aquaria (4 bass per aquarium) and provided with an excess amount of zooplankton. Bass were measured for length and then transferred from the holding aquaria into their own testing aquariums to undergo a series of behavioral assays. Upon completion of the assay procedure, bass were subjected to 1 of 3

angling experiments. Bass subjected to angling experiment 1 were underwent the series of behavioral assays a second time following the completion of the angling experiment. The bass that were subjected to angling experiments 1 and 2 were observed in the laboratory under three experimental behavioral contexts: 1) a familiar and safe environment, 2) a social environment (mirror-test), and 3) an environment where food and predators were present. Bass from angling experiment 3 were observed in a novel environment context, in addition to the three behavioral contexts that bass from angling experiments 1 and 2 were observed in.

Behavioral assay procedure

Behavioral assays followed a similar procedure as outlined in previous studies with this population of largemouth bass (Ballew in review). The testing aquaria were divided into two sections by an opaque vertical partition with the smaller section making up about 10% of the total volume. Individual bass used in angling experiment 3 were transferred into the smaller section of a testing tank and then left for approximately 45 minutes to recover from handling and to acclimate to the new environment. After the 45 minute acclimation period, novel context trials were initiated. The partition was raised approximately 10 centimeters above the floor of the aquarium using a pulley system, allowing the fish to swim from the smaller section into the larger section. For each sample, I measured the elapsed time from when the partition was raised until the fish swam into the larger area of the tank (up to 45 minutes). If after 45 minutes a fish had not moved to the larger section of the tank, I gently coaxed it out. Once a fish moved into the larger section of the tank, I lowered the partition so that it could not move back into the smaller section. An individual's score was calculated by subtracting the number of seconds that it waited before moving to the larger portion of the tank from 2700 (the maximum trial length). Thus, individuals with higher scores moved more quickly to the larger section of the tank. Individuals that did not leave the small section during the trial received a score of 0. Following

the completion of the novelty trial, I placed a mirror on the wall in the smaller section of the tank (not visible to the fish). Fish were then left overnight in the larger section of the tank to acclimate to their new surroundings. Bass subjected to angling experiments 1 and 2 were not observed in the novel environment trial. Instead of placing them in the smaller section of the tank, bass were simply placed in the larger section of the tank and left overnight to acclimate to their new surroundings.

The day after introducing a bass into a testing aquarium, I assayed its behavior in a familiar and safe context. I measured the amount of time the bass spent moving around the tank in the familiar environment (larger section of the tank). Fish were observed for 5 minutes and I summed the total time spent swimming (moving) to calculate the total number of seconds active per trial.

Immediately following the measurements taken in the familiar and safe environment trial, I conducted the social context (mirror-test) trial. I raised the partition to reveal a mirror on the wall in the smaller section of the tank. Once the partition was raised the trial commenced. Trials lasted for 10 minutes. I measured the number of bites, tail swipes, and rams at the mirror. At the end of the trial, the partition was lowered so that the mirror was no longer viewable. As the partition was lowered, fish in the path of the partition consistently retreated to the larger section of the tank. The number of bites, tail swipes, and rams were summed together to get an overall measure in this context. These behaviors were summed together because each was taken to be a specific form of agonistic behavior and other studies have shown that individuals often exhibit behavioral specificity so that they tend to primarily use their preferred method of a behavioral type (one individual may primarily use rams while another primarily uses bites; Uher 2011).

Approximately one hour after observing behavior in the presence of the mirror, the feeding in the presence of a predator trial was conducted. A live earthworm tied to monofilament fishing line (no hook) was lowered into the tank near one end. When the bass approached the worm, a model bird suspended on a string and pulley system positioned directly above the worm was released to strike the

surface of the water, simulating a predation attempt. The bird was then quickly lifted from the water, again using the string and pulley system. During this time, the fish most often retreated to a corner of the tank. Once the bird was appropriately positioned (10 centimeters above the water surface), the trial commenced. I recorded how many seconds it took the bass to re-approach the worm. An individual's score was calculated by subtracting the number of seconds that a fish waited before re-approaching the worm from the maximum trial length. Thus, individuals with higher scores re-approached the worm faster. Individuals that did not re-approach the worm during the trial received a score of 0. Upon completion of this final assay, bass were subjected to 1 of three angling experiments. Additionally, bass subjected to angling experiment 1 were re-assayed post-angling.

