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ORIGINAL ARTICLE

Individual behavioural traits not social context affects learning about novel objects in archerfish

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Abstract

Learning can enable rapid behavioural responses to changing conditions but can depend on the social context and behavioural phenotype of the individual. Learning rates have been linked to consistent individual differences in behavioural traits, especially in situations which require engaging with novelty, but the social environment can also play an important role. The presence of others can modulate the effects of individual behavioural traits and afford access to social information that can reduce the need for 'risky' asocial learning. Most studies of social effects on learning are focused on more social species; however, such factors can be important even for less-social animals, including non-grouping or facultatively social species which may still derive benefit from social conditions. Using archerfish, *Toxotes chatareus*, which exhibit high levels of intra-specific competition and do not show a strong preference for grouping, we explored the effect of social contexts on learning. Individually housed fish were assayed in an 'open-field' test and then trained to criterion in a task where fish learnt to shoot a novel cue for a food reward—with a conspecific neighbour visible either during training, outside of training or never (full, partial or no visible presence). Time to learn to shoot the novel cue differed across individuals but not across social context. This suggests that social context does not have a strong effect on learning in this non-obligatory social species; instead, it further highlights the importance that inter-individual variation in behavioural traits can have on learning.

Significance statement

Some individuals learn faster than others. Many factors can affect an animal's learning rate—for example, its behavioural phenotype may make it more or less likely to engage with novel objects. The social environment can play a big role too—affecting learning directly and modifying the effects of an individual's traits. Effects of social context on learning mostly come from highly social species, but recent research has focused on less-social animals. Archerfish display high intra-specific competition, and our study suggests that social context has no strong effect on their learning to shoot novel objects for rewards. Our results may have some relevance for social enrichment and welfare of this increasingly studied species, suggesting there are no negative effects of short- to medium-term isolation of this species—at least with regards to behavioural performance and learning tasks.

Keywords Social context · Inter-individual differences · Social learning · *Toxotes* · Exploratory tendency · Learning

Introduction

Learning enables rapid responses to change (Shettleworth 1972, 2009), but in order to learn about a novel object, an animal must first engage with it. Exploring a potential new food source can provide obvious foraging benefits but may expose an individual to potential risk from predation or noxious substances (Lima and Dill 1990). The social environment

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can play a large role in an individual's motivation to engage with novelty and subsequent learning opportunities (Boogert et al. 2006; Mirville et al. 2016; Langley et al. 2018; Kent et al. 2019; Hansen et al. 2020). Individuals can be more likely to approach novel foods with conspecifics present (Gómez-Laplaza and Morgan 1986; Sherwin 2003). For example, capuchin monkeys (*Cebus apella*) in social conditions had higher levels of engagement with and consumption of novel foods than solitary individuals (Visalberghi and Fragaszy 1995). Being in a group also affords learning opportunities through social learning mechanisms (Coussi-Korbel and Fragaszy 1995; Hoppitt and Laland 2013; Ward and Webster 2016) such as social facilitation (Zentall and Hogan 1976; Dindo et al. 2009). The social environment can also enhance learning effects through the 'social buffering of stress' (Smith et al. 1998; DeVries et al. 2003; Allen et al. 2009; Crane et al. 2018; Culbert et al. 2019), for example cichlids (*Cichlasoma paranaense*) in groups showed lower stress and faster learning rates than isolated individuals (Brandão et al. 2015). These social benefits are not limited to obligate social species. The solitary octopus (*Octopus vulgaris*) (Fiorito and Scotto 1992) and several non-grouping species of fish (Webster and Laland 2017), including solitary sharks (Vila Pouca and Brown 2019; Vila Pouca et al. 2020), use social learning. However, the effects of the social environment on learning can be complex.

Learning performance can depend on the social dynamics (Nicol and Pope 1999; Soma and Hasegawa 2004; Boogert et al. 2006; Grampp et al. 2019), behavioural traits (An et al. 2011; González-Bernal et al. 2014; Krueger et al. 2014), sex (Snijders et al. 2019) and level of familiarity (Guillette et al. 2016) of the individuals involved. In some species, individuals show no benefit from the presence of others when learning, for example the facultatively social tree skinks, *Egernia striolata*, (Riley et al. 2017, 2018). The presence of conspecifics can even worsen learning performance (Zajonc et al. 1969; Webster and Laland 2012; Fei et al. 2019).

