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 which is likely related to sex differences in cognitive flexibility rather than to spatial abilities. In the second experiment, 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 observed in most polygynous species investigated, suggesting a common pattern of cognitive sex differences across vertebrates.

Keywords: cognitive abilities; detour; evolutionary ecology; fish cognition; gender differences; *Poecilia reticulata*; route learning.

In several mammals, including humans, monkeys, rodents and carnivorans, males possess enhanced spatial abilities compared to 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 compared to 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 *M. alter*, females, that 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).

With regard to fish, there are very few data on sex differences in spatial cognition, although this taxon has been frequently used for research on spatial (Brown, Laland, & Krause, 2008) and other cognitive abilities (Bshary & Brown, 2014). Sovrano and colleagues (2003) testing redtail splitfin, *Xenotoca eiseni*, in a task that required the fish to learn the geometrical proprieties 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 range (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 et al., 2003; Croft, Krause, & James, 2004; Griffiths & Magurran, 1998). A capture-recapture study also found that females show high site fidelity, 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 suggests 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 in case of different habitat choice 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 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 × 54 cm) 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 7:30 to 19:30. 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 (approx. 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) anesthetised in a 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 inserted in an unfamiliar tank, individual guppies show a strong social tendency (Dadda, Agrillo, Bisazza, & Brown, 2015; Lucon-Xiccato, Dadda, & Bisazza, 2016), a response that likely derives from antipredator behaviours (Brown & Irving, 2013; Dugatkin & Godin, 1992). To exploit this social behaviour, in our experiments we inserted individual guppies into an unfamiliar tank with the possibility to 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 an 80 × 40 × 35 cm glass tank 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 × 35 cm) 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. Stimuli were 12 male and 12 female guppies from the same population of the subject that inhabited the tank for at least three 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 the subject 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 inserted in the start box, oriented in the opposite direction of 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 visible the stimuli, 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 familiarisation. 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 discarded. 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, Sladek, J. R., & Redmond, 1990; Wynne & Leguet, 2004) this might be an unnatural condition for most animals. For this reason, we used a totally transparent barrier for half of the subjects and for the other half of the subjects we used a semi-transparent barrier obtained by covering the transparent plastic panel with a grey mosquito net (0.1 × 0.1 cm grid).

Experiment 2 – Route learning

In experiment 2, we used a maze similar to that previously used to study spatial abilities in fish (Girvan & Braithwaite, 1998; Girvan & Braithwaite, 2000; Fig. 1b). Two plastic walls divided the arena into three sectors. The subjects could see the stimuli from the start box through a transparent panel covered by a mosquito net like the one described in experiment 1. Each wall was provided with two doors. Only one door allowed a fish to move to the next sector. The other door was blocked and led to a dead end closed by a grid. The shape of the arms prevented the subject from seeing the presence of this grid before entering the door. In the second barrier, the correct door was placed on the opposite side. For half of the subjects the sequence of correct doors was left-right, and for the other half it was the reverse. The bottom of the second sector was of a different colour (light yellow) to allow subject to note the difference between the first and second sectors. As in Girvan and Braithwaite's studies, two different small artificial plants were placed near each correct door.

Analysis of video recordings and statistical analysis

The performance was scored from the video recordings by an experimenter who was blind to aims of the experiment. To prevent as much as possible the experimenter from identifying the sex of the guppies, we used a low resolution camera, we did not directly light the subject tank, and the recordings were coded by number. We measured the time to solve the task, i.e. time taken to enter the goal box after exiting the start box. In experiment 1, we also measured the time that the subject spent trying to pass through the barrier, and in experiment 2 we additionally measured whether the first door chosen by the subject was correct or incorrect to calculate the accuracy.

Statistical analysis was performed in R version 3.2.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). Statistical tests were two tailed and significance threshold was $P = 0.05$, unless stated otherwise. For both experiments, we built linear mixed-effect models (LMMs) on the log(time to solve the task). We fit trial (from 1 to 5) and sex (male or female) as fixed effects and subject ID as random effect. We also fitted barrier type (transparent or semi-transparent) as fixed effect in experiment 1. In experiment 1, we similarly analysed the time spent by subjects in front of the barrier (after logarithmic transformation). To study choice accuracy in experiment 2, we initially built a generalized linear mixed-effects model (GLMM) with logit link function and binomial error distribution. As dependent variable we used the choice of the subject (correct or incorrect) at each pair of doors.