Angling Experiments

Experiment 1: Mesocosm context

36 bass that underwent the behavioral assay procedure were split randomly between two large (1000 liter) outdoor covered tanks. Bass were left in the tanks for 4 weeks. During the 4 week period, bass could feed on zooplankton *ad libitum*. Bass were exposed to a standardized angling procedure several days each week over the course of the 4 weeks. The angling procedure consisted of first uncovering the tanks. Then, from a distance of approximately 1 meter away from the edge of the tank, a hook (baited with an earthworm) was cast into the middle of the tank. 18 casts were made into each tank and I attempted to catch any bass that struck at the bait. Caught bass were identified and then returned to the tank. If after 1 minute no bass had struck at the worm, the worm was reeled in. Upon the completion of a cast (either due to a landing or 1 minute time limit), I waited 1 minute before re-casting into the center of the tank. During this 1 minute waiting period, I re-baited the hook (if necessary). Over the course of the four week angling experiment, one bass died in each tank. At the

conclusion of the angling experiment, the 34 surviving bass were exposed to the same three behavioral assays used pre-angling.

Experiment 2: Outdoor pond context

202 bass that underwent the behavioral assay procedure were stocked in an experimental pond (30 m wide and 2 m deep). Bass were exposed to angling several days each week over the course of a 4 week angling experiment. Angling lasted approximately 1 hour on days that angling took place. While standing at the edge of the pond, I casted a hook (baited with an earthworm) into the middle of the pond and then slowly reeled in the worm. If a bass struck at the hook, an attempt was made to land it. Successfully landed bass were identified and then returned to the pond to simulate catch-and-release style angling.

Experiment 3: Outdoor pond context with casts made directly onto bass nests

Reproductively mature bass that underwent the behavioral assay procedure in the spring were split randomly into 3 experimental ponds. I then snorkeled throughout the 3 ponds daily during the bass reproductive season to locate male nests. When nests were found, photographs were taken to quantify the number of eggs in each nest. Approximately one hour after finding a nest, I angled for the nest guarding male. Standing from shore, I made casts onto the nest. If the nest guarding male struck at the hook (baited with an earthworm), an attempt was made to land it. Successfully landed males were identified and then returned to their nests. If after 1 minute the male had not struck at the worm, the worm was reeled in. Up to 5 casts were made on each nest. Males that were caught on the first cast were given an angling vulnerability score of 5, males caught on the second cast a score of 4, and so on with males not caught being given a score of 0. I attempted to catch males from 36 nests.

Statistical analysis

All statistical analyses were conducted using R version 2.13 (R Development Core Team 2008). Scores for all variables were standardized (mean of 0 and standard deviation of 1). Previous studies on this population of largemouth bass indicate that context-specific personality traits underlie the expression of behavior in each of the contexts observed and that correlations exist between most of the context-specific traits (Ballew in review). To determine if the context-specific traits are sub-modules of a context-general trait (like boldness), I conducted a principal components analysis of the context-specific personality traits for the samples used in each of the angling experiments. The principal components analyses revealed a general personality trait interpreted as boldness in each sample population. This result is in line with other studies on this bass population (Ballew in review). Thus, in addition to the context-specific traits, the effect of the boldness trait (from the PCA) on angling vulnerability was also investigated in each angling experiment.

To investigate the effect of personality traits on angling vulnerability in experiment 1 (mesocosm context), I performed separate linear regressions for each personality trait and included bass length as a covariate; $\text{angling vulnerability} = \text{length} + \text{personality} + \text{length:personality}$. To investigate the effect of personality on angling vulnerability in experiment 2 (outdoor pond context), I performed separate logistic regressions for each personality trait and included length as a covariate; $\text{vulnerable to angling (Yes/No)} = \text{length} + \text{personality} + \text{length:personality}$. To investigate the effect of personality on angling vulnerability in experiment 3 (outdoor pond context with casts made directly onto bass nests), I performed separate linear regressions for each personality trait and included length and nest egg count as covariates; $\text{angling vulnerability} = \text{length} + \text{nest egg count} + \text{personality} + \text{length:personality} + \text{nest egg count:personality}$. Separate regressions were conducted on each personality trait because the boldness trait was taken to represent a combination of the traits.