Notwithstanding social factors, individual variation can also have significant effects on learning. Many of the commonly measured behavioural traits and syndromes relate to exploratory tendency and associated neophobia (aversion to novelty (Greenberg and Mettke-Hofmann 2001; Mettke-Hofmann 2017)), and these traits can affect learning, as well as cognitive performance more generally (Sih and Del Giudice 2012; Greggor et al. 2015; Morand-Ferron et al. 2016; Boogert et al. 2018; Dougherty and Guillette 2018). Several studies have shown that individuals which exhibit consistently high levels of exploratory tendency tend to show lower levels of neophobia and engage with/learn-to-associate cues with food rewards more quickly than individuals with low activity levels (An et al. 2011; Guenther et al. 2014; Guillette et al. 2015; Reader 2015; Mazza et al. 2018). Differences in response to stress and physiology may drive variation in learning. Individuals exhibiting specific 'coping styles' (Koolhaas et al. 1999) can perform differently in cognition studies (Zidar et al. 2017; Mazza et al. 2019). Several studies have shown that 'proactive' individuals, with low cortisol levels and high levels of exploratory activity, learn faster than 'reactive' individuals which tend to take longer to approach novel objects (Mesquita et al. 2015; Bensky et al. 2017; Raoult et al. 2017). These individual differences in behavioural traits can be moderated by social environment (Webster and Ward 2011; Jolles et al. 2016; Pearish et al. 2019; Tucker and Suski 2019); however, the importance of social context may depend on the species.

Studies exploring the effects of social context on learning have focused on relatively few highly social species, and there is current debate about the evolution of social learning on social and non-social species (Heyes 2012; Reader 2016). We were interested in exploring whether social context would facilitate learning in a species not generally considered social but capable of receiving social information, and whether this could overcome pre-existing variation in relevant traits such as exploratory tendency. Specifically, we tested the effect of different social context on the rate of learning an association between shooting novel objects and obtaining a food reward in archerfish, *Toxotes chatareus*. Famous for their ability to 'shoot' down prey (Bekoff and Dorr 1976; Dill 1977; Schuster 2007), archerfish exhibit low sociality with no grouping preference (Timmermans and Maris 2000), possibly linked to their highly competitive foraging behaviour (Rischawy et al. 2015) and tendency for intra-specific kleptoparasitism (Davis and Dill 2012). Previous work has suggested that they use social information (Schuster et al. 2006) and alter their shooting behaviour in response to a conspecific in a neighbouring tank (Jones et al. 2018). However, little else is known about their social behaviour and social effects on learning. Most research has focused on understanding the mechanisms underlying their shooting abilities (Timmermans and Vossen 2000; Gerullis and Schuster 2014; Reinel and Schuster 2018) and related abilities (Ben-Tov et al. 2018; Newport and Schuster 2020) including image search (Temple et al. 2010; Rischawy and Schuster 2013; Ben-Tov et al. 2015) and associated neurobiology (Schlegel and Schuster 2008; Ben-Simon et al. 2012; Machnik et al. 2018a, b). Archerfish have been shown to exhibit consistent individual differences in latency to shoot—with consequences for their performance in learning and discrimination trials (Jones et al. 2020): fish with low latencies were quicker to learn to shoot targets for reward. The effects of these individual differences have only been explored in fish in solitary conditions, and no social element has been tested. Our main question in this study was whether archerfish learn to shoot a novel object faster when housed in solitary conditions or with a visible conspecific. We included a variation of the open-field assay to determine whether individual variation in learning rates was also associated with individual differences in exploratory tendency.

Methods

Subjects

We tested 19 archerfish, *T. chatareus*, 12 ± 0.5 cm (total length), from animals housed at the University of St. Andrews. All fish were wild-caught as juveniles from a freshwater population, sourced from an accredited ornamental fish supplier. Fish were of unknown sex as archerfish are sexually monomorphic. The fish had been kept in their stock tanks for a minimum of 6 months prior to use in the study and had not been trained to shoot or exposed to experimental tanks in that time. Stock tanks (180 × 45 cm and 35 cm deep) held at temperatures between 25 and 26°C under a 12:12 h light:dark cycle, had environmental enrichment in the form of 3-cm-deep gravel substrate and several plastic plants. Water quality parameters (pH, nitrite, ammonia and nitrate concentrations) were measured weekly, and levels were kept within a range appropriate for archerfish (Newport et al. 2013; Jones et al. 2018), using external canister filters and regular water changes.

