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## Can personality predict individual differences in brook trout spatial learning ability?

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### ABSTRACT

While differences in individual personality are common in animal populations, understanding the ecological significance of variation has not yet been resolved. Evidence suggests that personality may influence learning and memory; a finding that could improve our understanding of the evolutionary processes that produce and maintain intraspecific behavioural heterogeneity. Here, we tested whether boldness, the most studied personality trait in fish, could predict learning ability in brook trout. After quantifying boldness, fish were trained to find a hidden food patch in a maze environment. Stable landmark cues were provided to indicate the location of food and, at the conclusion of training, cues were rearranged to test for learning. There was a negative relationship between boldness and learning as shy fish were increasingly more successful at navigating the maze and locating food during training trials compared to bold fish. In the altered testing environment, only shy fish continued using cues to search for food. Overall, the learning rate of bold fish was found to be lower than that of shy fish for several metrics suggesting that personality could have widespread effects on behaviour. Because learning can increase plasticity to environmental change, these results have significant implications for fish conservation.

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**1. Introduction**

Fish populations are comprised of individuals with substantial differences in behaviour and personality (Bell and Aubin-Horth 2010; Conrad et al., 2011; Thomson et al., 2011). Once thought to be a source of undesired and unexplained variation (Carere and Locurto, 2011; Cleasby et al., 2015), it is now recognized that explicitly measuring individual personality can improve population-level inferences on fish movement (Chapman et al., 2011; Fraser et al., 2011), growth (Adriaenssens and Johnsson, 2011a), metabolism (Sih, 2011), and even parasitic infection rate (Brick and Jakobsson, 2002). However, although work has recently begun to address the evolutionary significance and fitness consequences of individuals with different personalities (Smith and Blumstein, 2008; Conrad et al., 2011), how personality affects cognitive ability and decision making has not yet been resolved.

The bold-shy axis is the most studied personality trait in fish (Conrad et al., 2011; Carter et al., 2013). Of particular interest is how boldness covaries with other behaviours through space and time. The literature is rich with studies suggesting that boldness is characteristic of a proactive behavioural type that exhibits higher levels of aggression, risk taking, exploration, and growth (Rehage and Sih, 2004; Chapman et al., 2011; Sih and Del Giudice, 2012; Garamszegi et al., 2013). Taken together, correlations of these traits correspond to a behavioural syndrome that is hypothesized to be relatively inflexible; excelling more at repetitive tasks and in familiar environments (Thomson et al., 2011; Sih and Del Giudice, 2012; Beri et al., 2014; Millot et al., 2014). It has therefore been suggested that personality may influence an individual's ability to solve problems and adapt to novel environments (Adriaenssens and Johnsson, 2011a, b; Thomson et al., 2012; Frost et al., 2013).

To date, the ecological significance of individual personality, particularly as it relates to cognitive ability, remains poorly understood (Dugatkin and Alfieri, 2003; Conrad et al., 2011; Mittelbach et al., 2014). Few studies have attempted to correlate boldness to cognition, and those that have were unable to separate the effects of personality from motivation and habituation (Griffin et al., 2015). This could, in part, explain the equivocacy of previous results. For example, some suggest that bold individuals are better able to use cues to find a novel food patch. However, these studies are confounded by unaccounted for covarying behaviours: bold individuals generally explore more and may find a food patch by chance (Adriaenssens and Johnsson, 2011b; Sih and Del Giudice, 2012; DePasquale et al., 2014), are less fearful (Dugatkin and Alfieri, 2003), and may have a higher metabolism and be more motivated to find food (Hoogenboom et al., 2012). Alternatively, cognitive ability has been shown to decrease with increasing (albeit indirect) measures of boldness (Brown and Braithwaite, 2005), perhaps because shy individuals take longer to incorporate stimuli and assimilate information making them more adept at solving novel problems (Carere and Locurto, 2011; Sih and Del Giudice, 2012).

Stream salmonids are ideal study taxa for testing the influence of personality on spatial learning ability. Previous research has documented high inter-individual variation in personality within populations, including variation along the bold-shy axis of behaviour (Thomson et al., 2011). The habitat stability and complexity of high-elevation headwaters occupied by many stream salmonids produces a context under which visual cues could

provide reliable information that aids in navigation of the environment. While previous research has documented the ability of salmonids to use spatial cues (Braithwaite et al., 1996), studies have yet to correlate boldness to learning ability.

We tested whether boldness could predict the ability of brook trout (*Salvelinus fontinalis*) to use visual landmarks to solve a four-armed maze. After assessing boldness, fish were trained to find a hidden food patch in a maze staged with visual cues indicating the location of food. Following training, cues were relocated to test whether fish had learned to associate cues with food. Expanding on previous findings that bold individuals are less successful at adapting to novel situations (Brown and Braithwaite, 2005; Adriaenssens and Johnsson, 2011a; Sih and Del Giudice, 2012) and less flexible in their learning strategies (Coppens et al., 2010), the prediction was that boldness would be negatively correlated to learning rate and, consequently, bold fish would spend less time feeding and more time randomly searching the maze during training and testing.

