

TESTING MODELS OF THE ADAPTIVE EVOLUTION OF CONSISTENT INDIVIDUAL
DIFFERENCES IN BEHAVIOR USING STICKLEBACKS

BY

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DISSERTATION

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ABSTRACT

Traditionally considered one of the most plastic traits an individual could exhibit, there is now mounting evidence that individuals within the same population often differ in their behavior and that these differences are consistent over time and/or across context. This does not necessarily imply that individuals are rigid in their behavioral expression, but rather that each individual can only display a subset of the potential total behavioral variation. Therefore explaining these consistent individual differences in behavior is a recent challenge for evolutionary biology in general and behavioral ecology in particular. While there is some evidence that this limited behavioral plasticity may be a result of physiological or genetic constraints, there is growing theoretical evidence suggesting that instead, consistent individual differences may be the result of adaptive evolution.

Several mechanisms have been proposed to generate and maintain consistent individual differences in behavior. In particular, three ecological factors have been implicated in several models: competition, social interactions and environmental uncertainty. Therefore for my dissertation I tested whether these factors influence consistent individual differences as predicted by theory. Additionally, these models make several assumptions about the costs and benefits of different behaviors, which have yet to be tested as to whether they are realistic assumptions to make of natural populations. To test whether competition, social interactions and environmental uncertainty generate consistent individual differences, I measured the behavior of threespined sticklebacks in a foraging context. Foraging provides an ideal context because competition is an inherent quality of any foraging group of individuals, social interactions will occur among foragers, and it is easy to manipulate the level of uncertainty in resource availability.

The first hypothesis, the competition avoidance hypothesis, states that competition in a heterogeneous environment might promote consistent individual differences in behavior because among-individual behavior variation can help reduce direct competition among individuals. This hypothesis predicts that consistent individual differences in behavior should be greater when there is the opportunity to avoid competition, compared to when it is unavoidable. To test this, I tested groups of sticklebacks in two different foraging environments that differed in the number of available food patches: one environment contained only one patch at a time making competition unavoidable, whereas a second environment contained two patches where individuals could reduce competition by utilizing both patches. In support of the competition avoidance hypothesis, I found consistent individual differences in social foraging behavior in the two-patch environment; some individuals consistently used the second patch, whereas other individuals continued to only use the first patch. I also found that among-individual differences in foraging behavior grew stronger the longer the group of foraging sticklebacks had been together, evidence of positive feedback, a crucial assumption of most models. In addition, individuals maintained their foraging behavior even when placed in a new social group demonstrating that even though individuals can exhibit some plasticity from context to context, there is still rank-order consistency among individual behavior.

The second hypothesis, the social niche specialization hypothesis, states that repeated social interactions should favor consistent individual differences if predictable behavior helps individuals exploit interactions with others. The social niche specialization hypothesis therefore predicts that consistent individual differences in behavior should be greater in groups of individuals that are more familiar with each other. I explicitly tested this hypothesis by manipulating the opportunity for repeated social interaction and comparing the social foraging

behavior of groups of individuals that were familiar with one another to groups of individuals that were unfamiliar. Additionally, I tested whether individuals exhibited behavioral types by repeatedly measuring individual behavior in three different contexts: a novel environment, when presented with an opportunity to associate with conspecifics, and when confronted by an intruder. I found no evidence that repeated social interactions increased among-individual variation in social foraging behavior. Instead, variation in social foraging behavior was related to variation in behavioral types. In particular, high shoaling individuals took longer to utilize a new food patch while foraging in a social group compared to low-shoaling individuals. Altogether, the results of this experiment do not support the social niche specialization hypothesis that repeated social interactions generate consistent individual differences in behavior. Instead, they suggest that an individual's social behavior is largely influenced by their behavioral type.

The third hypothesis, the environmental uncertainty hypothesis, states that consistent individual differences in behavior are a result of individuals coping with uncertainty about their environment. This hypothesis predicts that consistent individual differences in behavior should be greater when individuals are in an uncertain environment, compared to a certain environment. I tested groups of foraging sticklebacks in a two patch environment where the patch profitability varied: one environment where patch profitability was certain and reliable, and a second environment where patch profitability varied and was uncertain. Additionally, most models on the influence of environmental uncertainty on consistent individual differences consider solitary foraging animals, however many animals forage in groups where the presence of conspecifics competitors may alter the costs and benefits of foraging behavior. Therefore all individuals were tested both while alone, and while in a group. In support of the environmental uncertainty

hypothesis, I found evidence for consistent individual differences in foraging behavior when individuals foraged alone. However, when individuals foraged in groups, consistent individual differences in foraging behavior were present under both certain and uncertain environments. There was also little carryover in how individuals behaved while alone and while in a group. Taken together these results suggest that while uncertainty about some factors such as resource availability may be important drivers of consistent individual variation in behavior when individuals are alone, the presence of social competition can mask these effects.

In conclusion my research has demonstrated that competitive interactions among individuals may be one of the most important drivers of consistent individual differences in behavior, at least in sticklebacks. While repeated social interactions did not appear to directly influence behavioral variation, this hypothesis may be more applicable to groups of animals with more stable social groups. Finally, whether or not environmental uncertainty influences consistent individual differences in behavior may be mediated again, by the competitive environment. This suggests that theories surrounding the role of environmental uncertainty may need to incorporate how uncertainty from different types of factors such as resources, or predators, or social partners can work in concert or opposition to influence individual behavior. While interest in consistent individual differences in animal behavior continues to grow, the field can only move forward with more empirical tests of theoretical predictions to determine under which ecological conditions we should expect to find consistent individual differences, and when we should not.

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CHAPTER 1: GENERAL INTRODUCTION

As evolutionary biologists we are inherently interested in the causes and consequences of biological variation. This variation can be genotypic or phenotypic and can be organized at several different levels, from species-typical variation, to population-specific and finally individual variation. Without individual variation, natural selection would be an ineffective force to shape patterns of biological diversity. Darwin recognized individual variation as the essential raw material upon which natural selection can act (Darwin 1859). However, even as individual variation has been recognized as a key component of evolutionary processes, until recently much of this type of variation was largely labeled as random noise around an optimal mean and ignored. Now the study of individual variation has received considerable interest in the past few decades as researchers recognized that the same processes that act to generate variation among populations or species may also be at work on individuals. Therefore individual variation may also represent the product of natural selection, not just its raw material (Wilson 1998).

Individual variation can exist in any phenotypic (or genotypic) trait. From morphology to life-history traits to behavior, no population consists of perfectly identical individuals. The increase in interest in individual variation has emerged from a number of different fields of study. For example, physiological researchers noticed that individual animals have different coping mechanisms to deal with stress (Koolhaas et al. 1999), in psychology differences are the very basis of human personality research (Buss 1995), and finally animal behaviorists began to notice that individual animals differed in their behavior and these differences were maintained over time (Sih et al. 2004). The study of individual differences is subtly shifting the traditional view of biological research. As opposed to measuring multiple individuals once in different

treatments and looking for mean treatment effects, the study of individual differences encourages a more comprehensive view of the organism. Individuals need to be measured repeatedly and/or in different contexts in order to determine how evolutionary processes may be acting on the individual as a whole unit, rather than on single traits in isolation.

Individual differences in behavior have received considerable attention recently possibly because behavior is often considered to be one of the most plastic traits. But now there is extensive evidence that individuals consistently differ from each other in how they behave and these differences are consistent over time and across context (Sih et al. 2004; Bell, Hankison & Laskowski 2009). Consistent individual differences in behavior does not necessarily suggest or require that individuals exhibit no plasticity in behavior, but rather even in the face of behavioral plasticity, rank-order differences among individuals can be maintained (Dingemanse et al. 2010). This type of consistent individual variation in behavior is comprised of two components: among-individual variation and within-individual consistency. The first, among-individual variation, describes the average differences among a set of individuals; some individuals are more active or aggressive than others, for example (e.g. Sih et al. 2003; Johnson & Sih 2005). The second component, within-individual consistency, refers to how similar an individual's behavior is when measured several times. A highly consistent individual would behave similarly time and time again; some individuals are always highly aggressive, whereas others alter their level of aggression depending on their opponent, for example (e.g. Benus et al 1987; Sih & Watters 2005). While there are several different terms currently being used in the literature to describe the confluence of among individual variation and within individual consistency in behavior (e.g. "personality," Wolf & Weissing 2010; "temperament," Reale et al. 2007; "behavioral type," Sih et al. 2004), they all describe the same phenomena: consistent individual differences in behavior.

The presence of consistent individual differences in behavior now appears to be the rule, rather than the exception. A recent meta-analysis demonstrated that across a wide variety of taxa, behaviors and contexts, differences among individual accounted for nearly ~40% of the total behavioral variation (Bell, Hankison & Laskowski 2009). This meta-analysis summarized available repeatability estimates reported in the literature. Repeatability is a common statistic used to describe the proportion of the total variation that is due to among-individual variation (Lessells & Boag 1987; Sokal & Rohlf 1995). Statistically, repeatability is defined as
$$R^2 = \frac{\sigma^2_{\text{among-individual}}}{\sigma^2_{\text{among-individual}} + \sigma^2_{\text{residual}}}$$
 where $\sigma^2_{\text{among-individual}}$ is the among-individual variance component and $\sigma^2_{\text{residual}}$ is the residual, or within-individual, variance component (Sokal & Rohlf 1995). Therefore, a significant repeatability estimate is interpreted as evidence that individuals consistently differ from each other in their behavior (Figure 1.1A). However, a non-significant repeatability should be interpreted with caution; it can be caused by very high within-individual variation (Figure 1.1B) or it can also be caused by very low-among individual variation (Figure 1.1C). This second scenario can mean that individuals behave consistently, *per se*, but they do not behave consistently *different* from each other. Therefore to fully understand the evolution of consistent individual differences in behavior, researchers need to explain the presence of both types of variation.

The widespread presence of consistent individual differences in behavior presents a challenge to behavioral ecology to uncover the mechanisms responsible for both among- and within-individual variation in behavior. In recent years, there has been an explosion of theoretical work modeling how consistent individual differences might be a result of adaptive evolution (reviewed in Wolf & Weissing 2010). Explaining the two components of consistent individual differences in behavior (among-individual variation and within-individual consistency) can be especially tricky as different evolutionary mechanisms may be at work. For

example, among-individual variation in behavior is likely maintained by similar mechanisms as have been proposed to maintain genetic variation (Mackay 1981, Lande 1982, Barton and Keightley 2002) such as negative frequency dependent selection (Wolf et al. 2008) or life-history trade-offs (Stamps 2007). Within-individual consistency could be a result of positive feedback (Wolf et al. 2008), state-dependence (Houston and McNamara 1999; Clark and Mangel 2000), learning (Sih and Bell 2008) or noisy information (Dall & Johnstone 2002; McElreath and Strimling 2006). Currently, the study of consistent individual differences has been descriptive; researchers have documented the presence of this type of behavioral variation across a wide variety of taxa (reviewed in Bell, Hankison and Laskowski 2009). In order to move the field forward, empirical tests of theory are needed to determine which mechanisms are at work generating this variation in order to build a general framework for when we would expect to see consistent individual differences in behavior and when we would not. In my thesis, I test three common predictions made by several different models.

The first prediction is that competition coupled with environmental heterogeneity can be the key factors promoting among-individual variation in behavior: the competition avoidance hypothesis. In these models, heterogeneity in environmental conditions can favor among-individual variation in behavior (Wolf et al. 2008; Dubois et al. 2010; Wolf et al. 2011; Mathot et al. 2012). For example, in a patchy foraging context, individuals can increase their food consumption if they have different patch use behavior than their group mates (e.g. the ideal free distribution, Fretwell & Lucas 1970). Intra-specific competition is already known to be a key driver in individual diet specialization as it helps reduce direct competition among conspecifics (Bolnick et al. 2003; Svanback & Bolnick 2007) and so seems a likely candidate to also favor individual differences in other behaviors. Therefore, these models predict that among-individual

variation in behavior should be greater when it helps individuals reduce competition within a group, compared to when competition is unavoidable.

A key assumption of several models is that positive feedback mechanisms will favor behavioral consistency (Wolf et al. 2008; Wolf et al. 2011). Wolf et al. (2008) assume that there is a cost associated with displaying a behavior and as that behavior is repeated, the cost is reduced, thereby generating positive feedback. This is akin to learning and can occur in either a social or a non-social environment (Shettleworth 1998). However, another potential non-exclusive mechanism to generate positive feedback is that repeated social interactions with the same individuals can increase the benefits of predictable, or consistent, behavior (Wolf et al. 2011). Importantly, repeated social interactions also have the potential to favor among-individual variation in behavior. This second prediction, recently termed the social niche specialization hypothesis (Bergmueller & Taborsky 2010; Montiglio et al. 2013), predicts that individuals benefit by specializing in behavior and consistently using that behavior when in a group. This hypothesis is especially appealing as there is support for it in other natural systems. For example, in human personality research there is strong support for the idea that humans specialize on certain tasks (Sterelny 2007), and the caste system in eusocial insects is an excellent example of the advantage of social niches. Essentially, when individuals in a group behave predictably, it can help reduce competition and increase individual payoffs. A broad example could be in a foraging context; if individuals have predictable patch use behavior then the group can more quickly arrange itself in the ideal free distribution, which will increase the payoffs to all individuals in the group. These models therefore predict that both among-individual variation and within-individual consistency should increase with the number of repeated social interactions with the same group-mates.

A third prediction states that uncertainty about the environment is an important driver of consistent individual differences in behavior (Dall & Johnstone 2002; McElreath & Strimling 2006; Mathot et al. 2012). These models state that the reason individuals differ from each other in behavior is because they use different strategies to cope with environmental uncertainty. This environmental uncertainty hypothesis states that it is the uncertainty coping mechanism that is the root cause of individual differences in behavior. For example, some individuals choose to sample their environment to gain more information about their potential options and reduce uncertainty that way, whereas other individuals may rely on insurance mechanisms which would not require sampling. This is well illustrated in a foraging context where individuals may be uncertain about how profitable different food patches are; some individuals may choose to sample the patches frequently, whereas other individuals may wait at one patch until the food returns. This would lead to among-individual variation in behavior. Interestingly, which strategy an individual uses to cope with environmental uncertainty can also impact their behavioral consistency: individuals that sample will need to sample more as the environment becomes more uncertain. This could cause those individuals to appear inconsistent because their behavior changes with increasing uncertainty. Therefore this model predicts that among-individual variation in behavior should be greatest when individuals are uncertain about their environment and that within-individual consistency should be linked to these behavioral differences.

My dissertation research has focused on investigating three factors which several models have hypothesized are key drivers of consistent individual differences in behavior: competition, repeated social interactions, and uncertainty about environmental conditions. Specifically I address the following predictions: 1) Competition within a social group should generate

consistent individual differences in behavior if behavioral variation helps reduce direct competition. 2) Repeated social interactions should generate consistent individual differences in behavior if predictable behavior helps increase individual payoffs. 3) Individuals consistently differ in their behavior because they use different tactics to reduce their uncertainty about environmental conditions. To test these predictions, I investigated the social foraging behavior of threespined sticklebacks. Sticklebacks are a small fish known for their consistent individual differences in a range of behaviors (Huntingford 1976; Bell 2005; Dingemanse et al. 2007) and for their extensive variation in diet and resource use (Milinski 1984; Bolnick et al. 2003; Webster & Hart 2006). The social foraging behavior of sticklebacks provides a suitable system in which to investigate these hypotheses because it is easy to manipulate the level of competition, the level of familiarity among group members and also the level of uncertainty about foraging profitability.

REFERENCES

- Barton, N. H. & Keightley, P. D. 2002 Understanding quantitative genetic variation. *Nature Reviews Genetics* **3**, 11-21.
- Bell, A. M. 2005 Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology* **18**, 464-473.
- Bell, A. M., Hankison, S. J. & Laskowski, K. L. 2009 The repeatability of behaviour: a meta-analysis. *Animal Behaviour* **77**, 771-783.
- Benus, R., Koolhaas, J. & Van Oortmerssen, G. 1987 Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour*, 105-122.
- Bergmueller, R. & Taborsky, M. 2010 Animal personality due to social niche specialisation. *Trends in Ecology & Evolution* **25**, 504-511.
- Bolnick, D. A. I., Svanback, R., Fordyce, J. A. A., Yang, L. A. H., Davis, J. M., Hulsey, C. A. D. & Forister, M. L. 2003 The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161**, 1-28.
- Buss, D. M. 1995 Evolutionary psychology: A new paradigm for psychological science. *Psychological Inquiry* **6**, 1-30.
- Clark, C. J. & Mangel, M. 2000 *Dynamic State-Dependent Models in Ecology*. New York, NY: Oxford University Press.
- Dall, S. R. X. & Johnstone, R. A. 2002 Managing uncertainty: information and insurance under the risk of starvation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **357**, 1519-1526.

- Darwin, C. 1859 *The origin of species by means of natural selection: or, the preservation of favored races in the struggle for life.*
- Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R. & Dawnay, N. 2007 Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology* **76**, 1128-1138.
- Dingemanse, N. J., Kazem, A. J. N., Reale, D. & Wright, J. 2010 Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution* **25**, 81-89.
- Dubois, F., Morand-Ferron, J. & Giraldeau, L. A. 2010 Learning in a game context: strategy choice by some keeps learning from evolving in others. *Proceedings of the Royal Society B: Biological Sciences* **277**, 3609-3616.
- Fretwell, S. D. & Lucas, H. J. 1970 On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16-36.
- Houston, A. I. & McNamara, J. M. 1999 *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.
- Huntingford, F. A. 1976 The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour* **24**, 245-260.
- Johnson, J. C. & Sih, A. 2005 Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioral syndromes. *Behavioral Ecology and Sociobiology* **58**, 390-396.

- Koolhaas, J., Korte, S., De Boer, S., Van Der Vegt, B., Van Reenen, C., Hopster, H., De Jong, I., Ruis, M. & Blokhuis, H. 1999 Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews* **23**, 925-935.
- Lande, R. 1982 A quantitative genetic theory of life history evolution. *Ecology*, 607-615.
- Lessells, C. & Boag, P. T. 1987 Unrepeatable repeatabilities: a common mistake. *The Auk*, 116-121.
- Mackay, T. F. 1981 Genetic variation in varying environments. *Genetical Research* **37**, 79-93.
- Mathot, K. J., Wright, J., Kempenaers, B. & Dingemanse, N. 2012 Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos* **121**, 1009-1020.
- McElreath, R. & Strimling, P. 2006 How noisy information and individual asymmetries can make 'personality' an adaptation: a simple model. *Animal behaviour* **72**, 1135-1139.
- Milinski, M. 1984 Competitive resource sharing: an experimental test of a learning rule for ESSs. *Animal Behaviour* **32**, 233-242.
- Montiglio, P.-O., Ferrari, C. & Reale, D. 2013 Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20120343.
- Reale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007 Integrating animal temperament within ecology and evolution. *Biological Reviews* **82**, 291-318.

- Shettleworth, S. J. 1998 *Cognition, evolution, and behavior*. New York, N.Y.: Oxford University Press.
- Sih, A., Kats, L. B. & Maurer, E. F. 2003 Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. *Animal Behaviour* **65**, 29-44.
- Sih, A., Bell, A. M. & Johnson, J. C. 2004 Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19**, 372-378.
- Sih, A. & Watters, J. V. 2005 The mix matters: behavioural types and group dynamics in water striders. *Behaviour*, *142* **9**, 1417-1431.
- Sih, A. & Bell, A. M. 2008 Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior* **38**, 227-281.
- Sokal, R. & Rohlf, F. 1995 *Biometry: The principles and practice of statistics in biological research*. New York, NY: W.H. Freeman and Company.
- Stamps, J. A. 2007 Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters* **10**, 355-363.
- Sterelny, K. 2007 Social intelligence, human intelligence and niche construction. *Philosophical Transactions of the Royal Society B: Biological Sciences* **362**, 719-730.
- Svanback, R. & Bolnick, D. I. 2007 Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences* **274**, 839-844.

- Webster, M. M. & Hart, P. J. B. 2006 Subhabitat selection by foraging threespine stickleback (*Gasterosteus aculeatus*): previous experience and social conformity. *Behavioral Ecology and Sociobiology* **60**, 77-86.
- Wilson, D. S. 1998 Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **353**, 199-205.
- Wolf, M., van Doorn, G. S. & Weissing, F. J. 2008 Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 15825-15830.
- Wolf, M. & Weissing, F. J. 2010 An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B* **365**, 3959-3968.
- Wolf, M., Van Doorn, G. S. & Weissing, F. J. 2011 On the coevolution of social responsiveness and behavioural consistency. *Proceedings of the Royal Society B-Biological Sciences* **278**, 440-448.