We fit trial, sex and sector (first or second) as fixed effects and subject ID as random effect. We did not include body size of the guppies in the models because in our population males are smaller than females, resulting in collinearity between sex and body size. In three previous studies in which we used a less dimorphic strain of guppies and could match the two sexes, we found no effect of body size on the performance (Lucon-Xiccato & Bisazza, 2014; Lucon-Xiccato & Bisazza, 2016; Lucon-Xiccato, Miletto Petrazzini, Agrillo, & Bisazza, 2015). Then, we compared choice accuracy of trials 2 to 5 (overall number of correct choices of each subject in these four trials / 8) of the two sexes to chance (accuracy expected by chance: 0.5). We calculated choice accuracy excluding the first trial because subjects were expected to perform randomly before the training. In each of the four trials considered in this analysis, subjects chose between two doors; thus, the overall number of choices made by a subject was $4 \times 2 = 8$.

Ethical note

Experiments were conducted in compliance with the law of the country (Italy) in which they were performed (Decreto legislativo 4 marzo 2014, n. 26). The experimental procedures were approved by the Ethical Committee of Università di Padova (protocol n. 151817). Subjects did not express distress during the experiments. After the test, we released the subjects in a tank used only for breeding.

RESULTS

Experiment 1 – Detour

The LMM revealed a significant effect of trial ($F_{4,176} = 13.185$, $P < 0.001$), indicating that time to solve the task decreased over trials. The LMM found also a significant effect of barrier type ($F_{1,44}$ = 34.280, P < 0.001) and sex ($F_{1,44}$ = 14.205, P < 0.001). The barrier type × sex interaction was also significant ($F_{1,44}$ = 7.989, P = 0.007). None of the remaining interactions were significant. To understand the meaning of the significant interaction, we ran two LMMs for the two barrier types separately (transparent or semi-transparent). Trial had a significant effect in both models (transparent barrier: $F_{4,88}$ = 9.253, P < 0.001; semi-transparent barrier: $F_{4,88}$ = 4.908, P = 0.001), but trial × sex interaction was not significant (transparent barrier: $F_{4,88}$ = 0.641, P = 0.635; semi-transparent barrier: $F_{4,88}$ = 0.205, P = 0.935). In the condition with the transparent barrier, females were significantly faster than males at solving the task (mean ± *SD*: females: 63.95 ± 33.80 s, males: 204.4833 ± 98.84 s; $F_{1,22}$ = 18.296, P < 0.001; Fig. 2a), while we found no significant effect of sex in the condition with the semi-transparent barrier (females: 35.52 ± 18.55 s, males: 36.73 ± 13.95 s; $F_{1,22}$ = 0.548, P = 0.467; Fig. 2b).

Time spent in front of the barrier trying to pass it accounted for a large proportion of the time to solve the task with the transparent barrier (83.57%), but not with the semi-transparent barrier (37.55%). The analysis conducted on this variable revealed substantially the same scenario as the analysis on the time to solve the task. In the initial LMM, there was a significant effect of trial ($F_{4,176}$ = 10.934, P < 0.001), barrier type ($F_{1,44}$ = 39.232, P < 0.001) and sex ($F_{1,44}$ = 5.815, P = 0.020). The barrier type × trial and barrier type × sex interactions were significant ($F_{4,176}$ = 2.981, P = 0.021 and $F_{1,44}$ = 6.303, P = 0.016, respectively). When we performed two LMMs on the data split according to the type of barrier, sex had a significant effect in the condition with the transparent barrier (females: 46.57 ± 32.17 s, males: 177.75 ± 102.72 s; $F_{1,22}$ = 8.126, P = 0.009; Fig. 3a) but not in the one with the semi-transparent barrier (females: 13.87 ± 9.82 s, males: 13.27 ± 7.30 s; $F_{1,22}$ = 0.009, P = 0.924; Fig. 3b). This indicated that the sex difference in the time to solve the task with the transparent barrier is likely to be due to the time the subjects spent in front of the barrier trying to pass it. In both the latter LMMs, trial had a significant effect (transparent barrier: $F_{4,88} = 9.459$, $P < 0.001$; semi-transparent barrier: $F_{4,88} = 3.542$, $P = 0.010$), but the trial × sex interaction was not significant (transparent barrier: $F_{4,88} = 0.661$, $P = 0.621$; semi-transparent barrier: $F_{4,88} = 0.244$, $P = 0.913$).