Each of four stock tanks held between 5 and 8 fish, with a total of 27 fish. We aimed to test groups of familiar fish so we selected 21 fish for the experiment to ensure all groups of fish came from the same stock tank. At the time of the experiment, the fish were estimated to be 18–24 months old, based on their size and date of arrival from the retailer; however, this is an estimate as the correlation between age and growth rate in captivity is not known for this species. The fish were fed daily with an alternating mixture of commercial fish food (Tetra Cichlid Sticks) and freeze-dried bloodworms. When moving fish into the experimental setup, fish were always captured from the same tank. Fish were measured as they were captured from the stock tank—using a ruler taped to the side of the tank, netted fish were gently pressed against the side of the tank to record their length before being moved to the experimental tank. All the fish that were tested were used only once in this experiment.

General procedure

Fish were tested in groups of three; each fish in a tested trio came from the same stock tank and had been kept together for at least 6 months prior to the experiment to ensure they were familiar with each other. Each fish was moved from the stock tank and introduced into one of three experimental tanks which had been randomly assigned to one of the social treatments. Each fish was then given a full day to acclimate to the experimental tank. After 24 h, the video recordings were taken for the behavioural assay. At the time of introduction and until after the behavioural assay, all barriers were kept in place such that all fish were in the same solitary conditions with no other fish visible to them.

Between 46 and 48 h after being moved into experimental tanks, the barriers were re-positioned in accordance with the social treatment assigned to each tank. Fish were then given another period of ~24 h acclimation to the conditions of their respective social treatment before training began. During the training period, the fish were trained to learn to shoot at a novel target to obtain a food reward. Archerfish will readily shoot novel targets and can learn to associate shooting a target with receiving food rewards (Newport et al. 2013; Karoubi et al. 2017). Each fish was given a single training session per day until it reached the training criterion: 10 on-target shots a day for two consecutive days. In each session, an initially novel target (a five-armed star-shaped cut from black plastic, max diameter 2cm) was placed on the glass 15 cm above the water level of the tank. A training session lasted 45 min, or until a fish had shot at the target 10 times. Shots were easily visible as they left water droplets on the underside of the transparent platform on which the target was placed, signalling where the shot had impacted. A shot was considered on-target if it was within 2 cm of the target; successful shots were rewarded with food, and the target was removed and repositioned on the glass for a subsequent trial. We continued training for all fish in each set until all three of the fish had reached the criterion or until the 50th session. Fish were given a maximum of 50 sessions to reach the criterion.

Experimental setup

Experimental tanks (55 × 55 cm and 45 cm deep) were each set up with an immersion heater (kept at 24.5 ± 0.5°C), a small internal filter (Eheim Biopower 200 Internal Filter), a 1-cm-deep gravel bottom, and plastic plants (positioned to provide structure and refuge but allow a clear view of neighbouring tanks). We used two replicate setups of three tanks each to run up two groups of fish at a time. In each setup, three tanks were set up side by side with a 0.5-cm gap between them, using the same setup as in Jones et al. (2018) (see Fig. 1). A 3-mm-thick black opaque plastic barrier could be easily inserted between each tank to block or allow vision between tanks. The barriers were used to create different social conditions detailed below, by controlling the visibility of the side tanks.

Behavioural assay

We scored fish in their experimental tanks using a simple ‘open-field’ assay. The ‘open-field test’ exposes animals to a novel area and allows measurements such as amount of activity and time spent in the open as a measure of exploratory behaviour, where animals that spend more time in the open are considered to have greater exploratory behaviour (Burns 2008). This assay is widely used in fishes (Webster et al. 2007; Chapman et al. 2011; Conrad et al. 2011; Lucon-Xiccato et al. 2020). For this assay, each fish was recorded for 10 min, and

