

Laboratory measures of boldness correlate to ecological niche in threespine stickleback

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February 4, 2022

Abstract

Research on among individual variation in behavior has increased rapidly in recent years. It is intuitively appealing that among individual variation in behavior has ecological consequences and among the most likely to be affected is trophic niche. Bold individuals, with the tendency to be explorative and risk tolerant, can be less likely to alter their foraging behavior across contexts and therefore forage more consistently. Stable isotopes are a useful tool to retrospectively estimate ecological niche and have been found to correlate to foraging behavior in the wild. It is now pressing to extent studies to further examine the ecological or evolutionary relevance of personality. We examined if common behavioral traits were correlated to ecological niche in the wild using a rapid behavioral assay and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes from fin and muscle reflecting ecological niche for the previous weeks and months. We found that latency to explore, as a proxy for boldness, correlated to values of $\delta^{13}\text{C}$ with bolder fish having lower $\delta^{13}\text{C}$ values. Moreover, latency to explore also explained variation in the change in individual stable isotope niche over time. These results highlight the long-term ecological importance of among individual variation in behavior and are among the first to support a correlation of laboratory measures of behavior and ecological niche in the wild.

Introduction

Research on among individual variation in behavior has increased rapidly in recent years, offering a more nuanced perspective on how populations are composed and may respond to the environment. Animal personality, when individuals consistently differ from each other in the expression of behavioral traits across time or contexts, has been frequently observed across taxa (Dingemanse et al., 2003; Sih, Bell and Johnson, 2004; Réale et al., 2007; Bell, Hankison and Laskowski, 2009). However, the average expression of any behavioral trait only partially reflects the personality of the individual and it is also important to consider how variable behavioral expression is within the individual (Nussey, Wilson and Brommer, 2007; Dingemanse et al., 2010; Mathot et al., 2012). Within individual variability in behavior can be directional, for example, habituation to a novel environment (Brown, 2001; Allan, Bailey and Hill, 2020), change in behavior appropriate to context, such as the level of risk (Steinhoff et al., 2020), but also random or unpredictable (Stamps, Briffa and Biro, 2012; O’Dea, Noble and Nakagawa, 2020). Furthermore, recent research has shown that even the expression of similar traits can have different underlying mechanism depending on the context (Mouchet & Dingemanse, 2021).

Nevertheless, it is expected that among individual variation in behavior has ecological consequences (Bolnick et al., 2003; Bolnick et al., 2011). Individual trophic specialization and its connection to foraging behavior is well known (Araújo, Bolnick and Layman, 2011; Bolnick et al., 2003), but has been researched mostly independently from animal personality. It is intuitively appealing that animal personality could result in both consistent differences in diet and trophic niche breadth. For example, bold stickleback have been found to be less likely to alter their foraging behavior across contexts (Ólafsdóttir & Magellan, 2016). Boldness was found to affect multiple foraging decisions in deer mice, but the effect of personality traits was also context

dependent (Boone, Brehm and Mortelliti, 2021). Correlations between animal personality and trophic niche could have significant implications for ecosystems as many current environmental impacts or stressor are expected to favor specific behavioral types, for example, bolder fish are more likely to disperse and form invasive populations (Cote et al., 2010; Myles-Gonzalez et al., 2015), fishing may be more likely to remove bolder (Biro & Post, 2008) and more sociable (Crespel et al., 2021) fish. Boldness has been shown to correlate positively with juvenile survival in damselfish (McCormick, Fakan and Allan, 2018).