FIGURES

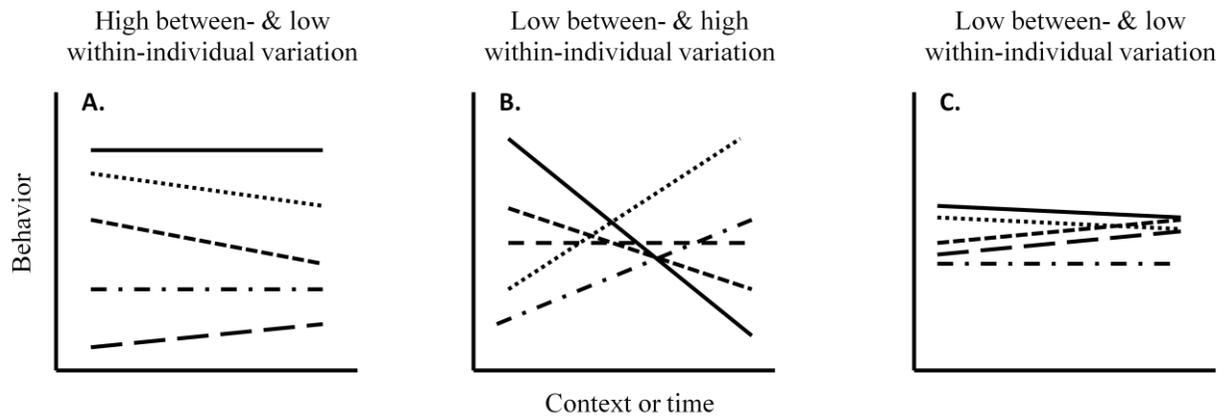


Figure 1.1 Patterns of among- and within-individual variation in behavior. Each line represents a different individual measured for a behavior over time or across contexts; among-individual variation can be summarized by the difference in the line averages whereas within-individual variation can be summarized by the slope of a particular line. When individuals exhibit both high among-individual and low within-individual variation in behavior the behavior is said to be “repeatable” (A.). In contrast, if individuals exhibit very low among-individual but high within-individual variation (B.) or low among-individual and low within-individual variation in behavior (C.), the behavior is not repeatable.

CHAPTER 2: COMPETITION AVOIDANCE DRIVES INDIVIDUAL DIFFERENCES IN RESPONSE TO A CHANGING FOOD RESOURCE IN STICKLEBACKS¹

ABSTRACT

Within the same population individuals often differ in how they respond to changes in their environment. A recent series of models predicts that competition in a heterogeneous environment might promote among-individual variation in behavioral plasticity. I tested groups of sticklebacks in patchy foraging environments that differed in the level of competition. I also tested the same individuals across two different social groups and while alone to determine the social environment's influence on behavioral plasticity. In support of model predictions, individuals consistently differed in behavioral plasticity when the presence of conspecifics influenced the potential payoffs of a foraging opportunity. Whether individuals maintained their level of behavioral plasticity when placed in a new social group depended upon the environmental heterogeneity. By explicitly testing predictions of recent theoretical models, we provide evidence for the types of ecological conditions under which we would expect, and not expect, variation in behavioral plasticity to be favored.

¹ This chapter appeared in its entirety in journal *Ecology Letters* and is referred to later in this dissertation as "Laskowski and Bell 2013". Laskowski, K.L and Bell, A.M. 2013. Competition avoidance drives individual differences in response to a changing food resource in sticklebacks. 16: 746-753. This article is reprinted with permission of the publisher and is available from <http://onlinelibrary.wiley.com/> and using DOI: 10.1111/ele.12105

INTRODUCTION

Consistent individual differences in behavior are difficult to explain because we expect natural selection to favor a single optimal behavioral strategy. These average differences in behavior among individuals (i.e. personality) are now well documented across many taxa and appear to be driven by a number of ecological factors with important consequences (Reale *et al.* 2007; Smith & Blumstein 2008). In addition to variation in personality, there is now growing evidence that individuals vary in the extent to which they adjust their behavior according to the environment, including the social environment (i.e. behavioral plasticity, Dingemanse *et al.* 2010; Mathot *et al.* 2012; Dingemanse & Wolf *in press*). For example, some individuals within a population might be more likely to exploit new food patches, while other individuals consistently forage in old patches, regardless of the behavior of others. Interest in among-individual variation in behavioral plasticity has triggered two key questions: First, are there adaptive reasons why individuals differ in plasticity? And second, what is the influence of changes in the environment on behavioral plasticity?

A growing number of models have provided ‘proof of principle’ support for the first question, showing that under certain conditions, variation in plasticity can be adaptive (reviewed in Dingemanse & Wolf *in press*). Adaptive mechanisms that might generate and/or maintain among-individual differences are state variable differences (Houston & McNamara 1999; Clark & Mangel 2000), temporal and spatial variation in environmental conditions (Wolf *et al.* 2008; Dubois *et al.* 2010) and repeated social interactions (Wolf *et al.* 2011). In these models, the presence of conspecifics can alter the payoff of the behavioral choices available to an individual (i.e. game theoretic dynamics). These competitive interactions can generate negative frequency-

dependent payoffs to plastic individuals, thereby promoting among-individual variation in behavior (e.g. Wolf *et al.* 2008; Wolf *et al.* 2011), a prediction which has empirical support in anti-predator behavior (Mathot *et al.* 2011). This mechanism could also be at work in other contexts; for example, in a patchy foraging context, individuals arrange themselves in a way that maximizes their own food intake, which generally is proportional to the food input at each patch (“ideal free distribution,” Fretwell & Lucas 1970). If a new food patch suddenly becomes available, a plastic individual may be able to take advantage of this opportunity more quickly than a less plastic individual. This should increase the payoff to the plastic individual, but also the non-plastic individual as the level of competition within a patch is reduced, increasing the likelihood of their using the same tactic again (i.e. positive feedback, Wolf *et al.* 2008). However, behavioral plasticity is assumed to carry a cost (DeWitt *et al.* 1998) and the advantage to a plastic individual is highest when it is rare in the population (Wolf *et al.* 2008). If all individuals in the population are plastic and constantly respond to changes in their environment, a non-plastic individual might do well if it can behave appropriately on average and not have to pay the costs associated with plasticity (Wolf *et al.* 2008). In this way, among-individual variation in behavior might be maintained when individuals have a mutual interest in avoiding competition in a heterogeneous environment.

As suggested by these models, social dynamics can play a key role in promoting variation in plasticity; however it is still unknown how changes in the social environment might influence behavioral plasticity (Reale *et al.* 2007; Stamps & Groothuis 2010). Individuals may be strongly influenced by the social composition and therefore exhibit context-specific behaviors that change as the context or social environment changes (*sensu* Coleman & Wilson 1998). For example, individual birds maintained a consistent producer or scrounger strategy in one social

group, but switched strategies when they were placed in a new social group (David *et al.* 2011; Morand-Ferron *et al.* 2011). Alternatively, individuals might exhibit very domain-general (*sensu* Coleman & Wilson 1998) behaviors that do not change when placed in a new context. Hyper-aggressive water striders maintained high levels of aggression regardless of the composition of the social group, even though their hyper-aggressiveness decreased mating success (Sih & Watters 2005). If behaviors are domain-general, then the behavior of an individual in a nonsocial situation is predictive of an individual's behavior in a social situation, and individuals maintain their behavior across different social groups (e.g. Beauchamp 2000; Magnhagen & Bunnefeld 2009). However, given dynamism and unpredictability of social interactions, we might also expect individuals to exhibit context-specific behaviors for each social environment.

Therefore, in this study, I 1) tested the prediction that there is more among-individual variation in plasticity in a social environment when there is the opportunity to avoid competition and 2) tested the influence of changes in the social environment on among-individual variation in plasticity in threespined sticklebacks (*Gasterosteus aculeatus*). Sticklebacks are a small fish known for their variation in behavior (Huntingford 1976; Bell 2005; Dingemanse *et al.* 2007). Additionally, individual sticklebacks differ in their resource use (Bolnick *et al.* 2003) and how they behave in a patchy foraging environment (Milinski 1984, 1994), suggesting that some individuals may be more sensitive to changes in food availability than others. Therefore as a measure of behavioral plasticity, I measured how quickly individuals within social groups responded to a newly available food patch in a two-patch foraging environment. This method quantifies plasticity as a single variable: the speed with which an individual moves into a newly

available food patch, allowing us to gather repeated measures of behavioral plasticity on the same individuals relatively quickly.

To alter the level of competition, I created two competitive regimes that differed in the number of food patches available at any one time: the ‘simultaneous patch’ regime had two patches available simultaneously, which gave plastic individuals the opportunity to reduce within-patch competition by moving into a newly available patch. The ‘sequential patch’ regime only had one patch available at a time therefore only one foraging opportunity was ever available. Given that most environments do not have perfectly reliable food patches, both regimes present ecologically-relevant challenges with obvious fitness consequences (food payoff). To determine the role of the social environment on individual behavior, I measured individuals’ behavior in two different social groups and I also measured a subset of the individuals while alone (not in a social group).

MATERIALS AND METHODS

All fish were wild-caught females from Putah Creek, CA, a freshwater stream. Fish were housed in large groups (~30 individuals) in the laboratory for six months prior to experiments. Fish were fed an *ad libitum* diet of bloodworms, mysis and brine shrimp daily. Fish were permanently marked with subcutaneous UV elastomer (Northwest Marine Technologies, Inc.) at least one week prior to testing. Three days prior to testing, fish were also marked with a small plastic tag on their dorsal spine to allow visual identification (Webster & Laland 2009). All experimental procedures were approved by the University of Illinois’s Institutional Animal Care and Use Committee protocol #09204

Measuring behavioral plasticity under two different competitive regimes. I created a feeding arena (113 x 30 x 35.5cm) with two food patches to which food could be added independently. Food was dropped into the patches by means of a conveyer belt with small cups; as the belt advanced, a cup upended into the patch. If the patch was receiving food, the cup contained a single small (~1cm) bloodworm in a small amount of distilled water (~2ml); if not, the cup only contained distilled water. Each patch was located on either end of the long axis of the aquarium and the aquarium was divided into three zones: two patches (30 cm long each) with a neutral zone (53cm long) in between.

I created six groups of six non-reproductive, size-matched (42-45mm) sticklebacks. I never detected an influence of body size on any behavioral measure (data not shown). Each group was tested in two trials per day on five consecutive days to assess the repeatability of behavior. Groups were tested in one of two competitive regimes that differed in the level of within-patch competition (Figure 2.1). In the ‘simultaneous patch’ regime, food was first added to one patch (12 bloodworms/minute) for five minutes and then at an equal rate to both patches for five minutes (6 bloodworms/minute). In this regime, individuals could reduce within-patch competition by switching to the new patch. In the ‘sequential patch’ regime food was first added to one patch for five minutes (12 bloodworms/minute) and then *only* to the other patch for five minutes (12 bloodworms/minute). In this regime, only one patch was available at a time, which forced foragers to switch patches and maintain a similar level of competition. In both regimes, the side that received food first was randomly assigned on the first trial of the day, however the same side could not receive food first for more than two consecutive days. To control for potential side biases, on the second trial of the day, the opposite patch received food first.

Influence of the social environment on behavioral plasticity. I assessed the influence of changes in the social environment by measuring individual behavior in two different social groups: their ‘original’ social group (described above) and a ‘shuffled’ social group. I randomly shuffled the fish from their original groups into three new groups with the restriction that only two individuals from each original group went into any one shuffled group. Fish were tested in the same regime in both their original and shuffled groups (Figure 2.1). Each shuffled group was tested in 10 trials as before.

I also tested whether individual behavior while in a group was related to individual behavior while alone. To do this, I measured the behavior of individuals from the ‘simultaneous patch’ regime while they were alone (Figure 1). Preliminary observations of lone sticklebacks suggested that individuals were unwilling to move into a new patch if the old patch was still receiving food, and if an individual switched to the new patch, it usually did so within two minutes. Pilot experiments showed that single fish became satiated after consuming ~25 bloodworms. Therefore in the ‘alone’ trials, individuals were tested in a modified regime where one patch received food for two minutes (5 bloodworms/minute) and then the other patch received food for two minutes (5 bloodworms/minute).

To test individuals while alone, a group was placed in the feeding arena where it remained for the week of testing. For this assay, two opaque dividers were lowered on either end of the feeding arena during testing (Figure S1), but remained up at other times so that fish could swim freely around the aquarium when a trial was not in session. When a trial began, all individuals except one were gently herded behind one divider. I then measured the behavior of the remaining individual in the feeding arena. Then, this fish was gently herded under the opposite divider. A new individual was gently herded from under the other divider into the arena

and tested. This continued until all fish had been tested in one trial. I waited 15 minutes and repeated the process until all fish had been tested a second time. This method allowed us to minimize stress to the fish from excessive netting and isolation from their group-mates. Fish were tested for five consecutive days and were performed two months after tests in the original and shuffled groups.

Data collection. Each trial was video-recorded with a high-definition JVC Everio camcorder and the videos were coded using JWatcher (Blumstein, Daniel & Evans; UCLA & Macquarie University). In all trials, I never observed overt aggressive interactions among group-mates suggesting that behavioral differences were not simply the result of differences in dominance. I measured 18 individuals in each regime in the original groups (n=36) however one individual in the ‘sequential patch’ regime and two in the ‘simultaneous patch’ regime died before they could be tested in their shuffled group (n=33). They were replaced with other fish to maintain the same group size but I did not include the extra fish’s behavior in the dataset. The two fish that died in the ‘simultaneous patch’ regime also meant that our sample size was n=16 for the ‘alone’ trials.

In each trial I recorded three variables for each fish. First, I recorded *switch delay*: the latency of an individual to move into the newly available food patch. If an individual never switched to the newly available food patch they were given a maximum *switch delay* of five minutes; if an individual was already within the new food patch before food was added, I could not assess whether they would have switched quickly or not at all so they were not given a *switch delay* for that trial. Second, I measured the number of *food items* an individual consumed in a single trial. Finally, I recorded an individual’s *sampling* behavior as the number of times an

individual moved from one patch to another. I restrict our results and discussion to variation in *switch delay* as I interpret this as a measure of behavioral plasticity in response to a change in the environment; *sampling* behavior occurred throughout the trial before and after the change in food availability and therefore I could not determine whether this was in direct response to the change in food (results for *sampling* behavior are shown in Table 2.1).

Data analysis. I used Bayesian statistics with Markov Chain Monte Carlo simulations using the MCMCglmm package (Hadfield 2010) in R 2.15 (<http://www.r-project.org/>.) I first tested for differences in average behavior between competitive regimes by including Regime as a fixed effect. To account for the non-independence of observations I included Group and Individual (nested within Group) as random effects. For all analyses I used non-informative proper priors (Hadfield 2010) with 500,000 iterations, thinning of 10 iterations and a burn-in of 1,000 iterations

To address our first research question of whether the opportunity to avoid competition promotes greater among-individual variation in behavioral plasticity, I estimated the repeatability of *switch delay* (our measure of behavioral plasticity) over the entire trial week within each of our regimes. Then, to determine whether among-individual variation in plasticity increased with time spent in the social group, I estimated repeatability of *switch delay* using only the first two, and the last two days of the trial week in each regime. Throughout all the following analyses, I mean-centered and scaled the variance to one for all our variables within each regime, although I present raw values in the figures for ease of interpretation. Repeatability (r) is the proportion of total variation that can be attributed to among-individual differences and I estimated ‘ r ’ using MCMC simulations which reports 95% credibility intervals which I use to interpret significance

(Nakagawa & Schielzeth 2010; Dingemanse & Dochtermann *in press*). I did not include any fixed effects in our models but rather only Group and Individual (nested within Group) as random effects. As all individuals were exposed to the same levels of any potential fixed effect (e.g. trial day), variation attributable to these factors would remain in the residual variance, thereby providing a conservative repeatability estimate (Nakagawa & Schielzeth 2010). Preliminary analysis showed that inclusion of the fixed effects had little effect on our estimates of repeatability (<0.02 change in r estimate and no change in CI interpretation, data not shown), therefore I provide the non-‘adjusted’ repeatability estimates to allow for broader generalization of our results (Nakagawa & Schielzeth 2010; Dingemanse & Dochtermann *in press*).

To determine how food intake and behavior were related, I used bivariate mixed models to estimate the covariance between *food intake* and *switch delay* (Dingemanse & Dochtermann *in press*). I ran a separate model for each regime and included Group and Individual (nested within Group) as random effects. This method allowed us to partition the covariance between the two behaviors at the among- (i.e. Individual covariance; e.g. individuals that switched quickly on average, ate more food, on average) and within-Individual level (i.e. residual covariance; e.g. when an individual switched more quickly during a trial, it ate more food compared to other trials).

Our second research question was whether individuals maintain their behavior when placed in a new social environment. I used a bivariate mixed model where I considered each individual’s *switch delay* in the original and shuffled groups as separate response variables and estimated the covariance between these variables (Dingemanse & Dochtermann *in press*).

RESULTS

1. *The opportunity to avoid competition promotes among-individual variation in behavioral plasticity*

Across both competitive regimes, individuals switched to the new patch in, on average, 120 ± 6 (s.e.) seconds, but there was individual variation in switch delay: some individuals switched within 2.4 seconds whereas others never switched (Figure 2A,B). I did not detect a difference in *switch delay* between regimes ('sequential patch': 114 ± 8 sec; 'simultaneous patch': 127 ± 9 sec.; posterior Regime estimate = $9.75 [-13.7, 34.6]$).

In support of our hypothesis, individuals in the 'simultaneous patch' regime exhibited consistent individual differences in *switch delay* (repeatability ' r ' = 0.18, 95% CI: [0.05, 0.38], Figure 2.2A). Individuals in the 'sequential patch' regime exhibited very low among-individual variation (Table 2.1), resulting in a repeatability estimate of 0 (95% CI: [3.0×10^{-10} , 6.6×10^{-9}], Figure 2.2B). Importantly, the CI's of the Individual variance (Table 2.1) and repeatability estimates of *switch delay* in each regime do not overlap demonstrating that there is greater among-individual variation in *switch delay* in the 'simultaneous patch' regime than in the 'sequential patch' regime. Moreover, the repeatability of *switch delay* in the 'simultaneous patch' regime significantly increased later in the testing week (first two days: $r = 0.006 [0.0009, 0.015]$; last two days: $r = 0.20 [0.05, 0.42]$), driven by a significant increase in the Individual variance component (Table 2.1), which is consistent with positive feedback increasing among-individual differences. This pattern was not apparent in the 'sequential patch' regime; the Individual variance component (Table 2.1) and repeatability of *switch delay* was always nearly zero (first two days: $r = 0.00 [1.9 \times 10^{-10}, 4.5 \times 10^{-9}]$; last two days: $r = 0.00 [1.2 \times 10^{-12}, 3.7 \times 10^{-11}]$).

I suspected individuals in the ‘sequential patch’ regime might be more influenced by their group mates than individuals in the ‘simultaneous patch’ regime. To assess this, I compared the amount of variation explained by the Group variance component. Over the entire week, in the ‘sequential patch’ regime, ~21% of the variance could be attributable to variation among Groups (0.23 [0.04,0.56]), whereas only 3% of the variance was attributable to variation among Groups (0.05 [0.009,0.12]) in the ‘simultaneous patch’ regime, a suggestive, but not significant difference. However, by the end of the week, the Group variance component explained significantly more variation in the ‘sequential patch’ regime (0.38 [0.007,0.94]) than in the ‘simultaneous patch’ regime (0.00 [<0.001 , <0.001], Table 2.1).

I found evidence for within-individual correlations across trials in how many *food items* an individual consumed and their *switch delay*, though in opposite directions in the two regimes. In the ‘simultaneous patch’ regime, when individuals took longer to switch (larger *switch delays*), they consumed more *food items* in that trial (residual covariance=0.15 [0.02,0.29], Figure 2.3A). Not surprisingly, the opposite pattern was apparent in the ‘sequential patch’ regime (residual covariance=-0.37[-0.54,-0.22], Figure 2.3B) as only individuals that switched would receive food in the second period of the trial. While I found no evidence for a significant covariance between an individual’s average *switch delay* and average *food items* in either regime this may have been influenced by the relatively small sample size of our study (Individual covariance: ‘simultaneous patch’=0.03[-0.14,0.21]; ‘sequential patch’= -8.9×10^{-5} [- 2.2×10^{-5} , 2.3×10^{-5}]).