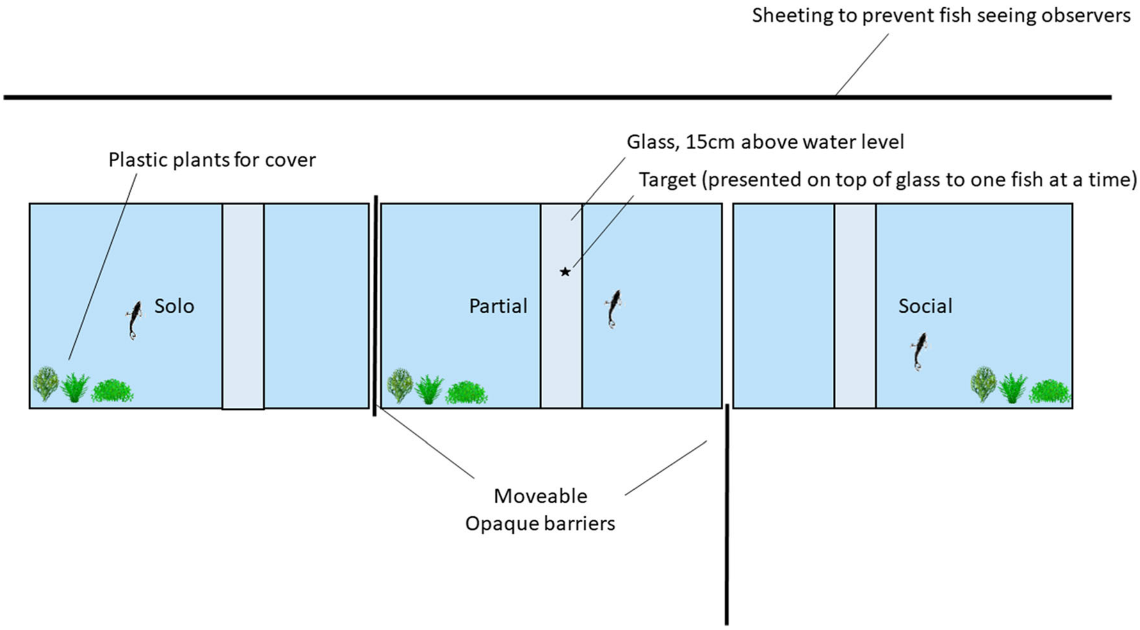

Fig. 1 Experimental set-up, from a top-down view as recorded by the camera above the tanks. The different experimental treatments and level of social context was manipulated by use of the opaque barriers. Solo treatments were always set up in one of the two end tanks

the proportion of time spent in the open, where the fish was more than 1 body length away from the plant shelter or corners of the tank, was recorded. We used a 24-h acclimation period prior to conducting the assay, informed by our previous work with this species in a similar setup (Jones et al. 2018); while a single measurement per individual is not ideal for a labile trait (Biro and Stamps 2010), suitable acclimation periods can provide more robust estimates of individual behavioural traits (Biro 2012), as demonstrated by high estimates of repeatability in guppy activity levels following acclimation (O'Neill et al. 2018). To minimize observer bias, blinded methods were used; specifically, a hypothesis naïve scorer was used to score videos of the behavioural assays.

We initially planned on testing 21 fish, but the social context of two fish (in a solo and partial treatment) may have been compromised as there was a gap in the barrier between the two tanks for at least one session. We noticed this on day 4 of testing this group. These two fish were excluded from the data and were not tested further except to provide a social context for the fish in the social treatment. Of the remaining 19 fish tested, one—in the social treatment—was unable to hit the target or shoot within 2 cm of it. This fish showed no obvious injury or morphological difference from other fish but was unable to reach training criterion for this reason. All other fish were able to shoot and hit the target.

Experimental treatments (social context)

The opaque barriers were employed to block visible contact between fish in neighbouring tanks. Fish in the 'solo' treatment were left in isolation, with no visible neighbour. In the 'partial' treatment, fish had partial social exposure: they were able to see a neighbouring fish when given opportunities to shoot the presented target. However, they could not observe when the neighbour was being trained. Fish in the partial treatment were therefore not exposed to social information about the presented target and associated food reward by other fish, but they may have been impacted by the presence of another fish. This presence could have had either positive impacts on learning rates through social buffering of stress, or, more likely, negative impacts due to the presence of potential competitors per (Simon et al. 2011; Jones et al. 2018). Fish in the 'social' treatment were exposed to full social conditions and had visible contact with a neighbouring fish at all times (including during the neighbour's training sessions), except when presented with the target itself. A visible neighbour fish may act as a potential distraction when shooting, as shown by Jones et al. (2018), so the social condition was designed to afford social information about the target while reducing the chance of distraction. The treatments were pseudo-randomly assigned to each tank prior to transferring fish into them. For each trio of fish tested, the solo treatment was randomly assigned to one of the two end tanks: the social and partial treatments were then randomly allocated a tank from the two remaining.

