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RESEARCH

Individual recognition in guppies does not require large brains

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Abstract It is often assumed that group-living animals require larger brains in order to deal with the various social challenges they encounter. One such key challenge is the need to recognize and discriminate between specific group members. Individual recognition is often deemed the most cognitively demanding form of recognition. Hence, one could expect this ability to be facilitated by the evolution of larger brains. So far, this hypothesis remains largely untested. In this study, we investigated the link between relative brain size and individual recognition, using Trinidadian guppies (*Poecilia reticulata*) from artificial selection lines for either increased or decreased relative brain size. In a first experiment, we compared the selection lines in their ability to spontaneously discriminate between a familiar and unfamiliar conspecific. In a second experiment, we actively trained guppies from the selection lines to associate a particular individual with the presence of food. Overall, we found evidence for individual recognition, confirming earlier research on this species. However, individual recognition was independent of brain size selection regime in both experiments. Guppies spontaneously recognized and preferably associated with a familiar individual. In the trained association experiment, however, fish showed no preference for either stimulus fish. Our study suggests that although small fishes like the guppy are capable of individual recognition, larger brains do not necessarily facilitate this ability. Our study demonstrates that to fully understand the link between sociality and cognition, one needs to verify which exact social challenges require the evolution of larger brains.

Significance statement Living in a group is a complex challenge, and is thus said to require relatively large brains. Despite this assumption, there is very little known about which particular aspects of group-living are actually cognitively demanding to a degree that they require a higher investment in brain tissue. Here, we tested the specific hypothesis that the ability to recognize and remember specific individuals, i.e. individual recognition, a keystone of sociality, is cognitively challenging by comparing guppies with known differences in relative brain size in their ability to recognize a familiar shoal-member and learn the difference between two new individuals. Although guppies demonstrated individual recognition, relative brain size did not affect their performance. Our results provide valuable insights in the evolution of sociality and its link with relative brain size.

Keywords Social Brain Hypothesis · Familiarity · *Poecilia reticulata* · Associative learning · Social preferences

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Introduction

Sociality can be a complicated undertaking. Group-living animals may face a multitude of challenges, e.g. the need to remember and maintain multiple relationships, keeping track of intra- and intergroup individuals, and predicting and manipulating the behavior of others (Dunbar 1998; Holekamp 2006; Speechley et al. 2024). It has often been postulated that to deal with such social challenges, group-living animals, especially those in complex social systems, require advanced cognitive skills and, therefore, larger brains (known as the Social Intelligence or Social Brain Hypothesis: Humphrey 1976; Dunbar 1992, 1998; Holekamp 2006). However, evidence for the Social Brain Hypothesis is mixed, as comparative research on various taxa has both supported (see e.g. Dunbar 1998; Perez-Barberia et al. 2007; van der Bijl and Kolm 2016; Street et al. 2017; Triki et al. 2019) and failed to confirm its predictions (e.g. Benson-Amram et al. 2016; Reddon et al. 2016; DeCasien et al. 2017). One possible explanation for these inconsistent results is that we lack a proper understanding of what makes group living cognitively demanding (Dunbar 2009; van der Bijl and Kolm 2016; Tumulty et al. 2023; Speechley et al. 2024). In other words, what specific social challenges require the evolution of larger brains?

One fundamental challenge for group-living animals is to recognize and discriminate between specific individual group members. Individual recognition is considered essential in maintaining coherent and stable social groups, reducing the cost of agonistic interactions, and developing differentiated social relationships (Tibbetts and Sheehan 2013; Kohda et al. 2015; Tumulty et al. 2023). It is thus potentially an important factor behind the evolution of cooperation (Crowley et al. 1996; Tumulty et al. 2023). For instance, Trinidadian guppies (*Poecilia reticulata*) and sticklebacks (*Gasterosteus aculeatus*) remember the predator inspection behavior of individual conspecifics, and preferably associate with better inspectors (Milinski et al. 1990; Dugatkin and Alfieri 1991). Although widespread across the animal kingdom (e.g. in reptiles: Carazo et al. 2008; arthropods: Tibbetts and Sheehan 2013; fish: Kohda et al. 2015; mammals: Gilfillan et al. 2016), individual recognition varies both across and within species (Gronenberg et al. 2008; Tibbetts and Sheehan 2013; Tumulty et al. 2023), and is typically assumed to be more developed in social taxa (Tibbetts and Dale 2007; Tumulty et al. 2023). Compared to more basic class-level recognition, where individuals use broad group-like characteristics to distinguish between classes (Ward et al. 2020), individual recognition requires animals to learn unique characteristics of conspecifics (visual, auditory, chemical or a combination thereof, Yorzinski 2017), remember them for extended periods of time (Tibbetts and Sheehan 2013) and use this to show individual-specific responses (Tibbetts and Dale 2007). Consequentially, individual recognition is considered the most cognitively challenging and complex form of recognition and is assumed to be costly (Tibbetts and Dale 2007; Tibbetts and Sheehan 2013; Yorzinski 2017; Ward et al. 2020; Tumulty et al. 2023).

Therefore, one could expect – in line with the Social Brain Hypothesis – that the emergence of individual recognition requires the evolution of higher information-processing capacity and thus, relatively larger brains with more neurons (Marhounova et al. 2019). However, so far there are hardly any studies that have tested whether relatively larger brains are necessary to facilitate individual recognition. The only study tackling this question found no differences in the size of the whole brain, nor of the visual centers, between paper wasp species (*Polistes* sp.) with and without face recognition (Gronenberg et al. 2008), suggesting that this ability could evolve without substantial neural investments. Till now, the cognitive costs of individual recognition remain unexplored in other taxa (Yorzinski 2017).