Stable isotopes are a useful tool to retrospectively estimate ecological niche as they reflect the diet and environment of the individual over the past days to months and, by combining tissue types, can reflect within individual variation in resource use (MacNeil, Skomal and Fisk, 2005, Gratton & Forbes, 2006). Measures of both behavior and stable isotope values could therefore offer an important on the ecological consequences of animal personality. The stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are commonly used in conjunction to examine trophic niche variation within and between groups (Post, 2002). $\delta^{13}\text{C}$ reflects local primary production and commonly differs along the axis of benthic – pelagic production and $\delta^{15}\text{N}$ is consistently enriched as it passes through the food web allowing its use as a metric of trophic level (Post, 2002; Chérel & Hobson, 2007). Studies combining laboratory measures of personality and stable isotope estimates of trophic niche are not common. Dhellemmes et al., (2021) found that exploratory behavior in juvenile lemon sharks (measured in a controlled test) correlates to $\delta^{13}\text{C}$ values representing sheltered or unsheltered foraging habitats but only when predators were abundant. A recent study on red knots found that observations of foraging behavior correlated to personality (exploratory behavior) but this was supported by stable isotope values suggesting a long-term effect of personality (Ersoy et al., 2021). Conversely, no effect was observed between dominance and stable isotope values of crayfish across different contexts (Glon, Larson and Pangle, 2016; Adey & Larson, 2020).

Much of animal personality research has been laboratory based and it is now pressing to further examine the ecological or evolutionary relevance of personality. However, laboratory measures of behavior are easily applied and controlled, for example, allowing measures of plasticity across controlled contexts and measures of subjects of known origin, such as, individuals of known relatedness. Because of the convenience and flexibility of laboratory measures it is valuable to understand how, or if, they have relevance for ecological traits in the wild. For this purpose, stable isotopes can be a useful as they retrospectively represent trophic niche in the wild over timeframes that are often unfeasible for direct observation in nature and can be as easily applied to aquatic species when field observations are difficult.

My objective was to examine if behavioral traits measured in the laboratory correlated to ecological niche in the wild, supporting that behavioral variation among individuals could have ecological or ecosystem consequences. For this aim we used a rapid behavioral assay to assess latency to explore and activity of individually identifiable threespine stickleback (*Gasterosteus aculeatus*). We then assessed if either individual intercept or slope for these traits, estimated across three trials, correlated to ecological niche or temporal change in ecological niche (as estimated by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes). We hypothesized that bolder and more active individuals may have higher $\delta^{15}\text{N}$ values, reflecting higher trophic levels, and lower $\delta^{13}\text{C}$ values reflecting less benthic foraging. Moreover, we expected bolder individuals to have less change in stable isotope niche over time, indicative of more consistent and generalist foraging. Finally, we expected that behavior would have only moderate effects on stable isotope values.

Materials & Methods

Study subjects and housing

We used a wild population of threespine stickleback, *Gasterosteus aculeatus*, caught with unbaited minnow traps from a vegetated freshwater lake in April 2021 (Syridalsvatn, 66° 7' N, 23° 14' W). Thirty-three fish of the size 4.0-4.1cm were transported the short distance to the laboratory (<15min). This size of fish most likely represents individuals that hatched in spring/summer 2019. All fish were placed in individual holding tanks of 9.5l (Aquaneering.com). Each tank was equipped with a single 12cm knee-shaped PVC pipe for cover. Temperature was kept at 12.0°C, with an 8:16 h light/dark cycle regime. The tanks were continuous

flow through, fitted with a biological filter, UV sterilization and aerated. After a single day of acclimating to the laboratory we began observations. Fish were fed defrosted frozen bloodworms (*Chironomus spp.*) on the day of capture and then to satiation daily after the experiment. Behavioral experiment without invasive or stressful procedures, such as the current experiment, do not require licensing by Icelandic law.