Statistical analyses

All analysis was conducted using R base package (R Core Team 2019) and specific packages as detailed below.

In order to determine whether the different treatments affected learning rates, we conducted a survival analysis using a Cox proportional hazards regression model, as per similar studies exploring time to reach the criterion in learning tasks (Bensky and Bell 2018). We used this approach as six of the 19 fish failed to reach criterion in the given 50 sessions. The numbers of sessions required to reach training criterion were used as the dependent variable. The social treatment (solo, partial, or social) and score from the behavioural assay (the proportion of time spent in the open) were the two independent variables included in the models. We fitted a model using the coxph function in the 'survival' package in R (Therneau 2019), with the variables detailed above, where survival equated to failing to reach the learning criterion. We included an interaction between the two independent variables, as we expected that the effect of social treatment may depend on the behavioural traits of individual fish. This analysis allowed us to explore the effects of the independent variables of interest on the probability of reaching learning criterion using all the available data.

Results

There was no effect of social context on the probability of reaching the learning criterion (Table 1; Fig. 2); however, the probability of an individual reaching criterion did depend on the proportion of time that the individual spent in the open in the open-field assay. Time spent in the open during the initial behavioural assay is significantly associated with time to learn: greater time spent in the open, our measure of exploratory tendency, is associated with increased learning rates (Table 1; Fig. 3).

Discussion

The social environment did not influence the associative learning rates of the archerfish in this experiment. Instead, learning rates were related to behavioural traits linked to exploratory tendency—specifically, time spent in the open in an open-field test. Fish which spent more time in the open (i.e., were more exploratory) were faster learners, taking fewer sessions on average to reach the criterion.

Table 1 Summary output of survival model

	Coef (β)	SE (coef)	z	Pr(>|z|)
Social treatment	2.411	1.735	1.389	0.1648
Solo treatment	1.181	1.422	0.83	0.4063
Open-field score	**11.14**	**5.154**	**2.162**	**0.0307**
Social: open-field score	−10.77	6.292	−1.711	0.0871
Social: open-field score	2.911	4.466	0.652	0.5146

Positive coefficients are associated with shorter time to reach learning criterion. Significant coefficients ($p < 0.05$) are highlighted in bold. Likelihood ratio test = 16.61 on 5 *df*, $p = 0.005$, concordance = 0.724

The link between individual behavioural traits and learning rates is apparent in an increasing number of species (Dougherty and Guillette 2018; Smit and van Oers 2019); our results complement earlier findings showing that inter-individual differences in latency to shoot relate to differences in learning in archerfish (Jones et al. 2020). Our inability to detect any effect of social context on learning rates is perhaps more interesting given that archerfish were affected by the presence of others in a previous experiment with similar conditions and setup: visible conspecifics in a neighbouring tank increased the latency to shoot and behaviour of shooting fish (Jones et al. 2018). It certainly raises more questions: is there no effect of social context on learning, or are these effects more subtle and therefore masked by the individual differences? Our limited sample size prevents us from being able to address this issue. Effects of social environment on learning can vary with behavioural phenotype where more exploratory individuals tend (relative to less exploratory individuals) to be less sensitive to external stimuli (Guillette et al. 2011; Kelly et al. 2020) and derive less benefit from social environment (Barou Dagues et al. 2020). The lack of significant effect in our study may therefore be a result of exploratory fish that are more likely to engage in risk-taking behaviour but less likely to use social information. Five fish that did not reach training criterion in the allotted time (but could shoot), and it is possible that these individuals may have been more affected by different social contexts. Given the large variation between individuals we found, future studies with a greater sample size will be needed to detect any social effects in less exploratory, potentially more socially sensitive fish, or at least be more confident that there is no social effect on learning to shoot a novel target in this species. Our results, however, do correspond with other studies, across several different species, which have shown that social context does not always have a strong effect on learning performance, at least not when there are strong inter-individual differences in behavioural traits (Seferta et al. 2001; Krueger et al. 2014; Riley et al. 2017, 2018).