2. Individuals maintain behavioral plasticity across two social environments in the ‘simultaneous patch’ regime

I evaluated whether individuals were influenced by changes in their social environment by measuring individual *switch delay* and *sampling* behavior in their original group and in a new shuffled group. I observed among-individual variation in *switch delay* within the original social groups in the ‘simultaneous patch’ regime and there was significant covariance between an individual’s *switch delay* in their original group and their *switch delay* in the shuffled group (Individual covariance=0.12 [0.003, 0.28], Figure 2.4A). In contrast, in the ‘sequential patch’ regime, I could not accurately estimate covariance between individual *switch delay* across the two social groups, as there was essentially zero variation in individual behavior within the original groups (Figure 2.2B, Table 2.1), which further supports that there is little carryover in behavior from one social context to the other.

As only individuals in the ‘simultaneous patch’ regime exhibited significant among-individual variation in *switch delay*, I also measured these individuals while alone. I found that these individuals also exhibited significantly repeatable variation in *switch delay* while alone ($r=0.26$ [0.07,0.52]). While not strongly supported, I did find evidence for cross-context repeatability in individual behavior while alone and in a social group as there were positive covariances between individual *switch delay* while alone and in their original groups (Individual covariance=0.10[-0.10,0.31]) and while alone and in their shuffled groups (Individual covariance=0.10[-0.02,0.24]). The fact that the CI’s overlapped zero should be interpreted cautiously but this still suggests that individuals with shorter *switch delays* while alone tended to have shorter *switch delays* in the social groups

Not surprisingly, when tested while alone, individuals that switched more quickly during a trial also received more food during that trial (residual covariance=-0.30[-0.45,-0.18]). Individuals that switched more quickly on average, tended to get more food overall, though there was not strong support for this (Individual covariance=-0.16[-0.43,0.05]).

DISCUSSION

While there is evidence that limited behavioral plasticity can constrain optimal behavior (Sih *et al.* 2004; Johnson & Sih 2005; Sih & Watters 2005), recent models have shown that individual variation in plasticity can be adaptive under some circumstances (e.g. Wolf *et al.* 2008; Wolf *et al.* 2011). Some of the most intriguing models have shown that competitive interactions among individuals might promote among-individual variation in behavior, including plasticity, when there is environmental heterogeneity (e.g. Wolf *et al.* 2008; McNamara *et al.* 2009; Dubois *et al.* 2010; Wolf *et al.* 2011). These models predict that individual differences in plasticity are most likely to emerge when access to foraging opportunities is temporally and/or spatially variable and these opportunities are limited by the presence of competitors. In this paper I provide strong support for this prediction by showing that consistent individual differences in *switch delay* were only apparent in the ‘simultaneous patch’ regime, i.e. under conditions where individuals that quickly switched to the new food patch could exploit a different foraging opportunity than non-plastic individuals. In addition, under these conditions (‘simultaneous patch’ regime), among-individual variation in *switch delay* increased the longer a group had been together, consistent with positive feedback, which is another prediction of these models (Wolf *et al.* 2008; Wolf *et al.* 2011). I also showed that the relative success of this behavior depended on the competitive regime, suggesting that ecological factors such as food

availability and predictability might influence variation in plasticity. Finally, I showed that the influence of the social environment on individual behavior depended on the competitive regime: individuals in the ‘simultaneous patch’ regime exhibited similar behavior across two social groups and while alone, whereas individuals in the ‘sequential patch’ regime did not.

The Ideal Free Distribution theory predicts that groups of foraging animals arrange themselves among patches to avoid competition and increase individual payoffs (Fretwell & Lucas 1970). I showed that this pattern might be driven by only a few individuals in the group that consistently respond more quickly than others to new foraging opportunities. Recent models argue that the presence of plastic individuals reduces within-patch competition: as plastic individuals utilize a new patch and the non-plastic individuals stay at the old patch, the payoffs to all individuals increase (Wolf *et al.* 2008). Because of this increase in payoff, all individuals, including non-plastic individuals, should be more likely to use the same strategy again (Wolf *et al.* 2008; Wolf *et al.* 2011). The repeatability of *switch delay* increased later in the week, demonstrating that among-individual variation in this behavior increased the longer the group had been together, suggestive of positive feedback. However, this positive feedback could be caused by several potential mechanisms. One possibility is that individuals became familiar with the patchiness of the competitive regime; as food at one patch became unavailable or reduced, they learned to quickly search for another. Alternatively, increasing familiarity among group mates may have caused positive feedback. As individuals learned their group mates’ reputation for patch use, they were able to avoid competition because individuals could be relied upon to behave in a certain way (e.g. Dall *et al.* 2004; McNamara *et al.* 2009). A promising future research direction is to determine if familiarity with the competitive regime or familiarity among group mates is the cause of the positive feedback.

Comparing the two competitive regimes revealed that how quickly an individual exploited a new patch influenced individual payoffs, but the direction of the relationship depended on the variation in food availability. In the ‘sequential patch’ regime, when an individual quickly responded to the change in food availability (faster *switch delay*), it received more food during that trial compared to other trials; however, in the ‘simultaneous patch’ regime the opposite pattern was the case. In this regime, when an individual quickly switched to the new food patch, it did worse during that trial (Figure 2.4). The fact that individuals that quickly responded did worse in the ‘simultaneous patch’ regime suggests that there is a cost associated with behavioral plasticity, which is a crucial assumption of these models (Wolf *et al.* 2008; Wolf *et al.* 2011). The most obvious cost under these conditions is travel time between patches, however, other costs have been suggested (e.g. maintenance and production costs, DeWitt *et al.* 1998; Wolf *et al.* 2008). Determining how costs maintain variation in behavioral plasticity is a promising topic for further work. The Wolf *et al.* (2011) model suggests that plastic individuals might be favored whenever individuals vary in their average behavior and our results suggest that the benefits of plasticity can also depend on variation in abiotic environmental factors, such as resource availability. Similar results have been found elsewhere that demonstrated that the success of different behavioral types depended on the distribution and abundance of resources (Dingemanse *et al.* 2004; Morand-Ferron *et al.* 2011). Environmental heterogeneity is pervasive in natural populations and along with maintaining variation in personality, might play a role in maintaining variation in behavioral plasticity within and across populations as well. Whether this extends to the maintenance of genetic variation in plasticity in sticklebacks is an obvious question for future work.

While adaptive models explain the origin and maintenance of variation in behavior over evolutionary time, another outstanding question is the extent to which current social conditions influence behavior within the individual's lifetime (e.g. Stamps & Groothuis 2010; Dingemanse & Wolf *in press*). Multiple studies have demonstrated the impact of changes in the social environment on individual behavior (e.g. Sih & Watters 2005; Magnhagen & Bunnefeld 2009), and here I offer insight into how changes in social group composition influence an individual's reaction to foraging opportunities. One extreme view might be that behavior is context-specific and therefore the most important influence on an individual's behavior is their current environment. Therefore, I would expect to see little carryover in behavior from one situation to the next. In contrast, another view suggests that behavior is most heavily determined by innate factors such as genetics and therefore I would expect individuals to exhibit very domain-general behaviors across multiple environments. In our study, I found evidence for both perspectives: the relative importance of the social environment varied between regimes.

Individuals in the 'simultaneous patch' regime maintained a similar level of behavioral plasticity across two different social contexts (original and shuffled groups), supporting the behavioral type hypothesis. If individuals do not change their behavioral type according to their social group, this might favor social selection, i.e. for individuals to choose the "best" group to join (e.g. Saltz 2011). There is support for this in sticklebacks: sticklebacks prefer to associate with familiar individuals (Barber & Ruxton 2000; Ward *et al.* 2002), groups of familiar sticklebacks find more food overall (Ward & Hart 2005) and share food more equitably with each other than non-familiar sticklebacks (Utne-Palm & Hart 2000). I also found tentative support that individual *switch delay* while alone was related to their *switch delay* while in a social group; however, this result was not strictly significant, potentially due to our low sample

size. This suggests that individuals may inherently differ in their response to a new food source, but that the presence of conspecifics may alter the benefits of this type of plasticity.

In contrast, results from the ‘sequential patch’ regime supported the hypothesis that behavior is strongly context-specific. Individuals in this regime did not display consistent individual differences in *switch delay* between the two social groups, demonstrating that the current social situation heavily influenced behavior. The failure to detect variation in plasticity in the ‘sequential patch’ regime was caused by low levels of among-individual variation in *switch delay*: individuals may have been displaying consistent levels of plasticity over time (low within-individual variation), but they did not consistently differ from one another (Figure 2.2). All individuals appeared to switch quickly, as would be expected given experience with the competitive regime as only individuals that switched would receive food in the second period of the trial. Interestingly, differences among the three original groups accounted for a significant portion of variation, suggesting that individuals may also have been using social cues from one another about when to switch. Similar among-group behavioral differences have been found in other studies (Mathot *et al.* 2011) and might be expected as sticklebacks are a schooling fish and behavioral synchrony within social groups is often vital for species that rely on social defenses against predation (Magurran & Pitcher 1987; Webster & Hart 2006).

While there is accumulating evidence that among-individual variation in behavioral plasticity is common, I still know little about the ecological factors contributing to its evolution. Our study provides strong evidence that competition can play a key role in promoting variation in behavioral plasticity. The field of animal personality will continue to progress as more studies test the predictions of models that articulate when and why I expect to observe consistent individual differences in behavior.

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REFERENCES

- Barber, I. & Ruxton, G. D. 2000 The importance of stable schooling: do familiar sticklebacks stick together? *Proceedings of the Royal Society of London. Series B: Biological Sciences* **267**, 151-155.
- Bell, A. M. 2005 Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology* **18**, 464-473.
- Beauchamp, G. 2000 Learning rules for social foragers: implications for the producer-scrouter game and ideal free distribution theory. *Journal of Theoretical Biology* **207**, 21-35.
- Bolnick, D. A. I., Svanback, R., Fordyce, J. A. A., Yang, L. A. H., Davis, J. M., Hulsey, C. A. D. & Forister, M. L. 2003 The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* **161**, 1-28.
- Clark, C. J. & Mangel, M. 2000 *Dynamic State-Dependent Models in Ecology*. New York, NY: Oxford University Press.
- Coleman, K. & Wilson, D. S. 1998 Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour* **56**, 927-936.
- Dall, S. R. X., Houston, A. I. & McNamara, J. M. 2004 The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters* **7**, 734-739.
- David, M., Cezilly, F. & Giraldeau, L. A. 2011 Personality affects zebra finch feeding success in a producer-scrouter game. *Animal Behaviour* **82**, 61-67.

- DeWitt, T. J., Sih, A. & Wilson, D. S. 1998 Costs and limits of phenotypic plasticity. *Trends in Ecology & Evolution* **13**, 77-81.
- Dingemanse, N. J., Both, C., Drent, P. J. & Tinbergen, J. M. 2004 Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**, 847-852.
- Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R. & Dawnay, N. 2007 Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology* **76**, 1128-1138.
- Dingemanse, N. J., Kazem, A. J. N., Reale, D. & Wright, J. 2010 Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution* **25**, 81-89.
- Dingemanse, N. J. & Wolf, M. 2013 Between-individual differences in behavioural plasticity within populations: causes and consequences. *Animal Behaviour* **85**, 1031-1039.
- Dingemanse, N. J. & Dochtermann, N. 2013 Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology* **82**, 39-54.
- Dubois, F., Morand-Ferron, J. & Giraldeau, L. A. 2010 Learning in a game context: strategy choice by some keeps learning from evolving in others. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **277**, 3609-3616.
- Fleeson, W. 2004 Moving personality beyond the person-situation debate. *Current Directions in Psychological Science* **13**, 83-87.
- Fretwell, S. D. & Lucas, H. J. 1970 On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16-36.

- Hadfield, J. D. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**, 1-22.
- Houston, A. I. & McNamara, J. M. 1999 *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.
- Huntingford, F. A. 1976 The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour* **24**, 245-260.
- Johnson, J. C. & Sih, A. 2005 Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioral syndromes. *Behavioral Ecology and Sociobiology* **58**, 390-396.
- Magnhagen, C. & Bunnefeld, N. 2009 Express your personality or go along with the group: what determines the behaviour of shoaling perch? *Proceedings of the Royal Society of London. Series B: Biological Sciences* **276**, 3369.
- Magurran, A. & Pitcher, T. 1987 Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **229**, 439-465.
- Mathot, K. J., van den Hout, P. J., Piersma, T., Kempenaers, B., Reale, D. & Dingemanse, N. J. 2011 Disentangling the roles of frequency- vs. state-dependence in generating individual differences in behavioural plasticity. *Ecology Letters* **14**, 1254-1262.
- Mathot, K. J., Wright, J., Kempenaers, B. & Dingemanse, N. 2012 Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos* **121**, 1009-1020.

- Milinski, M. 1984 Competitive resource sharing: an experimental test of a learning rule for ESSs. *Animal Behaviour* **32**, 233-242.
- Milinski, M. 1994 Long-term memory for food patches and implications for ideal free distributions in sticklebacks. *Ecology* **75**, 1150-1156.
- Mischel, W. 1996 *Personality and assessment*. Mahwah, N.J.: Lawrence Erlbaum Associates, Inc.
- Morand-Ferron, J., Gi-Mike, W. & Giraldeau, L. A. 2011 Persistent individual differences in tactic use in a producer-scrounger game are group dependent. *Animal Behaviour* **82**, 811-816.
- McNamara, J. M., Stephens, P. A., Dall, S. R. X. & Houston, A. I. 2009 Evolution of trust and trustworthiness: social awareness favours personality differences. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **276**, 605-613.
- Nakagawa, S. & Schielzeth, H. 2010 Repeatability for Gaussian and non Gaussian data: a practical guide for biologists. *Biological Reviews* **85**, 935-956.
- Reale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007 Integrating animal temperament within ecology and evolution. *Biological Reviews* **82**, 291-318.
- Saltz, J. B. 2011 Natural genetic variation in social environment choice: context-dependent gene-environment correlation in *Drosophila melanogaster*. *Evolution* **65**, 2325-2334.
- Sih, A., Bell, A. M. & Johnson, J. C. 2004 Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19**, 372-378.

- Sih, A. & Watters, J. V. 2005 The mix matters: behavioural types and group dynamics in water striders. *Behaviour*, **142** **9**, 1417-1431.
- Smith, B. R. & Blumstein, D. T. 2008 Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* **19**, 448-455.
- Stamps, J. A. & Groothuis, T. G. G. 2010 Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**, 4029-4041.
- Ward, A. J. W., Botham, M. S., Hoare, D. J., James, R., Broom, M., Godin, J. G. J. & Krause, J. 2002 Association patterns and shoal fidelity in the three-spined stickleback. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **269**, 2451-2455.
- Ward, A. J. W. & Hart, P. J. B. 2005 Foraging benefits of shoaling with familiars may be exploited by outsiders. *Animal behaviour* **69**, 329-335.
- Webster, M. M. & Hart, P. J. B. 2006 Subhabitat selection by foraging threespine stickleback (*Gasterosteus aculeatus*): previous experience and social conformity. *Behavioral Ecology and Sociobiology* **60**, 77-86.
- Webster, M. M. & Laland, K. N. 2009 Evaluation of a non-invasive tagging system for laboratory studies using three-spined sticklebacks *Gasterosteus aculeatus*. *Journal of Fish Biology* **75**, 1868-1873.
- Wolf, M., van Doorn, G. S. & Weissing, F. J. 2008 Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 15825-15830.

Wolf, M., Van Doorn, G. S. & Weissing, F. J. 2011 On the coevolution of social responsiveness and behavioural consistency. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **278**, 440-448.

Utne Palm, A. C. & Hart, P. J. B. 2000 The effects of familiarity on competitive interactions between threespined sticklebacks. *Oikos* **91**, 225-232.

TABLES

	Simultaneous	Sequential	Alone
Switch Delay			
Entire week			
Group	0.05 [0.01,0.12]	0.23 [0.04,0.56]	1.1e ⁻⁸ [1.6e ⁻⁹ ,2.8e ⁻⁸]
Individual	0.25 [0.04,0.64]	2.7e ⁻⁹ [3.7e ⁻¹⁰ ,7.1e ⁻⁹]	0.40 [0.08,0.99]
Residual	1.02 [0.80,1.25]	0.88 [0.69,1.08]	0.98 [0.74,1.21]
Repeatability	0.18 [0.05,0.38]	2.5e ⁻⁹ [3.0e ⁻¹⁰ ,6.6e ⁻⁹]	0.26 [0.07,0.51]
First two days			
Group	0.14 [0.03,0.34]	0.24 [0.04,0.58]	1.3e ⁻⁹ [2.0e ⁻¹⁰ ,3.4e ⁻⁹]
Individual	0.006 [0.001,0.02]	1.7e ⁻⁹ [2.6e ⁻¹⁰ ,4.7e ⁻⁹]	0.32 [0.05,0.77]
Residual	0.98 [0.65,1.34]	0.89 [0.58,1.25]	1.04 [0.64,1.46]
Repeatability	0.006 [0.0009,0.02]	1.6e ⁻⁹ [1.9e ⁻¹⁰ ,4.5e ⁻⁹]	0.22 [0.05,0.45]
Last two days			
Group	5.8e ⁻⁹ [7.9e ⁻¹⁰ ,1.5e ⁻⁸]	0.38 [0.007,0.94]	0.17 [0.003,0.40]
Individual	0.29 [0.05,0.71]	1.7e ⁻¹¹ [2.3e ⁻¹² ,4.6e ⁻¹¹]	0.53 [0.09,1.31]
Residual	1.06 [0.71,1.44]	0.96 [0.65,1.28]	0.91 [0.57,1.26]
Repeatability	0.20 [0.05,0.42]	1.4e ⁻¹¹ [1.1e ⁻¹² ,3.7e ⁻¹¹]	0.30 [0.09,0.58]
Food items			
Entire week			
Group	3.7e ⁻⁸ [4.7e ⁻⁹ ,9.8e ⁻⁸]	0.004 [0.007,0.01]	0.06 [0.01,0.16]
Individual	0.52 [0.09,1.28]	0.28 [0.05,0.70]	0.54 [0.10,1.34]
Residual	1.05 [0.83,1.28]	0.93 [0.73,1.13]	0.88 [0.68,1.09]
Repeatability	0.30 [0.10,0.57]	0.21 [0.05,0.42]	0.33 [0.11,0.60]
Samples			
Entire week			
Group	0.06 [0.01,0.16]	0.23 [0.04,0.55]	Cannot be estimated – no variation
Individual	0.28 [0.05,0.69]	0.09 [0.02,0.23]	
Residual	0.99 [0.78,1.20]	0.90 [0.73,1.10]	
Repeatability	0.22 [0.03,0.56]	0.07 [0.01,0.19]	
First two days			
Group	0.38 [0.07,0.94]	0.61 [0.10,1.47]	Cannot be estimated – no variation
Individual	0.16 [0.03,0.40]	0.02 [0.005,0.06]	
Residual	1.12 [0.74,1.53]	0.78 [0.54,1.07]	
Repeatability	0.13 [0.02,0.32]	0.02 [0.003,0.05]	
Last two days			
Group	3.7e ⁻⁸ [5.0e ⁻⁹ ,9.7e ⁻⁸]	0.10 [0.002,0.25]	Cannot be estimated – no variation
Individual	0.42 [0.07,1.05]	0.07 [0.01,0.18]	
Residual	1.08 [0.73,1.45]	0.91 [0.62,1.25]	
Repeatability	0.33 [0.05,0.83]	0.06 [0.006,0.14]	

Table 2.1. Variance component estimates and repeatability estimates for behaviors measured within original groups across two competitive regimes and while alone. Numbers in [] indicate the 95% CI for the estimate.