Experimental protocol

The experiment started on the day following capture and was repeated on three consecutive days for all fish (trial 1-3). Each fish was removed from its home tank using a small hand-net and transferred the short distance (~1.5m) to the experimental tank where it was placed in a release compartment at one end of the tank. The release compartment was 30x40cm and darkened using black plastic on all sides and top covering. As soon as the fish was in the release compartment an opaque plexiglass divider was lifted by 5cm allowing the fish access to the main arena. The main arena was 60x40cm with all sides covered with blue and green aquarium background (plant patterned) preventing the experimental fish from seeing outside the tank. The main arena was visually divided in three equal areas by black lines on the bottom of the tank. Four food patches were placed within the arena each with two bloodworms taped to a small glass petri dish. Two of the patches were sheltered by a round of four small stones and two were unsheltered. The food patches were in areas two and three while the first area, closest to the release compartment, was empty (Fig. 1). The water level in the experimental tank was 10cm with continuous flow of aerated and chilled (12.0°C) water. The behavior of fish in the experimental tank was videoed from above for 10-min. From the 10-min videos recorded we extracted (1) latency to explore, i.e. the fish fully moved out of the release tank; (2) latency to forage, the time to locate and attempt to feed at any of the food patches and (3) activity, the number of times a fish fully crossed between the three areas in the tank. It was also noted if feeding took place at an open or sheltered food patch.

Stable isotope analysis

Immediately following the behavioral experiment all fish were euthanized with an overdose of phenoxyethanol. Fin and muscle samples were rinsed with deionized water and cleaned by carefully removing any skin or bone from the muscle samples. Samples were then dried at 55°C until fully dry. Elemental analysis-isotope ratio mass spectrometry was used for the carbon and nitrogen isotope analysis by the company Iso-Analytical (<https://www.iso-analytical.co.uk/>) using their standard quality control methods. The reference material used for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was soy protein (IA-R068). The analysis was completed in batches, with the reference sample tested between each batch. Stable isotope analysis was repeated for every sixth sample. Repeat values all fell within a 0.20 of repeated analyses of the reference materials was less than 0.10 values were within 0.10 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicating both good precision and accuracy. The quality control samples used were soy (IA-R068), L-alanine (IA-R038) and tuna protein (IA-R046). All control samples were calibrated against international comparison standards distributed by the International Atomic Energy Agency.

Statistical analysis

Thirty-three stickleback (size range 4.0-4.1) were used for this analysis. Data from day three of the experiment was missing for four fish resulting in a total number of observations, $n = 95$. We used the software R v. 3.1.3 (<http://www.r-project.org>) (R Core Team 2012) for all statistical analysis and visualization. Preliminary data exploration showed that latency to explore and latency to forage were highly correlated and that foraging at a sheltered or open food patch did not appear to differ between individuals or day or trial. Therefore, statistical analysis was focused on latency to explore and activity. The statistical analysis and data visualization were done in R 4.0.3 (R Core Team 2021), tidyverse 1.3.0. (Wickham, 2019) and the packages cited below. All gathered data is presented in Supplementary Table 1.

First, we used lme4 1.1-27.1. (Bates et al., 2015) to fit a generalized linear mixed model using a Poisson distribution to examine change in latency to explore and activity across the three daily behavioral trials and to get estimates of intercepts and slopes for each fish for both behaviors. This allowed us to reduce the measurements of the three trials to two values. The intercept represents the rank level of that individual and in the current context highly reflects the initial response of the fish to the trial, for example, if they

started exploring/foraging early in the first trial. The slope represents the plasticity of the individual across trials and in the current context is likely to reflect habituation to the trial, for example, a high negative slope for latency to explore will show a fish that was initially hesitant (first trial) but subsequently bolder. Note that fish that were either bold or shy for all trials would both have estimated slopes close to zero.

Second, we examined the correlation of individual behavior and stable isotope niche. As estimates of the individual personality we used intercept and slope for both latency to explore and activity. Slope was included to also capture plasticity in behavior across trials. We used two approaches to do this. First, we used a generalized linear model to estimate the significance of the correlation of stable isotope values (both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to either intercept or slope of the behavioral traits. A Poisson distribution was used in these models. Second, we wanted to see if behavior correlated to within individual variation in stable isotope niche. For that purpose, we calculated the Euclidian distance from individual stable isotope values of muscle samples and fin samples (reflecting different turnover times). We then used that distance as the response variable in two linear model with the intercept and slope of each of activity and latency to explore as factors with an interaction effect. A Gaussian distribution was used in this model. The residual distributions of all models were examined using the R package DHARMA 0.4.4. (Hartig 2021).

