

RESEARCH ARTICLE

Artificial selection for schooling behaviour and its effects on associative learning abilities

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ABSTRACT

The evolution of collective behaviour has been proposed to have important effects on individual cognitive abilities. Yet, in what way they are related remains enigmatic. In this context, the 'distributed cognition' hypothesis suggests that reliance on other group members relaxes selection for individual cognitive abilities. Here, we tested how cognitive processes respond to evolutionary changes in collective motion using replicate lines of guppies (*Poecilia reticulata*) artificially selected for the degree of schooling behaviour (group polarization) with >15% difference in schooling propensity. We assessed associative learning in females of these selection lines in a series of cognitive assays: colour associative learning, reversal learning, social associative learning, and individual and collective spatial associative learning. We found that control females were faster than polarization-selected females at fulfilling a learning criterion only in the colour associative learning assay, but they were also less likely to reach a learning criterion in the individual spatial associative learning assay. Hence, although testing several cognitive domains, we found weak support for the distributed cognition hypothesis. We propose that any cognitive implications of selection for collective behaviour lie outside of the cognitive abilities included in food-motivated associative learning for visual and spatial cues.

KEY WORDS: Cognition, Social behaviour, Collective motion, Poeciliidae

INTRODUCTION

Understanding how the evolution of social complexity is related to the evolution of cognition has been a key challenge for social behaviour studies. Cognition refers to mechanisms that animals have for taking in information through their senses, retaining it, and using it to adjust their behaviour to local conditions (Shettleworth, 2010b). Consequently, individuals base their decisions on current sensory input and previous experience. When individuals are in social situations, processing of information is affected both by the individual itself, and by changes in the social environment (Couzin and Krause, 2003; Sosna et al., 2019). Social cognition refers to the ability to respond flexibly during social interactions by integrating the behaviours of others with memories of past interactions and predictions of future behaviour in real time (Prounis and Ophir,

2020; Schradin, 2013; Weitekamp and Hofmann, 2014). Animals living in groups are frequently required to make collective decisions about detecting and avoiding predators, or locating food (Dall et al., 2005), which in turn often results in more accurate decisions being made by groups than those made by individuals (Couzin, 2009; Ward et al., 2011). These interactions result in social dynamics where decision-making potentially demands cognitive abilities, making cognition a central part of social behaviour (Brothers, 2002; Prounis and Ophir, 2020).


Coordinated behaviour of animal groups such as schools of fish, flocks of birds or swarms of insects has been associated with decision-making by individuals that are highly synchronized and coordinated (Couzin, 2009). In such groups, individuals often experience a highly dynamic group structure, where spatial positions, orientations and neighbours change rapidly, and where social transmission of information may facilitate coordination of motion and effective responses to complex environments (Strandburg-Peshkin et al., 2013). Individuals respond to the local movements and positions of their neighbours through decision-making processes in which they gather information from multiple sensory inputs (Herbert-Read, 2016). Such behavioural flexibility has been suggested to mediate mechanisms for assessing, evaluating and responding to a variety of cues that lead to the evolution of improved cognition (Fernald, 2014; Shettleworth, 2010a; Weitekamp and Hofmann, 2014). Cohesive and coordinated group behaviours emerge from decision rules individuals use to interact in groups (Herbert-Read et al., 2017). Collective motion may thus act as a source of individual cognitive challenges, and be an important driver of how individuals process information and learn. Shoaling fish rely on movement decisions of individuals to shape attraction–repulsion dynamics by decreasing the critical distance between individuals (Herbert-Read et al., 2017), and their sociability and activity are associated with aggregation and coordinated movement (Sumpter et al., 2018). In particular, shoaling refers to a group of fish that remain together for social reasons, whereas schools are shoals that are polarized and coordinated (Miller and Gerlai, 2012; Pitcher, 1983; Pitcher and Parrish, 1993). We therefore focus our study on guppies, a species in which females tend to shoal to avoid being harassed by males (Dugatkin and Godin, 1992), and facultatively school, particularly in response to a perceived predation threat (Seghers, 1974). We artificially selected for their polarized and coordinated behaviour to test for a possible connection between individual cognition abilities and group-level decision-making.