Experiment 2 – Route learning

The GLMM conducted on the accuracy revealed no significant effect of trial ($\chi^2_4 = 6.753$, $P = 0.150$) or sector ($\chi^2_1 = 0.011$, $P = 0.915$). Sex had a significant effect on the model ($\chi^2_1 = 4.184$, $P = 0.041$), indicating that male accuracy was higher than female accuracy (Fig. 4a). However, there was also a significant trial × sex interaction ($\chi^2_4 = 11.846$, $P = 0.019$). We therefore ran two GLMMs for males and females separately. Trial had a significant effect for males ($\chi^2_4 = 14.447$, $P = 0.006$), but not for females ($\chi^2_4 = 3.784$, $P = 0.436$). In both these GLMMs, the effect of sector was not significant (males: $\chi^2_1 = 0.172$, $P = 0.678$; females: $\chi^2_1 = 0.281$, $P = 0.596$), nor was the trial × sector interaction (males: $\chi^2_4 = 2.669$, $P = 0.615$; females: $\chi^2_4 = 2.023$, $P = 0.732$). A GLMM fitted on data of males from trial 1 to trial 2, found a significant effect of trial ($\chi^2_1 = 6.840$, $P = 0.009$), indicating that males increased their accuracy already in the second trial. Overall accuracy (calculated on trials 2 to 5) was significantly greater than chance for males (68.75 ± 16.48%; $t_{23} = 4.754$, $P < 0.001$) but not for females (54.69 ± 21.43%; $t_{23} = 1.047$, $P = 0.306$).

The LMM on the time to solve the task revealed a significant effect of trial ($F_{4,184} = 6.896$, $P < 0.001$). Sex and trial × sex interaction had no significant effect in the LMM ($F_{1,46} = 2.092$, $P = 0.155$ and $F_{4,184} = 0.705$, $P = 0.590$, respectively; Fig 4b), suggesting that males and females did not differ regarding the time required to solve the task.

DISCUSSION

Research on mammals, birds and reptiles suggests that sex differences in spatial abilities may evolve when males and females show different ecological demand for the use of space. In this study, we found partial support for this hypothesis in a fish. Male guppies, which live in a more complex environment and range more than females, performed better in a route learning spatial task (experiment 2). However, in a simple detour task we did not find evidence of better male performance; in one condition, males performed worse than females.

In experiment 1, we tested male and female guppies for their ability to learn to detour around a barrier to reach a goal that was visible behind it. When the barrier was semi-transparent—making the obstacle evident—we found no performance difference between the two sexes; a rapid decrease in the time needed to pass the barrier indicated that both males and females easily learned the task. A clear sex difference has emerged, however, when guppies had to detour around a totally transparent barrier. Here, males took more than three times longer than females to solve the task, a difference that was particularly marked in the first trial.

Detour behaviour has been studied in a large number of organisms including children, monkeys, dogs, birds, frogs and fish (e.g. Collet, 1982; McKenzie & Bigelow, 1986; Regolin, Vallortigara, & Zanforlin, 1995; Schiller, 1949; Taylor et al., 1990; Zucca, Antonelli, Vallortigara, 2005). In general, improvement of performance can be observed over the course of the trials but there are exceptions (Zucca et al., 2005). Sometimes individual differences have been reported. For example, only one out of four quokkas, *Setonix brachyurus*, that were tested in a detour task showed improvement over repeated trials (Wynnie & Leguet, 2004). Very few investigations have looked at sex differences in detour tasks. A study of 10-, 12- and 14-month-old children found a clear effect of age but no effect of sex in detouring around a barrier to reach the mother (McKenzie & Bigelow, 1986). Sex differences have been observed in domestic chicks, *Gallus gallus domesticus*, but they seem to be due to the type of reward used rather than to spatial skills. Males have been observed to be better than females when the target was conspecifics, but the reverse occurred when food was the target (Vallortigara, Cailotto, & Zanforlin, 1990).