Here, we test the hypothesis that individual recognition is facilitated by relatively larger brains, using Trinidadian guppies selectively bred for small or large relative brain size (Kotrschal et al. 2013). Wild guppies typically forage in small shoals ranging from two to 50 members, in a highly dynamic fission–fusion system (Croft et al. 2003). Female and juvenile guppies are capable of individual recognition; they preferably associate with familiar individuals (e.g. Magurran et al. 1994; Griffiths and Magurran 1997b, 1998, 1999; Sievers and Magurran 2011; Cattelan et al. 2019) and females remember group members even after several weeks of separation (Bhat and Magurran 2006). Male guppies show no preference for shoal-mates when wild-caught, likely due to their more dynamic shoal-shifting (Griffiths and Magurran 1998), but they develop such preferences after ‘forced’ familiarization with other males in captivity (Croft et al. 2004) and in the lab they retain specific information about particular conspecifics, such as their past cooperation in predator inspector trials, and adjust their behavior accordingly (Dugatkin and Alfieri 1991). Despite the fission–fusion dynamics, wild female guppies are known to form stable social interactions with specific shoal-members over extended time periods (> 10 days) which go beyond simple morphological assortment (Croft et al. 2005a, b). Furthermore, during periods of drought, rivers inhabited by guppies may shrink to a series of isolated pools, in which confined guppies are known to develop familiarity (Kelley et al. 1999). Lab-experiments have also shown that familiarity decreases aggression between male guppies, presumably due to the establishment of social status (Price and Rodd 2006; Sogawa et al. 2023). Furthermore, familiarity makes female guppies more likely to cooperate in risky predator inspections and increases the degree of cooperation while doing so (Croft et al. 2005a), facilitates social learning of a novel foraging behavior (Swaney et al. 2001), and increases shoal cohesiveness thus facilitating efficient antipredator behavior (Davis et al. 2017). In a mating context, guppies also prefer unfamiliar mates (Kelley et al. 1999; Mariette et al. 2010). These examples demonstrate that the ability to recognize specific individuals likely has important fitness-consequences for guppies in nature.

Here, we tested guppies' ability to discriminate between individual conspecifics both spontaneously and after active training. Based on the putative high cognitive demand of individual recognition (Ward et al. 2020; Tumulty et al. 2023) we expect that fish with relatively larger brains would demonstrate greater individual recognition abilities.

Methods

Study species and set-up

We used guppies taken from the ninth generation of an artificial selection experiment for relative brain size, which is explained in greater detail in Kotrschal et al. (2013). Briefly, selection lines were established from three independent stocks ('replicates') of wild-type guppies. In each of these, an up- and down-selected line was created by only retaining the offspring of parents with the largest and smallest brains respectively, corrected for body size. By the fifth generation, up- and down-selected lines differed approximately 15.4% in relative brain size and 11.9% in relative neuron number. More details on the differences between these selection lines can be found in Kotrschal et al. (2017) and Marhounova et al. (2019). Associated changes in cognitive performance are also well-established between these lines (see e.g. Kotrschal et al. 2013; Kotrschal et al. 2015; Buechel et al. 2018). Guppies in this study have gone through active selection from the first till the fourth generation, and on the seventh generation, with rounds of random breeding in between. In total, 108 fish were used as focal individuals in the experiments, selected from both sexes and all brain size selection lines, and ranging in age from 16 to 22 months old. In addition, 96 fish from the same selection lines, and 120 wild-type guppies were used as stimulus fish. Prior to the experiments, the guppies had been housed in 7 L tanks enriched with java moss, in groups ranging from six to twelve same-sex individuals, and were fed six times per week with either commercial flakes or freshly hatched *Artemia* sp.

To test the link between relative brain size and individual recognition, we conducted two separate binary-preference experiments. These are standard protocols to measure social preference in guppies (see e.g. Griffiths and Magurran 1997b; Bhat and Magurran 2006; Corral-Lopez et al. 2017; Cattelan et al. 2019). First, we tested whether guppies (N = 48, equally divided over sex, selection line and replicate) with divergent brain sizes would differ in their ability to spontaneously recognize a familiar conspecific with whom they had been housed together for more than one year. Guppies typically prefer to associate with familiar individuals (e.g. Griffiths and Magurran 1997b, 1999; Croft et al. 2004; Bhat and Magurran 2006), and these selection lines do not differ in shoaling behavior (Kotrschal et al. 2018). Hence, variation in with whom fish spent more time will likely reflect differences in the ability to recognize familiar individuals, rather than in grouping behavior. Nonetheless, to better understand the role of learning and memory in preference for familiar individuals, we conducted a second experiment in which we actively trained fish (N = 60, equally divided over sex, selection line and replicate), to associate with one new individual over another. Experiments were conducted from May until June 2023 in several batches (two per experiment). For logistic reasons, experiments were conducted in two separate rooms simultaneously (both ~ 26 °C and under a 12:12 light–dark cycle). The person collecting and analyzing the data was blind to the identity of both the stimuli and focal fish, in order to minimize observer bias.

Spontaneous choice experiment

In the first experiment, fish were tested on their ability to spontaneously discriminate between a familiar and unfamiliar conspecific in a binary-preference test (cfr. Bhat and Magurran 2006; Corral-Lopez et al. 2017; Cattelan et al. 2019). Fish were taken from same-sex groups consisting of up to twelve males and nine females respectively, separated by replicate and selection line. These groups had been housed together for at least one year prior to the start of the experiment, giving fish ample time to familiarize (Griffiths and Magurran 1997b; Croft et al. 2004; Bhat and Magurran 2006; Sievers and Magurran 2011). Focal fish were housed individually in medium-sized (7 L) tank facing two smaller (3 L tanks) with one stimulus fish each: a 'familiar' fish, from the same tank as the focal fish, and an 'unfamiliar' fish from a different tank. One challenge in familiarity-experiments is to know whether individuals show individual recognition, or classify conspecifics as familiar versus unfamiliar based on general group-like characteristics ('class-level recognition') (Tibbetts and Dale 2007; Yorzinski 2017; Ward et al. 2020). Examples of the later include e.g. similarity in phenotypes, context-based cues or chemical cues indicating shared habitat/diet or relatedness (Ward et al. 2004, 2009, 2020; Webster et al. 2008). As familiar and unfamiliar fish belonged to the same replicate, sex and age, the chances of phenotype matching were minimized. Since focal and stimuli fish were placed in separate tanks, all in a new environment, we also eliminated possible context-based and chemical cues that could have facilitated such class-level recognition. While this meant that guppies had access to visual cues only, previous research has shown that those alone are sufficient to allow guppies to recognize familiar individuals (Griffiths and Magurran 1999; Sogawa et al. 2023). Note that this experiment did not allow us to establish whether fish showed ‘true individual recognition’ (TIR) *senso stricto*, as this would require demonstrating that individuals retained specific information of specific individuals (Tibbetts and Dale 2007; Saeki et al. 2018). However, as the chances that fish were using group-based characteristics were minimized, we believe that any discrimination between familiar and unfamiliar fish in this experiment would likely be based on individual-based characteristics and should, in line with Steiger and Müller (2008), be considered as a form of individual recognition. We hence refer to it as such throughout this study.