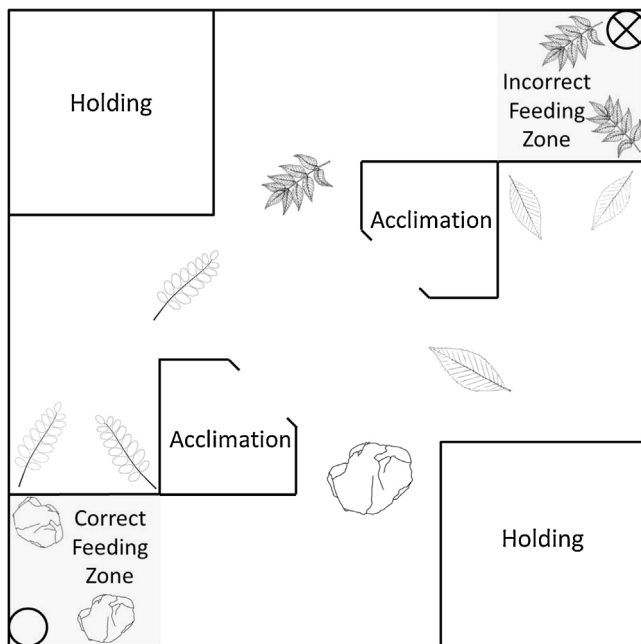
**2. Methods**

Fish used in this study were two-year-old brook trout obtained from a Virginia Department of Game and Inland Fisheries hatchery in January 2013. Prior to data collection in January 2015, approximately 20 fish were housed in each of three 90-L aquaria maintained at 18 °C. While in housing fish were fed bloodworms once daily. We used a random selection of 14 fish in this study ranging in size from 102 to 136 mm total length. Unique identifying marks were unnecessary as subjects were housed individually during training and testing.

*2.1. Boldness assay*

We screened for boldness using an open field test, an assay that is widely regarded as the most reliable assessment of boldness in fish (Burns, 2008; Conrad et al., 2011; Toms et al., 2010). A subject was placed in the center of a 0.69 m long × 0.55 m wide × 0.8 m deep rectangular enclosure and given 15 min to acclimate before initiating a 10-min trial. The duration of time that a subject spent in the center of the enclosure during the trial was quantified using EthoVision XT9 software (Noldus Information Technology), with more time spent in the center indicating bolder individuals. The center was defined by a 0.48 m long × 0.39 m wide area using EthoVision, and was thus invisible to the subject during testing. This arena design, specifically the increased depth compared to open field trials conducted in other fish families, was necessary to minimize stress and make the task ecologically appropriate for brook trout, a species that occupies deep pools and drift feeds in the middle of the water column.

All subjects were fed the evening before the open field trial. All open field trials were completed between 0600 and 1000 h, after which an automatic feeder was installed in the enclosure. The feeder dispensed bloodworms every five minutes and operated for at least five hours. Though fish were accustomed to being fed bloodworms, this acclimation period allowed fish to be trained to the sound of the feeder and to accept worms from a novel delivery mechanism before being placed in the maze. For all subjects, the open field test and feeder training were completed in the morning and afternoon, respectively, of the same day. Before com-



**Fig. 1.** Four-armed maze used for training and testing. All walls were constructed from opaque plastic and dividers at the end of each arm could be removed such that any arm could grant access to feeding zones. The rock cue always signified the location of the functional feeder (open circle in the correct feeding zone). The other three arms had a plant cue, including the arm that contained a sham feeder (circled-X in the incorrect feeder zone).

pleting feeder training, subjects were observed for at least 20 mins to ensure that they had fixated on the feeder and were consuming worms every time the feeder turned on.

## 2.2. Maze design

Learning was assessed by documenting a subject's ability to use visual cues to locate a hidden food patch in a four-armed maze constructed from opaque plastic (Fig. 1). The perimeter of the maze was 1.5 m × 1.5 m and was placed inside a circular tank 1.6 m in diameter and 0.8 m deep. The tank was draped in black plastic to minimize disturbance. In two corners of the maze there were opaque holding areas where fish were individually housed between training trials. At the start of each trial, subjects were placed in one of two opaque acclimation areas. One side of the acclimation area had an opening in the middle of the water column which, once located, subjects could freely exit from to enter the center of the maze.

Three of the maze arms were unrewarded including two dead end arms and one arm that contained a sham feeder. The sham feeder operated every 30 s but provided only visual and olfactory cues via small holes that bloodworms could not escape from. Each of the unrewarded arms contained unique plant landmarks. The fourth arm, designated by a rock landmark, had a functional feeder that delivered bloodworms every 30 s. Importantly, the terminus of each arm (dead ends, sham feeder, functional feeder) was not visible to subjects from the center of the maze and a fish had to enter an arm before it could determine which stimulus was present. The 15 cm surrounding the functional and sham feeders were labeled the correct and incorrect feeding zones, respectively, and dead end arms were separated from feeding zones by removable opaque walls. Cues were placed at both the opening and end of each arm. Water freely circulated around the outside of the maze, thereby diluting any possible sources of olfactory cues aside from the two feeders and making sources of flow inside the maze negligible.

