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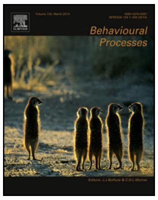

# How ecology shapes prey fish cognition

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ABSTRACT

Fish exhibit diverse cognitive capacities: they cooperate, punish, develop cultural traditions, learn to map their environment and communicate their intentions to one another. Skills such as these have helped fish radiate to colonize the many and diverse aquatic niches available. Prey fish are no exception to this, and several recent studies have shown them to be a rich resource for understanding the evolutionary ecology of animal cognition. Many fish have to cope with the threat of predation, but some environments contain more predators than others. These environments deliver the opportunity to investigate how predation pressure shapes fish cognition and behaviour. Here we compared the ability of fish from two high and two low predation habitats to learn a sequential choice spatial task. We also investigated their ability to solve the maze after it was rearranged. Fish from high predation sites made more errors as they learned to navigate the maze than fish from low predation sites. The fish also varied in the cues that they learned to help them solve the maze. These did not vary by levels of predation pressure, rather, they differed between rivers, with fish from one river learning to use landmark cues, and those from the other river learning the sequence of left and right turns. As the different populations varied in how well they learned to navigate through a reconfigured maze, it seems likely that predation pressure is not the only factor influencing spatial behavior in these fish.

## 1. Introduction

To understand individual variation in learning and memory, it is necessary to consider the ecological and evolutionary context of the species being studied. Fish experience a wide variety of environments and challenges. Over evolutionary time these have produced a comparably wide range of cognitive skills in response (e.g. Teyke, 1989; Kelley & Magurran, 2003; Laland et al., 2003; Schuster et al., 2004; Burt de Perera and Guilford, 2008). There are many factors that can influence what information is learned and remembered such as the reliability of the information (Biegler & Morris, 1996a, 1996b; Girvan & Braithwaite, 1998), the time interval over which Q2 information remains relevant (Coolen et al., 2003), and the presence of competitors (Utne-Palm and Hart, 2000) or predators (Burns & Rodd, 2008; Brown & Braithwaite, 2005). Each of these factors varies with ecological niche or habitat. Such variability of experience makes fish a valuable arena in which to explore cognitive ecology.

When facing a pike (*Essox lucius*), a single mistake is likely to cost a minnow (*Phoxinus phoxinus*) its life. This high potential cost of any predator interaction means that anti-predator defenses are often quickly acquired though mechanisms such as one-trial learning (Brown, 2003). Nonetheless, more subtle learning processes still occur as incorrect information must be updated, or a single learned cue generalized to the broader realm of circumstance that fish must face over the course of their life history.

Predators can also shape aspects of memory not directly associated with predation. Work by Brown and Braithwaite (2005) using a tropical Poecilid, the Panamanian bishop fish (*Brachyrhaphis episcopi*) showed that fish from four high predation riverine sites were slower to solve tasks involving finding a food reward or shelter than fish from paired low predation sites. It was found that low predation fish utilized within-maze cues than the high predation fish, giving them an advantage in learning the locations of the food reward and shelters. Although it might at first be hypothesised that high predation fish should be selected to learn these locations more rapidly, this was clearly not the case. Instead, it may be that the pressure of predation prevents the more thorough investigation of surrounding habitat that low predation fish have the luxury of, and this increased exploration may give the low predation fish an opportunity to learn more about the spatial cues in their habitat. These same populations have been shown to differ in temperament across high and low predation regimes, with the high predation fish generally being more bold and active than low predation fish

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(Brown & Braithwaite, 2004; Brown et al., 2005). More bold mammals tend to establish more rigid routines than shy mammals, and are additionally less likely to recognise small changes in their surroundings (Benus et al., 1990; Bolhuis et al., 2004). This supports the hypothesis that bolder animals may pay less attention to their environment, a potential hindrance towards learning new cues or information.

To elucidate the effect of predation pressure on cognition, we designed a study that compared the performance of different populations of *B. episcopi* fish as they learned to solve a maze task. The fish were sampled from areas with either high or low risk of predation, where high predation populations consistently show bolder behavior than fish from low predation sites. As boldness appears to affect how much attention individuals pay to their environment (Bolhuis et al., 2004), we wanted to test whether this affected the kinds of spatial information the fish learned to use. The maze was based on a design similar to that used by Girvan and Braithwaite (1998) such that two kinds of spatial information could guide the fish along its route; (i) the fish could reach the goal chamber by learning that plant landmarks were reliable markers of the correct route, or (ii) they could learn a list of turn directions to make when at decision points (i.e. take left route or right route). As high predation environments may demand increased vigilance and attention compared to areas occupied by fewer threats, we wanted to determine whether there were differences in the spatial information used by different populations (Girvan & Braithwaite, 1998). In addition, we tested whether populations varied in their ability to update their spatial information by changing the lay-out of the maze once they had learned a specific route in order to quantify flexibility in cognitive ability.