FIGURES

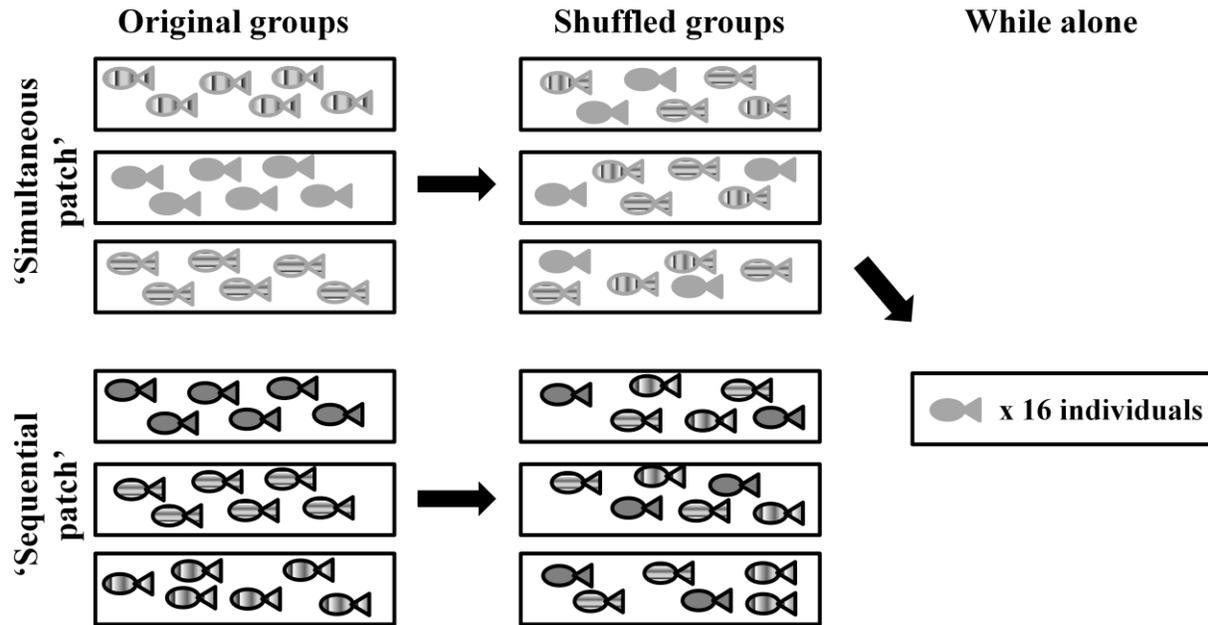


Figure 2.1. Experimental design. 18 individuals were tested in the ‘simultaneous patch’ regime and 18 individuals were tested in the ‘sequential patch’ regime. The three original groups within each regime are represented with different patterns. All individuals were first tested in an original group and then randomly reassigned and tested in a shuffled group. Individuals from the ‘simultaneous patch’ regime were then also tested while alone (see methods). Each group was tested in ten trials over five days.

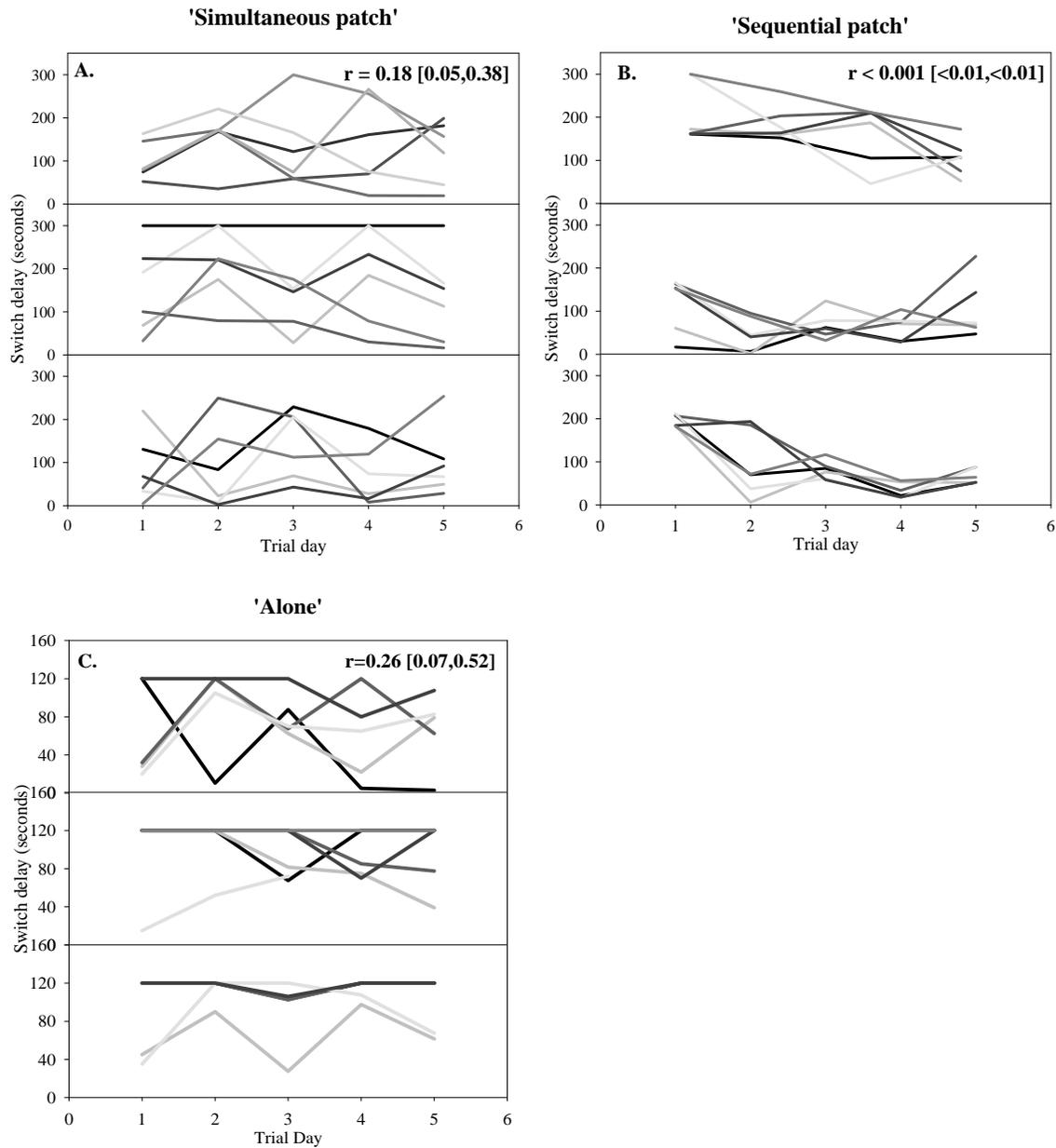


Figure 2.2. Individuals consistently differed in *switch delay* in the ‘simultaneous patch’ regime (A) and while alone (C), but not the ‘sequential patch’ regime (B). Each line represents a different individual and the panels show different original groups within each regime. The value ([95% CI]) in the upper right of each panel represents the repeatability estimate for that regime over the entire testing week. When the lines do not cross, there is perfect rank-order consistency over time, e.g. between days 4 and 5 in the second panel of (A). One cause of a low estimate of repeatability is when there is little among-individual variation, e.g. in (B).

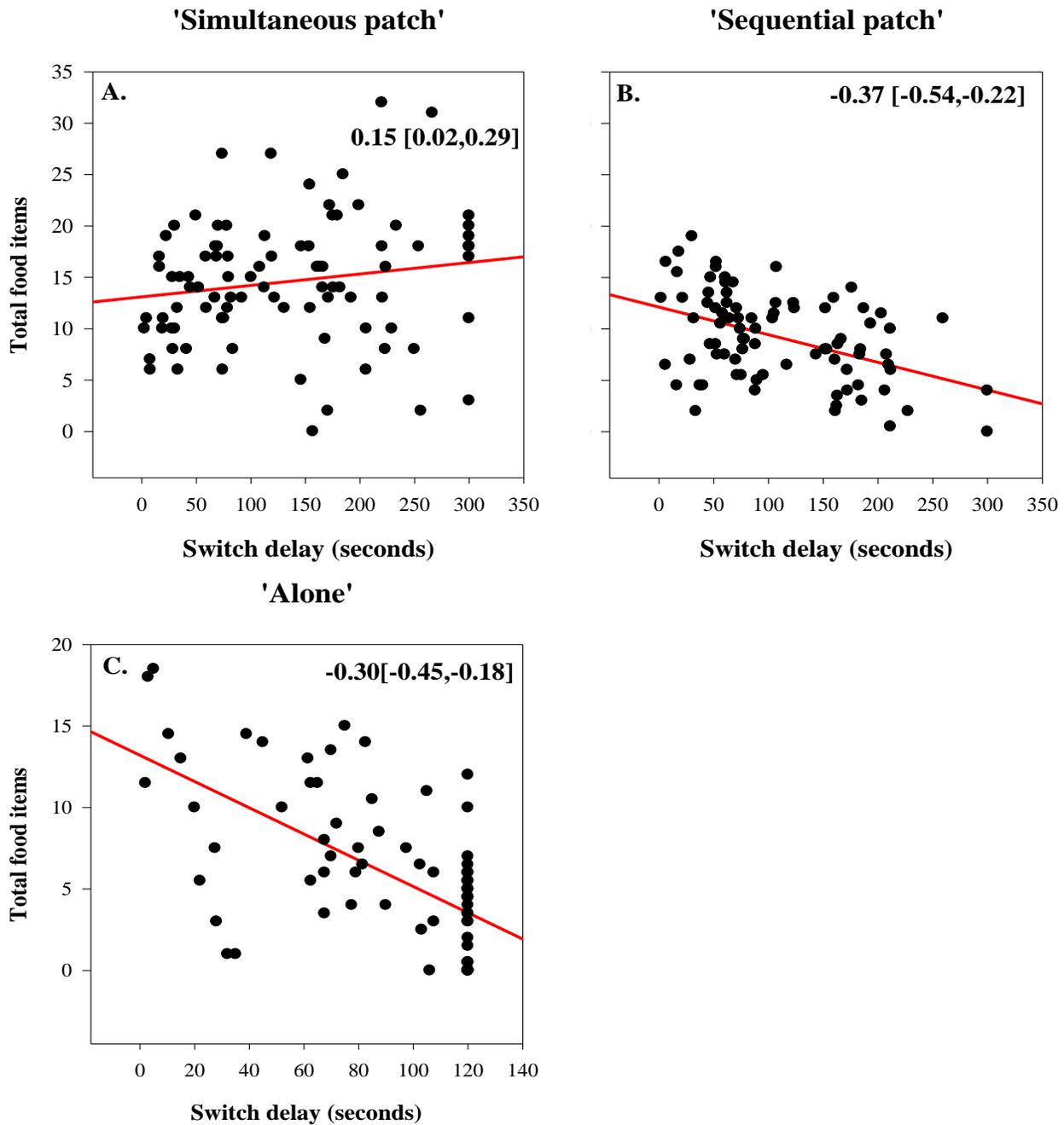


Figure 2.3. When individuals switched more quickly in the ‘simultaneous patch’ regime they received less food during that trial compared to other trials (A), but when individuals switched more quickly in the ‘sequential patch’ regime (B) and while alone (C) they received more food during that trial compared to other trials. Each dot represents a trial so a single individual is represented by ten dots. The value in the upper right represents the residual covariance between *switch delay* and *food items* ([95% CI]). The regression line is included for illustrative purposes only.

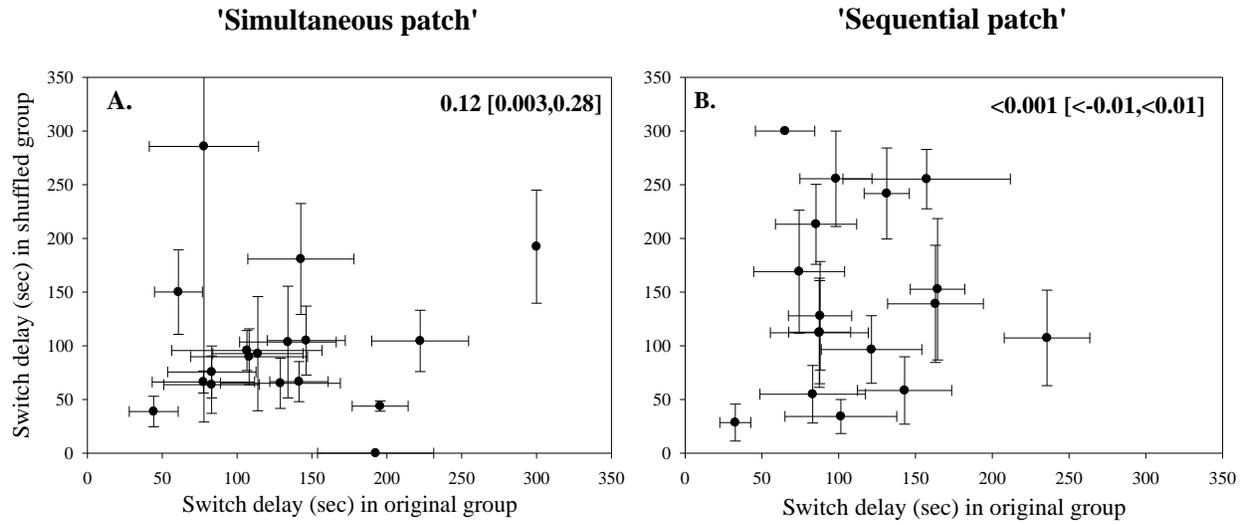


Figure 2.4. There was significant covariance between individuals' *switch delay* across two social groups in the 'simultaneous patch' regime, but not in the 'sequential patch' regime. Each dot represents one individual and their average behavior in their original and shuffled group ± 1 standard error. The value in the upper right shows the covariance estimate between individual *switch delay* ([95% CI]).

CHAPTER 3: STRONG PERSONALITIES, NOT SOCIAL NICHE, DRIVE INDIVIDUAL DIFFERENCES IN SOCIAL FORAGING BEHAVIORS

ABSTRACT

Understanding the mechanisms responsible for consistent individual differences in behavior is a challenge for behavioral ecology. Recent models predict that repeated social interactions can increase the benefits of predictable behavior, thereby generating individual differences (the social niche specialization hypothesis). We explicitly test this hypothesis by manipulating the opportunity for repeated social interactions in threespined stickleback. We compared the social foraging behavior of groups of individuals that were familiar with one another to groups of individuals that were unfamiliar. Additionally, we tested whether individuals exhibited behavioral types by repeatedly measuring individual behavior in three different contexts: a novel environment, when presented with an opportunity to associate with conspecifics, and when confronted by an intruder. We found no evidence that repeated social interactions increased among-individual variation in social foraging behavior. Instead, variation in social foraging behavior was related to variation in behavioral types. In particular, high shoaling individuals took longer to utilize a new food patch while foraging in a social group compared to low-shoaling individuals. Altogether, these results do not support the hypothesis that repeated social interactions generate consistent individual differences in behavior. Instead, they suggest that an individual's social behavior is largely influenced by their behavioral type.

INTRODUCTION

Understanding the mechanisms responsible for consistent individual variation in behavior is a long-standing goal of psychological and behavioral research. New models predict that repeated social interactions can generate and maintain differences among individuals in behavior (Wolf et al. 2008; Wolf et al. 2011; e.g. “social niche specialisation hypothesis” Bergmueller & Taborsky 2010; Montiglio et al. 2013). The presence of other individuals might cause individuals to behave differently from each other to reduce direct competition, thereby generating among-individual variation in behavior (Wolf et al. 2008). Once individuals behave differently from each other, the presence of other individuals may increase the benefits of behaving predictably, thereby maintaining those differences through positive feedback mechanisms (Wolf et al. 2011). For example, in a patchy foraging environment, individuals generally arrange themselves among patches to maximize their own food intake by reducing direct competition with other foragers (i.e. the ideal free distribution, Fretwell & Lucas 1970). If an individual forages in a predictable way, then the group should be able to achieve the ideal free distribution more quickly in repeated encounters. This hypothesis predicts that individuals within groups that have repeatedly interacted with each other should exhibit greater among-individual differences in behavior compared to individuals within groups that have not had the opportunity for repeated social interactions.

A recent study on threespined sticklebacks provided indirect support for this hypothesis (Laskowski & Bell 2013): individual sticklebacks consistently differed in how quickly they utilized a new food patch in a social setting, and individual differences increased with familiarity. Familiarity has many benefits for shoaling fishes (reviewed in Griffiths 2003; Ward & Hart 2003), and studies have shown that fish take advantage of these benefits by preferentially

associating with familiar conspecifics, thereby generating ample opportunity for repeated social interactions in natural populations (reviewed in Ward & Hart 2003; Croft et al. 2005).

While the results in Laskowski & Bell (2013) may have resulted from positive feedback caused by repeated social interactions, it is also possible that the increase in among-individual variation in social foraging behavior was caused by individuals learning about the patchiness of the foraging environment (a mechanism that does not require familiarity among group members). Therefore in this study we explicitly test the hypothesis that repeated social interactions among individuals within groups increase among-individual variation in social foraging behavior. We followed methods used in (Laskowski & Bell 2013) to measure social foraging behavior. However we varied the length of time groups of individuals had spent together prior to being measured. We predicted that among-individual variation in social foraging behavior would be greater in groups of fish that had spent more time together (i.e. that were familiar with each other), compared to groups of fish that were recently formed (i.e. were unfamiliar with each other).

A nonexclusive, alternative explanation for among-individual variation in social foraging behavior is that it reflects individuals' behavioral types, i.e. correlated behaviors outside of the foraging context (Sih et al. 2004). Therefore, we repeatedly measured the behavior of the same individuals in three different contexts to determine whether individual differences in social foraging behavior could be explained by variation in other behaviors. We chose to measure exploratory, shoaling, and aggressive behavior because there were *a priori* reasons to suspect that they might be related to an individual's willingness to utilize a new food source in a social setting. For example, individuals that are highly exploratory and willing to enter and explore novel environments might be more likely to find and utilize a novel food source or patch, as has

been found in wild blue tits (Herborn et al. 2010). Alternatively, or in addition, less social (low shoaling) individuals might be more willing to leave a social group (Cote & Clobert 2007; Rosa et al. 2012) which may increase their odds of finding a new food source. Finally, less aggressive individuals might be excluded from an established food patch, making it more likely for less aggressive individuals to switch patches (e.g. Milinski 1984). This hypothesis also predicts that if behavioral type is important, then a group's social foraging behavior should reflect the average behavioral types of its members.

MATERIALS AND METHODS

Overview

We created eight groups of six size-matched, non-reproductive sticklebacks and assigned four of these groups to a “Familiar” treatment and four groups to a “Non-familiar” treatment (Figure 3.1). After becoming familiar with other individuals within their group (or not), individuals within each group were repeatedly measured for their social foraging behavior where we kept track of each individual's social foraging behavior. We tested whether the individuals in the Familiar treatment exhibited greater among-individual variation in social foraging behavior, compared to individuals in the Non-familiar treatment. Additionally, prior to being assigned to their familiarity treatment groups, we repeatedly measured individual behavior in three standardized assays designed to measure exploratory, shoaling and aggressive behavior. Individuals were assigned to their familiarity groups randomly and blind to their behavior in these other contexts. These data allowed us to test whether social foraging behavior could be predicted by exploratory, shoaling or aggressive behavior.

Animal care and maintenance

All individuals were wild-caught non-reproductive adult sticklebacks from the Navarro River in Northern California. Fish were kept in the lab for three months prior to testing and fed a daily *ad libitum* diet of bloodworms, mysis and brine shrimp and kept on a 12:12 light:dark cycle at 20 C for the entirety of the experiment. One month prior to experimentation all fish were permanently marked with subcutaneous UV elastomer (Northwest Marine Technologies, Inc., Shaw Island, WA, USA) for individual identification. All fish were housed in 10 gallon aquaria with six fish per aquarium. Opaque dividers were placed between aquaria to prevent visual interactions. All experimental protocols were approved by the University of Illinois' Institutional Animal Care and Use Committee protocol #11128.

Creating Familiar and Non-familiar groups

We generated groups of individual fish that differed in the amount of time they had spent together prior to being measured for their social foraging behavior. To create groups of familiar fish ("Familiar" treatment), four groups of six focal individual fish were housed together for three weeks prior to the social foraging behavior test. Previous work has demonstrated that preference for familiar individuals in fishes can occur anywhere within 24 hours to 3 weeks (Van Havre & Fitzgerald 1988; Griffiths & Magurran 1997; Ward et al. 2005). We choose a three week familiarization period to maximize the chances that all fish had become highly familiar with others within their group. To create groups of non-familiar fish (the "Non-familiar" treatment), focal individuals were housed with five other "background" individual sticklebacks for three weeks, then were measured for social foraging behavior with five other focal individuals that were unfamiliar (Figure 3.1). Therefore in this experimental design, all fish,

regardless of treatment, experienced a similar social environment in terms of group density throughout the experiment; the only difference was whether the group-members were familiar or unfamiliar during the social foraging behavior test. As all fish were caught from a large wild population (Navarro River, California), it is possible that individuals in the Non-familiar groups might have interacted in the field previously. However, three months elapsed between capture and testing, and we assumed that if there had been previous social interactions in the field, that they no longer influenced behavior during the time of testing.