## 2.3. Maze training

Before training, subjects were acclimated to an empty maze by running two trials where landmarks and feeders were absent and dividers at the ends of all four arms prevented fish from accessing both feeding zones. The morning after feeder training a subject was placed into a randomly selected acclimation area. The subject was allowed to exit the acclimation area at will, and then swim freely around the empty maze for four hours. After four hours, the subject was placed in one of the holding areas. The same process was repeated in the afternoon for the same subject, only the opposite acclimation area was used. For the second empty maze trial, we recorded the amount of time a subject spent in each maze arm for the first 20 mins of the trial to ensure there was no location bias before beginning training. This habituation procedure ensured behaviour during early trials, and thus modeled learning rates, were not confounded by individual differences in comfort level in an unfamiliar environment.

On the morning after empty maze trials we randomly assigned landmarks to maze arms and removed two dividers allowing access to the correct and incorrect feeding zones. Fish were trained to locate the correct feeding zone during 10 trials conducted over five days. For each trial, the subject was placed in a randomly selected acclimation area and we recorded the amount of time before the subject exited. Subjects that had not exited acclimation after 60 mins were guided out with a net. Once a subject exited, a 20-min trial was initiated and we recorded the amount of time spent in each arm, the amount of time in each feeding zone, and the latency to enter the arm with the functional feeder. At the conclusion of each trial, the subject was removed from the maze and placed in the holding area.

Two trials occurred each day with at least four hours separating each trial. Methods for the second trial were identical to those described above except the subject was placed in the opposite acclimation area from that used for the first trial of the day. Alternating acclimation areas made egocentric cues unreliable and intra-maze and extra-maze cues (overhead lights and the PVC frame holding the plastic drape) the only sources of spatial information. Bloodworms that were not consumed were removed at the conclusion of each trial, and subjects were not fed outside of training trials.

## 2.4. Spatial strategy test

The morning after the last training trial we conducted a 20-min testing trial and measured the same variables as mentioned above for training. Prior to testing, rock landmarks were moved to a randomly selected, previously unrewarded arm of the maze. All other landmarks were moved such that the position of each landmark relative to the rock landmark remained consistent, but each landmark now occupied a new arm. For testing, both feeders were sham feeders providing visual and olfactory cues, but neither delivered bloodworms. This removed the possibility of a subject spending time in the arm with the rock simply because it was delivering food (i.e., preference for the arm would be evidence of learning rather than attraction to a food reward). A randomly selected acclimation area was used for each subject. At the conclusion of testing, subjects were measured for total length and placed in a new housing aquarium separate from untested fish.

## 2.5. Data analysis

Data were collected using EthoVision software and a camera mounted approximately 2 m from the water surface. Data for open field trials were collected with automated features in EthoVision, thus removing potential sources of collector bias. However, because of interference with landmarks, we could not use software to track

subjects in the maze and scored maze trials manually. To minimize bias, a subject's boldness score was unknown to the scorer at the time of data collection.

Data were analyzed using hierarchical and non-hierarchical Bayesian beta regression models (see Supplementary material Table S1 for detailed model descriptions). Accordingly, results do not rely on p-values to make inferences. Rather, 90% Bayesian credible intervals (BCIs), which are analogous to confidence intervals in frequentist statistics, are reported alongside the calculated probability associated with estimated parameters supporting each hypothesis. For all models three parallel Markov chains were run with each chain beginning with a different random starting value. From a total of 50,000 samples from the posterior distribution, the first 30,000 samples of each chain were discarded and then every third sample was retained for a total of 20,001 samples used to characterize the posterior distribution. The scale reduction factor ( $\hat{R}$ ), a convergence statistic, for each parameter, trace plots, and plots of posterior distributions were examined to assess convergence. Analyses were completed using JAGS in the R2jags package (Plummer, 2011) run within R (R Core Team, 2014).

### 2.5.1. Estimating individual learning rate

A hierarchical (varying intercept, varying slope) beta regression model was fitted to estimate subject-specific learning rates. Learning rate was characterized by an increased ability to navigate the maze and find food over the duration of the ten training trials. Accordingly, learning rate was quantified by the slope obtained from the regression of behavioural variables against trial number (level 1 of the hierarchical model; Table S1). A separate regression was performed for each of four behavioural variables including time spent in the correct arm with the rock landmark, time spent in the correct feeding area, latency to enter the arm with the rock landmark, and latency to leave the acclimation area. We do not report data for first arm choice because it is highly correlated to latency to enter the correct arm (i.e., a subject that chose the correct arm first had a short latency). Further, unlike first choice, latency to enter the correct arm accounts for subjects that may have chosen the correct arm first, but only after a significant delay.

Notably, we hypothesized the direction of the regression slope to differ among variables. Specifically, learning rate was hypothesized to be defined by a positive slope for time spent in the correct arm and correct feeding zone as subjects that have learned the location of food should spend more time near the functional feeder in later training trials. However, we hypothesized the slope would be negative for latency to enter the focal arm and latency to leave the acclimation area as fish should learn to complete these tasks faster over time.

The response variable ( $y$ ) was the proportion of time spent in an area or the latency to complete a task, and was assumed to follow a beta distribution (see Ferrari and Cribari-Neto, 2004 for more details). To meet model expectations, response variables were transformed using the equation  $(y \cdot (n - 1) + 0.5) / n$ , where  $n$  is the sample size (Smithson and Verkuilen, 2006).