The side on which the familiar individual was presented was counterbalanced. All tanks contained a ~ 1 cm layer of white gravel, a plastic plant (either left or right, randomized, in the tank for easier anchoring) and a tube for aeration. The walls of the tank were opaque except for the contact zone between focal and stimuli fish (Fig. 1). A set-up to hold a camera was always present above the focal tank.

Fish were habituated to the experimental tanks for 24 h during which visual contact between tanks was blocked with an opaque divider. Thereafter, we removed the divider and allowed the focal fish to socialize with the stimulus fish for ten minutes. All trials were filmed from above (GoPro HERO 5 Black) for subsequent behavioral scoring (see below).

Trained association experiment

In the second experiment, fish were actively trained to discriminate between two conspecifics. The experimental set-up was similar to the spontaneous choice experiment. Focal fish were collected from the selection lines, but stimuli fish (N = 120) were wild-type guppies, both completely new to the focal individual. Stimulus fish were the same sex as their focal fish. Petri dishes (⌀ 5.5 cm) were placed on both sides of the contact zones (Fig. 1). Fish were habituated to the

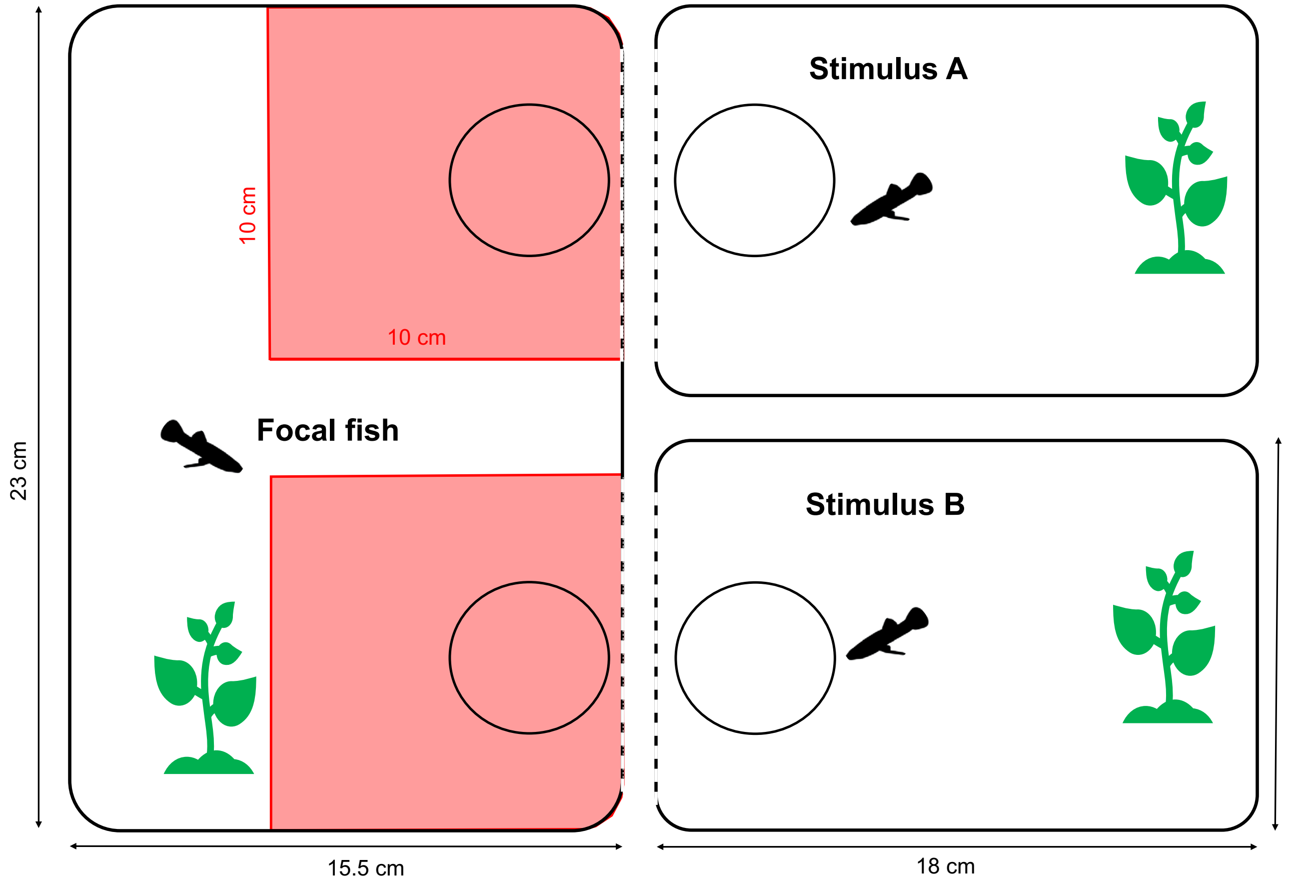

Fig. 1 Experimental set-up for the binary preference test. Choice zones are indicated in red. Black circles represent the petri dishes in the trained association experiment. Dotted lines indicate the visual contact zones

experimental tanks for three days prior to the start of the experiment.

In order to train fish, we would consistently feed the focal fish in front of the same stimulus individual. This way, the focal fish was expected to associate the presence of this specific individual with receiving food. Training took place over seven days, with a break during the weekends, meaning that focal fish could familiarize over the course of twelve days, which was shown to be an adequate time frame in previous studies on guppies (Griffiths and Magurran 1997b; Croft et al. 2004; Sievers and Magurran 2011). Ten minutes before a feeding session, an opaque divider was placed between focal and stimuli fish, to provide a clear signal of when a feeding was about to start. After the divider was removed, food (a pastry mix of pulverized flakes) was pipetted in the petri dish close to the 'rewarded' individual. The petri dish near the 'unrewarded' individual was left empty. Stimuli fish were fed at the same time, to make sure that focal and stimuli fish were close to each other while feeding. Training sessions lasted one hour, after which food leftovers were removed. Fish were trained three times per day, with two hours in between consecutive sessions, so for a total of 21 sessions. To avoid spatial learning, the stimuli tanks, and thus the side where focal fish feeding took place, were switched daily after the second session.