RESULTS

Angling experiment 1: Mesocosm context

A general personality trait interpreted as boldness was uncovered from the principal components analysis on the three context-specific personality traits measured prior to exposure to angling. Bolder individuals (higher scores on axis 1) were significantly more active in the safe and familiar environment context, more aggressive in the mirror-test context, and less hesitant to approach the food in the food and predator present context. The principal components analysis on the three traits measured after exposure to angling produced the same result. Overall, boldness explained 41% of the variation observed in the three context-specific traits prior to angling and 46% of the variation observed in the context specific traits after angling.

Linear regressions of the effect of bass length and personality on angling vulnerability in the 1000L holding tanks showed that bass that hesitate shorter periods of time to approach food in the presence of predators are significantly more vulnerable to angling (Table 17). Further, bass that are bolder are also significantly more vulnerable to angling. In addition, an interaction between length and some of the personality traits, such as the initial boldness measure, had a negative effect on angling vulnerability (Figure 14). Overall, angling vulnerability was moderately determined by the food and predator present context-specific trait and the interaction between this trait and length ($R^2 = 0.34$ for pre-angling measurements and 0.31 for post-angling measurements).

Angling experiment 2: Outdoor pond context

A boldness trait similar to the one found in the sample population used in angling experiment 1 was uncovered in the sample population used in angling experiment 2 (Boldness = Axis 1 from PCA and explains 40% of the variation). Logistic regressions of the effect of length and personality on angling vulnerability in the experimental pond revealed that larger bass were significantly more vulnerable to

angling (Table 18). Additionally, more aggressive bass in the mirror-test context and bolder bass were more vulnerable to angling (Figure 15). However, only the result in the mirror-test context was statistically significant (Table 18).

Angling experiment 3: Outdoor pond context with casts made directly onto bass nests

A boldness trait similar to the ones found in the sample populations used in angling experiments 1 and 2 was uncovered in the sample population used in angling experiment 3. Bolder individuals (higher scores on axis 1) were significantly less hesitant to enter a novel environment, were more active in the safe and familiar context, were more aggressive in the mirror-test context, and were less hesitant to approach the food in the food and predator present context. Overall, boldness explained 42% of the variation observed in the four context-specific traits.

Linear regressions of the effect of bass length, nest egg count, and personality on angling vulnerability in nest guarding males showed that males guarding nests containing more eggs were significantly more vulnerable to angling (Table 19). Additionally, each of the personality traits was positively correlated with angling vulnerability. However, only the safe and familiar context trait and boldness significantly affected angling vulnerability (Figure 16). Overall, 31% of the variation in nest guarding male angling vulnerability was determined by the number of eggs being guarded and a male's boldness.

DISCUSSION

The results of this study demonstrate that personality can affect angling vulnerability in a range of angling contexts. Further, the personality trait that affects angling vulnerability depends on the specifics of the angling context. In the mesocosm context, bolder bass, and specifically those that hesitated less before foraging in the behavioral assays, were more vulnerable to angling. Thus, it

appears that bass struck at the bait in this angling context primarily to forage. In the outdoor pond context, bass that were more aggressive towards the mirror in the laboratory were more vulnerable to angling. Thus, it appears that bass strikes in this context were primarily the result of aggressive responses to the bait. In the outdoor pond context where casts were made directly onto bass nests, the activity measure in the safe and familiar context had the greatest effect on nest angling vulnerability. I predicted that strikes at the bait were likely made by bass to protect offspring and as a result, male bass that were more aggressive in the mirror-test context would be more vulnerable to nest angling. It appears that strikes were in fact made to protect offspring as bolder males were also more vulnerable to angling. However, nest angling vulnerability may be determined more by parental diligence as opposed to overt aggression.

This study demonstrates for the first time that the selective capture of fish by recreational angling may be dependent on the specifics of the angling context that takes place. This is important to conservation biologists as the relationship between personality and vulnerability to recreational and commercial harvesting practices may result in selection pressures that result in fisheries-induced evolution (Sutter et al. 2012; Philipp et al. 2014; Mittelbach et al. 2014). If personality selection in any of these angling contexts were to result in fisheries-induced evolution, fished populations would almost certainly experience a decline in catchability on a population level scale, a scenario that would be undesirable for recreational anglers (Philipp et al. 2009; Dorow et al. 2010). To date, the majority of studies on angling vulnerability in fish have focused on life-history or physiological correlates of angling vulnerability, such as growth rate and resting metabolic rate (Cooke et al. 2007; Redpath et al. 2009). The current study is set apart from others in that the direct target of selection was investigated. However, as in prior studies, the current study also found that other factors, in addition to personality traits, were important for determining angling vulnerability.