### 2.5.2. Modeling the effect of boldness on learning rate

Level 2 of the hierarchical model quantified the effect of personality on learning by modeling the slope parameter from level 1 of the model (i.e., subject-specific learning rates) as a function of boldness (a subject-specific covariate; Table S1). This was also performed for each of the four behavioural response variables separately. Boldness was standardized as described in the previous paragraph for trial number and the proportional means for each subject (i.e., the subject-specific intercepts) were not modeled. The variance-covariance matrix was modeled using the scaled inverse-Wishart distribution (Gelman and Hill, 2007).

### 2.5.3. Spatial strategy test

A non-hierarchical model was used to test whether boldness influenced a subject's ability to solve the rearranged maze (a hierarchical model was not necessary because there were not multiple observations per fish in the spatial strategy test). If a subject learned during training that the rock landmark signified the location of food, then during testing it should spend more time searching for food in the maze arm that contained the rock even though the location of the rock was now in a previously unrewarded arm. However, if a subject had formed a spatial map independent of the provided landmark cues (e.g., using extra-maze cues, which were spatially constant during training and testing), it was expected to return to the arm that was previously rewarded during training. A lack of preference for either arm would indicate that a subject failed to form a spatial relationship of the environment.

Two variables were examined to test these hypotheses: the proportion of time the subject spent in the feeding zone in the arm that contained the rock landmark and the proportion of time the subject spent in the arm that was previously rewarded during training. Variables were analyzed using a beta regression as outlined above; however, there were no individual-level random effects and a single precision parameter was estimated. Proportion of time in the feeding zone that contained the rock was used as the response variable because it is a stronger measure of learning than time spent in the entire arm (though the result of that analysis produces similar results).

## 3. Results

Of the 14 subjects tested, six spent less than 200 s (30%) of time in the center of the open field arena and six subjects spent more than 400 s (60%) in the center. The remaining two subjects spent approximately equal time in the center and on the perimeter. There was no correlation between boldness and total length ( $R^2 = 0.04$ ).