Information acquisition and the associated cognitive tasks necessary for decision-making processes can be accomplished by individual fish, but can be performed more efficiently when animals form groups (Giraldeau, 1984; Ioannou et al., 2011). A group is viewed as a collection of individuals who may have to compromise their own motives to conform to a mean group level behaviour

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(Brown and Irving, 2014). A major benefit of social interactions is access to information at relatively low cost (Dall et al., 2005), given it does not require direct sampling of the environment (Ioannou, 2017). This sharing of information means that cognitive performance for relevant tasks can be improved either for each individual within the group, or for the group as a whole (Ioannou, 2017). Although the movement of individuals in a group may appear uniform, quantification of behaviour has demonstrated consistent heterogeneity between individuals (Jolles et al., 2020). Individual differences over a range of cognitive tasks appears to be repeatable (Cauchoix et al., 2018), but less is known in terms of whether each group member in a group differs in their 'general' cognitive abilities. Although variation in individual cognition is critical for the emergence of collective behaviour, the link between collective dynamics and individual learning remains rarely tested (but see Cook et al., 2020). Differences in individual cognitive abilities could be explained by the 'distributed cognition' hypothesis, as it posits that social complexity selects for effective information sharing, which may relax selection for individual cognitive abilities (O'Donnell et al., 2015), and potentially reduce metabolic costs (Cheng, 2018). Indirect support for this idea comes from comparative analyses in wasps (O'Donnell et al., 2015), woodpeckers (Fedorova et al., 2017) and mole rats (Kverkova et al., 2018), which all show an inverse relationship between social complexity and brain size. The benefits accrued from a group feature such as schooling have the potential to be associated with greater differentiation of cognitive labour, resulting in a relaxation of the selection pressures on individuals' cognitive abilities, as suggested by the distributed cognition hypothesis (O'Donnell et al., 2015; Theiner, 2018). The costs of individual cognitive abilities with increased schooling propensity may stem from greater attention required to increase alignment (Lemasson et al., 2009), or with the metabolic costs of swimming faster (Miller and Gerlai, 2012). These costs may be alleviated by the constant repetition of interactions between group members, which may compensate for individual cognitive limitations. Experimental data allowing causal conclusions, however, are currently lacking. Controlled evolution of collective behaviour via artificial selection can provide such data and allow for experimental evaluation of the distributed cognition hypothesis in this context.

Here, we made use of female guppies artificially selected for collective behaviour, specifically on an individual's ability to 'align' (i.e. coordinate) with other group members, to test whether this form of social decision-making in fish is associated with individual learning abilities. Schooling is common among fish species, making them ideal models with which to investigate individual cognitive traits within a social framework, but the cognitive ability of each individual within the group is less well studied. By artificially selecting for an increase in social coordination, we intended to capture any possible change in individual decision-making processes. Here, we focused on a general form of individual cognitive ability that is closely linked to fitness: associative learning, the learning of an association between two stimuli or events (Pearce, 2013; Shettleworth, 2010b). Our learning assays are based on a reward paradigm associated with foraging. Individuals in highly aligned, polarized groups can potentially communicate more effectively, making foraging more efficient (Davis et al., 2017). Indeed, foraging time tends to decrease with an increasing shoaling size (Pitcher et al., 1982), although the link with polarization may also depend on hunger levels and swimming speed when seeking food (Wilson et al., 2019). By testing various aspects of associative learning in the polarization selection lines, we thus provide an experimental test of the relationship between the evolution of collective behaviour and

individual associative learning abilities. Following the distributed cognition hypothesis, we predicted that individuals from more polarized groups would perform worse than those from the less polarized control groups.

MATERIALS AND METHODS

Polarization selected lines

We examined the relationship between schooling behaviour and cognitive abilities in laboratory lines of Trinidadian guppies (*Poecilia reticulata* Peters 1859) that were selected for schooling behaviour by means of polarization in an artificial selection experiment (Kotrschal et al., 2020; Szorkovszky et al., 2018). Briefly, in each generation, 16 groups of eight females were subjected repeatedly to open field assays in which their level of polarization (i.e. the average degree to which the individuals in each group moved in the same direction) was quantified. Polarization was thus used as a measure of schooling behaviour, capturing their alignment as a characterization of their coordination (which facilitates information transfer; Rosenthal et al., 2015; Strandburg-Peshkin et al., 2013). Female behaviour was chosen for the artificial selection experiment given their higher propensity to shoal than males (Croft et al., 2003; Magurran, 2005). Three up-selected polarized lines were bred by pairing individuals from the most polarized groups with unselected males, while three control lines were established by pairing randomly selected females from the remaining groups with unselected males (i.e. three replicates for each line). This procedure was repeated for three generations. This selection procedure resulted in polarization lines with a 15% higher polarization after three generations of selection compared with control lines (Kotrschal et al., 2020). Changes in polarization also resulted in a correlated response in cohesiveness (crucial for predator response; Hamilton, 1971). The fish used in this study were the offspring of F₃ fish. See Szorkovszky et al. (2017), Szorkovszky et al. (2018) and Kotrschal et al. (2020) for full details. Fish were kept at 25°C under a 12 h:12 h light:dark schedule. All behavioural trials in the present study were performed blind to social treatment.