For a fish, the ability to detour around a visible obstacle to reach a goal is likely to be exploited continuously in the natural environment, such as when it has to reach a refuge, a foraging patch, prey or social companions, or when it has to navigate around a rival to reach a potential mate. It would not be surprising that this simple navigation system had evolved early in vertebrates, and consequently is common in males and females as suggested by our data on guppies with the semi-transparent barrier.

The explanation of the differences observed in the condition with the transparent barrier is less straightforward. Low performance with the transparent barrier has been documented in other species, including primates (Taylor et al., 1990). In some cases, such as for herring gulls, *Larus cachinnans*, the animal failed to solve this task (Zucca et al., 2005). What is the cause of this difficulty? A detailed analysis of our data revealed that the poor male performance with the transparent barrier is largely due to the fact that they spent a lot of time trying to pass through the barrier rather than detour around it. Although it is commonly used in the literature, the transparent barrier is a condition that animals never experience in nature. The ecological relevance of this test may be limited, especially regarding the measure of spatial abilities.

As indicated by other lines of investigation (Hernik & Southgate, 2012; Jentsch, Roth, & Taylor, 2000; Thompson, Harmon, & Yu, 1984), the capacity to detour around a transparent barrier may reflect the level of persistence and cognitive flexibility of an animal. In this view, our result with the transparent barrier might be due to a greater persistence of male guppies, rather than to reduced spatial abilities. A similar result has been previously found in this species with a reversal learning experiment. Lucon-Xiccato and Bisazza (2014) trained to criterion male and female guppies to select one of two colour options to obtain a food reward and then reversed the reward contingency. Females rapidly learned to select the newly rewarded colour, but males persisted much longer in choosing the previously rewarded option. There is evidence of increased male persistence also in pig-tailed macaques, rats and chicks (Guillamón, Valencia, Calés, & Segovia, 1986; Ha, Mandell, & Gray, 2011; Rogers, 1974). Although the evolutionary and proximate causes are still not clear, our finding aligns with a previous hypothesis suggesting that greater male persistence may be selected in polygynous species as it helps males to overcome females resistance to mate (Rowe, Cameron, & Day, 2005; Lucon-Xiccato & Bisazza, 2014).

In experiment 2, using a more complex route learning task, we found that males solved the problem in the five trials allowed whereas females' performance did not differ from chance. Before concluding that this sex difference in performance is due to greater male spatial ability, we should consider an alternative explanation. Male superiority might be due to greater general learning abilities compared to females. Although our results do not allow us to disentangle these two possibilities, the available literature on cognitive sex differences in guppies suggests the absence of a difference in general learning abilities between the two sexes. In four different experiments that involved learning in contexts other than spatial, males and females showed an almost identical learning performance (Lucon-Xiccato & Bisazza, 2014; Lucon-Xiccato & Bisazza, 2016); a sex differences favouring females has emerged only in one experiment on a very particular type of learning, the reversal learning (Lucon-Xiccato & Bisazza, 2014).

Therefore, our results are more likely to be due to a sex difference in spatial abilities. The direction of this sex difference is apparently in line with the initial hypothesis underpinning this work: enhanced spatial abilities are selected for in the sex with the greater ecological demand for spatial cognition. Male guppies live in a more spatially complex environment and tend to disperse farther than females (Croft et al., 2003; Croft et al., 2004; Croft et al., 2006; Darden & Croft, 2008; Griffiths & Magurran, 1998). Therefore, males are expected to be selected for greater spatial abilities.

The analysis on performance in trial 1 and trial 2 revealed that males' accuracy significantly increased in this interval. This is suggestive of one-trial learning of the route to the goal zone, as previously found in other fish (Cognato et al., 2012). One-trial learning is commonly associated to the reaction to dangerous situations. Rapidly learn how to avoid a predator, for example, is essential to survive during successive encounters (Ferrari, Wisenden, & Chivers, 2010). In our experiment, we tested guppies in a tank that was unfamiliar and thus likely perceived as dangerous; therefore, it is possible that males exploited one-trial learning to memorise the position of the safe goal zone. Since male guppies tend to live near the shoreline where cover is more abundant whereas females tend to live in open deep waters (Croft et al., 2006; Darden & Croft, 2008), one-trial learning of safe refuges is likely to be an effective strategy to cope with predation risk only for males. Females are expected to cope with predation risk with other strategies, such as shoaling. In line with this idea, a recent work found that female guppies outperform males in a cognitive task that required to discriminate the larger between two different shoals (Lucon-Xiccato et al., 2016).