The social foraging behavior assay was carried out in a two-patch foraging environment. In order to allow individuals to become familiar with their group members' foraging behavior, during feeding in the familiarization period we simultaneously dropped food into the aquarium via two pipettes at either end of the long-axis of the aquarium.

Measuring social foraging behavior

The experimental protocol for the trials is a modification of previously published experiments (Laskowski & Bell 2013). After the familiarization period, fish were marked with small plastic tags on their pelvic spines to ensure visual identification in the social foraging behavior trials. One group of fish was then transferred to the social foraging behavior arena where the trials took place and acclimated for two days. The social foraging behavior arena was a long aquarium (113 x 30 x 35.5cm) with a food patch at either end and a neutral area in between. Food could be dropped independently into either patch. Each group of fish was tested in ten trials over the course of five days with two trials per day separated by an hour. Briefly, each trial consisted of two five-minute periods. In the first period, bloodworms were added at a rate of 10 bloodworms per minute to only one patch of the arena. In the second period,

bloodworms were then added at a reduced rate (5 bloodworms/minute) to both patches. We recorded the latency of each individual to move into a new food patch during the second period of each trial (Laskowski & Bell 2013).

Measuring exploratory, shoaling and aggressive behaviors

To determine whether behavior in the social foraging assay reflected an individual's behavioral type, we measured all individuals in three contexts designed to measure exploratory, shoaling, and aggressive behavior. To ensure that behavior in these contexts was not influenced by the familiarity treatment, these assays were carried out two weeks prior to the familiarization period. Each fish was measured in each context twice to determine whether individuals behaved consistently within each context.

Quantifying exploratory behavior

As all fish were housed in their home aquariums at this point (prior to being placed in their Familiarity treatment), we randomly chose a home aquarium and then haphazardly netted an individual from the aquarium. We quickly checked the fish's UV elastomer marking and if it was an experimental fish it was placed into a water-filled cup and then transferred to a small opaque cylinder in the center of the exploratory arena. The exploratory arena consisted of a 1.8m blue plastic kiddie pool divided into nine equal-area sections: one circular center section and eight sections around the outside (Figure 3.2). The center section contained a small plastic plant next to the acclimating cylinder and each of the outside sections contained a small rock pile for cover.

The fish was allowed to acclimate in the cylinder for three minutes, after which the cylinder was raised remotely from behind a blind exposing the focal fish. Once the cylinder was removed from the arena, we measured the time it took for the individual to begin freely swimming. After the individual began swimming, we then measured its behavior for an additional five minutes. As our measure of exploratory behavior we measured the *total number of sections* an individual swam between. Individuals that did not begin swimming within five minutes were given a score of “1” for the *total number of sections* explored (this occurred on 28 out of 76 trials) and the trial was terminated. After the trial was complete we noted the section where the focal individual was located and began the shoaling behavior assay.

Quantifying shoaling behavior

The shoaling behavior assay was performed immediately after the exploratory assay. To begin, we haphazardly selected two conspecific sticklebacks from a large group of ~30 sticklebacks and placed them in a water-filled glass flask. The conspecifics were all given time to settle after being placed in the flask and before being used in a trial to reduce any stress-related behavior. The flask was placed in the section directly clockwise to where the focal individual fish was. If the focal individual was located within the middle circular section, the flask was always placed in section 3. This was done to ensure that the conspecifics were located a similar distance away from the focal individual across all focal individuals. The conspecifics were from the same population; however they were not used for any other part of this experiment.

After the conspecifics were added to the arena, the focal individual was given five minutes to orient toward the flask. Orienting behavior occurred when the focal individual turned

to place the flask within its field of view directly in front of itself. After the focal individual oriented toward the flask, we then measured the *total time spent within a body length* of the flask for five minutes as our measure of shoaling behavior. If a focal individual did not orient toward the flask within five minutes, the trial was terminated and the individual received a “0” for the *total time spent within a body length* of the flask (30 of 76 trials). After completion of the shoaling behavior trial, the focal individual was gently netted out of the arena and randomly placed in to an aggression observation arena by itself. As we had 12 separate aggression observation arenas, we performed observations on 12 individuals per day.

Quantifying aggressive behavior

After completion of the exploratory and shoaling behavior observations, we allowed the individuals to acclimate overnight in their aggression observation arena (35.5 x 35.5cm square aquarium; Figure 3.3) as preliminary observations demonstrated this time period promoted dominance and aggression in the focal individuals. Preliminary observations demonstrated that the use of a slightly smaller intruder, promoted more aggressive behavior in the focal individual compared to when a larger intruder was used. At the beginning of an aggressive behavior trial, we randomly selected a 10% smaller “intruder” (conspecific stickleback) from a large pool of non-experimental individuals. The intruder was placed into an opaque cylinder within the aggression observation arena and allowed to acclimate for three minutes. After three minutes, the cylinder was lifted remotely and removed from the arena exposing the intruder.

A focal individual was give five minutes to orient toward the intruder, after which time we measured the *total number of bites* directed toward the intruder by the focal individual for five minutes. If the focal individual did not orient to the intruder within five minutes, the trial

was terminated, and the focal individual was given a “0” for the *total number of bites* directed toward the intruder (9 out of 76 trials). After the trial was completed, the intruder was removed and the focal individual was gently netted and placed back into their home tank.

Determining exploratory, shoaling and aggressive behavioral types

After we measured all focal individuals for their exploratory, shoaling and aggressive behavior, the fish were placed back in their home tanks. One week (7 days) later, we re-measured all individuals for these same behaviors using the same protocols to determine whether individuals exhibited consistent individual differences in these behaviors.

Data analysis

We first tested for average differences in latency to utilize the new food patch between the familiarity treatments using a linear mixed model with Treatment as a fixed effect. Treatment Group and Individual (nested within Group) were included as random effects. To test whether familiarity among group members increased consistent individual differences in behavior, we compared the repeatability and variance components of latency to utilize a new food patch between the two familiarity treatments. Repeatability (R) is the proportion of total variation that can be attributed to among-individual differences in repeated measures data. We ran a separate model for each treatment. As variance estimates are inherently tied to the total variation present in the response variable, to enable comparison across models, we first mean-centred and scaled the variance of our response variable to one within each treatment. We used Markov Chain Monte Carlo simulations to estimate the variance components as this is an especially powerful method to estimate the variance associated with different random factors (Dingemanse &

Dochtermann 2013). We used ‘MCMCglmm’ in R 2.14.0 (Hadfield 2010) to partition the variation into its components, which we then used to estimate repeatability (Dingemanse & Dochtermann 2013; Nakagawa & Schielzeth 2010). Bayesian methods such as MCMC are useful for variance component comparison as they return 95% credibility intervals which we use to test whether a component estimate is significantly different from zero, and significantly different from other estimates. For each simulation, we used weakly informative inverse-gamma distribution priors (Hadfield 2010), though changing the priors had little to no effect on the repeatability estimates (data not shown). We ran a total 500,000 iterations with a 1,000 burn-in and thinning every 100 iterations for each model.

Our data also allowed us to assess whether individual behavior in the foraging trials could be predicted by differences in exploratory, shoaling or aggressive behavior. To determine whether individuals exhibited behavioral types we first estimated the repeatability of each behavior from the two testing periods. Additionally, to test for the presence of a larger behavioral syndrome, we ran Pearson’s correlations among exploratory, shoaling and aggressive behavior. To test whether an individual’s exploratory, shoaling and/or aggressive behavior predicted their social foraging behavior, we regressed each individuals’ average latency to utilize a new food patch on each individual’s average exploratory, shoaling and aggressive behavior. Additionally, to test for a relationship between the groups’ average behaviors, we regressed each group’s average latency to utilize a new food patch on to each group’s average exploratory, shoaling or aggressive behavior.

RESULTS

Familiar groups had greater among-group variation, not among-individual variation

Fish in the Non-familiar treatment took an average of 105.7 (± 8 s.e.) seconds to utilize a new food patch, whereas fish in the Familiar treatment switched to a new food patch within 92.0 (± 7) seconds. The difference in average latency to utilize a new food patch did not differ between familiarity treatments ($F_{1,6}=0.72$, $p=0.43$).

Within each treatment, there was extensive variation among individuals in latency to utilize a new food patch: variation spanned the entire range (0.5-300 seconds) in both treatments. The repeatability of latency to utilize a new food patch was significantly greater than zero in both familiarity treatments (Table 3.1). However, contrary to our prediction, the repeatability of latency to utilize a new food patch was not greater in the Familiar fish, compared to the Non-familiar fish (Fam: $R=0.09$, 95% CI:[0.02,0.22]; Non-fam: $R=0.16$ [0.04,0.35]). In particular, the Individual variance component, which estimates the amount of variation among individuals, did not differ between familiarity treatments (Table 3.1).

Although the two familiarity treatments did not differ in the extent of variation among individuals, they did differ in the extent of variation among groups within the treatments: among-Group variation accounted for a significant portion of the variation in the Familiar treatment (Group variance estimate= 0.19 [0.03,0.46], Figure 3.4), whereas there was essentially zero variation among Groups in the Non-familiar treatment (Table 3.1, Figure 3.4).

Variation in shoaling behavior predicts variation in social foraging behavior

There was consistent individual variation in exploratory, shoaling and aggressive behavior. Individuals explored between 1-59 sections during the five-minute exploratory trial (average=7.8 sections (± 1.2)), and this behavior was repeatable over time ($R=0.43$ [0.21, 0.66]). Individuals also exhibited consistent individual differences in the total time they spent shoaling with conspecifics ($R=0.22$ [0.07, 0.38]) with some individuals shoaling not at all, and others shoaling for nearly the entire five-minute trial (279 seconds). Finally, there was also dramatic individual variation in aggressive behavior, some individuals never bit the intruder while others bit 151 times during the five-minute trial (average=25 times). Individual variation in aggressiveness was also consistent over time ($R=0.62$ [0.42,0.80]). There was evidence of a behavioral syndrome linking all exploratory, shoaling and aggressive behavior (Table 3.2). All three behaviors were significantly positively correlated; though after a Bonferroni correction for multiple testing the correlation between exploratory and shoaling behavior was marginally significant ($p=0.02$, Table 3.2).

We tested whether individual variation in exploratory, shoaling and aggressive behavior could explain the differences in latency to utilize a new food patch among our treatment groups. Contrary to our predictions, we found no evidence that individuals that were more exploratory or less aggressive exhibited faster latencies to utilize a new food patch (exploration: $R^2_{1,36}=0.07$, $p=0.10$; aggression: $R^2_{1,36}=0.01$, $p=0.52$). However, individuals that spent less time shoaling with conspecifics were more likely to quickly utilize a new food patch ($R^2_{1,36}=0.11$, $p=0.034$, Figure 3.5).

The fact that individual behavior during the social foraging trials was related to behavioral types suggests that differences among groups in social foraging behavior might reflect the non-random distribution of behavioral types across groups. Indeed, individual differences in shoaling behavior translated into group-level differences in social foraging behavior (Figure 3.6): the average shoaling behavior of the individuals that comprised a group significantly predicted the group's average latency to utilize a new food patch ($R^2_{1,6} = 0.73$, $p = 0.007$, Figure 3.6B). Specifically, groups that were comprised of fish that exhibited low shoaling behavior quickly utilized a new food patch (Figure 3.6B). There was not a detectable relationship between a group's average exploratory ($R^2_{1,6} = 0.06$, $p = 0.56$, Figure 3.6A), or aggressive ($R^2_{1,6} = 0.08$, $p = 0.51$, Figure 3.6C) behavior and the group's average latency to utilize to a new food patch.

DISCUSSION

Contrary to our hypothesis, we found no evidence that repeated social interactions among group members resulted in greater among-individual variation in social foraging behavior in sticklebacks. Instead, among-individual variation in social foraging behavior was related to variation in behavioral types. In particular, the individuals that shoaled less with conspecifics were also the individuals that were more likely to quickly utilize a new food patch in the social foraging assay.

Understanding the mechanisms responsible for among-individual variation in behavior is a primary goal for the study of animal personality. Recent theoretical models predict that individuals within groups may differentiate and specialize on certain behaviors in an effort to reduce competition with group members (Wolf et al. 2008; Wolf et al. 2011). Individual diet

specializations can be driven by intraspecific competition (Bolnick et al. 2003), and recently this idea has been expanded to the social context (i.e. “social niche specialization” Bergmueller & Taborsky 2010, Montiglio et al. 2013) making this a likely mechanism to drive among-individual variation in social foraging behaviors. In a recent study, Laskowski & Bell (2013) found that among-individual variation in a social foraging behavior, latency to utilize a new food patch, increased the longer the group had been together. The results of the current study suggest that this pattern was probably not caused by repeated social interactions *per se*, but might instead have been caused by learning: with repeated testing some individuals learned how to quickly exploit a new food patch.

It is possible that familiarity does not promote individual variation in sticklebacks because their social structure is fairly fluid, marked by fission-fusion dynamics (Croft et al. 2005; Ward et al. 2002). Individual sticklebacks leave and join shoals throughout the day (Ward et al. 2002) and while certain pairs of individual sticklebacks are found together more often than predicted by random chance, these pairs are still frequently found within larger groups of (potentially non-familiar) sticklebacks (Croft et al. 2005), which might mask any effect of repeated social interactions within the pair. Evidence that group member interactions promote personality variation might be more likely to be found in species with more stable social groups, e.g. cichlids (Schurch et al. 2010), social spiders (Pruitt & Riechert 2011) and marmots (Armitage 1986).

Although these results are not consistent with the social niche specialization hypothesis, they are consistent with the hypothesis that an individual’s behavior while in a social group reflects its behavioral type. Individuals exhibited stable individual differences in exploratory, shoaling and aggressive behavior, and their shoaling behavioral type was related to their latency

to utilize a new food source. This suggests that an individual's tendency to associate with other individuals might be an important determinant of their social foraging behavior: low shoaling individuals might be especially willing to leave the safety of the group, as has been found in several other species (Herborn et al. 2010; Cote & Clobert 2007).

While social foraging behavior was related to individual differences in shoaling behavior, it was not related to exploratory or aggressive behavior. One possible explanation for the failure to find a relationship with exploratory behavior is that the sticklebacks might not have perceived the social foraging arena as novel and potentially risky because they were allowed to acclimate to the arena for two days prior to testing. Moreover, while an earlier study found that more aggressive sticklebacks excluded less aggressive sticklebacks from a food patch (Milinski 1984), it is possible that aggressiveness was not related to social foraging behavior in this study because we never observed overt aggressive interactions among any individuals during the social foraging trials.

Variation in individual behavior resulted in variation among groups in terms of the group's average behavior. Even though all focal individuals were randomly assigned to their treatment group blind of their exploratory, shoaling or aggressive behavior, there must have still been non-random assignment of certain behavioral types to certain treatment groups. Given the small number of treatment groups in total, this possibility is not un-realistic. However, this does demonstrate that the average behavior of groups of foraging individuals can vary quite dramatically depending upon group composition (e.g. Pruitt & Riechert 2011). This suggests that groups of foraging individuals cannot be considered equivalent; some groups may be more successful at utilizing new food patches than others. In our experiments, each group was given the same, finite amount of food which was always fully consumed; however, in the wild,

variation among groups could obviously translate into differences in overall and individual food intake and is a promising direction for future research.

Altogether this study provides strong support for the hypothesis that individuals can retain their distinctive personalities even in a dynamic social situation. These results are consistent with studies showing that this population of sticklebacks exhibited a strong behavioral syndrome (Bell 2005) and that the way an individual foraged while alone predicted their foraging behavior in a group (Laskowski & Bell 2013). However, these findings are in direct contrast to other studies that have suggested that individual behavior is socially-contingent: the behavior of birds (David et al. 2011; Morand-Ferron et al. 2011) and fish (Webster et al. 2007) changed dramatically when placed in a new social context. There is great interest in the field as to how an individual's behavioral type and their social context interact (see Bergmueller & Taborsky 2010; Montiglio et al. 2013; Webster & Ward 2011) and so there is a need for further theory and data to explain why individual behavior is socially-contingent in some species, or in some situations, but not others.

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REFERENCES

- Armitage, K. 1986 Individuality, social behavior, and reproductive success in yellow-bellied marmots. *Ecology* **67**, 1186-1193.
- Bell, A. M. 2005 Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *J. Evol. Biol.* **18**, 464-473.
- Bell, A. 2013 Randomized or fixed order for studies of behavioral syndromes? *Behav. Ecol.* **24**, 16-20.
- Bergmueller, R. & Taborsky, M. 2010 Animal personality due to social niche specialisation. *Trends in Ecology & Evolution* **25**, 504-511.
- Bolnick, D. A. I., Svanback, R., Fordyce, J. A. A., Yang, L. A. H., Davis, J. M., Hulsey, C. A. D. & Forister, M. L. 2003 The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**, 1-28.
- Cote, J. & Clobert, J. 2007 Social personalities influence natal dispersal in a lizard. *Proc. R. Soc. B.* **274**, 383-390.
- Croft, D., James, R., Ward, A., Botham, M., Mawdsley, D. & Krause, J. 2005 Assortative interactions and social networks in fish. *Oecologia* **143**, 211-219.
- David, M., Cezilly, F. & Giraldeau, L. A. 2011 Personality affects zebra finch feeding success in a producer-scrounger game. *Anim. Behav.* **82**, 61-67.
- Dingemanse, N. J. & Dochtermann, N. 2013 Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J. Anim. Ecol.* **82**, 39-54.
- Fretwell, S. D. & Lucas, H. J. 1970 On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16-36.

- Griffiths, S. W. & Magurran, A. E. 1997 Familiarity in schooling fish: How long does it take to acquire? *Anim. Behav.* **53**, 945-949.
- Griffiths, S. W. 2003 Learned recognition of conspecifics by fishes. *Fish Fish.* **4**, 256-268.
- Hadfield, J. D. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Soft.* **33**, 1-22.
- Herborn, K. A., Macleod, R., Miles, W. T. S., Schofield, A. N. B., Alexander, L. & Arnold, K. E. 2010 Personality in captivity reflects personality in the wild. *Anim. Behav.* **79**, 835-843.
- Laskowski, K. L. & Bell, A. M. 2013 Competition avoidance drives individual differences in response to a changing food resource in sticklebacks. *Ecol. Lett.* **16**, 746-753.
- Milinski, M. 1984 Competitive resource sharing: an experimental test of a learning rule for ESSs. *Anim. Behav.* **32**, 233-242.
- Montiglio, P.-O., Ferrari, C. & Reale, D. 2013 Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Phil. Trans. R. Soc. B* **368**, 20120343.
- Morand-Ferron, J., Gi-Mike, W. & Giraldeau, L. A. 2011 Persistent individual differences in tactic use in a producer-scrounger game are group dependent. *Anim. Behav.* **82**, 811-816.
- Nakagawa, S. & Schielzeth, H. 2010 Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol. Rev.* **85**, 935-956.
- Pruitt, J. N. & Riechert, S. E. 2011 How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proc. R. Soc. B* **278**, 1209.
- Rosa, P., Nguyen, V. & Dubois, F. 2012 Individual differences in sampling behaviour predict social information use in zebra finches. *Behav. Ecol. Socio.* **66**, 1259-1265.

- Schurch, R., Rothenberger, S. & Heg, D. 2010 The building-up of social relationships: behavioural types, social networks and cooperative breeding in a cichlid. *Phil. Trans. R. Soc. B* **365**, 4089-4098.
- Sih, A., Bell, A. M. & Johnson, J. C. 2004 Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**, 372-378.
- Van Havre, N. & FitzGerald, G. 1988 Shoaling and kin recognition in the threespine stickleback (*Gasterosteus aculeatus* L.). *Biol. Behav.* **13**, 190-201.
- Ward, A. J. W., Botham, M. S., Hoare, D. J., James, R., Broom, M., Godin, J. G. J. & Krause, J. 2002 Association patterns and shoal fidelity in the three-spined stickleback. *Proc. R. Soc. B.* **269**, 2451-2455.
- Ward, A. J. W. & Hart, P. J. B. 2003 The effects of kin and familiarity on interactions between fish. *Fish Fish.* **4**, 348-358.
- Ward, A. J. W., Holbrook, R. I., Krause, J. & Hart, P. J. B. 2005 Social recognition in sticklebacks: the role of direct experience and habitat cues. *Behav. Ecol. Socio.* **57**, 575-583.
- Webster, M., Ward, A. & Hart, P. 2007 Boldness is influenced by social context in threespine sticklebacks (*Gasterosteus aculeatus*). *Behaviour* **144**, 351-371.
- Webster, M. M. & Ward, A. J. 2011 Personality and social context. *Biol. Rev.* **86**, 759-773.
- Wolf, M., van Doorn, G. S. & Weissing, F. J. 2008 Evolutionary emergence of responsive and unresponsive personalities. *P. Natl. Acad. Sci. USA* **105**, 15825-15830.
- Wolf, M., Van Doorn, G. S. & Weissing, F. J. 2011 On the coevolution of social responsiveness and behavioural consistency. *Proc. R. Soc. B.* **278**, 440-448.