Larger bass were significantly more vulnerable to angling in the outdoor pond context. Why length may affect angling vulnerability in this context but not the other two is not immediately clear. However, one possibility is that larger bass may be capable of accelerating towards the lure at a greater speed and as a result, strike at the lure before their smaller conspecifics. In the mesocosm context, bass tended to hesitate before striking at the lure and the length of hesitation was dependent on boldness. Thus, any advantage in swimming speed that length may entail would likely not affect angling vulnerability in this context. In the angling context focusing on nest guarding males, angling attempts targeted individual males. Therefore, swimming speed would not be expected to affect angling vulnerability in this context.

The number of eggs in a male's nest affected nest guarding male angling vulnerability. This result is consistent with the hypothesis that the value of a nest to a nest guarding male increases with the number of eggs it contains. Thus, we would expect males to more diligently protect nests that contain more eggs. Such a relationship between nest size and nest-guarding male angling vulnerability has the potential to have major consequences for populations that are heavily fished during the nesting season. The selective removal (either through harvest or temporary removal resulting from catch-and-release) of individuals with the greatest potential for high reproductive success has been hypothesized to have strong effects on individual fitness and population dynamics (Philipp et al. 1997; Suski and Philipp 2004; Sutter et al. 2012). Thus, in response to either harvest or catch-and-release nest angling, fish in exploited largemouth bass populations would generally be expected to evolve traits that reduce their exposure to nest angling. Such an evolutionary response could also reduce the level of diligence that males display when protecting their nests. The potential ramifications of this adaptive response to angling on recruitment would of course depend upon the amount of harvest mortality, or for catch-and-release fisheries, the intensity of catch-and-release angling of male bass on nests (Enberg et al. 2010). Angling of nest-guarding bass has been a selective force acting on many bass populations in North

America for several decades. Thus, many populations are likely to already contain fish that are less vulnerable to capture than non-fished populations (Sutter et al. 2012; Philipp et al. 2014). If evolutionary changes in personality and life history prove to reduce recruitment, then management strategies designed to reduce or even remove the underlying selective pressure (angling nest-guarding male largemouth bass) may need to be implemented.

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APPENDIX

Table 17. Linear regressions of the effect of length and personality on angling vulnerability in angling experiment 1 (mesocosm context). Each model has 30 degrees of freedom. Angling vulnerability = Length + Personality + Length:Personality.

Personality Trait	Intercept	Length Coefficient	Personality Coefficient	Length:PT Coefficient	R-squared
SFCT_1	0.045	-0.082	0.106	0.310	0.10
SFCT_2	-0.029	-0.180	-0.025	0.206	0.07
MTCT_1	-0.002	-0.147	0.107	-0.069	0.04
MTCT_2	0.007	-0.310	0.125	-0.458 *	0.14
FPCT_1	-0.177	-0.109	0.351 *	-0.571 **	0.34
FPCT_2	-0.317	0.031	0.636 **	-0.677 **	0.31
Boldness_1	-0.043	-0.136	0.207	-0.487 *	0.23
Boldness_2	-0.090	-0.172	0.387 *	-0.443	0.17

Note: SFCT = Safe and familiar context trait, MTCT = mirror-test context trait, FPCT = food and predator present context trait. _1 = scores from the assays conducted prior to the angling experiment. _2 = scores from the assays conducted after the angling experiment. * = $P \leq 0.05$; ** = $P \leq 0.005$.

Table 18. Logistic regressions of the effect of length and personality on angling vulnerability in angling experiment 2 (outdoor pond context). Each model has 198 degrees of freedom. Vulnerable to Angling (Yes/No) = Length + Personality + Length:Personality. For comparison, the null model deviance was 253.80.

Personality Trait	Intercept	Length Coefficient	Personality Coefficient	Length:PT Coefficient	Residual Deviance from model
SFCT	-0.843 **	0.846 **	-0.192	0.256	227.81
MTCT	-0.780 **	0.899 **	0.393 *	0.508	222.08
FPCT	-0.759 **	0.860 **	0.196	0.089	227.77
Boldness	-0.781 **	0.87 **	0.284	0.203	224.36

Note: SFCT = Safe and familiar context trait, MTCT = mirror-test context trait, FPCT = food and predator present context trait. * = $P \leq 0.05$; ** = $P \leq 0.005$.