Although males' level of accuracy remained above that of females until the fourth trial, it appeared to decrease after the initial peak. This counterintuitive finding might be explained with a change in the motivation to flee due to habituation to the testing tank. This effect is typical of studies that exploit the reaction of fish to novel environments. For example, Sovrano and colleagues (2003) trained redtail splitfin to choose the correct door of a maze to exit from an unfamiliar environment and join a group of conspecifics, a set up similar to ours. They found that the frequency of attempts to enter a door decreased over trials indicating habituation to the testing tank. In guppies and sticklebacks, *Gasterosteus aculeatus*, social motivation deriving from the exposure to an unfamiliar tank decreases with time (Thünken, Eigster, & Frommen, 2014; Lucon-Xiccato, Dadda, Gatto, & Bisazza, submitted manuscript). Accordingly, in our experiment, after repeated trials, the tank could have become more and more familiar for the males, which may have decreased their antipredator behaviour while leading them to increase other activities, such as exploration, and to reduce the motivation to choose the correct door.

Given the greater accuracy of males, one would expect that they were also faster in reaching the goal zone compared to females. Inspection of Fig. 4b shows that, excluding the first trial, time to reach the goal zone was on average shorter for males than for females. This difference however was not significant possibly because we did not have enough statistical power. An interesting alternative is that females used a different strategy than males to solve the task, for example choosing at random between the two doors but then rapidly switching to the alternative door if the initial choice was incorrect.

In the present study, we found that male guppies outperform females in a relatively complex spatial task, whereas females showed greater cognitive flexibility in detouring a transparent obstacle, two sex differences that are similar to the ones observed in most polygynous species investigated, suggesting a common pattern of cognitive sex differences across vertebrates. Recently, several other studies have focussed on cognitive sex differences in guppies. For many of the tasks investigated, including shape discrimination learning, object recognition memory, concept learning, use of ordinal information and discrimination of food quantities, males and females showed comparable abilities (Lucon-Xiccato & Bisazza, 2014; Lucon-Xiccato & Bisazza, 2016; Lucon-Xiccato & Dadda, 2016; Lucon-Xiccato et al., 2015; Miletto Petrazzini, Lucon-Xiccato, Agrillo, & Bisazza, 2015). In a few contexts—cognitive flexibility, shoal size discrimination and social learning—females showed better performance (Lucon-Xiccato & Bisazza, 2014; Lucon-Xiccato et al., 2016; Reader & Laland, 2000). Several hypotheses have been proposed to explain why in guppies, and other species, males and females differ in some cognitive tasks but show equal performance in others, such as the existence of task-specific selective pressures, by-products of selection on other traits or functional pleiotropy of cognitive functions (e.g. Jones et al., 2003; Lucon-Xiccato et al., 2016). However, many more data on this and other species are required to formalise and test these hypotheses.

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FIGURE CAPTIONS

Figure 1.

Aerial view of the apparatuses. (a) Experiment 1 and (b) experiment 2.

Figure 2.