Results

The $\delta^{13}\text{C}$ values ranged from -17.58 to -11.46 $\delta^{15}\text{N}$ values ranged from 6.92 to 8.66 (Supplementary Table 2 for full dataset).

The experimental fish left the release compartment within 10-min in most trials. The results of the GLMM showed that as a group the experimental fish left the compartment quicker with subsequent trials, but activity did not differ across days of the experiment (Table 1). Similarly, there was little variation among individuals in activity but high in latency to explore (Table 1).

The results from the generalized linear model of the estimated intercepts and slopes of behavioral traits (latency to explore and activity) and stable isotope values showed that the intercept of latency to explore was correlated to $\delta^{13}\text{C}$ values of both fin and muscle. The effect was not large, R^2 for both tissue types was 0.16, $p = 0.02$ (see also Fig. 3). Other correlations were not significant.

The calculated Euclidean distance between fin and muscle stable isotope values varied between fish with a mean value of 0.74 and $SD = 0.39$. The slope of latency to explore, as well as the interaction between slope and intercept, explained variation in the distance (Table 2, Fig. 4). The model R^2 was 0.23 suggesting that the model moderately reflected variation in the stable isotope distance. No significant result was observed for activity.

Discussion The current result show that latency to explore, a common proxy for boldness, assessed in a rapid laboratory array, correlated to retrospective measures of threespine stickleback trophic niche. Specifically, bolder fish had lower $\delta^{13}\text{C}$ values (Fig. 3) and their stable isotope niche changed more over time (Table 2). These results are among the first to support such a relationship.

The $\delta^{13}\text{C}$ values of bolder stickleback were consistently lower in both muscle and fins (Fig. 2). Comparing isotopic values of multiple tissues allows estimation of the relative temporal stability of the individual niche (Phillips & Eldridge, 2006; Maruyama et al., 2017). It is currently uncertain how much threespine stickleback fin and muscle differ in turnover rates but estimates for bony fish commonly vary on the scale of a few weeks to months (Willis et al 2013; Busst & Britton 2018; Barton et al., 2019; Winter et al., 2019). The stickleback fin and muscle stable isotope values were highly correlated (Fig. 3). The current study did not include $\delta^{13}\text{C}$ values of potential prey items within the lake, making inferences on how these patterns relate to the diet of the fish difficult. However, based on previous studies of stable isotope ecology in northern freshwater lakes the lower $\delta^{13}\text{C}$ values are expected to indicate more pelagic foraging or foraging on invertebrates that rely on pelagic production (France, 1995). Lower $\delta^{13}\text{C}$ values of bolder individuals could therefore be consistent with a “landscape of fear” (Gaynor et al., 2019), that shyer individuals keep to the more sheltered benthic habitat. It should be noted that in the current experimental setting the intercept will

highly reflect initial boldness (latency to explore during the first trial). Both in the current experiment and previous studies stickleback from this population have been found to adjust or habituate to the experiment as many individuals would initially be slow to explore but become quicker in subsequent trials (Ólafsdóttir & Magellan, 2016; Ólafsdóttir et al., 2014). Therefore, the current results should be taken to indicate that initial shyness/boldness is correlated to $\delta^{13}\text{C}$ values, whether those individuals were consistently shy/bold or adjusted their exploratory speed to context.

Boldness was also linked to change in stable isotope niche over time, that is, to the difference between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in fin and muscle. Both the estimated slope of latency to explore and the interaction of intercept and slope had significant effect on the change in individual stable isotope niche (Table 2). High positive slope (individuals that were initially shy but progressively bold) was correlated to less change in stable isotope niche (Table 2). This is also reflected by the significant interaction effect and is, at least in part, explained by that initially shy individuals will most often have (steep) negative slopes and vice versa. Visualization of these effects can be seen in Fig. 4 and may indicate that the pattern is largely driven by a few individuals. These results highlight that the correlation of trophic niche and behavior can be nuanced but also the need to consider not only the average behavior but also plasticity when relating animal personality to foraging (Coomes et al., 2021).