## 2. Materials and methods

Fish were collected from field sites in Soberania National Park, Panama using seine and dip nets. They were then transported to the aquatic laboratory facilities at Penn State University, USA. Fish were collected from the River Macho and River Quebrada Juan Grande (QJG). Each river had a pair of sampling sites, one upstream and one downstream, with a waterfall acting as a geographical barrier separating the populations. River Macho, high predation site: 9° 1’ 03“N, 79° 45’ 42“W; low predation site: 9° 11’ 02“N, 79° 45’ 36“W. River QJG high predation site: 9° 08’ 37“N, 79° 43’ 00“W; low predation site: 9° 08’ 37“N, 79° 42” 57“W. Above the waterfalls only two species of fish are present, *B. episcopi*, and the killifish *Rivulus brunneus*. Below the waterfalls, there are significantly more piscivorous predators including cichlids (*Geophagus* and *Aequidens* spp*)* and tigerfish (*Haplies* spp) (see Brown & Braithwaite, 2004 for details on the range and density of fish fauna). As previous studies with this species have documented behavioral differences between the sexes (Simcox et al., 2005; Archard & Braithwaite, 2011a), we chose to use only adult females in the current study.

Groups of fish were housed in glass aquaria (30 cm wide × 30 cm high × 90 cm long), in 65 L water maintained at 25 °C ± 1 °C, with a gravel substrate, and an internal, air-operated, box filter. Fish were separated by population across two tanks (a total of 8 population tanks) and were fed daily with flaked fish food and live brine shrimp nauplii. Tanks were cleaned once weekly, and were enriched with plastic plants and dark plastic shelters. Lighting came from overhead fluorescent tubes for 11 h per day, supplemented at lower levels by standard 40 W lamps for an additional half hour at the start and end of each day. Fish were accustomed to routine maintenance and the presence of people.

Prior to the experiment, individual fish were anaesthetized by placing them into a buffered MS222 solution, until they lost their balance and lay on their side. The fish were then removed from the solution, positioned on a wetted paper towel and given a unique coloured elastomer tag on both sides of their body behind their gill cover (procedure was approved by IACUC protocol # 36902). The color tag patterns allowed individual fish to be identified during the experiment. After marking, fish were transferred to the housing compartment of the test tank (Fig. 1). Fish were given 6 days after tagging to allow acclimation to the test tank. The sample size was 12 for each population (4 populations × 12 = 48 fish in total).

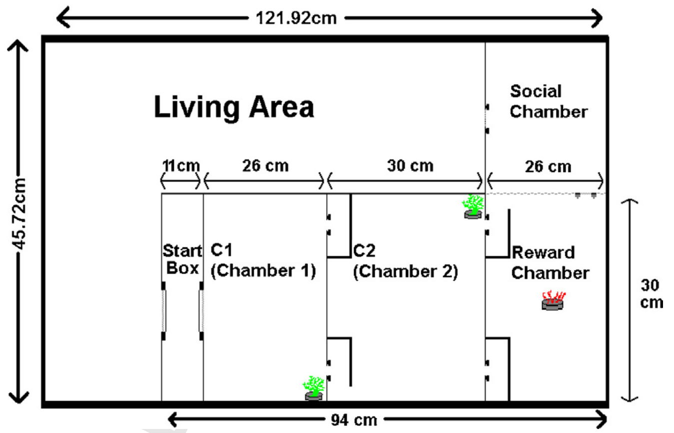

**Fig. 1.** Schematic overview of the maze and the separate living area for the fish. The different compartments were made accessible or sealed off by sliding trap-doors operated by remote pulleys. Landmarks were positioned next to open doorways.

## 3. Tank set-up

Training and trials were performed daily between the hours of 1000–1600. Maze test tanks were constructed within glass aquaria (121.92 cm L × 45.72 cm W × 53.34 cm H) that were filled with 16–18 cm depth of water. Each tank was divided into 6 chambers (Fig. 1). When not performing in trials, the fish remained in the housing area. At the beginning of a trial, an individual fish was moved into the start box. On leaving the start box, the fish could progress through the maze by swimming into a series of chambers separated by partition walls before reaching a final reward chamber. Each wall had two doorways. One door led to a dead-end while the other gave access to the next chamber. Once the fish reached the reward chamber, they had access to food as well as visual contact with a stimulus shoal maintained in a compartment separated by a clear plexi-glass window. After the fish had consumed the food they were allowed to enter the social chamber via a small trap door (Fig. 1).

Opaque black plastic covered the four sides of the tank to minimize disturbance or distractions during trials. Small viewing slits were cut into one of the sides to allow the observer to monitor the movement of individual fish as they moved through the maze. Trap doors between the living area, the start box, chamber 1, as well as the reward and social chamber were operated with a remote pulley system. This trap door system was used to prevent fish from back tracking and also allowed the separation of fish that had completed a trial from those that were still to be tested.

Throughout the experiment, *B. episcopi* were kept on a 12L:12D photoperiod. Fish were fed daily via the food reward and then *ad libitum* with flake food after all trials were conducted. Food rewards were freeze-dried bloodworms (Chironomid larvae) secured in a weighted plastic cup (1.2 cm deep and 2.8 cm diameter) filled with Vaseline.

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