On the eighth day, all focal fish were tested on their preference for either stimulus fish during a final experimental trial. The trial followed the same procedure as the feeding sessions, but this time no food was delivered in the petri dishes. Fish were then filmed for ten minutes. Videos were scored afterwards to see near which individual the focal fish spent more time (see further).

Size measurement of stimulus fish

Upon completion of the trials, stimulus fish were either anesthetized (spontaneous choice experiment) or euthanized (trained association experiment) with an appropriate dose of benzocaine and photographed from both sides with a Nikon D5300 camera to measure individual body length with ImageJ (v1. 54d) (Schneider et al. 2012). All focal fish and stimulus fish from experiment 1 were translocated back to group tanks for re-use and breeding purposes. Stimulus fish from experiment 2 were euthanized due to their advanced age.

Video scoring

Video recordings were analyzed with the BORIS (v. 8.19.3) software (Friard and Gamba 2016). In the videos, the focal tanks were divided in three zones: two choice-zones (i.e. 10 × 10 cm squares adjacent to the contact zones) and one neutral zone (i.e. the remainder of the tank) (Fig. 1). We then scored how much time focal fish spent in each zone, as spatial proximity is a standard measure of social associations (Cattelan et al. 2019). We also counted how many times focal fish visited a choice zone as a measure of sampling behavior.

All videos were scored by the same observer, who was blind to the identity of focal and stimuli fish. As guppies' social preferences can change over time (Corral-Lopez et al. 2017), videos were scored both for the whole ten minutes, and for the first and last five minutes separately. Behavioral scores in the last five minutes were calculated by subtracting the scores in the latter from the scores in the former. In total, data for five individuals (all small-brained males) were lost, one from the spontaneous choice task and four from the trained association experiment due to various reasons (i.e. stimulus fish jumping out, corrupted files, or scoring errors resulting in inconsistent times).

Statistical analyses

Data were analyzed in three different time intervals: the first five minutes, the last five minutes, and the whole ten-minute trial. Per time interval, we scored each focal individual's preference, by calculating the difference in time spent with each stimulus fish and dividing it by the total amount of time in the choice zones (Corral-Lopez et al. 2017):

$$\frac{Time_{\text{Familiar}} - Time_{\text{Unfamiliar}}}{Time_{\text{Familiar}} + Time_{\text{Unfamiliar}}} \quad \text{or} \quad \frac{Time_{\text{Rewarded}} - Time_{\text{Unrewarded}}}{Time_{\text{Rewarded}} + Time_{\text{Unrewarded}}}$$

A preference ratio score of zero indicates that the focal fish spent an equal amount of time with both options, while scores closer to 1 or -1 indicate a preference for the familiar/rewarded fish and unfamiliar/unrewarded fish respectively. Fish that did not visit any of the choice zones were assigned an 'NA' value. As some fish took more than five minutes to leave the neutral zone, sample sizes vary per time interval ($N_{\text{spontaneous choice}} = 42 - 44$, $N_{\text{trained association}} = 52 - 56$).

Data were analyzed using linear models (LMs). First, to investigate whether preference differed from chance, we ran a series of null models per experiment and per time interval, with the preference ratio scores as response variables, and tested whether the intercept differed from zero. Next, we tested the effect of relative brain size on individual recognition, by constructing a series of LMs with the preference ratio score as response variable, and selection line (large versus small-brained), sex (male versus female) and their interaction as fixed effects. The side of the familiar/rewarded individual (left versus right) was included as an additional fixed effect. To control for the possibility that fish preferred the side with the plastic plant (even though it was outside the choice zones), we added the side of the plant (unfamiliar/unrewarded versus familiar/rewarded) as a fixed effect to the model. Batch, replicate and experimental room were also included as controlling variables, but stepwise removed (backward) from the model in case of non-significance. Lastly, we wanted to control for potential dominance effects. To do so, we calculated the relative size difference between the familiar/rewarded and unfamiliar/unrewarded stimulus fish (with positive scores indicating that the familiar/rewarded fish was the larger one of the two) and included this as a covariate in the models. Separate models were run for each experiment and for each of the three time intervals. Non-significant interactions were removed from the model, but only if exclusion improved or did not change the model fit based on Akaike's information criterion ($\Delta AIC < 2$) (Bolker 2008; Symonds and Moussalli 2011; Gaudreau 2012). Otherwise, no predictors were eliminated (see Table S1-S2).

Next, we tested whether the first choice of the fish (1 = familiar/rewarded fish, 0 = unfamiliar/unrewarded fish) differed between selection lines and sexes, by constructing two generalized linear models (GLMs, one for each experiment) with identical model structure as the aforementioned LMs.

Finally, we wanted to know whether fish differed in how much they sampled both options, i.e. the number of visits to both choice zones. Sampling behavior was analyzed using a series of GLMs with a negative binomial distribution ('MASS' package, Venables and Ripley 2002). The same predictors were included as in the previous models, with the exception that we now included the size difference between the largest and smallest stimulus fish as additional covariate (as fish may require more sampling if both options are closer in size, regardless of the direction). Data from fish that did not sample (did not visit or change choice zone within a time interval) were not included in these analyses.

All models were run in R version 4.2.1 (R Core Team 2022). Model assumptions were checked using the 'performance' package (Lüdecke et al. 2021) and data was Box Cox- or arcsine transformed where required. Arcsine-transformation was necessary for some of the null models as logit- or logistic regressions are not possible with negative proportional data. Significance was tested using the 'Anova' function ('car' package, Fox and Weisberg 2019) based on F- or Wald Chi-square tests, and post-hoc tests to compare groups were conducted with the 'emmeans' package, using the Tukey-adjustment for multiple testing (Lenth et al. 2019). As the preference-ratio and sampling data were tested repeatedly in three time intervals, we performed p-value adjustment for multiple testing on the final models following the Benjamini & Hochberg procedure (Benjamini and Hochberg 1995). Full model outcomes are presented in Supplementary Tables S1–S2.

