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Sex differences in spatial abilities and cognitive flexibility in the guppy

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When males and females differ in their spatial ecology, selection is expected to promote sex differences in spatial abilities. Although this prediction applies to many species, few studies have looked at sex differences in spatial abilities outside mammals. Here, we addressed this hypothesis in the guppy, *Poecilia reticulata*, a polygynous fish in which males disperse more than females and inhabit more spatially complex environments. We compared the performance of male and female guppies in two spatial tasks to test whether males have been selected for enhanced spatial abilities. In a detour task (experiment 1), the two sexes showed similar ability to navigate around an obstacle to reach a target. However, males were more persistent in trying to pass through the transparent obstacle, an effect that is likely to be related to sex differences in cognitive flexibility rather than to spatial abilities. In the second experiment, with a more complex maze in which guppies had to choose between alternative routes to reach the target, males learned the task after only one presentation, whereas females did not show any evidence of learning after five trials. The direction of these differences is the same as that observed in most polygynous species investigated, suggesting a common pattern of cognitive sex differences across vertebrates.

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In several mammals, including humans, monkeys, rodents and carnivorans, males possess better spatial abilities than females (Gaulin & FitzGerald, 1986; Jonasson, 2005; Lacreuse, Herndon, Killiany, Rosene, & Moss, 1999; Perdue, Snyder, Zhihe, Marr, & Maple, 2011; Voyer, Voyer, & Bryden, 1995). Exceptions to this rule have been reported for some monogamous species (Gaulin & FitzGerald, 1986; Perdue et al., 2011). Since, in mammals, males often have a larger home range than females, and tend to be the dispersing sex, several authors have suggested that sex differences in spatial abilities arise because sexual selection favours different reproductive strategies and different use of space in the two sexes (reviewed in Jones, Braithwaite, & Healy, 2003).

This hypothesis has received support in the few studies that have looked for sex differences in spatial abilities in birds and reptiles (Astié, Kacelnik, & Reboreda, 1998; Carazo, Noble, Chandrasoma, & Whiting, 2014; González-Gómez et al., 2014). In the polygynous lizard *Eulamprus quoyii*, males have a larger home range and perform better than females in spatial learning (Carazo et al., 2014). Conversely in two obligate brood-parasitic cowbirds, *Molothrus bonariensis* and *Molothrus alter*, females, which need to accurately remember the position of many host nests, outperform males in spatial tasks (Astié et al., 1998; Guigueno, Snow, MacDougall-Shackleton, & Sherry, 2014). To test the idea that sex differences in spatial abilities evolve when the ecological demand for the use of space is greater in one sex, it is important to gather data on many more species, especially outside mammals (Jones et al., 2003).

There are very few data on sex differences in spatial cognition in fish, although this taxon has been frequently used for research on spatial (Brown, Laland, & Krause, 2008) and other cognitive abilities (Bshary & Brown, 2014). Sovrano, Bisazza, and Vallortigara (2003) testing redtail splitfin, *Xenotoca eiseni*, in a task that required the fish to learn the geometrical properties of a rectangular environment found that males were somewhat more efficient than females. However, there is no information about the use of space by this species in nature. In the freshwater blenny, *Salaria fluviatilis*, males learned a two-choice maze faster than females. However, in this species females have larger home ranges (Costa et al., 2011; Fabre, García-Galea, & Vinyoles, 2014).

We investigated sex differences in spatial abilities in the guppy, *Poecilia reticulata*. The spatial ecology of guppies has not been exhaustively described but there is evidence that males are more mobile than females, perhaps because they increase mating success by searching for receptive females (Croft, Krause, & James, 2004; Croft et al., 2003; Griffiths & Magurran, 1998). A capture - recapture study also found that females show high site fidelity,

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while males tend to disperse further (Croft et al., 2003). Moreover, in rivers with high predation risk and in some rivers with low predation risk, males preferentially inhabit shallow waters with complex spatial environments and abundant vegetation whereas females prefer to live in open waters (Croft et al., 2006; Darden & Croft, 2008). Thus, the available ecological data suggest that, if sex differences in spatial abilities have evolved in this species, males should show better performance.

Sex differences in cognition might be due not only to diverse selective pressures on males and females, but also to differences in the environmental conditions experienced during development, such as different habitat choices or differential predation (see discussion in Lucon-Xiccato & Bisazza, 2016). We designed our experiments to study sex differences due to selective pressures on males and females. We used laboratory-reared subjects that descended from guppies of a high predation risk site; thus, environmental conditions experienced during development were identical for male and female subjects and eventual sex differences are likely to be due to evolutionary processes.

Our experiments studied sex differences in the ability to solve two spatial tasks to reach a visible goal. In experiment 1, males and females were required to detour around a transparent or semi-transparent barrier to reach a group of conspecifics. In experiment 2, the task was more complex and consisted of learning the correct route to cross two successive barriers.