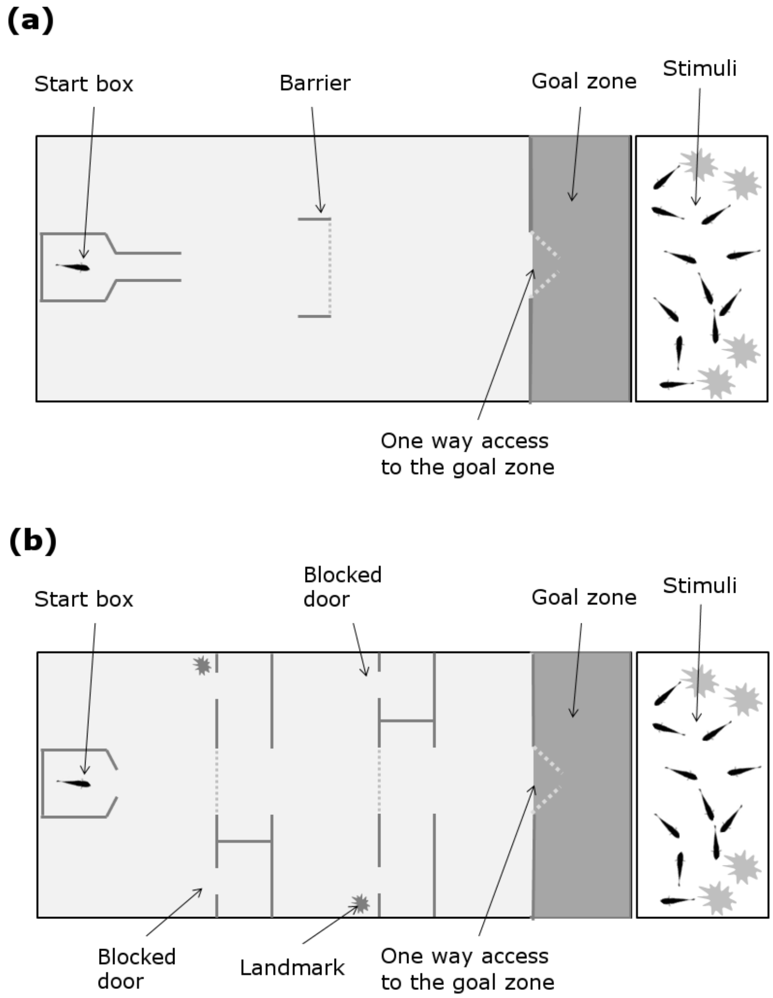
Time to solve the detour task (experiment 1) of males (grey) and females (dark). (a) Transparent barrier and (b) semi-transparent barrier. Data points represent mean ± *SEM*.

Figure 3.

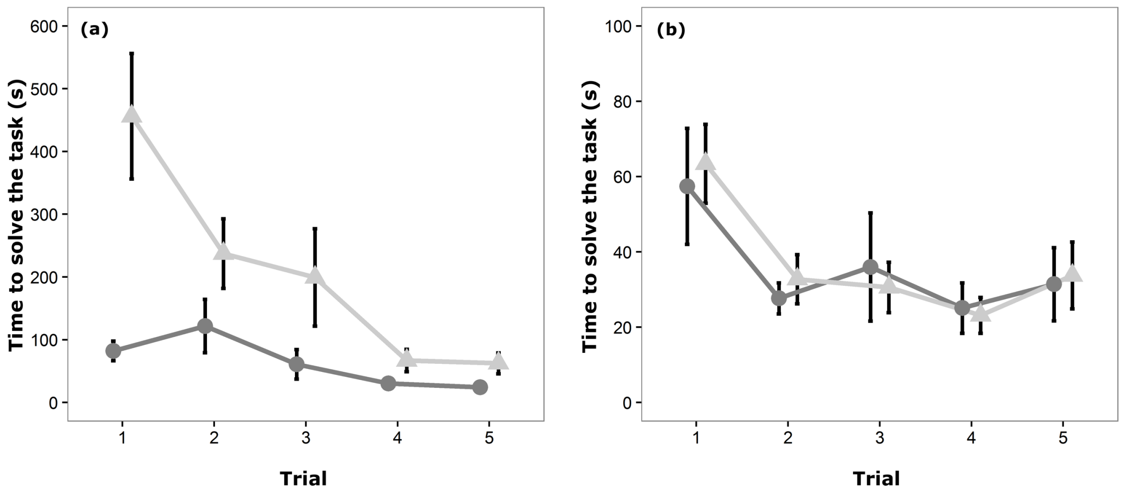
Time spent in front of the barrier in the detour task (experiment 1) of males (grey) and females (dark). (a) Transparent barrier and (b) semi-transparent barrier. Data points represent mean ± *SEM*.