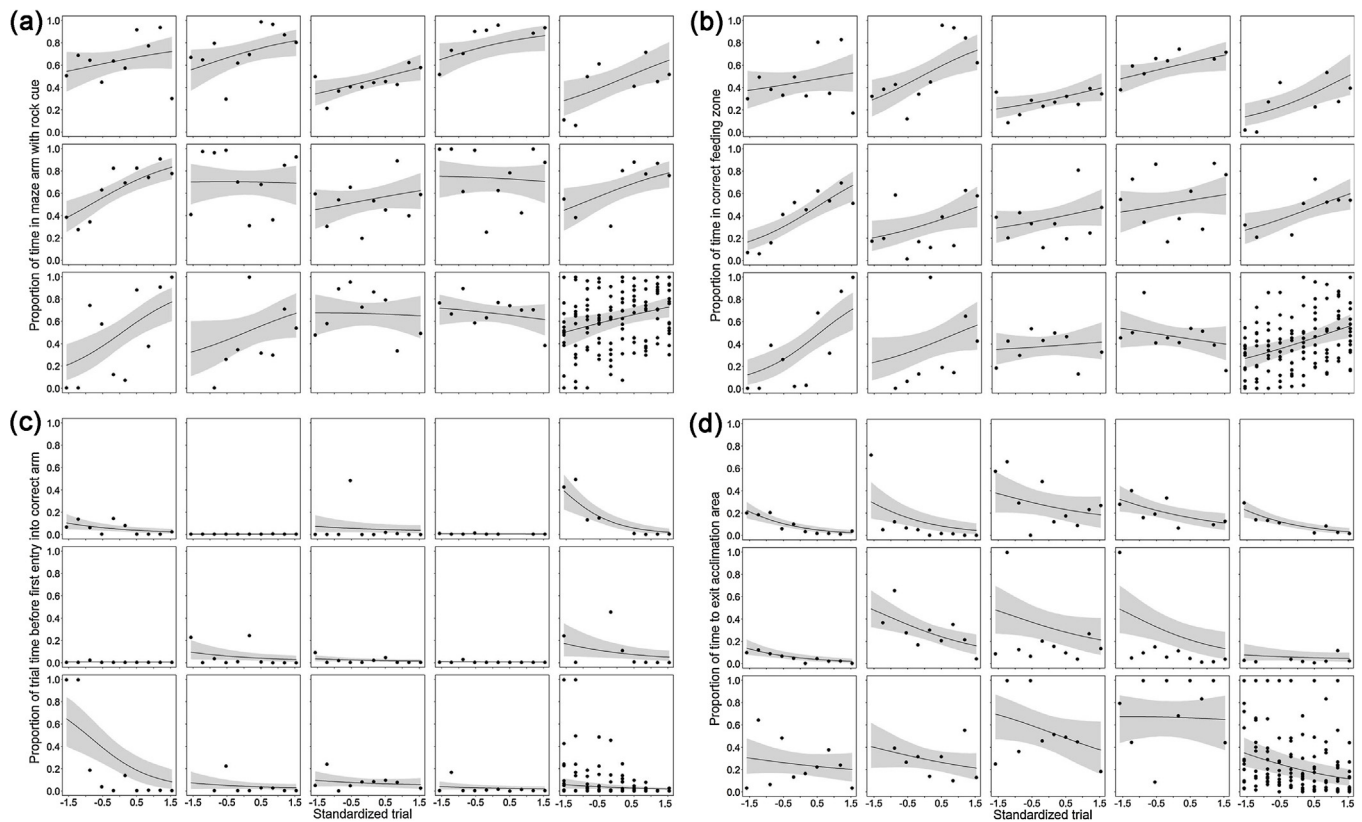
### 3.1. Individual learning rate

Based on a hierarchical beta regression model that excluded the effect of boldness at level-2 of the model (i.e., the model was unconditional at level-2), most subjects showed evidence of learning for all four behavioural variables analyzed. The probabilities that learning rate slopes were positive for time spent in the correct arm and time spent in the correct feeding zone both exceeded 98% (i.e., subject-specific regression slopes were  $>0$ ) indicating that, across all fish, subjects spent more time, on average, near the functional feeder in later trials. However, there was considerable heterogeneity in learning rates among fish, with estimated slopes ranging from 0.07 to 0.58 for time spent in the correct arm and from 0.16 to 0.65 for time spent in the correct feeding zone.

The time it took subjects to first enter the correct maze arm declined over time, and there was a 98% probability that learning rate slope was negative (range of slopes was 0.63 to  $-0.11$ ). Subjects also learned to exit the acclimation area faster with an over 99% probability that learning rate slope was negative (range of slopes was  $-0.71$  to 0.23, Fig. 2, Table 1).

### 3.2. Effect of boldness on learning rate

With 78% and 74% probability, learning rate decreased with boldness for time spent in the correct arm and time spent in the correct feeding zone, respectively. There was a weakly positive correlation between latency to enter the correct arm and boldness with a 59% probability that latency increased with boldness. There was a 96% probability that shy subjects learned to exit acclimation faster than bold subjects (Fig. 3, Table 1).



**Fig. 2.** Subject-specific learning rates defined by the slope for the proportion of time in the maze arm with the rock cue (a), proportion of time in the correct feeding zone (b), latency to enter the correct feeding arm (c), and latency to exit acclimation (d). Within each subplot, subjects are plotted by boldness score, ascending from left to right starting in the upper left. The last panel in each subplot represents the model fit across all fish. The 90% BCIs are shown in grey.

**Table 1**

Summary statistics for Bayesian beta regression models. Learning rate, the effect of boldness on learning rate, and how boldness influenced behaviour during testing were modeled using multiple response variables. For each variable, the posterior mean for the estimated slope, 90% Bayesian credible interval, and the probability that the effect is in the direction of the estimated posterior mean  $\text{Pr}[\text{direction of posterior mean}]$  are reported. Parameters are reported on the logit scale.