Results

Spontaneous choice experiment

Overall, we found evidence that guppies discriminated between familiar and unfamiliar conspecifics. Initially, during the first five minutes, preference did not differ from random (null model intercept ± SE = 0.158 ± 0.129, $F_{1,41} = 1.510$, $p = 0.226$), showing that an equal amount of time was spent with both stimulus fish. However, preference ratios were significantly higher than zero, i.e. fish spent more time with the familiar conspecific, during the last five minutes (0.161 ± 0.078, $F_{1,43} = 4.253$, $p = 0.045$) and when looking at the whole ten minutes (0.144 ± 0.069, $F_{1,43} = 4.373$, $p = 0.042$) (Fig. 2a). The ability to recognize familiar individuals was unaffected by relative brain size, as the two selection lines did not differ in preference ratio scores within any timeframe (all $p_{adj} > 0.1$), regardless of their sex (all $p > 0.1$, Table S1, $N_{\text{large brain}} = 22–23$, $N_{\text{small brain}} = 20–21$). Preference did not differ between sexes (all $p_{adj} > 0.1$, Table S1, $N_{\text{female}} = 20–21$, $N_{\text{male}} = 22–23$). Similarly, first choice was neither predicted by selection line ($\chi^2_1 = 0.105$, $p = 0.745$), sex ($\chi^2_1 = 0.064$, $p = 0.8$) or their interaction ($\chi^2_1 = 0.058$, $p = 0.809$). During the first five minutes, we observed higher preferences for the familiar fish, if it was presented on the side with the plastic plant ($F_{1,36} = 13.214$, $p_{adj} = 0.004$). In the last five minutes, such side-biases were not observed (all $p_{adj} > 0.1$, Table S1). Size differences between stimulus fish did not affect preferences (all $p_{adj} > 0.1$, Table S1).

Brain size did not affect sampling behavior within any time interval (all $p_{adj} > 0.1$, Table S1). In contrast, there was a much stronger sex-effect. Males sampled more frequently than females in the whole ten-minute trial ($\chi^2_1 = 6.477$, $p_{adj} = 0.044$), particularly in the first ($\chi^2_1 = 9.591$, $p_{adj} = 0.012$) but not the last five minutes ($\chi^2_1 = 3.171$, $p_{adj} = 0.112$) (Fig. 3). Size-differences between stimuli fish did not affect sampling behavior (all $p_{adj} > 0.1$, Table S1).

Trained association experiment

During the trained association experiment, we found no evidence for individual discrimination. Within the first five minutes, the preference ratio was marginally lower than zero, showing that fish tended to associate more with the 'unrewarded' companion, but this was non-significant (null model intercept ± SE: –0.237 ± 0.120, $F_{1,54} = 3.904$, $p = 0.053$; Fig. 2b). This effect was also mostly pronounced within the second batch ($F_{1,48} = 5.365$, $p = 0.025$; batch 1 intercept: 0.026 ± 0.111, $p = 0.815$; batch 2 intercept: –0.355 ± 0.116, $p = 0.004$). Preference ratios were not different from chance in the last five minutes (0.013 ± 0.107, $F_{1,55} = 0.014$, $p = 0.908$) or the whole ten-minute trial

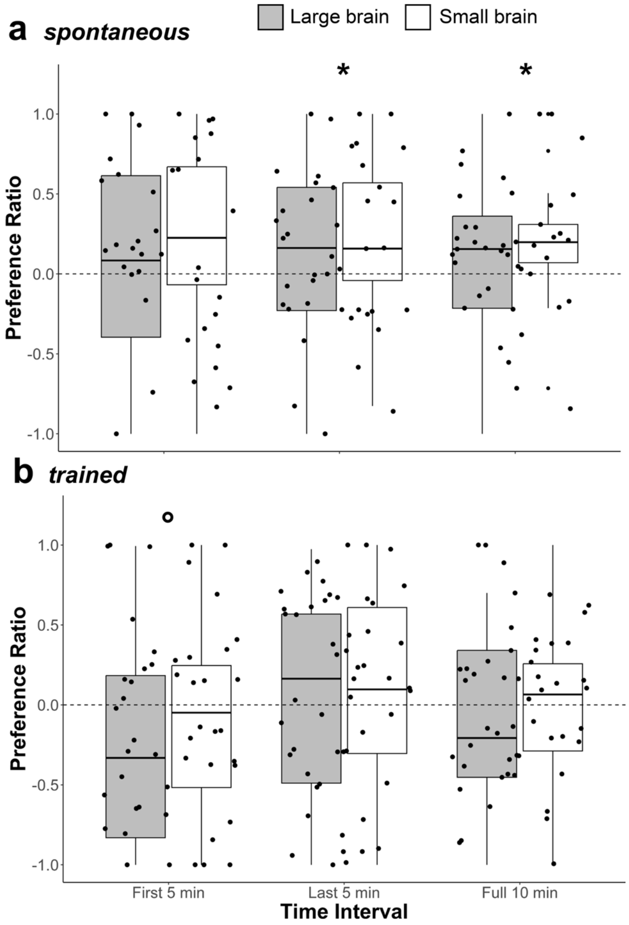

Fig. 2 Preference ratio scores per time interval for **a**) the spontaneous choice ($N=42$–44) and **b**) the trained association experiment ($N=55$–56). Boxes show the inter quartile range (IQR), with the central lines indicating the medians and the whiskers extending to 1.5 times the IQR. Grey indicates large-brained fish, white indicates small-brained fish. Positive preference ratios indicate a preference for the familiar (a) and rewarded (b) stimulus fish respectively, negative scores a preference for the unfamiliar (a) and unrewarded (b) one. '*' indicates that preference scores were significantly ($p<0.05$) different from zero, as shown by the intercept in the null model, and means that fish were choosing non-randomly. '°' indicates a statistical trend ($p<0.10$) for preference scores being different from zero

(-0.059 ± 0.069, $F_{1,55}=0.752$, $p=0.390$). We also found no evidence that the preference was affected by relative brain size ($N_{\text{large brain}}=29$–$30$, $N_{\text{small brain}}=26$) or sex ($N_{\text{female}}=30$, $N_{\text{male}}=25$–26), nor by the side on which the rewarded individual or plant was presented or their size difference (all $p_{adj}>0.1$, Table S2). Lastly, first choice did not differ between selection lines or sexes either (all $p>0.1$, Table S2).