METHODS

Subjects

We used descendants of wild guppies of the lower Tacarigua River (Trinidad) reared in our laboratory since 2002. The stock population was maintained in plastic tanks (100 × 70 cm and 54 cm high) with a 1:1 sex ratio. Water was constantly filtered and kept at 26 ± 1 °C. The environment was enriched with a gravel bottom, abundant plants and artificial shelters. A 36 W fluorescent lamp illuminated each tank from 0730 to 1930 hours. Guppies were fed three times per day, with alternate commercial food flakes (Fioccomix, Super Hi Group, Ovada, Italy) and live *Artemia salina* nauplii. We tested 24 males and 24 females (approximately 6 months old) randomly selected from the stock population in each experiment (48 males and 48 females overall). Standard length of a random subsample of subjects (12 males and 12 females) anaesthetized in an MS-222 solution and measured after the experiments was 20.73 ± 2.15 mm for females and 18.56 ± 0.89 mm for males. Each subject was tested only once; thus, data of the two experiments were independent.

Overview of the Experiments

We used the same apparatus and procedure in the two experiments. To motivate guppies to solve the task, we used a social reward. When put into an unfamiliar tank, individual guppies show a strong social tendency (Dadda, Agrillo, Bisazza, & Brown, 2015; Lucon-Xiccato, Dadda, & Bisazza, 2016), a response that probably derives from antipredator behaviours (Brown & Irving, 2013; Dugatkin & Godin, 1992). To exploit this social behaviour, in our experiments we put individual guppies into an unfamiliar tank in which they could reach a group of conspecifics by passing through a central arena and solving the spatial task. We repeated this trial five consecutive times for each subject in each experiment and used performance improvement as a measure of spatial learning ability.

Apparatus

The experiments were performed in glass tank (80 × 40 cm and 35 cm high) filled with 10 cm of filtered water (Fig. 1). On one side of the tank, we built a white plastic start box (10 × 10 cm) that led to a central arena with the spatial task (described below). The bottom of the start box and the central arena, as well as the walls, were covered with white plastic. On the opposite side of the tank, we built a goal zone (15 × 40 cm) with gravel on the bottom and green plastic walls simulating the colour of natural vegetation. The goal zone was adjacent to a second, smaller, glass tank (50 × 20 cm and 35 cm high) with social stimuli that served as a reward. The tank for social stimuli was provided with natural gravel, natural plants, a water filter and two 15 W fluorescent lamps. The background was white to improve the visibility of the stimuli. These were 12 male and 12 female guppies from the same population as the subject; they had inhabited the tank for at least 3 days before the start of the experiment. From the start box, the subject could see the stimulus fish through the glass walls of the tanks. We used a panel that could slide between the two tanks to regulate the sight of the stimulus tank during the different phases of the experiments (see Procedure). The entrance of the goal zone was a V-shaped one-way corridor (Fig. 1) made of transparent plastic; the subject could easily enter the goal zone, but the shape of the corridor worked as a trap preventing it from swimming back to the arena. The apparatus was placed in a dark room, and the experimental tank was illuminated indirectly from the stimulus tank. A digital camera on the ceiling recorded the tests.

Procedure

At the beginning of the trial, the subject was netted from the maintenance tank and slowly put into the start box, oriented in the opposite direction to the stimuli. During this phase, the sliding panel prevented the subject from seeing the stimuli. After 5 s, the sliding panel between the two tanks was removed making the stimuli visible, and we started the recording. The subject was free to decide when to emerge from the start box. Since the procedure exploited the response of guppies to unfamiliar environments, we used a short acclimation (5 s) to avoid familiarization. The experimenter observed the trial from a distant monitor connected to the camera that also served to record the session. In both experiment 1 and experiment 2, after the subject reached the goal zone, it was left there for 5 min with the social reward. The sliding panel was then inserted again for 2 min, after which the subject was netted and moved to the start box for the following trial. Each subject performed five consecutive trials. Subjects that took longer than 20 min to complete a trial (two males and three females in experiment 1 and two males and two females in experiment 2) were removed from the experiment. These subjects were replaced to maintain a final sample size of 24 males and 24 females in each experiment.

Experiment 1: Detour

In experiment 1, male and female guppies had to detour around a barrier to reach the stimuli. The barrier was a 15 × 10 cm panel made of transparent plastic material that was displaced in the middle of the arena, 20 cm from the start box (Fig. 1a). The barrier was U-shaped and two lateral green plastic panels impeded guppies from accidentally detouring around the barrier by simply sliding along the main panel. Subjects could detour around the barrier either from the right or the left side. Although the barriers employed in a detour task are normally totally transparent (Boogert, Anderson, Peters, Searcy, & Nowicki, 2011; Taylor, Roth,

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