TABLES

Estimate	Familiar	Non-Familiar
Group	0.19 [0.03, 0.46]	$6.9e^{-9}$ [$5.7e^{-10}$, $1.1e^{-8}$]
Individual	0.11 [0.02, 0.28]	0.20 [0.04, 0.49]
Residual	0.95 [0.75, 1.16]	0.95 [0.76, 1.15]
Repeatability	0.09 [0.02, 0.22]	0.16 [0.04, 0.35]

Table 3.1. Variance component estimates ([95% credibility interval]) for latency to respond to a new food patch in the familiar and non-familiar treatments as estimated by Markov Chain Monte Carlo simulations (see methods). Repeatability of the latency to utilize a new food patch was calculated as the Individual variance component divided by the total variance; estimates that do not overlap zero are considered statistically significant.

	Exploratory	Shoaling	Aggressive
Exploratory	--	0.38	0.57
Shoaling	p = 0.02	--	0.48
Aggressive	p = 0.0002*	p = 0.002*	--

Table 3.2 Pearson's correlations among exploratory, shoaling and aggressive behaviors. Above the diagonal are correlation coefficients and below the diagonal are p-values. Those p-values marked with a "*" remain significant after a Bonferroni correction for multiple testing.

FIGURES

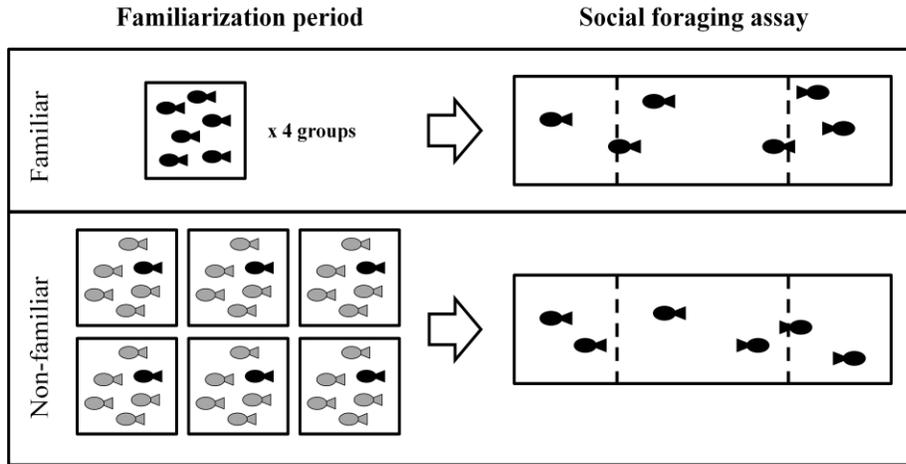


Figure 3.1. Schematic depicting the experimental design to create familiar and non-familiar groups of fish. All individuals were housed in these treatments for three weeks prior to being measured for their social foraging behavior (latency to utilize a new food patch).

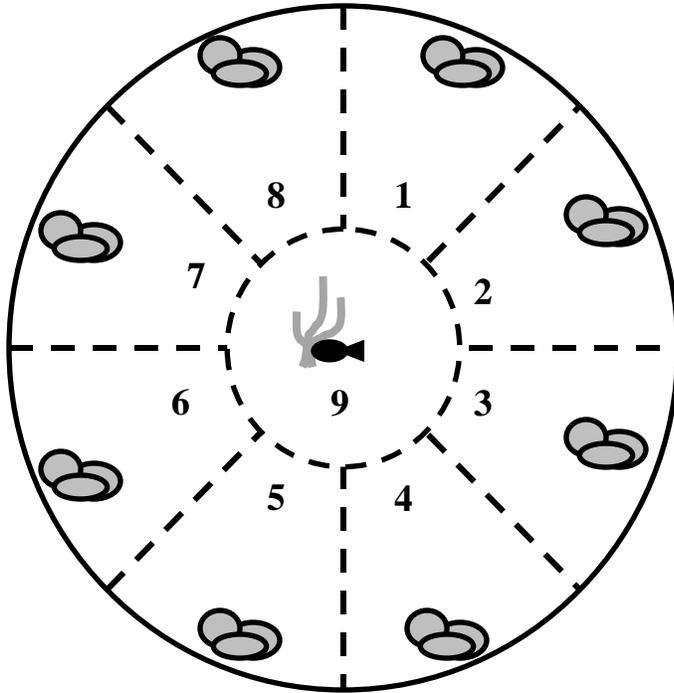


Figure 3.2. Schematic of the exploratory and shoaling behavior arena. The arena was a 1.8m diameter plastic kiddie pool. The fish was placed in an opaque cylinder in the center area and allowed to acclimate for three minutes. We then removed the cylinder and the fish was free to swim around the arena for five minutes. We recorded the total number of sections the fish swam through as our measure exploratory behavior.

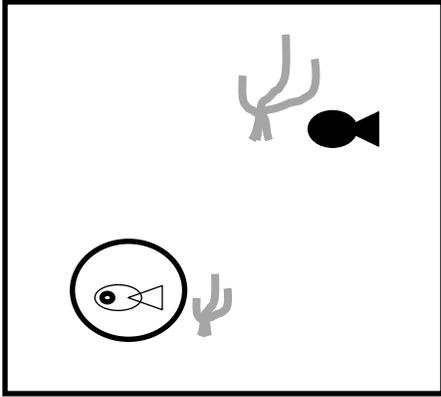


Figure 3.3. Schematic of the aggression observation arena. The focal individual (black) was allowed to acclimate in the chamber overnight. The arena contained gravel on the bottom and two small plastic plants for refuge. The intruder (gray) acclimated in an opaque cylinder for three minutes prior to the start of the assay. Once the cylinder was removed, we counted the total number of bites directed toward the intruder by the focal individual as our measure of aggression.

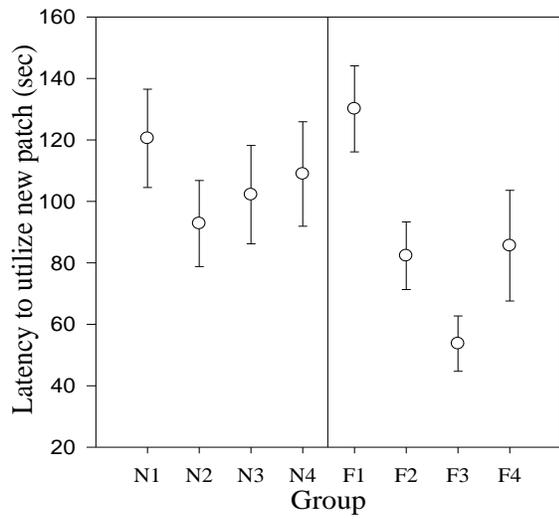


Figure 3.4. Average latency to utilize a new food patch in each treatment group. Each data point shows group mean \pm 1 standard error. Groups labeled with an ‘N’ indicate the Non-familiar treatment groups and groups labeled with an ‘F’ indicate the Familiar treatment groups.

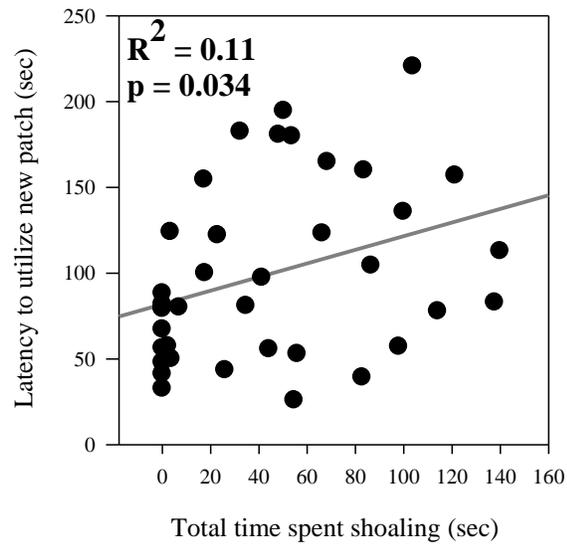


Figure 3.5. Relationship between individual differences in time spent shoaling (average across two trials) and individual differences in latency to utilize a new food patch (average across 10 trials). Individuals that spent more time shoaling were slower to utilize the new food patch.

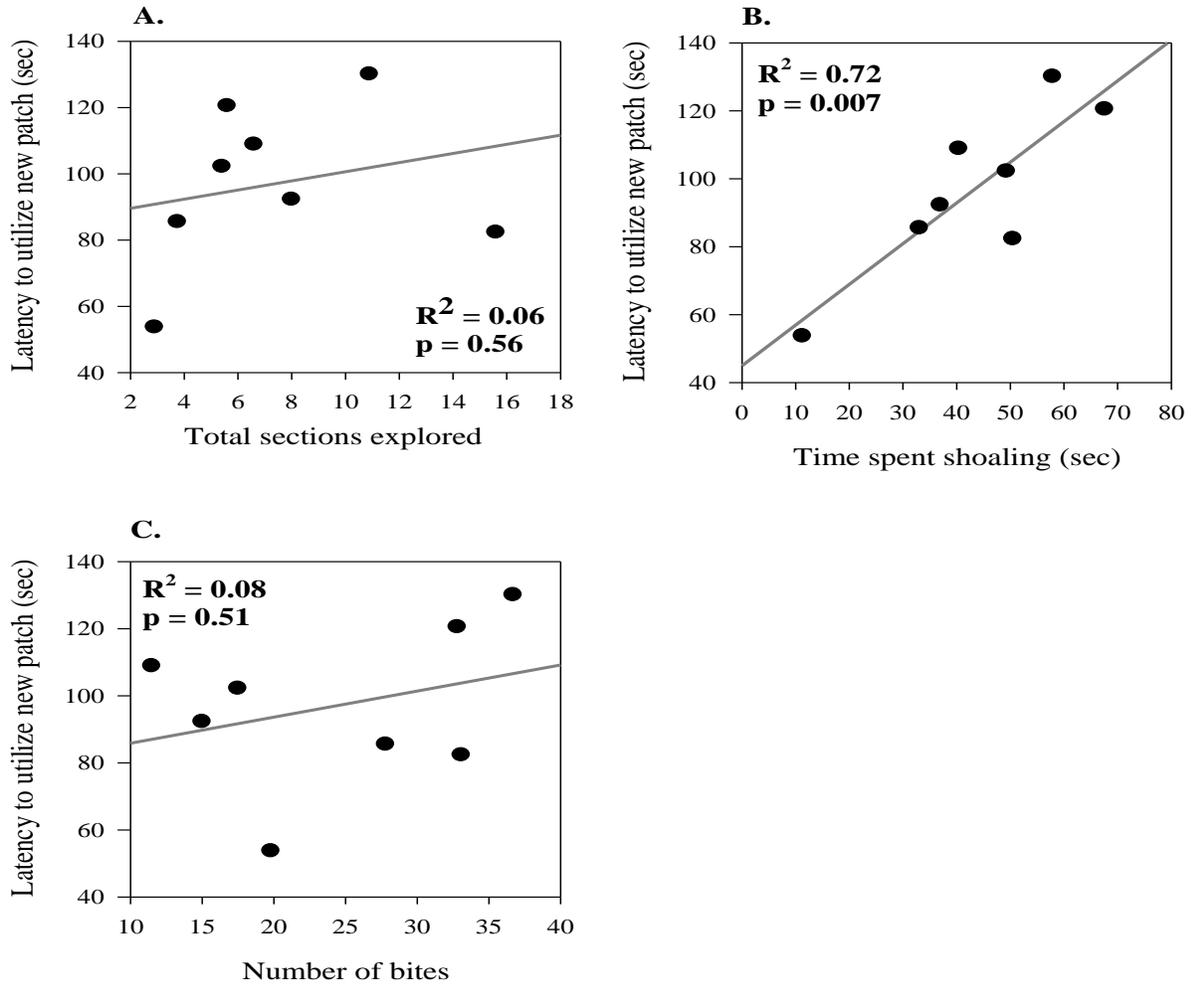


Figure 3.6. Relationship between a group's average latency to utilize a new food patch and the group's average exploratory (A), shoaling (B) and aggressive (C) behavior. Each data point represents a separate group.

CHAPTER 4: THE INFLUENCE OF ENVIRONMENTAL UNCERTAINTY ON CONSISTENT INDIVIDUAL DIFFERENCES IN FORAGING BEHAVIORS

ABSTRACT

Uncertainty about environmental conditions is ubiquitous. Recent models suggest that coping with environmental uncertainty might be an underlying ecological cause of consistent individual differences in behavior. Here I test the hypothesis that uncertainty about environmental factors generates consistent individual differences in behavior in threespined sticklebacks. I manipulate uncertainty in a patchy foraging environment. I tested individuals while alone and while in a group to determine whether the response to uncertainty about foraging opportunities is similar to the response to uncertainty caused by a dynamic social environment. When individuals were alone, consistent individual differences in competitive ability were more apparent in the certain environment, but differences in insurance behavioral tactics were more apparent in the uncertain environment, supporting our hypothesis. However, when tested in a competitive social group, consistent individual differences in tactic use disappeared, suggesting this is not a viable tactic in a social setting. Taken together our results demonstrate that uncertainty about non-social factors, such as food availability, can generate consistent individual differences in foraging behavior, but the presence of social competitors can mask this effect.

INTRODUCTION

Consistent individual differences in behavior are now widely documented across many animal taxa (Bell et al. 2009) and are known to affect fitness (reviewed in Smith & Blumstein 2008). Explaining the presence of widespread consistent individual variation in behavior is a recent challenge for behavioral ecology. New models have demonstrated that in principle, consistent individual differences in behavior can be adaptive, therefore representing the result of natural selection, rather than just its raw material (Wilson 1998; reviewed in Wolf & Weissing 2010). However, there are few empirical tests of these models.

Several models have proposed that environmental uncertainty might generate consistent individual differences in behavior (Dall & Johnstone 2002; McElreath & Strimling 2006; Mathot et al. 2012). In general, animals frequently have limited or noisy information about current environmental conditions, therefore deciding what is the appropriate behavioral response can be difficult (Schmidt et al 2010). From overlooking a particularly high quality food patch to being injured or killed if a predator is nearby, inappropriate behavioral responses to environmental uncertainty can be costly. Therefore, natural selection is expected to favor tactics by which individuals can cope with uncertainty. There are a number of different tactics available for animals to use to reduce uncertainty or limit its effects; such as sampling options, bet-hedging, specializing, or generalizing (Schmidt et al. 2010, Mathot et al. 2012). By sampling, an individual can reduce uncertainty about potential options. However, sampling can be costly if it involves, for example, travel time, energy or neural requirements to process the information (Stephens 1987). Another mechanism an individual can use to cope with uncertainty is by insuring themselves against its potential negative consequences (Dall & Johnstone 2002, Mathot et al. 2012). This can be done by maintaining the availability of different options; that is by not

specializing and making a behavioral decision too quickly, an individual can wait until the “proper” choice becomes more apparent. For example, by waiting to make a decision about which patch to forage in an individual can limit the potential cost of lost travel and foraging time if it later becomes apparent that a different patch is more profitable. In general, these models predict that the ecological cause of consistent individual differences in behavior is that they are a result of an underlying uncertainty coping mechanism, or decision making rule (Dall & Johnstone 2002, McElreath & Strimling 2006, Mathot et al. 2012). Therefore understanding the variation in the uncertainty coping mechanisms should better predict when we expect individuals to exhibit consistent individual differences in behavior. If these models are supported, a main prediction is that consistent individual variation in tactics for coping with uncertainty should be greater in uncertain compared to certain environments.

Theoretically any aspect of the environment can be uncertain. Here I consider two: foraging opportunities and social interactions. A rich literature has shown that foragers maximize food intake under a variety of conditions (i.e. optimal foraging theory, Krebs et al. 1978), including when foraging opportunities are variable and unpredictable (i.e. variance sensitive foraging, Stephens 1981). However, little is known about whether uncertainty in foraging opportunities can generate consistent individual differences in foraging behaviors. Moreover, most models on the influence of environmental uncertainty on consistent individual variation in behavior consider individuals in a solitary context, or at least do not explicitly consider the influence of other individuals (Dall & Johnstone 2002, McElreath & Strimling 2006, Mathot et al. 2012). However social interactions can strongly influence individual behavior (reviewed in Webster & Ward 2011), and can also themselves be uncertain. Therefore uncertainty associated with dynamic social interactions may also cause consistent individual variation in behavior.

In this study, I address the following questions: 1) Does uncertainty about environmental conditions generate consistent individual differences in behavior while alone, and while in a group setting? 2) Do these behaviors influence food consumption? And 3) Is individual's behavior while alone predictive of behavior in a group setting?

I address these questions by measuring the foraging behavior of individual sticklebacks in a patchy environment with either certain patch profitability, or uncertain patch profitability. Individual sticklebacks are a small fish known for their consistent individual differences in a behavior (Huntingford 1976, Bell 2005, Dingemanse et al. 2007) including foraging behavior (Milinski 1984, Milinski 1985, Svanback & Bolnick 2007, Laskowski & Bell 2013). The foraging context provides an ideal context in which to investigate the influence of environmental uncertainty on individual behavior because uncertainty can be easily manipulated by changing the profitability of food patches. Additionally, it is relatively easy to quantify two of the behaviors that individuals may use to cope with uncertainty: sampling and insurance. In a patchy foraging environment, an obvious way to reduce uncertainty is to sample between the patches. A second option is to insure against the consequences of uncertainty: by waiting to determine which patch is most profitable, individuals can reduce the costs of making the wrong choice.

MATERIALS AND METHODS

Overview

I created eight groups of six size-matched adult sticklebacks. Each group was assigned to either a "Certain environment" (n=4 groups) or an "Uncertain environment" (n= 4 groups) which differed in the reliability of food. Each individual was measured five times for their foraging behavior and food consumption while alone, and five times while in a group (Figure 4.1). This

design allowed us to test whether environmental uncertainty increased consistent individual differences, how individual differences in foraging behavior were related to food consumption, and whether individual behavior while alone was predictive of behavior while in a group.

Animal care and maintenance

Individuals were wild-caught adult, non-reproductive sticklebacks from the Navarro River in Northern California. Fish were kept in the lab for one month prior to testing and fed a daily *ab libitum* diet of bloodworms, mysis and brine shrimp and kept on a 12:12 light:dark cycle for the entirety of the experiment. Two weeks prior to experimentation all fish were permanently marked with subcutaneous UV elastomer (Northwest Marine Technologies, Inc., Shaw Island, WA, USA) for individual identification. All fish were housed in 10 gallon aquaria with ~10 fish per aquarium prior to being placed in the treatment groups.

Measuring foraging behavior while alone and while in a group

To determine whether there was greater among-individual variation in behavior in an uncertain environment, we measured the foraging behavior of adult sticklebacks in a two-patch environment in either a 'Certain' or 'Uncertain' environment. Tests were carried out in a long aquarium (113 x 30 x 35.5cm) divided into three zones: a food patch at either end and a neutral zone in the middle. Each patch could have food added to it independently. The food items were small (~1cm) frozen bloodworms; we added a single bloodworm in a small amount (~2ml) of water.

I placed a single group (n=6 individuals) in the foraging arena where it was allowed to acclimate for two days. To measure foraging behavior while alone, we gently herded all but one

individual under an opaque divider placed on one side of the arena. The divider was lowered, leaving the single individual in the arena. I then measured the foraging behavior of this individual according to its treatment (Certain or Uncertain, described further below). After the trial was complete, I checked the individual for its elastomer marking and gently herded it under another opaque divider placed on the other side of the arena. I then lifted the divider and allowed another individual to enter the arena and measured its foraging behavior. I continued this process until all individuals within a group had been measured. I measured the foraging behavior of each individual while alone once a day for five days.

After completion of the foraging trials while alone, I placed a small colored plastic tag on the pelvic spines of each individual within a group to allow visual identification (Webster & Laland 2009). The group was then allowed to rest in the arena for two days until the start of the social foraging trials while in a group. To measure foraging behavior while in a group, the entire group (n=6 individuals) remained in the arena during the trial. I measured the behavior of each individual in the group once a day for five days.