Brain size did not affect sampling within any time interval (all $p_{adj}>0.1$, Table S2). No other variables predicted sampling behavior (all $p_{adj}>0.1$, Table S2).

Discussion

Individual recognition is considered the most cognitively challenging form of recognition (Tibbetts and Dale 2007; Tibbetts and Sheehan 2013; Yorzinski 2017; Ward et al. 2020; Tumulty et al. 2023). It was therefore expected that this ability would be facilitated by the evolution of larger relative brain size. While we did find evidence that fish could recognize and discriminate between particular conspecifics, the ability to do so did not differ between selection lines.

During the spontaneous choice experiment, guppies preferred to associate with the familiar conspecific, which is in line with previous studies on this species (e.g. Magurran et al. 1994; Griffiths and Magurran 1997b, 1998, 1999; Bhat and Magurran 2006; Hain and Neff 2007; Sievers and Magurran 2011). Interestingly, this preference only developed after five minutes. This could indicate that fish require some time sampling to distinguish between familiar and unfamiliar individuals, at least when social interactions can only occur via visual cues, supporting the idea that individual recognition is cognitively challenging. Alternatively, we saw that in the first five minutes, guppies preferably spent time on the side with the plastic plant, even though the plant was not in the choice zone. This could reflect a stress response at the start of the trial, which may have slowed down the acquisition of individual recognition. This seems supported by the fact that fish sampled less during the first five minutes (mean ± SE: 6.238 ± 0.634 visits) compared to the last five minutes (8.452 ± 1.033). Importantly though, our results show that side biases are not responsible for the preference for a familiar conspecific in the last five minutes.

In the trained association experiment, there was no evidence for individual recognition, except for a small trend in the first five minutes, which was mostly pronounced in the second batch. On one hand, this could indicate that fish were unable to learn the individual identities of two conspecifics within the allocated timeframe and might require longer periods of familiarization. This is unlikely, as twelve days have consistently been shown as enough time to familiarize in guppies (Griffiths and Magurran 1997b; Croft et al. 2004; Hain and Neff 2007; Sievers and Magurran 2011). Perhaps more direct interactions are necessary to learn the (multimodal) cues required for individual recognition. Alternatively, focal fish may have been able to recognize the two stimuli fish, but failed to associate one of them with the presence of food. While fish from these selection lines are fully capable of learning discrimination tasks with food as a reward in a similar number of trials (Kotrschal et al. 2013; Buechel et al. 2018; Boussard et al. 2020), it is possible that individual discrimination of conspecifics is based on more complex characteristics, e.g.