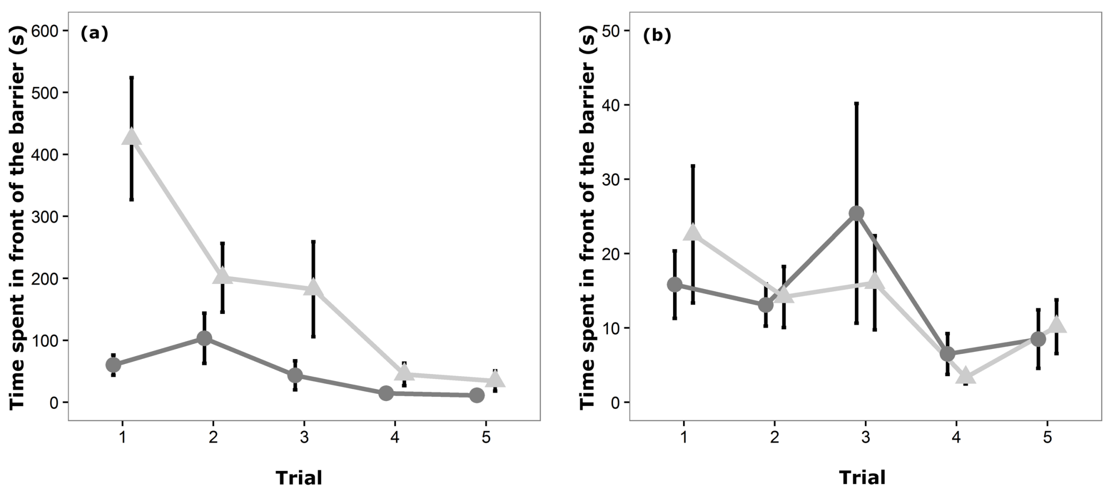
Figure 4.

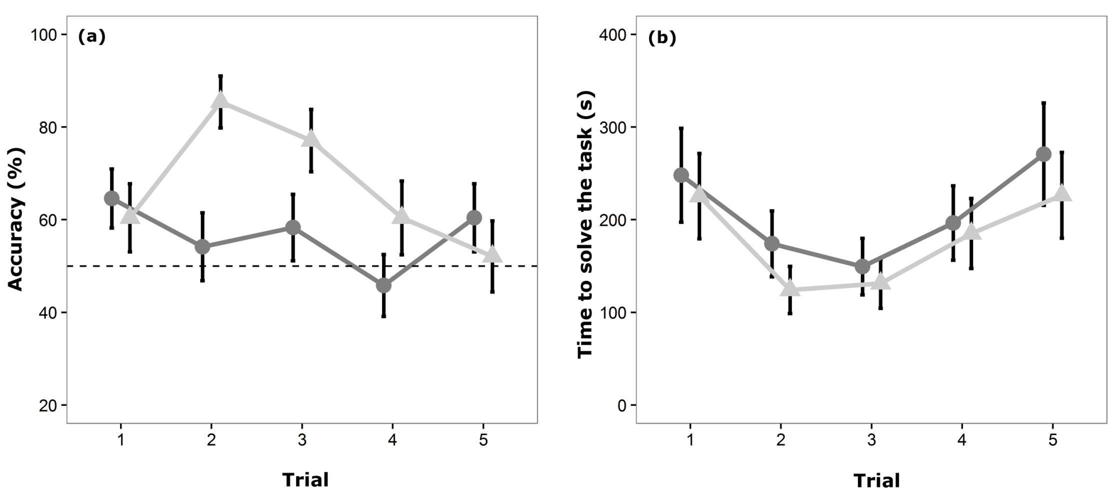
Results of experiment 2. (a) Accuracy in route learning of males (grey) and females (dark); data points represent mean ± *SEM* percentage of choice for the correct door; dashed line represents chance performance. (b) Time to solve the task of males (grey) and females (dark); data points represent mean ± *SEM*.



(a)
Start box
Barrier
Goal zone
Stimuli
One way access
to the goal zone
(b)
Start box
Blocked
door
Goal zone
Stimuli
Blocked
door
Landmark
One way access
to the goal zone


(a)
(b)
Time to solve the task (s)
Trial
600
500
400
300
200
100
0
80
60
40
20
1
2
3
4
5


(a)
(b)
Time spent in front of the barrier (s)
Trial
600
500
400
300
200
100
0
50
40
30
20
10
1
2
3
4
5


(a)
(b)
Accuracy (%)
Time to solve the task (s)
Trial
100
80
60
40
20
400
300
200
100
0
1
2
3
4
5