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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-

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