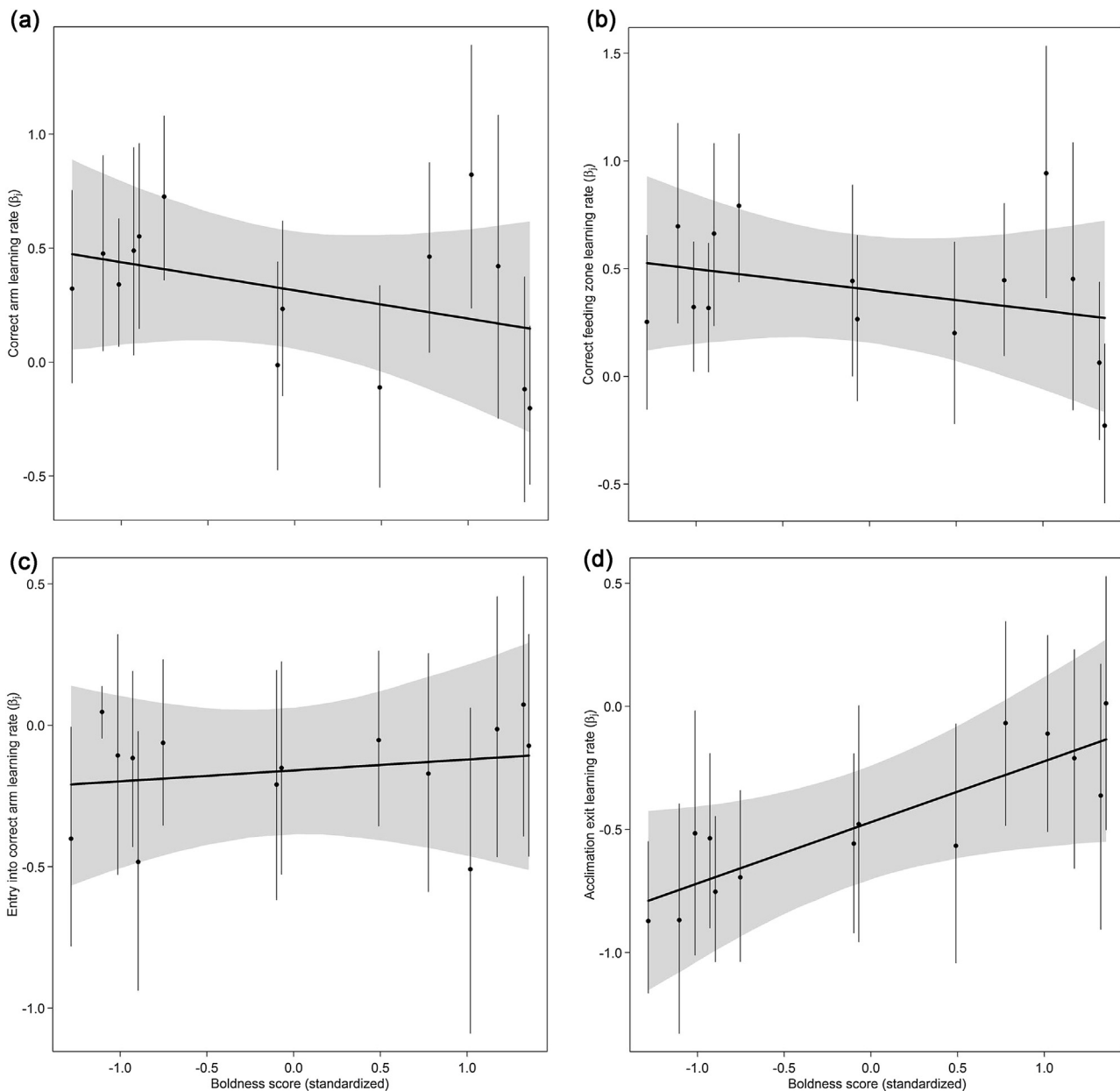
Model and response variable	Predicted direction of correlation	Posterior mean of the estimated slope	90% BCI	$\text{Pr}[\text{direction of posterior mean}]$
<b>Learning rate (<math>\mu\beta</math>)</b>				
Correct Arm	+	0.32	0.07, 0.58	0.98
Correct feeding zone	+	0.40	0.16, 0.65	1.00
Latency to correct arm	–	–0.37	–0.63, –0.11	0.98
Latency to exit acclimation	–	–0.47	–0.71, –0.23	1.00
<b>Effect of boldness on learning rate (<math>\gamma_1^\beta</math>)</b>				
Correct Arm	–	–0.12	–0.39, 0.15	0.78
Correct feeding zone	–	–0.10	–0.35, 0.16	0.74
Latency to correct arm	+/–	0.04	–0.24, 0.32	0.59
Latency to exit acclimation	–	0.25	0.01, 0.48	0.96
<b>Subject testing (<math>\tau_1</math>)</b>				
Feeding area with rock cue	–	–0.84	–1.16, –0.52	1.00
Previously rewarded arm	+	0.15	–0.16, 0.45	0.79

### 3.3. Spatial strategy test

The probability that boldness influenced the proportion of time spent in the correct feeding zone during testing exceeded 99% indicating shy fish learned to associate the rock cue with a food reward during training, and switched arm preference to track the rock cue during testing (Fig. 4, Table 1). There was 79% probability that the proportion of time spent in the previously rewarded arm increased with boldness. However, the proportion of time bold fish spent in the previously rewarded arm did not exceed that which would be expected by chance, and the positive relationship was driven by a preference for the arm with the rock cue by shy fish which, subsequently, spent little time in the previously rewarded arm.

### 4. Discussion

We found that high inter-individual variation in learning ability could be attributable, at least in part, to differences in personality. In a four-armed maze staged with visual cues, bold fish were less successful at locating a hidden food patch during training trials. When the maze was rearranged, shy fish continued to use cues to search for food, whereas bold fish randomly searched the maze and did not use inter- or extra-maze cues to track food resources. Together, these results suggest that bold and shy individuals differ in the learning and memory processes that help them locate and track resources in their environment.