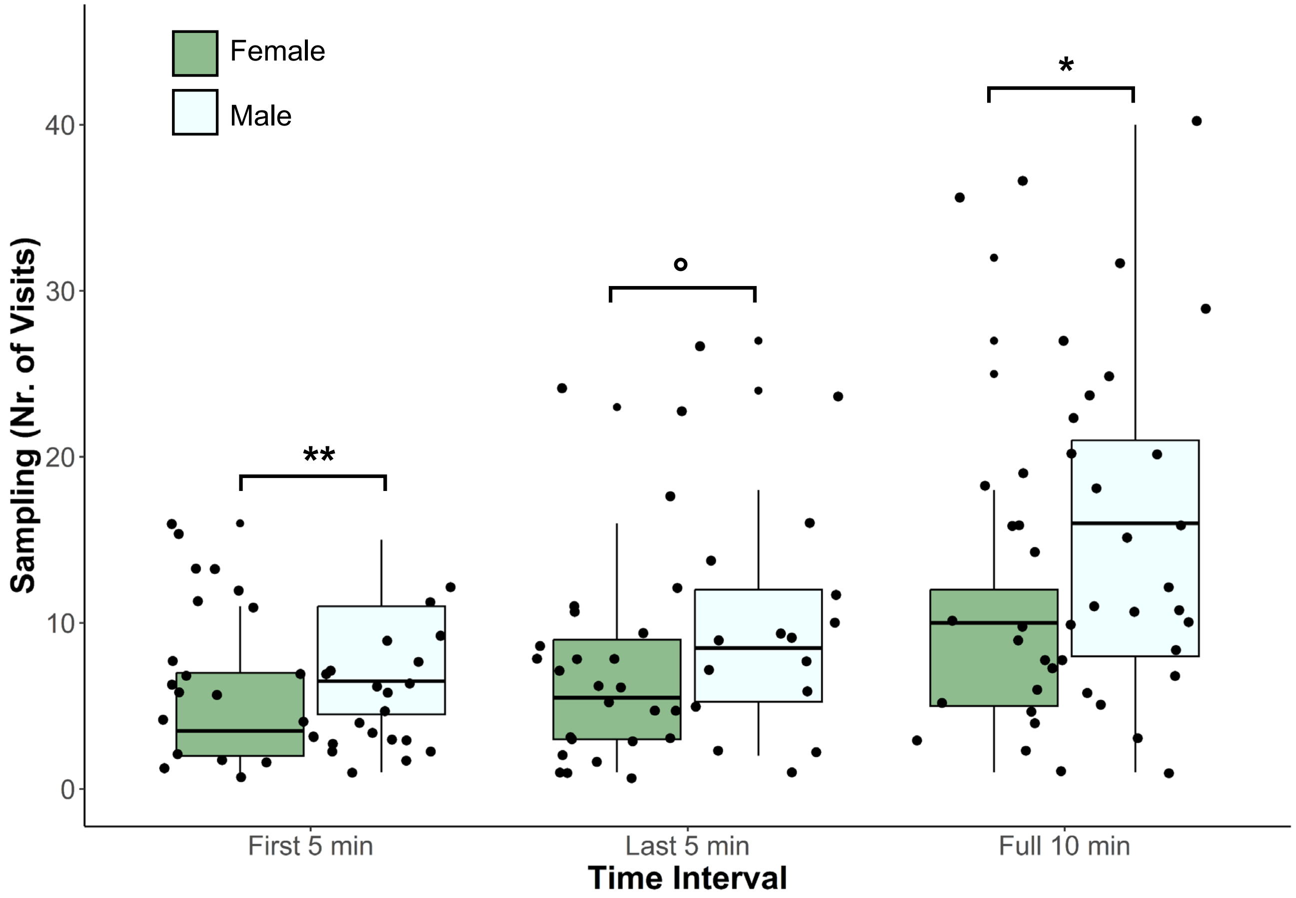

Fig. 3 Sex-differences in sampling behavior (number of visits to both choice zones) per time interval for the spontaneous choice experiment (N=42–44). Boxes show the inter quartile range (IQR), with the central lines indicating the medians and the whiskers extending to 1.5 times the IQR. Statistically significant differences are indicated as follows: '°' $p<0.10$, '*' $p<0.05$, '**' $p<0.01$

facial features (Sogawa et al. 2023), that require longer to associate with food than the simple patterns or colors typically used in (our) conditioning tasks. The apparent lack of learning is especially remarkable given that both selection lines failed to discriminate, whereas in a similar protocol (being fed in front of a stimulus), large-brained females outperformed small-brained females on a numerical discrimination task (Kotrschal et al. 2013). These results parallel those from a recent study by Pardo-Sanchez et al. (2025), where paper wasps (*P. fuscatus*) from populations differing in social complexity demonstrate clear differences in individual face learning, but not in other types of cognitive tasks. This suggests that the mechanisms to learn to recognize conspecifics are different than those involved in other learning processes both in fish and insects. Another explanation is that our focal individuals were continuously exposed to both stimuli fish, whereas in our typical learning assays stimuli are only shown when food is present. The fact that the majority of the day there was no food near the rewarded fish may have hindered the associative learning process as well. Furthermore, it is possible that competitive interactions directed at the focal fish from the stimulus fish during feeding also prevented the formation of such an association. Importantly, the lack of individual preferences was not a result of any side biases in this experiment.

Taken together, we can conclude that guppies are capable of discriminating between individual conspecifics, but only during the spontaneous choice experiment. Our results thus corroborate previous research (see e.g.Magurran et al. 1994; Griffiths and Magurran 1997b, 1998, 1999; Bhat and Magurran 2006; Sievers and Magurran 2011; but see e.g. Cattelan et al. 2019 for a counterexample). Interestingly, the overall preference for familiar individuals, while different from chance, was not very strong. This is most likely due to a large degree of interindividual variation in preferences, as also observed in previous work on guppies (Cattelan et al. 2019). Most likely individuals within each selection line still vary greatly in both their ability to remember familiar individuals and their motivation to associate with them. For example, preference for unfamiliar mates in female guppies is related to their general attraction to novelty (Lucon-Xiccato et al. 2019). Guppy personality also influences the strength and number of connections they maintain in their social network (Croft et al. 2009). As focal individuals and familiar fish were taken from larger groups, it is also possible that individuals differ in their preference for specific individuals within their previous group. Indeed, Cattelan et al. (2019) showed equitable social preferences within pairs of familiar guppies.

Surprisingly, the preference for familiar individuals did not differ between large- and small-brained guppies. This is in contrast with our initial hypothesis. Perhaps fish did not exhibit individual recognition at all, and rather relied on other, cognitively less demanding mechanisms, such as class-level recognition (Ward et al. 2004, 2020; Tibbetts and Dale 2007). In the most straightforward form of class-level recognition, animals use more general group-specific cues to distinguish one class of individuals from another (Tibbetts and Dale 2007; Ward et al. 2020). We do believe that our experimental design minimized the chances of such class-level recognition. For instance, fish may recognize familiar individuals based on context-based cues, i.e. temporal or spatial cues provided by the shared environment rather than the individual (Ward et al. 2020), but testing fish in a novel environment should have eliminated such cues. Fish may also preferably associate with familiar individuals based on phenotype matching (Engeszer et al. 2004; Croft et al. 2005b; Hain and Neff 2007), but as both stimuli fish belonged to the same age class, sex, selection line and replicate as the focal fish, we consider it highly unlikely that familiar fish would be consistently more similar to the focal fish than the unfamiliar one. Also, size differences between stimuli fish did not affect preferences, suggesting that body size was not used as a cue for familiarity. Alternatively, guppies' preference for familiar individuals could be due to a preference for individuals with whom they share environmental experiences (e.g. similar diet, habitat or even tank) (Ward et al. 2004, 2009; Webster et al. 2008). Yet, such 'environmental' matching is based on chemical cues (Ward et al. 2004, 2009), which fish in our experiment had no access to. Nevertheless, a second type of class-level recognition has been proposed in which animals can learn individual characteristics, but simply use them to categorize individuals as e.g. familiar, without retaining more specific individual information about them as is the case for 'true individual recognition' (Tibbetts and Dale 2007; Saeki et al. 2018). It is difficult to rule out this possibility in binary-preference experiments. But as explained before, it has been argued that this type of class-level recognition is essentially a form of individual recognition (Steiger and Müller 2008), and should be cognitively demanding due to the necessity to remember individual characteristics of multiple group-members. It is also important to point out that guppies have shown evidence of TIR, as they adjust their behavior during predator inspection trials based on the past behavior of their partner (Dugatkin and Alfieri 1991).

Based on these arguments, we are confident that our guppies demonstrated at least some form of individual recognition during the spontaneous choice task, yet independent of relative brain size. While somewhat surprising, our results do align with previous work on paper wasps, where species with and without face recognition do not differ in relative brain size, although the former do possess smaller olfactory centers (Gronenberg et al. 2008). Alternatively, individual recognition could be linked to the size of specific brain regions, e.g. the optic tecta, rather than the whole brain. However, in these guppy brain size selection lines, all brain regions show similar changes in size, meaning that small-brained guppies also have smaller optic tecta, relative to their body size, compared to their up-selected counterparts (Kotrschal et al. 2017).