Table 19. Linear regressions of the effect of length, nest egg count, and personality on angling vulnerability in angling experiment 3 (nest guarding males). Angling vulnerability = Length + Nest Egg Count + Personality + Length:Personality + Egg Count:Personality. Each model has 30 degrees of freedom.

Personality Trait	Intercept	Length Coefficient	Egg count Coefficient	Personality Coefficient	Length:PT Coefficient	Egg count :PT Coefficient	R-squared
NECT	0.058	-0.265	0.470 *	0.274	0.181	-0.288	0.21
SFCT	0.048	-0.293	0.453 *	0.405 *	0.186	-0.375	0.29
MTCT	0.002	-0.366	0.540 *	0.149	0.010	-0.192	0.22
FPCT	0.036	-0.317	0.519 *	0.223	0.128	-0.231	0.24
Boldness	0.057	-0.308	0.479 *	0.253 *	0.066	-0.213	0.31

Note: NECT = novel environment context trait, SFCT = Safe and familiar context trait, MTCT = mirror-test context trait, FPCT = food and predator present context trait. * = $P \leq 0.05$.

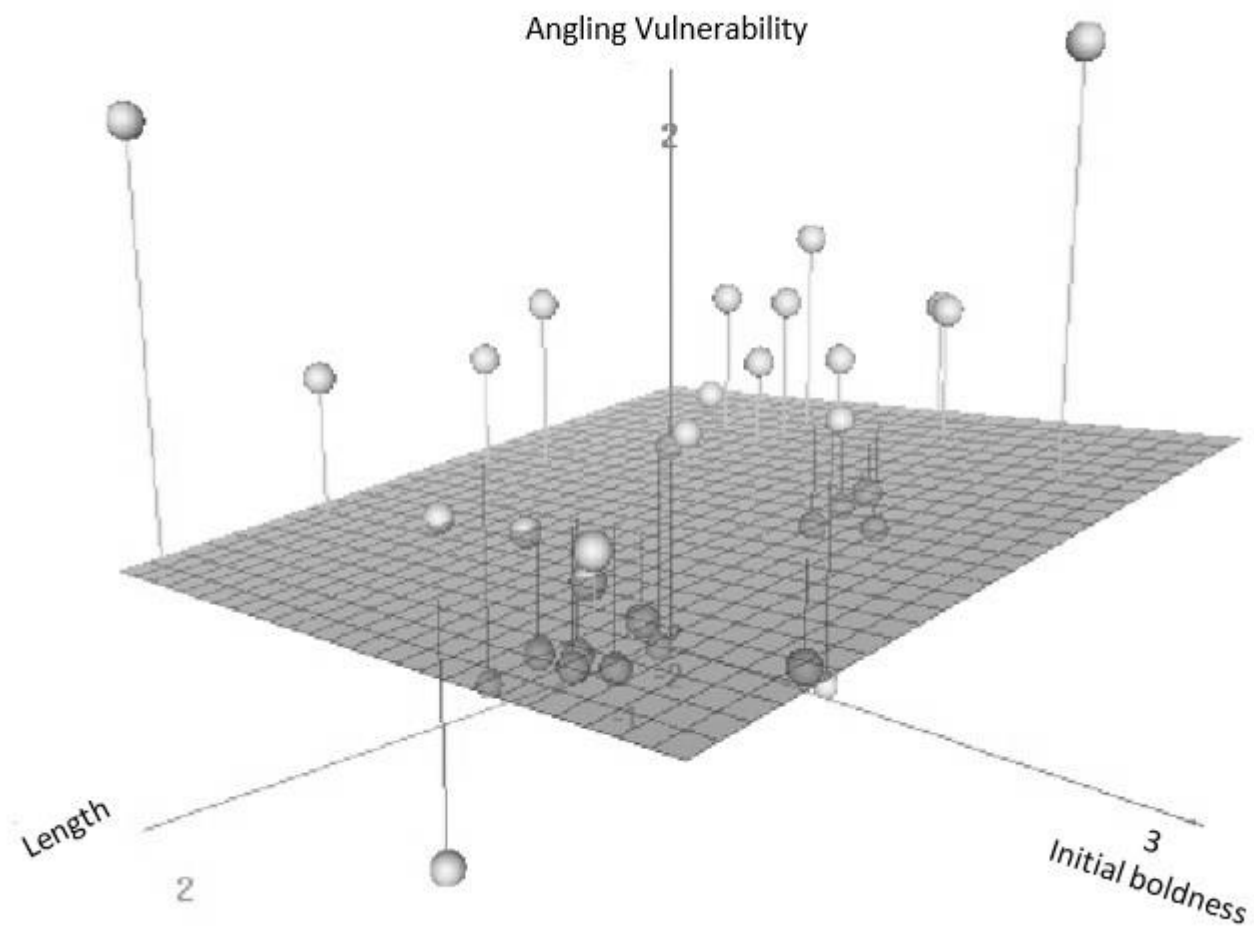


Figure 14. The effect of initial boldness, length, and the interaction between them on angling vulnerability in a mesocosm experiment. The circles represent individuals and the lines from the circles to the plane indicate individual residual values.

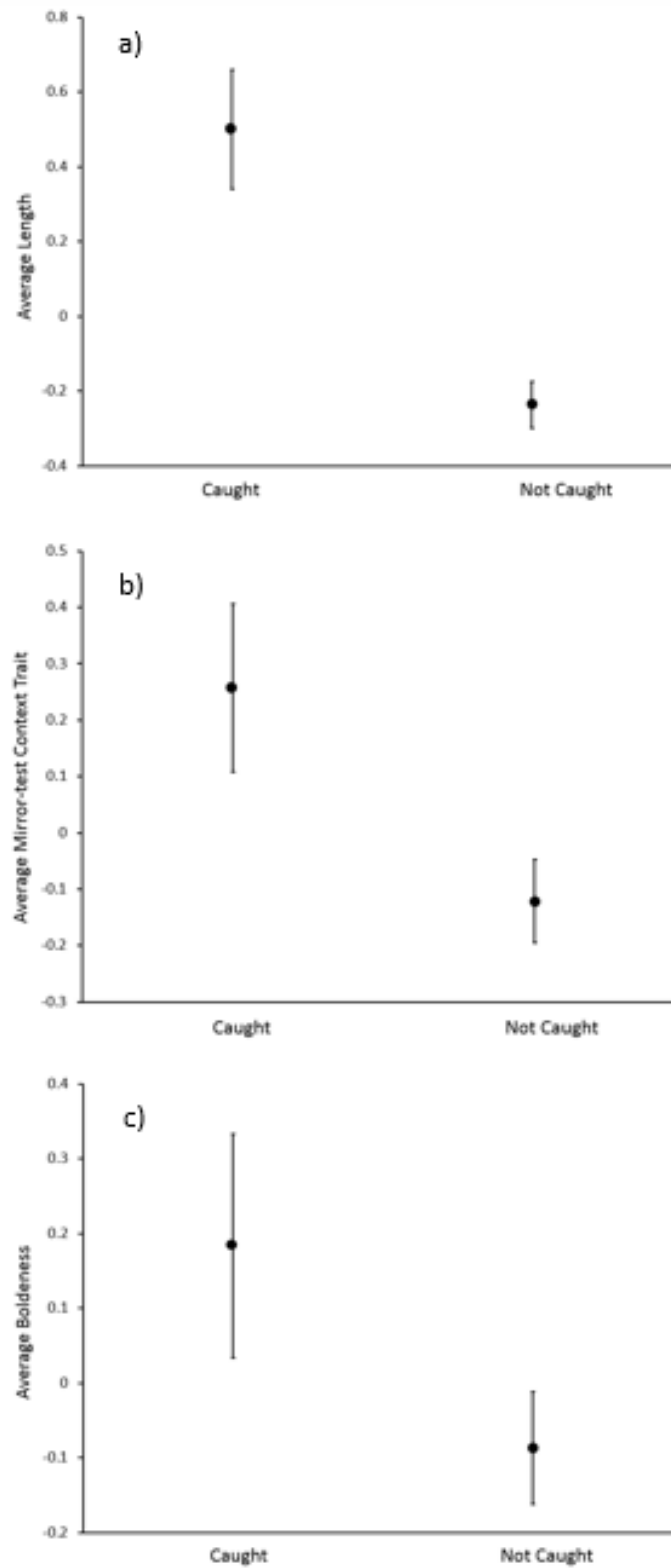


Figure 15. a) Average length, b) average mirror-test context trait, and c) average boldness of bass that were caught and those that were not caught in an outdoor pond. Error bars indicate the standard error of the mean.