Generating certain and uncertain environments

In the Certain environment, both food patches received the same number of bloodworms at the same rate during the entire trial; individuals in this treatment could be certain of the profitability of the patches without sampling the patches. The rate of food addition and trial length differed slightly between the alone and group trials; preliminary observations showed that individuals became satiated more quickly and could not eat the bloodworms as quickly as a group of six individuals. Therefore, while alone, bloodworms were added at a rate of five per minute (one every 12 seconds) for three minutes to both patches. However, while in a group,

bloodworms were added at a rate of eight bloodworms per minute (one every 7.5 seconds) for five minutes to both patches.

In contrast, in the Uncertain environment treatment, the profitability of both patches varied within and across trials; individuals in this treatment could not be certain of which patch was more profitable without sampling the patches. In the Certain environment, the time interval between bloodworm additions was always fixed. So to generate uncertainty in this environment, we varied the time interval between the addition of each bloodworm: short time intervals would increase the profitability of the patch, whereas longer intervals would decrease the profitability. In order to generate randomness in the time intervals, I generated Gaussian distributions with different mean values. These mean values represent the average time interval (in seconds) between the addition of each bloodworm; however, this could vary around this mean. During a trial, the interval distribution changed every minute for each patch creating uncertainty in the profitability of each patch across trials.

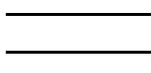
When measuring individuals while alone in the Uncertain environment, I used interval distributions with means of 7, 10 and 13 seconds. The variance of all distributions remained the same (variance = 4). For the three minutes of each alone trial, each patch was randomly assigned an interval distribution for each minute. The total number of bloodworms dropped into the arena during an Uncertain arena was made to match that of a trial in the Certain environment (n=30 bloodworms per trial). When measuring individuals while in a group in the Uncertain environment, I used interval distributions with means of 4, 7, 10 and 13 seconds. Again, for each minute during the five minute trial, the interval distribution for each patch changed with the restriction that the total number of bloodworms added during the entire trial matched the total number of bloodworms added during a Certain trial (n=80 bloodworms).

In both the ‘alone’ and ‘group’ trials, I recorded the following behavioral variables on each individual: the number of samples, how long an individual spent in the neutral zone between the patches each time it entered the neutral zone, and the number of food items (bloodworms) an individual consumed. For sampling behavior, I recorded the number of times an individual swam from one patch across the neutral zone and into the other patch. While this behavior may be correlated with general activity levels, individuals had to swim across the entire aquarium and personal observations suggest that individuals are doing this for the purpose of determining food availability in that patch. Therefore I refer to this behavior as “sampling” behavior.

Data analysis

My first research question was whether environmental uncertainty increased consistent individual differences in foraging behavior both while alone and while in a group. To address this, I investigated a number of different aspects of the data. First, I tested for average differences in behavior in the two environments. To do this, I ran a separate mixed model for each behavior (samples, time in neutral zone and food items) and included Environment as a fixed effect. The effect of Environment was modeled as a contrast; therefore positive effects of Environment indicate that the level of behavior was greater in the Certain environment compared to the Uncertain environment. We also included an effect of Trial and the interaction between Environment x Trial to test whether changes in foraging behaviors over time differed between the environments. Second, I estimated the among- and within-individual variance components of each behavior in each environment. To do this, I ran a separate mixed model for each behavior in each environment (Certain vs. Uncertain) and each social context (Alone vs. Group). I

included Individual ID and Group as random effects to account for the repeated measures. Estimating the among- and within-Individual (residual) variance components allowed me to calculate a repeatability estimate. Repeatability is a measure of the proportion of the variance that is attributable to among-individual differences and because it is standardized for the total variance of each behavior, repeatability estimates have the benefit of being comparable across models (Lessells & Boag 1989, Nakagawa & Schielzeth 2010). And finally, to investigate whether environmental uncertainty increased individual consistency in behavior, I also calculated each individual's intra-individual variability (IIV) for both sampling and time in the neutral zone in each social context (alone and in a group; Stamps et al. 2012). IIV is a measure of the amount of short-term, reversible variation an individual exhibits in a particular situation and has the advantage of accounting for systematic changes that may occur with repeated testing (i.e. the effect of trial; Stamps et al. 2012). It is calculated by running a separate linear regression for each individual, with the behavior of interest as the response variable and the repeated testing variable (i.e. Trial) as a fixed covariate. By including Trial as a covariate, I was able to determine the expected systematic changes in the individual's behavior due to repeated testing. I used this regression to calculate the predicted values of an individual's behavior at each trial and then summed the absolute values of the residuals. I used this to calculate each individual's variance and then square-rooted the variance to estimate the residual standard deviation associated with each individual. Statistically, the measurement of IIV that I report here

is summarized as:  Measurements of IIV have the advantage of being an individual-level statistic of individual consistency in behavior, whereas repeatability estimates are a population-level statistic (Stamps et al. 2012). Therefore it is important to note that each individual received a single IIV score for each behavior. The score summarizes the variation that

individual expressed in that behavior over the entire five trials; higher scores indicate greater individual variance whereas lower scores indicate lower individual variance (or greater individual consistency). I then tested whether average IIV of each behavior differed between the two environments in each social context by running a model with Environment as a fixed effect.

For my second research question I was interested in how individual behavior and individual variation in behavior (IIV) influenced food consumption. I tested this in two different ways. First, I ran a bivariate mixed model with the behavior of interest (samples or time in neutral zone) and food items consumed for each environment and social context as response variables (Dingemane & Dochtermann 2013). This allowed me to estimate the among- and within-individual covariance between behavior and food items consumed. I standardized the covariances according to the variances in each behavior to estimate the among- and within-individual correlation coefficients, which are directly comparable across models (Dingemane & Dochtermann 2013). A among-individual correlation demonstrates that individuals that perform more (or less) of one behavior (e.g. samples) on average across the five trials, also consume more (or less) food items on average across the five trials, compared to other individuals. A within-individual correlation demonstrates that when an individual performed more (or less) of a behavior during a single trial, it consumed more (or less) food items during that trial compared to the other trials. Secondly, I also wished to determine if an individual's variance in behavior (IIV) influenced their average food intake. Because each individual only had one IIV score per behavior, this required me to average the food items consumed over the entire five trials; therefore the resulting correlation is an among-individual correlation. I used a Pearson correlation to determine the relationship between sampling IIV and time in neutral zone IIV, and food consumption.

Finally, our last research question asked whether an individual's behavior while alone was related to their behavior while in a group. To test this, I ran a bivariate mixed model to estimate the among-individual covariance and correlation in sampling, time in the neutral zone and food items across the two social contexts. The behavior of interest in each social context (alone and in a group) was included as the response variables and a separate model was run for each behavior in each environment. I also wished to determine if individuals were consistent in behavioral variance (IIV) in each context; therefore I also estimated the Pearson correlation between the IIV scores for each behavior across the two social contexts.

For all analyses I used mixed models with MCMC estimation using MCMCglmm (Hadfield 2010) in R v2.14.0 (<http://www.r-project.org/>). Bayesian mixed model approaches such as these are especially powerful for estimating the among- and within-individual (residual) variance components even for non-Gaussian data which I needed to address several of my research questions. Additionally, Bayesian methods such as these have the advantage of returning both fixed and random effect estimates (including repeatability estimates) with their corresponding 95% credibility intervals (CI). If the 95% CI does not overlap zero, I interpret this as evidence for a significant effect of that variable. For all models I used weakly-informative proper priors (Hadfield et al. 2010), 500000 iterations, a 1000 burn-in and thinning every 100 iterations. Changing the priors did not alter the interpretations of our results (data not shown).

As a count variable, sampling behavior was Poisson distributed and therefore we used a Poisson error distribution with additive overdispersion for all models with this behavior as the response variable. Additionally, estimating the repeatability of Poisson distributed behaviors requires an adjustment of the residual error (see Nakagawa & Schielzeth 2010). I square-root transformed time in the neutral zone to approximate a Gaussian distribution, though I report raw

means for ease of interpretation. Number of food items consumed was Gaussian distributed and required no transformation for any analysis. The distribution of IIV scores for each behavior was also Gaussian and therefore I used Pearson correlations for determining the relationship between IIV and other behaviors throughout.

RESULTS

Consistent individual differences in foraging behavior depend upon environmental uncertainty when tested alone

While alone, I did not detect any difference in foraging behavior between the Certain and Uncertain environments. Individuals sampled the patches an average of 2.37 ± 0.24 in the Certain environment, and 2.38 ± 0.22 in the Uncertain environment (effect of Environment: 0.08 [-0.05, 0.21]). Sampling behavior did not change over time in either environment (Trial: 0.08 [-0.05, 0.21]; Environment x Trial interaction: 0.06 [-0.13, 0.23]). Similarly, there was no difference in the average time spent in the neutral zone between environments, across trials or their interaction (Environment: -6.67 [-38.43, 22.13]; Trial: -0.68 [-7.18, 5.44]; Environment x Trial: 2.67 [-6.45, 11.56]). However, there was a significant interaction between Environment and Trial for the number of food items consumed (Environment x Trial: -0.54 [-1.05, -0.005]). The number of food items consumed decreased over the course of the repeated trials in both environments (Trial: -0.78 [-1.14, -0.40]), however this happened much more precipitously in the Uncertain environment (Figure 4.1).

I predicted that consistent individual variation in behavior would be greater in the Uncertain environment. In support of this hypothesis, the repeatability of time in the neutral zone was higher in the Uncertain environment ($R=0.20$ [0.06,0.41], Table 4.1) than in the Certain

environment ($R=0$ [0,0], Table 4.1). This pattern was driven by both significantly greater among-individual variation and significantly lower within-individual (residual) variation in the Uncertain environment (Table 4.1). Contrary to my expectations, the repeatability of sampling was higher in the Certain environment ($R=0.59$, 95% CI: [0.37,0.78]; Table 4.1) compared to the Uncertain environment ($R=0.002$ [0,0.36], Table 4.1). This pattern appeared to be mainly driven by greater among-individual variation in the Certain environment (Table 1). The repeatability estimates for number of food items consumed were significantly different from zero in each environment, and not different from each other (Certain: $R=0.06$ [0.007, 0.22]; Uncertain: $R=0.03$ [0.006, 0.19]); however given their small values it is unclear whether these are biologically meaningful.

There was a range of intra-individual variability (IIV) scores, from highly consistent to very inconsistent (sampling IIV range: 0-3.4; time in neutral zone IIV range: 0-120). However, there was no evidence that IIV differed between the environments (effect of Environment on sampling IIV: 0.16 [-0.38, 0.64]; effect of Environment on time in neutral zone IIV: -5.96 [-18.91, 6.89]).

Therefore altogether, there was mixed evidence that environmental uncertainty can generate consistent individual differences in foraging behaviors while alone. While there was greater among-individual variation and repeatability in time spent in the neutral zone in the Uncertain environment, the repeatability of sampling behavior was higher in the Certain environment.

Sampling behavior positively influenced food consumption while alone

Sampling behavior influenced how many food items individuals consumed in both environments. In the Certain environment there was a significant positive among-individual correlation (0.77 [0.42, 0.93], Table 4.2) such that individuals that sampled more often on average across all five trials also ate more food on average across all five trials. There was no evidence for a significant within-individual correlation in this environment (0.14 [-0.15, 0.44], Table 4.2). Sampling behavior also influenced food intake in the Uncertain environment, but only at the within-individual level: when an individual sampled more frequently during a single trial, it also ate more food during that trial compared to the other trials (0.37 [0.07, 0.56], Table 4.2). There was no evidence for a among-individual correlation (0.35 [-0.34, 0.73], Table 4.2). Additionally, there was a significant effect of an individual's sampling IIV on their food consumption, but only in the Certain environment (Pearson=0.55, $p=0.005$, $N=24$, Table 4.2). Individuals that were more variable in their sampling behavior consumed more food items in this environment. There was no evidence for a similar effect in the Uncertain environment (Pearson=0.19, $p=0.38$, $N=24$, Table 4.2).

I found no evidence that time spent in the neutral zone influenced food intake in either environment when individuals were tested while alone (Table 4.2). Time in the neutral zone IIV also had no influence on food consumption in either environment (Table 4.2)

While in a group, environmental uncertainty does not generate consistent individual differences in foraging behaviors

On average, behavior did not differ between the Certain and Uncertain environments. Individuals in the Certain environment sampled the food patches on average 2.3 ± 0.20 times and

individuals in the Uncertain environment sampled 3.07 ± 0.27 times (effect of Environment: -0.03 $[-0.67, 0.63]$). There was no difference in the average time in the neutral zone between environments (Certain: 9.16 ± 0.67 seconds; Uncertain: 10.7 ± 0.74 seconds; effect of Environment: 8.84 $[-10.00, 29.97]$), but there was a significant effect of Trial (-6.54 $[-10.84, -1.95]$) and this effect did not differ between the environments (Environment x Trial interaction: -0.41 $[-6.05, 5.74]$). That is, individuals in both environments spent less time in the neutral zone with each successive trial (Figure 4.2). There was also no difference in the average number of food items consumed between the environments (Certain: 11.30 ± 0.50 ; Uncertain: 9.50 ± 0.34 , effect of Environment: -1.67 $[-4.23, 1.09]$; Environment x Trial interaction: -0.02 $[-0.65, 0.70]$). However, there was a marginal main effect of Trial on food items consumed; individuals in both treatments tended to eat more food items on average in both environments over time (Trial: 0.47 $[-0.02, 0.99]$, Figure 4.3).

While there were significant consistent individual differences in sampling in both environments, contrary to my prediction I did not find evidence for greater consistent individual variation in the Uncertain environment (Certain: $R=0.26$ $[0.01, 0.49]$; Uncertain: $R=0.33$ $[0.14, 0.59]$, Table 4.1). Although there were consistent individual differences in time spent in the neutral zone while alone, this consistent individual variation disappeared when individuals were tested in a group setting (Table 4.1). This lack of repeatability was mainly driven by zero among-individual variation in both environments; however the within-individual (residual) variance was significantly smaller in the Uncertain treatment (residual estimate: 1.03 $[0.77, 1.31]$, Table 4.1), compared to the Certain environment (residual: 50.25 $[37.89, 63.65]$).

The number of food items consumed was repeatable in both environments (Table 4.1), with a trend for greater consistent individual variation in the Certain environment ($R=0.37$ [0.19, 0.58]) than in the Uncertain environment ($R=0.15$ [0.03, 0.34]).

There was also a range of IIV scores in sampling and time in the neutral zone in both environments. Contrary to my predictions, average sampling IIV scores were higher in the Uncertain environment compared to the Certain environments (effect of Environment: 0.43 [0.01, 0.80]), demonstrating that individuals in the Uncertain environment were more variable in their sampling behavior. However, this difference was not apparent in the time in the neutral zone IIV scores: there was no evidence for average differences between the two environments (Environment: 2.28 [-5.43, 9.93]).

Taken together, these data does not support the hypothesis that environmental uncertainty generates consistent individual differences while in a group; in fact, there is some evidence that individuals are more variable in their behavior when in an Uncertain environment.

Time spent in the neutral zone negatively influenced food consumption while in a group

There was no evidence that sampling behavior influenced food consumption in a group in either environment (Table 4.2). In general, as time spent per trip in the neutral zone increased, food consumption decreased. This might be expected if time in the neutral zone takes away from time available to compete for food. For example, in the Certain treatment, individuals that on average spent more time in the neutral zone on each trip consumed fewer food items (among-individual: -0.53 [-0.82, -0.03]). In the Uncertain treatment, when an individual spent more time per trip to the neutral zone during a trial, it received fewer food items during that trial compared

to other trials (within-individual: -0.19 [-0.37, -0.007]). There was no evidence that IIV in either sampling or time in the neutral zone influenced food intake in either environment (Table 4.2).

Individual behavior while alone not predictive of behavior while in a group

I found no evidence that an individual's sampling behavior or time in the neutral zone while alone was related to the individual's behavior in a group in either environment (Table 4.3). However, individuals that consumed more food items while alone consumed more food items while in a group but only in the Certain environment (correlation coefficient=0.62 [0.07, 0.86]; Table 4.3), suggesting that competitive differences among individuals are more apparent when food availability is predictable in the food patches. There was also a significant positive correlation between time in the neutral IIV while alone and when in a group, again only in the Certain environment (Pearson=0.48, $p=0.02$, $N=24$, Table 4.3).

DISCUSSION

Uncertainty about environmental conditions is ubiquitous and can have negative consequences if individuals choose an inappropriate response. Therefore, selection should favor mechanisms that can either help reduce uncertainty, or limit its negative effects (Stephens 1987; Dall & Johnstone 2002; Mathot et al. 2012). Here, I tested the hypothesis that environmental uncertainty can generate (or reveal) consistent individual differences in behavior in a foraging context. I found support for this hypothesis when individuals were foraging alone. There was greater consistent individual variation in how individuals used the neutral zone when the environment was uncertain compared to when the environment was certain. However, when individuals were tested in a social group, there was no evidence that uncertainty increased

consistent individual differences in foraging behavior. Together, these two results suggest that competitive social interactions may mask the effects of environmental uncertainty. An individual's behavior influenced how many food items it consumed, though different behaviors (sampling or time in the neutral zone) were advantageous when alone and in a group. Finally, I found little evidence to suggest that behavior while alone was related to behavior in a group, again reinforcing the strong influence of the dynamic social environment on individual behavior.

When tested alone, individuals consistently differed in foraging behavior in both the certain and uncertain environments. In the Certain environment where patch profitability was reliable, individuals consistently differed in sampling behavior. It might be expected that sampling would decrease over time in this environment as individuals learned that both patches were equally profitable. However, sampling did not change over time in the Certain environment. In this environment, sampling behavior was positively correlated with food intake, suggesting that high sampling individuals were able to consume more food by utilizing both patches. Without the presence of other competitors, a high sampling individual did not have to be immediately present in the profitable patch as there were no other fish to eat the bloodworm. It is possible that sampling behavior is a measure of an individual's activity level, however, given that an individual needs to completely swim from one patch into the other patch suggests that individuals are purposefully sampling between the patches. It seems likely that rather than being a tactic for reducing uncertainty or mere activity, sampling in this experiment was a tactic to increase food consumption. This is likely a result of the low cost of sampling under these conditions. Other studies have found costs of sampling in a patchy environment in that sampling more frequently reduced food intake (e.g Morand-Ferron et al. 2011a; Laskowski & Bell 2013). These studies suggested travel time between patches might be an important cost; however they

were also all performed using foraging groups of individuals. My finding that individuals can increase their food consumption while alone by sampling suggests that it is the presence of competitors and not the patch distance that incurred a cost.

In contrast, in the Uncertain environment, individuals consistently differed in their use of the neutral zone: some individuals quickly passed through the neutral zone as they swam to the opposite patch, whereas others spent longer in the neutral zone, potentially using it as an “insurance” policy (Dall & Johnstone 2002). These individuals may have been waiting in this center neutral zone until it observed where the next available bloodworm was located, therefore keeping their patch use options open. Even though individuals consistently differed in this behavior, use of the neutral zone did not influence food consumption. Models predict that among-individual variation in uncertainty coping mechanisms, such as insurance, can be maintained because individuals are able to achieve similar fitness due to differential cost/benefit functions associated with each tactic (Dall & Johnstone 2002; McElreath & Strimling 2006).

When I measured the foraging behavior of sticklebacks in a social group, I found different patterns of consistent individual variation in behavior compared to when I measured them while alone. Specifically, the repeatability of sampling in both environments was significant and also the consistent individual variation in neutral zone use completely disappeared even in the Uncertain environment. Interestingly, while previous studies have found sampling behavior to be related to food consumption (e.g Milinski 1984; Morand-Ferron et al. 2011a), I did not find that connection in this study in the group setting. As sampling positively related to food consumption in the Certain environment while alone, it seems likely that the presence of other competitors removed the benefits of this tactic in the group setting. For example, while an individual was swimming to the opposite patch, a competitor who was already

present in that patch could quickly eat the bloodworm. However, an individual's neutral zone use influenced their food consumption in both environments, though at slightly different levels, a pattern that was not present in the alone trials. Individuals that spent more time in the neutral zone on average ate fewer food items on average (among-individual correlation) in the Certain environment. Whereas, in the Uncertain environment, the relationship between time in the neutral zone and food items was at the within-individual level, when individuals spent more time in the neutral zone during a single trial, they ate fewer food items during that trial. The reason for this negative relationship seems obvious: when in a competitive foraging group, any time spent outside the patches reduces the amount of time an individual has to compete for food.