Despite the potential benefits of social learning, public information use appears to be species-specific (Webster et al. 2019), and individual biases can have a greater effect on learning than social information even when it is employed (Szabo et al. 2017). Even in species known to use social information, social learning may be dependent upon an individual having some experience with novel foraging opportunities, as recently shown in American crows (*Corvus brachyrhynchos*) (Pendergraft et al. 2020) and stickleback species (Webster and Laland 2018). While it is likely that archerfish do use social information, given previous findings suggesting social learning in this species (Schuster et al. 2006), many factors may impact the use of social leaning or our ability to detect it. Especially, as both social and asocial learning may depend on the same basic mechanisms (Heyes 2012) and factors that

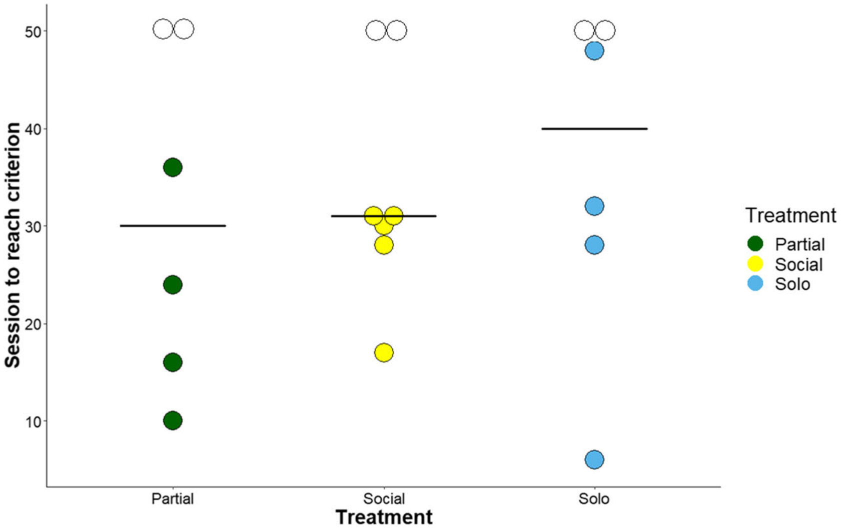

Fig. 2 Effect of different social contexts on time taken to reach training criterion. The treatments relate to level of exposure to a visible conspecific: solo (no social exposure); partial (visual social contact except during training of neighbours); social (full visual social contact including during training of neighbours). Only fish with 'social' exposure had access to social information regarding the novel objects and associated food rewards. Black lines indicate median number of sessions to reach criterion for each treatment; coloured dots represent data points for individual fish. White points indicate fish which failed to reach criterion within 50 sessions

constrain learning (Shettleworth 1972). In addition to showing no preference for shoaling with conspecifics as juveniles (Timmermans and Maris 2000), archerfish are highly competitive predators (Rischawy et al. 2015). Intra-specific competition can be a major driver of individual differences in behaviour, with stronger competition potentially leading to more defined inter-individual differences (Bolnick et al. 2003; Svanbäck and Bolnick 2007; Laskowski and Bell 2013) and archerfish like other predators show strong inter-individual variation in latency to respond to and attack prey (Szopa-Comley et al. 2020a, b). These individual differences may override effects of the social environment, particularly in social species—as shown in threespine sticklebacks (*Gasterosteus aculeatus*) where, individual differences were suppressed in certain social contexts, but bolder individuals were more likely to feed first in social conditions (McDonald et al. 2016). Our experimental design limited our ability to detect more subtle effects or interactions of this nature. Archerfish do respond to the presence of other fish by increasing their latency to shoot (Jones et al. 2018) and exhibit lower shooting accuracy in the presence of others (Simon et al. 2011). This may have impacted training results of fish in the partial social condition, the only condition in which subject fish were exposed to a visible conspecific when given opportunities to shoot. The presence of other fish may have inhibited learning through distraction by the conspecific (as demonstrated in zebrafish *Dario rerio*; Ayoub et al. 2019) or inhibition from potential conspecific competition.