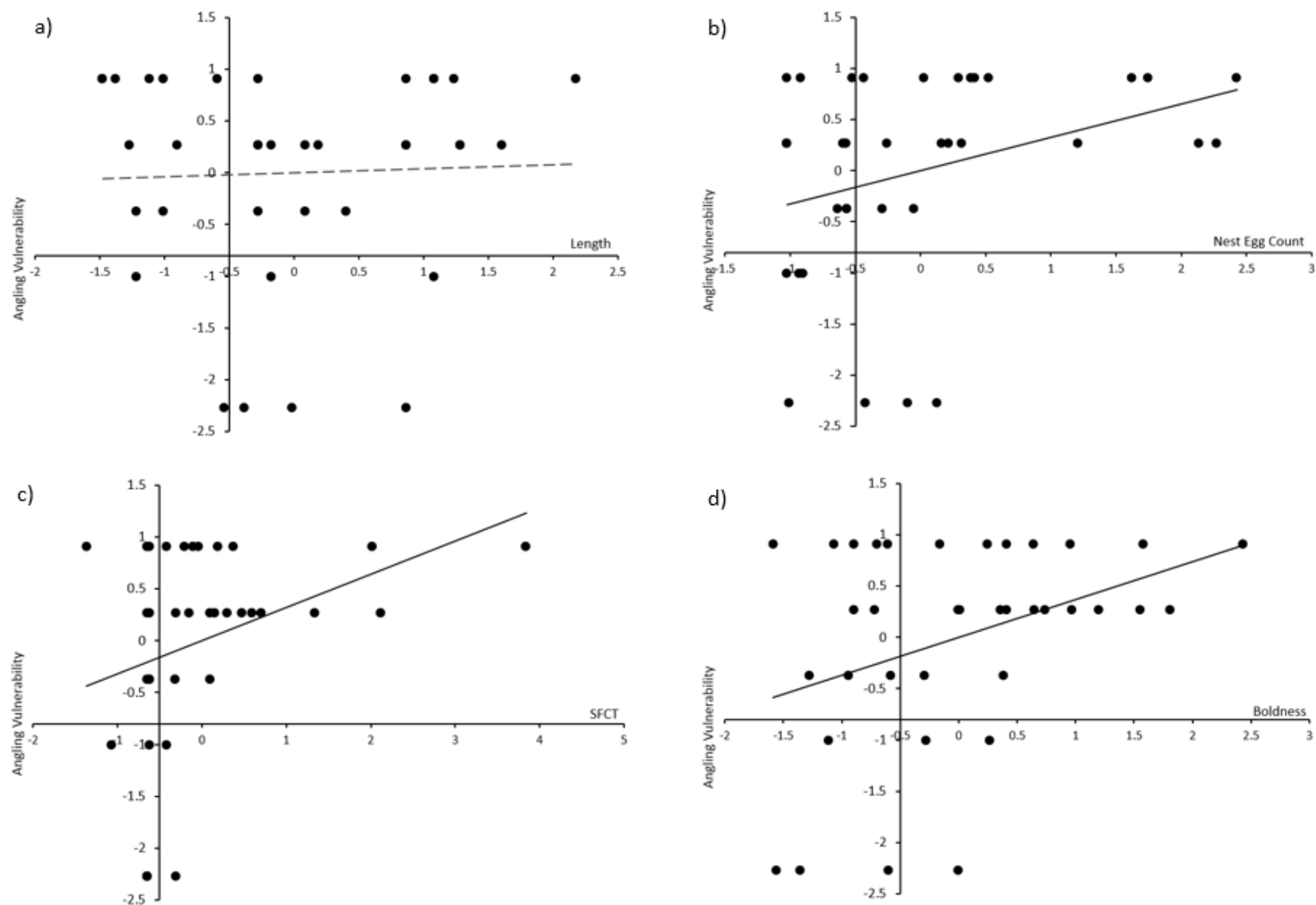


Figure 16. Effects of a) length, b) nest egg count, c) the safe and familiar context trait, and d) boldness on angling vulnerability of nest guarding male bass in an outdoor pond. Solid black lines indicate significant relationships (b-d) while dashed lines do not.

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