There was very little evidence that individual behavior while alone correlated with their behavior while in a group in either environment. However, I did find that the number of food items consumed and individual variability (IIV) in neutral zone use were positively correlated across both social contexts, but only in the Certain environment. Given that time in the neutral zone was negatively related to food consumption in a group setting, it seems likely that this represents consistent individual differences in competitive ability, or potentially hunger levels (e.g. Milinski 1984; David & Giraldeau 2012). While I attempted to standardize individual body condition and competitive ability by using size-matched fish and starving fish for one day prior to testing, it is still possible that differences in body condition persist. Previous work has found mixed results about the influence of the social (or lack thereof) environment on individual behavior: under some conditions an individual signature is apparent across social contexts (e.g. Beauchamp 2000; Sih & Watters 2005; Magnhagen & Bunnefeld 2009), whereas under others it is not (e.g. David et al. 2011; Morand-Ferron et al. 2011a&b). Most models on the influence of environmental uncertainty on consistent individual differences in behavior consider animals in a

solitary situation (Dall & Johnstone 2002; Mathot et al. 2012). However, given the fact that I found different patterns of behavioral variation while in a group, compared to while alone, and little carryover in behavior from one social context to the next, demonstrates that the presence of social competitors presents a more complex problem to understanding how environmental uncertainty influences behavior. Understanding how the social environment and individual behavior interact is a question with considerable interest in the field right now (Bergmueller & Taborsky 2010; Webster & Ward 2011; Montiglio et al. 2013) demonstrating the need for increased theory about when we might expect individuals to retain their behavior across contexts, and when they should not.

I chose our environmental conditions to be as different as possible (completely certain and predictable food availability, to completely uncertain and random) in order to maximize the chances of finding an effect of environmental uncertainty, if there was one. However, in most natural settings, the environment is rarely completely unpredictable and perfectly random. Current information about changing conditions and an individual's own past experiences can help shape an individual's expectations about an environment (Schmidt et al. 2012). In the Uncertain environment, an individual could sample the patches to reduce uncertainty, but as the time interval between bloodworms switched every minute, this information would be quickly outdated. An exciting potential for future direction would be to study consistent individual variation in foraging behaviors over a range of environmental uncertainties.

In conclusion, I found mixed evidence to support the hypothesis that environmental uncertainty generates consistent individual differences in behavior. When individuals were measured while alone, individuals did differ in their use of a neutral zone which seems likely to be an insurance tactic, allowing the individual to not fully commit to a patch until they are sure

of its profitability. However, when tested in a social group setting, this insurance tactic was not beneficial; individuals would miss out on foraging opportunities if they were not present in a food patch. Social interactions can in themselves be very dynamic, potentially representing a different type of environmental uncertainty, and one that certainly warrants inclusion into the literature on the influence of environmental uncertainty on individual behavior.

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REFERENCES

- Beauchamp, G. 2000 Learning rules for social foragers: implications for the producer-scrounger game and ideal free distribution theory. *Journal of Theoretical Biology* **207**, 21-35.
- Bell, A. M. 2005 Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology* **18**, 464-473.
- Bell, A. M., Hankison, S. J. & Laskowski, K. L. 2009 The repeatability of behaviour: a meta-analysis. *Animal Behaviour* **77**, 771-783.
- Bergmueller, R. & Taborsky, M. 2010 Animal personality due to social niche specialisation. *Trends in Ecology & Evolution* **25**, 504-511.
- Dall, S. R. X. & Johnstone, R. A. 2002 Managing uncertainty: information and insurance under the risk of starvation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **357**, 1519-1526.
- David, M., Cezilly, F. & Giraldeau, L. A. 2011 Personality affects zebra finch feeding success in a producer-scrounger game. *Animal Behaviour* **82**, 61-67.
- David, M. & Giraldeau, L. A. 2012 Zebra finches in poor condition produce more and consume more food in a producer-scrounger game. *Behavioral Ecology* **23**, 174-180.
- Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R. & Dawnay, N. 2007 Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology* **76**, 1128-1138.
- Dingemanse, N. J. & Dochtermann, N. 2013 Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology* **82**, 39-54.
- Hadfield, J. D. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**, 1-22.

- Huntingford, F. A. 1976 The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour* **24**, 245-260.
- Krebs, J. R., Kacelnik, A. & Taylor, P. 1978 Test of optimal sampling by foraging great tits. *Nature* **275**, 27-31.
- Laskowski, K. L. & Bell, A. M. 2013 Competition avoidance drives individual differences in response to a changing food resource in sticklebacks. *Ecology Letters* **16**, 746-753.
- Lessells, C. & Boag, P. T. 1987 Unrepeatable repeatabilities: a common mistake. *The Auk*, 116-121.
- Magnhagen, C. & Bunnefeld, N. 2009 Express your personality or go along with the group: what determines the behaviour of shoaling perch? *Proceedings of the Royal Society B: Biological Sciences* **276**, 3369.
- Mathot, K. J., Wright, J., Kempenaers, B. & Dingemanse, N. 2012 Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos* **121**, 1009-1020.
- McElreath, R. & Strimling, P. 2006 How noisy information and individual asymmetries can make 'personality' an adaptation: a simple model. *Animal behaviour* **72**, 1135-1139.
- Milinski, M. 1984 Competitive resource sharing: an experimental test of a learning rule for ESSs. *Animal Behaviour* **32**, 233-242.
- Milinski, M. 1985 Fading short-term memory for patch quality in sticklebacks. *Animal Behaviour* **33**, 678-680.

- Montiglio, P.-O., Ferrari, C. & Reale, D. 2013 Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20120343.
- Morand-Ferron, J., Gi-Mike, W. & Giraldeau, L. A. 2011a. Persistent individual differences in tactic use in a producer-scrounger game are group dependent. *Animal Behaviour* **82**, 811-816.
- Morand-Ferron, J., Varennes, E. & Giraldeau, L. A. 2011b. Individual differences in plasticity and sampling when playing behavioural games. *Proceedings of the Royal Society B-Biological Sciences* **278**, 1223-1230.
- Nakagawa, S. & Schielzeth, H. 2010 Repeatability for Gaussian and non Gaussian data: a practical guide for biologists. *Biological Reviews* **85**, 935-956.
- Schmidt, K. A., Dall, S. R. X. & Van Gils, J. A. 2009 The ecology of information: an overview on the ecological significance of making informed decisions. *Oikos* **119**, 304-316.
- Sih, A. & Watters, J. V. 2005 The mix matters: behavioural types and group dynamics in water striders. *Behaviour*, **142** **9**, 1417-1431.
- Smith, B. R. & Blumstein, D. T. 2008 Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* **19**, 448-455.
- Stamps, J. A., Briffa, M. & Biro, P. A. 2012 Unpredictable animals: individual differences in intraindividual variability (IIV). *Animal Behaviour*.
- Stephens, D. W. 1981 The logic of risk-sensitive foraging preferences. *Animal Behaviour* **29**, 628-629.
- Stephens, D. 1987 On economically tracking a variable environment. *Theoretical Population Biology* **32**, 15-25.

- Svanback, R. & Bolnick, D. I. 2007 Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences* **274**, 839-844.
- Webster, M. M. & Laland, K. N. 2009 Evaluation of a non-invasive tagging system for laboratory studies using three-spined sticklebacks *Gasterosteus aculeatus*. *Journal of Fish Biology* **75**, 1868-1873.
- Webster, M. M. & Ward, A. J. 2011 Personality and social context. *Biological Reviews* **86**, 759-773.
- Wilson, D. S. 1998 Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **353**, 199-205.
- Wolf, M. & Weissing, F. J. 2010 An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B* **365**, 3959-3968.

TABLES

Social context	Estimate	Certain environment	Uncertain environment
Samples			
While alone	Individual	1.45 [0.42, 2.80]	0.22 [0, 0.53]
	Residual	0.38 [0.09, 0.73]	0.56 [0.20, 0.93]
	Repeatability	0.59 [0.37, 0.78]	0.002 [0, 0.36]
While in a group	Individual	0.27 [0, 0.59]	0.45 [0.10, 0.87]
	Residual	0.26 [0.04, 0.54]	0.37 [0.12, 0.63]
	Repeatability	0.26 [0, 0.49]	0.33 [0.14, 0.59]
Food items			
While alone	Individual	1.30 [0.11, 3.06]	1.16 [0.11, 2.99]
	Residual	9.13 [6.58, 11.64]	13.32 [9.63, 16.99]
	Repeatability	0.06 [0.007, 0.22]	0.03 [0.006, 0.19]
While in a group	Individual	11.84 [3.77, 22.0]	2.54 [0.34, 5.29]
	Residual	17.86 [12.85, 23.33]	11.50 [8.38, 14.86]
	Repeatability	0.37 [0.19, 0.58]	0.15 [0.03, 0.34]
Time in neutral zone			
While alone	Individual	$6.8e^{-5}$ [$5.0e^{-11}$, $1.8e^{-7}$]	0.53 [0.11, 1.07]
	Residual	149.8 [114.9, 191.0]	1.69 [1.21, 2.20]
	Repeatability	0 [0, 0]	0.20 [0.06, 0.41]
While in a group	Individual	$5.8e^{-6}$ [$5.8e^{-10}$, $2.6e^{-6}$]	$2.5e^{-5}$ [$2.4e^{-10}$, $3.4e^{-4}$]
	Residual	50.25 [37.89, 63.65]	1.03 [0.77, 1.31]
	Repeatability	0 [0,0]	0 [0,0]

Table 4.1. Summary of the variance component and repeatability estimates for each behavior in each environment. Repeatability estimates that are significantly different from zero are bolded.

Behavior	Type of correlation	Certain environment	Uncertain environment
While alone			
Sampling	Among-individual	0.77 [0.42, 0.93]	0.35 [-0.34, 0.733]
	Within-individual	0.14 [-0.15, 0.44]	0.37 [0.07, 0.56]
IIV Sampling	Among-individual	0.55 (p=0.005)	0.19 (p=0.38)
Time in neutral zone	Among-individual	-0.05 [-0.77, 0.80]	-0.04 [-0.43, 0.35]
	Within-individual	-0.004 [-0.20, 0.15]	-0.02 [-0.20, 0.18]
IIV Time in neutral zone	Among-individual	-0.34 (p=0.11)	-0.30 (p=0.15)
While in a group			
Sampling	Among-individual	-0.35 [-0.67, 0.28]	0.25 [-0.37, 0.70]
	Within-individual	-0.03 [-0.34, 0.30]	0.25 [-0.04, 0.52]
IIV Sampling	Among-individual	0.18 (p=0.40)	-0.05 (p=0.80)
Time in neutral zone	Among-individual	-0.53 [-0.82, -0.03]	0.14 [-0.55, 0.55]
	Within-individual	-0.04 [-0.25, 0.14]	-0.19 [-0.37, -0.07]
IIV Time in neutral zone	Among-individual	0.06 (p=0.78)	-0.03 (p=0.91)

Table 4.2. Correlations between food intake and foraging behaviors in each environment in each social context. All correlations were estimated using a mixed model with MCMC estimation (see methods) to partition the variance into its among- and within-individual components, except for the correlations between food intake and IIV scores; these were estimated using a Pearson correlation as there is only one IIV score per individual, preventing the estimation of a within-individual correlation. Coefficients that are significantly different from zero are bolded.

Behaviors	Certain environment	Uncertain environment
Samples	0.28 [-0.11, 0.72]	0.06 [-0.32, 0.58]
Food items	0.62 [0.07, 0.86]	0.48 [-0.32, 0.86]
Time in neutral zone	-0.11 [-0.85, 0.84]	0.34 [-0.81, 0.79]
IIV samples	-0.08 (p=0.72)	0.29 (p=0.18)
IIV time in neutral zone	0.48 (p=0.02)	-0.12 (p=0.58)

Table 4.3. Summary of the correlation coefficients of each behavior ([95% CI] or p-value) across the two social contexts in each environment. Coefficients that are significantly different from zero are bolded.

FIGURES

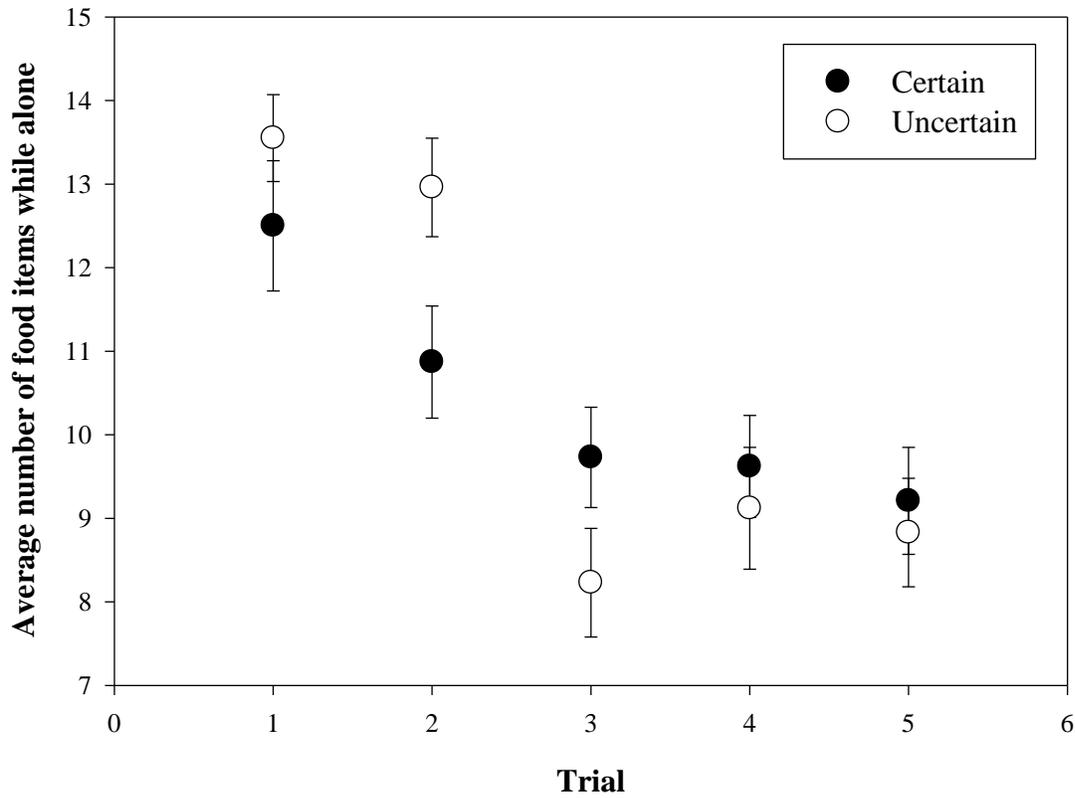


Figure 4.1. While alone, fish in both environments ate fewer food items over the five trials of the experiment, however this effect was significantly more pronounced in the Uncertain environment (Environment x Trial interaction: -0.54 [$-1.05, -0.005$]).

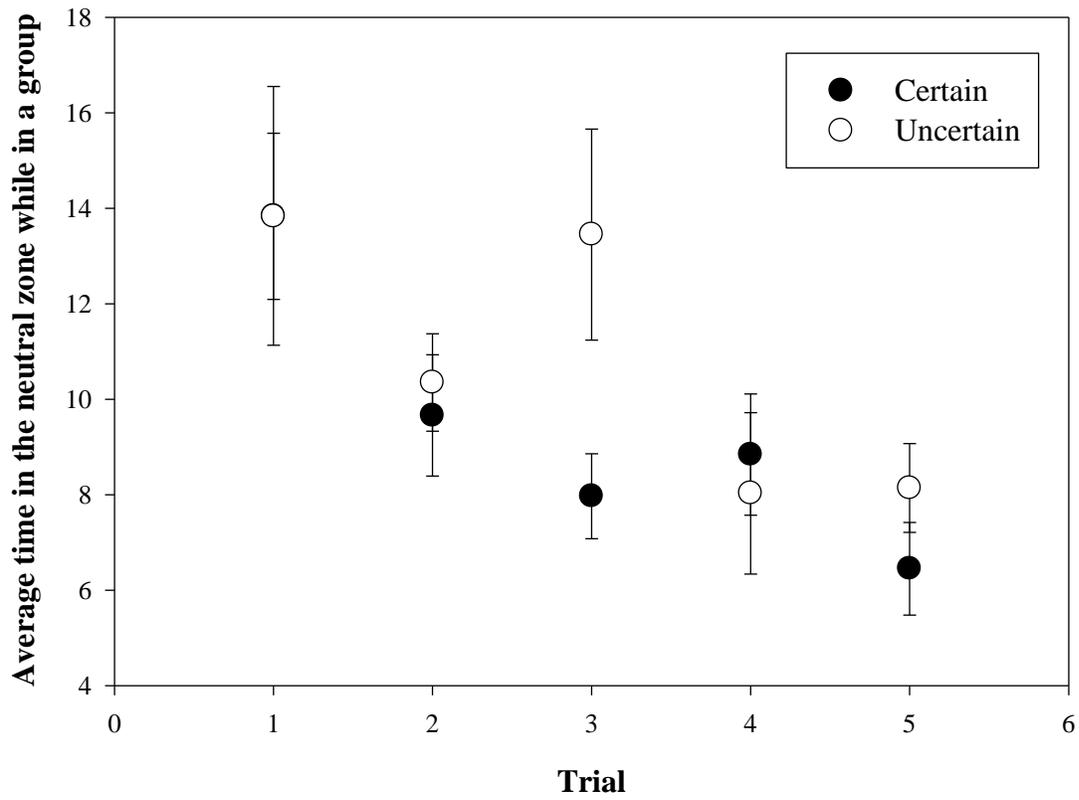


Figure 4.2. While in a group, fish in both environments spent less time in the neutral zone (effect of Trial: -6.54 [-10.01, -1.95]).

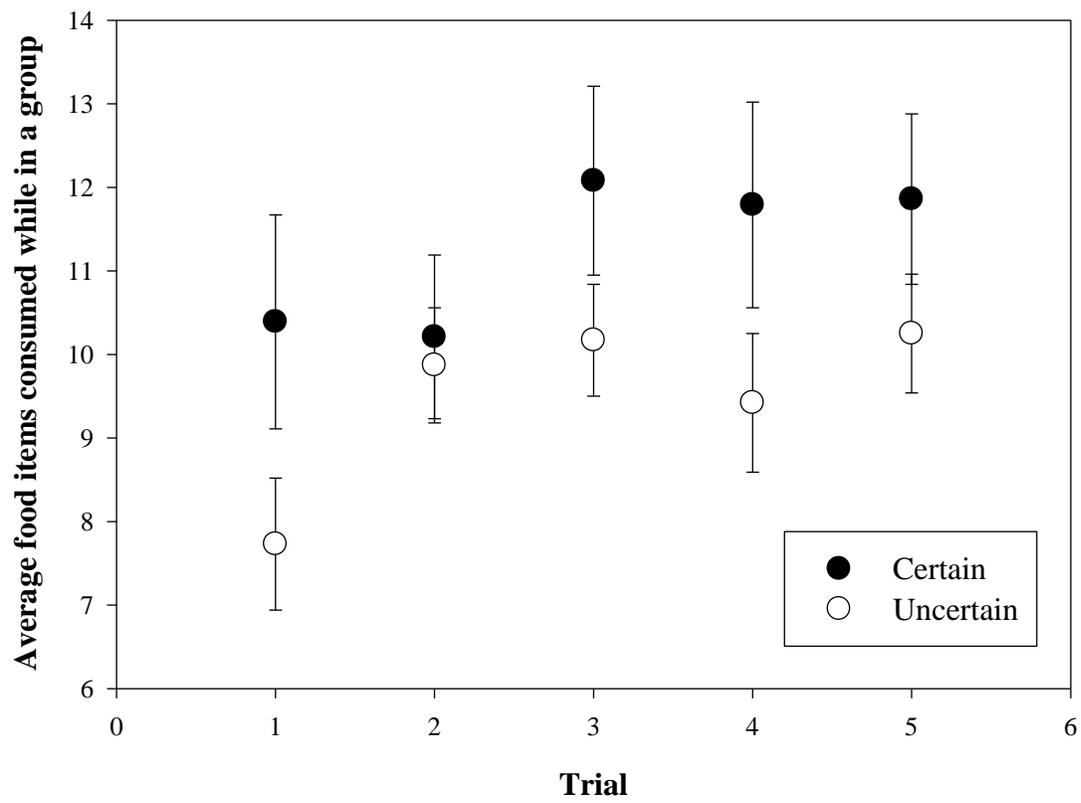


Figure 4.3. While in a group, fish in both environments tended to eat more food items with repeated trials (effect of Trial: 0.47 [-0.02, 0.99]).