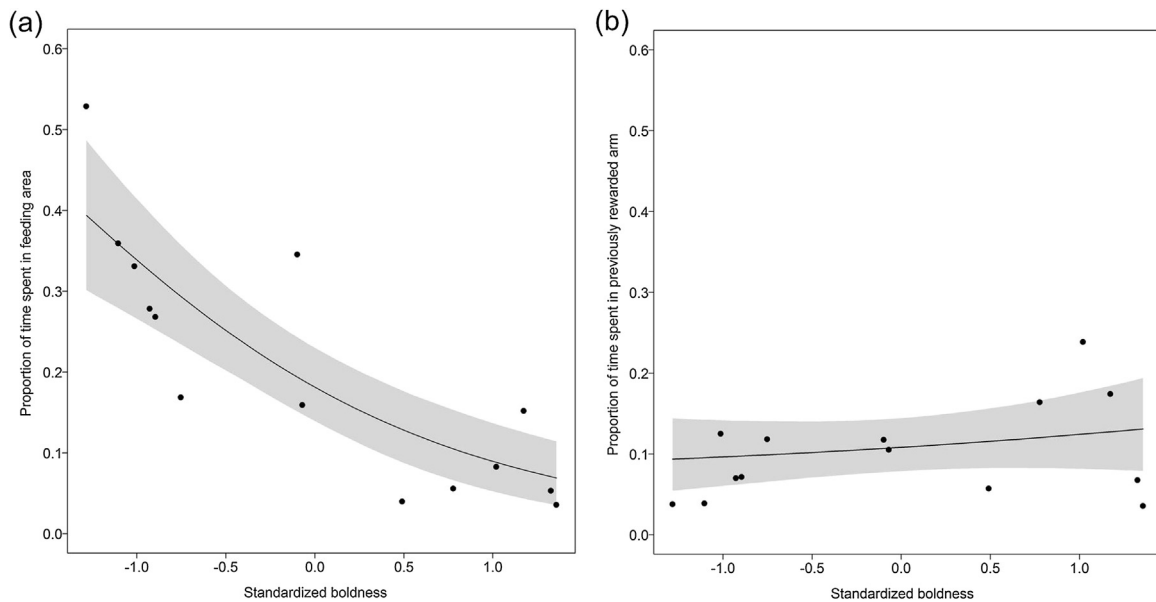


**Fig. 3.** Effect of boldness on subject-specific learning rate as defined by time spent in the correct arm (a), time spent in the correct feeding zone (b), latency to enter the correct arm (c), and latency to leave the acclimation area (d). Points represent subject-specific learning rates with 90% BCI bars. The 90% BCIs for the hierarchical regression line (solid black line) are shown in grey.

Correlations between boldness and exploration have led some to hypothesize that boldness confers an adaptive advantage by allowing individuals to rapidly learn about a diverse range of environmental conditions (Adriaenssens and Johnsson, 2011b; Sih and Del Giudice, 2012). Results here question how much spatial information bold individuals acquire and retain as they move through the environment. It is plausible that bold fish use resources that were not available in the maze to map their habitat (e.g., flow, olfaction, forage quality: Braithwaite and de Perera, 2006). Equally possible is that bold fish randomly explore the environment irrespective of cues or only superficially inspect the environment with limited assimilation of information (Sih and Del Giudice, 2012). However, the inefficiency of a random walk strategy and temporal instability of non-spatial cues in headwater stream environments would suggest that these are less reliable navigation methods for

brook trout. Subsequently, bold fish may be less capable of relocating preferred habitat patches once abandoned.

Bold and shy phenotypes are maintained in natural environments suggesting that there must be fitness trade-offs to personality. The conservation of boldness may correspond to patterns of long-distance dispersal that lead to occupation of new habitat patches (Fraser et al., 2001; Rehage and Sih, 2004; Conrad et al., 2011). These movements through dendritic landscapes require short-term occupancy of habitats with low energetic profitability, but are especially important in dynamic headwater streams where resiliency to disturbance and genetic connectivity are important for population survival (Chapman et al., 2011). Conversely, shy individuals may be more adept at integrating social and spatial information to optimize energetic profitability at smaller spatial scales (Sih and Del Giudice, 2012).



**Fig. 4.** Effect of boldness on proportion of time spent in the feeding area with the rock cue (a) and proportion of time spent in the previously rewarded arm (b) during testing. Light grey regions represent 90% BCIs.

Cognitive capacity increases behavioural plasticity and, by allowing individuals to adapt to changing conditions, may decrease the rate of population extirpation due to habitat degradation and climate change (Kotrschal and Taborsky, 2010; Hoffman and Sgrò, 2011). However, the natural maintenance of bold and shy phenotypes in fish populations may be threatened by anthropogenic directional selection for bold personality types in hatchery environments (Sundström et al., 2001; Huntingford, 2004; Mittelbach et al., 2014; Wilke et al., 2015). Stocking an excessive proportion of a single phenotype may increase population stochasticity and loss by reducing cognitive flexibility and homogenizing behaviour (Wolf and Weissing, 2012). Further, the effects of stocking may be long-lasting as it could take several generations of wild reproduction to restore phenotypic stability (Jonsson and Jonsson, 2014). As such, accounting for individual differences in cognition and personality could increase the efficacy of stocking programs and increase population resilience by promoting behavioural plasticity.

Using a single measure of personality is common practice in fish behaviour research (e.g., Ahmad and Richardson, 2013; Archard and Braithwaite, 2011; Mosciki and Hurd, 2015); however, there has recently been some question about the validity of this approach. This surge in skepticism is likely the product of many novel, unevaluated, personality measures such as latency to emerge from a start box (Brown and Braithwaite, 2004), latency to approach a food source (Jenjan et al., 2013), or willingness to forage in the presence of a predator (Bell and Sih, 2007) that have become increasingly common but have not yet been rigorously tested. In contrast, open field tests were pioneered by psychologists and biomedical researchers and have been used in animal behaviour research for over 40 years (Walsh and Cummins, 1976) to reliably measure boldness. Open field tests have more recently been validated in fish, including Burns (2008) who subjected guppies to multiple temperament assays and concluded that open field tests were the most reliable for assessing personality. Further, Schjolden et al. (2005) found a correlation between neuroendocrine responses and behaviour in an open field arena in salmonids, indicating that the assay reliably captures physiological differences in the stress response of bold and shy individuals. Given the validity of the assay, repeated measures of open field tests are not only unnecessary (Réale et al., 2007), but potentially confounded by the effects of

habituation and learning that are difficult to measure and inflate variance of the personality measurement.