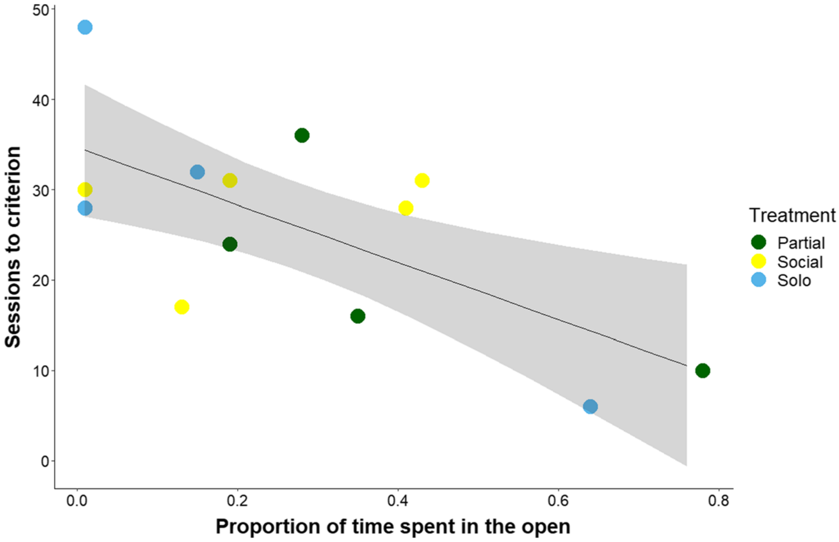

Fig. 3 Relationship between the proportion of time spent in the open and number of sessions taken to reach training criterion. Each point represents a single fish that reached criterion ($n = 13$) and is coloured according to the social treatment they were exposed to. The predicted response and estimated standard error from a linear model are given by the black line and grey shading, respectively

One area where our results may be useful is in informing future studies, particularly with regard to acclimation, training and related ethical and welfare concerns. Archerfish, like other animals perhaps especially other wild caught animals—which may be slower or less likely to engage with novel objects than captive-bred or urban individuals (Gajdon et al. 2004; Jarjour et al. 2020)—can require extended periods to acclimate and train (Archard and Braithwaite 2010; Patton and Braithwaite 2015). Acclimation can play an important role in the expression of behaviours and performance in behavioural assays (O'Neill et al. 2018), and sufficient acclimation may help reduce the issues inherent in measuring cognition in the laboratory (Webster and Rutz 2020). Cognition studies may be particularly susceptible to factors affecting stress and environmental conditions which can affect measures (Pritchard et al. 2016), and this is especially important when exploring consistent individual variation (Strand et al. 2010; Rowe and Healy 2014; Griffin et al. 2015; White et al. 2017; Boogert et al. 2018; da Silva et al. 2020). There have been no studies of archerfish welfare, and further work into social and environmental enrichment is required, but our study suggests that keeping archerfish alone may not be detrimental to their welfare in the short term. Learning rates are one measurable aspect of animal welfare and benefit of enrichment (Strand et al. 2010) and the lack of visible conspecifics had no negative effects on learning rates in our study, for the fish that completed training. However, it also suggests that the relatively long training and acclimation periods required for learning in this species may not be easily reduced by including a visible conspecific. This may be important for other species where social effects are relatively unstudied, and where they are likely to be increasingly used as a model species.

Archerfish are not a highly social species but do modify their shooting behaviour in response to the presence of conspecifics. The lack of variation in learning rates with social context in this study suggests that learning about what to shoot and the decision to take a shot may not be affected equally by social factors. Other non-grouping species may similarly be less likely to show strong effects of social context on learning behaviour, even when their behaviour can be affected by social context in other situations.

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Availability of data The data analysed for this study are available at: https://osf.io/us9t7/?view_only=743ea515b7ff4201b16dd7ed896edff9.

Author contribution NARJ, MW, and LR designed the study. NARJ and HCS-J collected the data. NARJ conducted the analyses. HCS-J acted as initially naïve video scorer. NARJ wrote the manuscript. All authors edited and commented on the paper.

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Declarations

Ethics approval This research was approved by the University of St Andrews Animal Welfare and Ethics Committee (AWEC). No procedures required U.K. Home Office licensing. All tanks were enriched with gravel and plastic plants for cover. All fish were retained in the laboratory after the study period to be used in future projects. Handling was kept to a minimum, and when fish had to be moved between tanks, they were caught using two large hand nets to reduce the likelihood of extended capture periods. In the experimental tanks, fish were kept singly in a volume of at least 125 l. Archerfish are not considered a social species. There are no published studies on the effects or preference for any social context and or isolation in this species, but several previous studies have maintained archerfish in isolation with no reported ill effects or perceived likelihood of stress (Gabay et al. 2013; Gerullis and Schuster 2014; Newport et al. 2014, 2018). During our study, we closely monitored each fish, specifically for signs of reduced feeding rate, responsiveness, stereotypic behaviour and colour changes. We observed few instances of these signs: all of the instances of short-term colour change occurred immediately post-transfer between tanks and reduced feeding rate for the first 12 h post-transfer.

Consent for publication All authors consent to publication of this article.

Conflict of interest The authors declare no conflict of interest.

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