Based on the current data it is not possible to fully distinguish between three underlying scenarios. First, innate boldness, as a general trait expressed consistently in the laboratory and in the field, results in different foraging patterns and those foraging patterns are reflected in stable isotope values. Second, previous diet was unrelated to innate behavior but induced the observed differences in behavior in the laboratory, for example, through nutrient state or condition. The experimental fish were deliberately chosen to be of approximately the same size and weight, but more detailed variation of condition, fatty deposits, lipid content etc., was not considered. Should previous diet affect behavior the timing of behavioral test could highly determine the results, for example, in the current study behavioral test were conducted with only a single day for fish to adjusting to laboratory conditions. This was necessary to limit the effect of the identical laboratory diet on stable isotope values but could have augmented variation on the boldness-shyness axis, as acclimatization has been found to affect measures of behavioral traits (Biro, 2012; O'Neill et al., 2018) but also resulted in increased variation in nutrient state. Third, both growth rates and standard metabolic rate have been linked to stable isotope turnover rate and are therefore reflected in stable isotope values (Gorokhova, 2018; Scharnweber et al., 2021), although these factors may explain less of the values than diet (Johnston et al., 2021). Varying growth rates of the stickleback in the wild prior to capture could have relevance for the current results, both in that fast-growing individuals would be both bolder and with lower $\delta^{13}\text{C}$ values, without any causal link, but boldness and growth could also have been correlated in the wild. It has been previously supported that boldness, metabolic rate and growth could be connected in a “pace of life” syndrome (Réale, 2010). Finally, it should be noted that overall the relationship of behavior and stable isotope niche in the current study was small and that no significant correlations were found for activity or $\delta^{15}\text{N}$.

Conclusions

We expected that if a trait such as boldness resulted in difference in diet it would be that bolder, more active individuals had higher $\delta^{15}\text{N}$ values (reflecting higher trophic levels), lower $\delta^{13}\text{C}$ values (reflecting more foraging in open waters) and that their niche would change less over time. Previous research showed mixed support of a relationship of laboratory measures of behavior and stable isotope values. Therefore, we did not expect a strong effect. Conversely, the current results showed a clear link between a single behavioral trait, latency to explore, and long-term ecological niche although it was not possible to determine if the relationship is because of innate differences in behavior resulting in different resource use, by ecological niche affecting condition that in turn caused differences in behavior or by interaction of behavior, growth rate and stable isotope values. We suggest that further studies could be designed to determine if there is a causal link between behavior and ecological niche but also highlight the need to consider that the relationships of behavior and stable isotope niche is likely to be very context and trait dependent.

Acknowledgements

We would like to thank Kolbeinn Sæmundur Hrólfsson for helping prepared the stable isotope samples and Ragnar Edvardsson for producing the drawing of the experimental set-up presented in Fig. 1.

Data accessibility

All data used in this paper has been made available in the supplementary tables.

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	Latency to explore	Latency to explore	Latency to explore	Latency to explore	Activity	Activity
Random effects	Variance	SD			Variance	SD
ID intercept	3.359	1.833	-	-	0.506	0.711
Slope	0.803	0.896	-	-	0.165	0.406
Fixed effects	Estimate	SE	z-value	t-value		
Intercept	4.918	0.321	15.308	<0.001	2.716	0.149
Trial #	-0.309	0.157	-1.968	0.049	-0.015	0.083

Table 1. Results from the GLMM from which the individual intercepts and slopes were estimated.

	Estimate	SE	t-value	p-value
Model intercept	1.395	0.379	3.671	0.001
LE intercept	-0.117	0.079	-1.479	0.149
LE slope	-0.704	0.263	-2.674	0.012
LE intercept:slope	0.119	0.053	2.241	0.032

Table 2 . Results from the GLM examining the effect of behavior, latency to explore intercept and slope, on the change in stable isotope values. Significant effects are boldfaced.