Quantifying consistency of behaviour across independent contexts can also validate personality assessments (Wilson and Stevens, 2005). In fish, another common boldness measure is the time it takes a subject to exit an enclosure (Toms et al., 2010). Using this alternative assay, we compared average time to exit the maze acclimation area with results from the open field trials and confirm a significant correlation (Spearman rank correlation:  $r_s = 0.71$ ,  $p = 0.002$ ), indicating consistency in personality designation. However, while the expectation is that bold individuals will exit acclimation sooner (presumably showing an increased willingness to enter a potentially dangerous, novel environment), we found that shy fish consistently exited faster. There are two explanations for this result. First, unlike open field tests, time to exit a start box has not been rigorously validated and hypotheses about how different personalities will react are poorly supported. Second, our acclimation arena was not designed to measure personality. Specifically, the arena was not a refuge (there was no overhead cover and subjects were exiting into a familiar environment) and the exit was located in the middle of the water column forcing fish to actively search for the opening in order to leave. In fact, we often observed bold fish circling around the bottom of the arena for nearly an hour appearing to look for an opening, whereas shy fish would often immediately exit once calm. Accordingly, while the strong trends we found are indicative of learning, results cannot be compared to other studies where acclimation arenas had fundamentally different designs and objectives.

Though difficult to quantify, our results are unlikely an artifact of motivation (Griffin et al., 2015). All fish were fed ad libitum the day before maze training, at which point the only source of food was the maze feeder which was not delivering enough food to satiate subjects. However, if motivation was different among fish, it would likely result in the learning rate of bold fish to be overestimated and shy fish underestimated. To meet the energetic demand of higher metabolism (Sih, 2011; Mittelbach et al., 2014), bolder fish should have been more motivated to locate and occupy the feeding zone, particularly in later training trials as bold fish went consecutive days with decreased food intake. Heightened motivation in later trials would have increased time spent near the functioning feeder,

and thus increased the slope of the modeled learning rate. However, this effect was not observed. Similarly, shy fish continued to spend the majority of time in the correct feeding zone during later training trials, indicating no decrease in motivation despite high food intake (Odling-Smee et al., 2008).

Previous studies have documented the use of allocentric and egocentric cues by fish to form cognitive spatial maps (Warburton, 1990; Rodriguez et al. 1994; Odling-Smee and Braithwaite, 2003). While the studies did not measure personality, there was high inter-individual variation suggesting the potential for fish-specific learning rates (Braithwaite et al., 1996). Results here show that individual learning rates differed by over 150% for some metrics (Fig. 2), and that boldness was a significant predictor of learning ability (Fig. 3). This suggests that failure to measure individual-specific performance may exclude valuable data that would lend to more ecologically relevant conclusions about the significance of population phenotypic diversity. In particular, explicitly measuring animal personality may provide a powerful explanatory variable that decreases unexplained variation while allowing for inferences across a larger sample population.

While hierarchical beta regression has been used sparingly in behavioural research, our analytical methods are comparable to other published studies. Specifically, our analysis is a mixed model in similar form to that prescribed by Dingemans et al. (2010) for quantifying changes in behaviour. Specifically, both analyses use a varying intercept, varying slope model to account for repeated measures and to quantify individual behavioural heterogeneity. This allows fish-specific covariates (e.g., boldness) to be incorporated, allowing a more robust analysis that allows uncertainty to be propagated, and thus accounted for, between the observation- and fish-levels of the analysis. The only major difference between the two approaches is that Dingemans et al. (2010) use a Gaussian error distribution whereas we assumed a beta distribution. A Gaussian distribution assumes that errors are normally distributed and continuous between negative to positive infinity. This assumption is inappropriate for many animal behaviour datasets, including proportional data that are non-normal and bounded between 0 and 1. Alternatively, the beta distribution is an expansion of the generalized linear model (GLM) to regress predictor variables on dependent variables that are continuous and bounded between 0 and 1. Beta distributions have been shown to be more accurate and efficient parameter estimates and we encourage readers with similar datasets to consider this approach.

The other fundamental difference in our analysis is the use of Bayesian estimation. Because we used diffuse priors, our results would have been comparable to those if we conducted the analysis in a frequentist framework (for example, the correlation between boldness and testing performance, Fig. 4a, when calculated using least-squares regression is significant with  $R^2 = 0.71$  and  $P < 0.001$ ). However, with Bayesian estimation we can make probabilistic statements about effects, thereby avoiding the need to rely on arbitrary decisions about statistical significance.

Few studies have attempted to correlate cognitive processes to personality (Griffin et al., 2015). Results here suggest that personality may influence learning and cognition, and the significance of this finding across taxa and habitats will be a fruitful line of future research. In particular, several hypotheses for the maintenance of inter-individual cognitive abilities were discussed, but determining the population effects of individual behaviour will further emphasize the need for a behaviourscapes approach (White et al., 2014) to wildlife management.

### Conflict of interests

We declare that all authors have no conflict of interest.

### Compliance with ethical standards

The experimental protocol was approved by the Institutional Animal Care and Use Committees of The Pennsylvania State University and Randolph–Macon College. Fish were cared for in accordance to the ASAB/ABS Guidelines for the Use of Animals in Research and suffered no negative effects from the experimental protocol.

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### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2016.08.009>.

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