Individual recognition is considered a cornerstone of sociality (Kohda et al. 2015; Gokcekus et al. 2021). If individual recognition does not require large neural investments, as our results together with the aforementioned paper wasp study imply, then it is possible that some sorts of group-living may evolve without the need for larger brains. This could also explain why individual recognition seems to be so widespread throughout the animal kingdom, even appearing in species with relatively small brains (Tibbetts and Sheehan 2013; Gokcekus et al. 2021). Yet, we should acknowledge that our tasks might have been relatively easy compared to individual recognition in more natural situations. Our guppies were housed with up to eleven conspecifics, while wild shoal sizes range from two to 47 individuals with quite dynamic membership (Croft et al. 2003). Preference for familiar individuals is also weaker in guppies sampled from larger populations, demonstrating that guppies can only remember a limited number of individuals (Griffiths and Magurran 1997a), although this was contradicted by a more recent study showing no effect of group size (up to 96 individuals) on the preference for unfamiliar mates (Mariette et al. 2010) (Note, however, that neither of these studies controlled for class-level recognition mechanisms). It is possible that larger brains do not facilitate the ability to discriminate between individuals per se, rather, they increase the upper limit of individuals that can be remembered. This would correspond with the traditional correlation found between forebrain size and group size in primates (Dunbar 1992, 1998) and the recently established link between population density and forebrain size and cell count in cleaner fish (*Labroides dimidiatus,* Triki et al. 2019). Our selection lines could provide an excellent opportunity to test the link between brain size and the upper limit of the number of remembered individuals experimentally. Additionally, brain size might also affect how much information of past experiences and actions can be remembered per individual, thus allowing more complex and nuanced social networks (Shultz and Dunbar 2010; Hahn et al. 2025).

We also found no differences in individual recognition between sexes. Male guppies in wild populations are relatively mobile and frequently move between shoals, and therefore have less time to familiarize with shoal mates (Griffiths and Magurran 1998). However, our results are in line with Croft et al. (2004), showing that male guppies are capable of individual recognition if they are constrained to the same group for an extended period of time. Furthermore, this is the first evidence that male and female guppies, despite their different social behavior, do not vary in individual recognition abilities.

One question we could ask is what are the mechanisms behind individual recognition in our experiment. For instance, which characteristics did they use to recognize the familiar or rewarded fish? Surprisingly, size did not play a major role. It is thus likely that guppies used other characteristics to discriminate between and recognize individuals. For instance, several fish species, including guppies, have demonstrated recognition based on facial features (e.g. Kohda et al. 2015; Wang and Takeuchi 2017; Sogawa et al. 2023; see Kohda et al. 2024 for a more complete list). Future experiments could be designed to untangle which features guppies use to recognize familiar individuals, and whether brain size affects what information is used.

Finally, we tested whether relative brain size affected the sampling behavior of our guppies, as indicated by the number of visits to both choice zones. Larger brains should facilitate a higher degree of information gathering and prompt individuals to behave more proactive (Kotrschal et al. 2014). Large-brained guppies from these selection lines are indeed known to be more explorative than their small-brained counterparts (Kotrschal et al. 2014). Surprisingly, however, sampling behavior did not differ between selection lines in this experiment. In a similar study, guppies' brain size did also not affect information gathering in a mate choice context (Corral-Lopez et al. 2018). Perhaps our tasks were indeed too simple, and differences in information gathering would have been more outspoken in the face of a more difficult problem to solve. We did, however, observe that males were sampling more frequently than females, especially in the first five minutes. This is in line with the higher boldness and activity often observed in male guppies (Harris et al. 2010; Irving and Brown 2013; Herczeg et al. 2019), as inspecting a new individual could be considered a risk, e.g. due to aggressive behavior (Sogawa et al. 2023). Alternatively, male guppies in the wild switch more often between shoals and therefore spend less time familiarizing (Griffiths and Magurran 1998). They may thus require more sampling to discriminate between unfamiliar and familiar individuals.

To summarize, guppies demonstrated individual recognition, albeit only after a long period of familiarization and independent of their relative brain size. This suggests that individual recognition, in the broad sense, can evolve without substantial neural investments into overall brain size. Given the putative importance of individual recognition in the evolution of group-living, this in turn could shed new light on why brain size is not universally associated with sociality. Many aspects of group-living are often considered cognitive challenging, and are therefore believed to require the evolution towards larger brains. However, our study highlights the importance of disentangling for which social challenges of group-living this actually holds true. Such insights are critical to move forward our understanding of how sociality and cognition co-evolve.

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Author contributions GDM: conceptualization, methodology, validation, formal analysis, data curation, writing – original draft, writing – review and editing, visualization, supervision. DB: conceptualization, methodology, formal analysis, investigation, writing – review and editing. MW: methodology, writing – review and editing. JM: software, writing – review and editing. JF: methodology, writing – review and editing. AK: conceptualization, methodology, resources, writing – review and editing. NK: conceptualization, methodology, resources, writing – review and editing, supervision, project administration, funding acquisition.

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Data availability Data and R-scripts are available on Figshare via [https://doi.org/10.6084/m9.figshare.c.7499958] (De Meester et al. 2025).

Declarations

Ethics approval All experiments were approved by the Stockholm Animal Research Ethical Permit Board (permit nr: 17362–2019, 12211–2021 and 17402–2020), followed local laws, and adhered to the ASAB/ABS Guidelines for the use of animals in behavioral research and teaching. Animals were monitored daily for general health and welfare, both during and outside the experiments. Stress during the experimental trials was reduced by videotaping the animals with no human observers in the same room, and focal fish in the trained association experiment were isolated for no longer than 24 h. Two stimulus fish died during the experiments by jumping out of their tank (trained association experiment), and one focal fish after the trials (spontaneous choice experiment). Fish were anaesthetized by immersing them in a water bath with a low dose of benzocaine (67 mg/L) until they fell on their side and then we waited another 10 s to make sure they were unconscious. All fish that were anesthetized during the photography fully recovered. After the experiments, focal fish were placed back in their home tanks in line with the ethical permits. Stimulus fish in the trained association experiment were euthanized after the experiment due to their advanced age, by immersing them in a water bath with a higher dose of benzocaine (400 mg/L) for 10 min. After taking pictures, their brains were destroyed to ensure death.

Competing interests The authors declare no competing interests.

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