Ethics

The experiment was performed in accordance with ethical applications approved by the Stockholm Animal Research Ethical Permit Board (Dnr 17362-2019, 223/15 and N173/13).

Experimental apparatus

We performed four different associative learning assays using an experimental apparatus as described by Buechel et al. (2018). Each experimental tank consisted of a home compartment and an experimental compartment which were separated by one transparent and one opaque sliding door (Fig. 1). Females from each treatment were allocated randomly to the tanks. Females were housed in the home compartment throughout the experiment and were allowed visual contact between the home tanks to minimize any stress that could impair learning (Bouton, 2007; Miletto Petrazzini et al., 2012). The experimental compartment was only accessible during the test trials and was visually isolated to avoid potential effects of social learning and copying (Dugatkin and Godin, 1992; Laland and Williams, 1997). The experimental compartment contained a white plate with 20 circular indentations (5 mm deep, 10 mm diameter), two of which contained a frozen adult *Artemia* that was covered with either a yellow or a red plastic disc (14 mm diameter). One of the two discs could be dislodged by the female for her to eat and associate it as a reward, while the other disc was rendered immovable by a glued-on knob (unrewarded stimulus). A food reward was hidden underneath both discs to control for olfactory cues. The red and

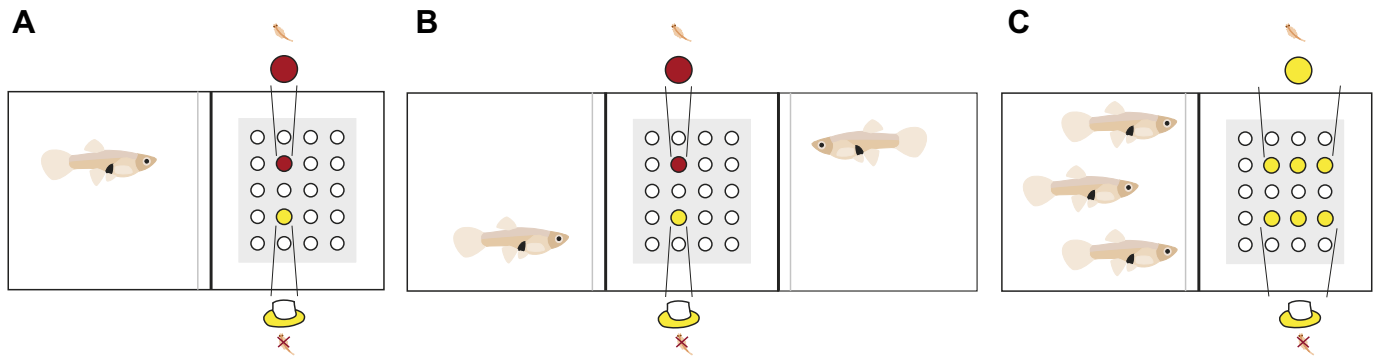


Fig. 1. Experimental apparatus (top view) to test associative learning by colour and side discrimination, respectively. (A) Colour discrimination and reversal learning assays, (B), social learning assay and (C) side-rewarded association for the individual and collective learning assay. A home compartment was separated by an opaque and a transparent sliding door. Females learned to dislodge a rewarded disc (red for A and B, and left disc in C in this example) to find a frozen *Artemia* underneath. Note that for C, the association is right or left from the fish perspective. The unrewarded stimulus was blocked by a glued-on silicon knob so that the fish would not have access to the reward, which is indicated by the crossed *Artemia*. In B, females were able to observe a demonstrator on each trial perform the correct choice. In C, females were tested either individually or in groups of three. See Materials and Methods for details.

yellow colours used as stimuli were chosen based on their relevance for food selection and mate choice (Buechel et al., 2018; Houde, 1997; Rodd et al., 2002).

Individual and collective spatial associative learning assays were performed in the same experimental set-up, but these tanks held three fish in the home compartment for part of the experiment (see details below). For these assays, the plate in the experimental compartment contained yellow discs only, and females were trained to associate a food reward to either the left or the right side (see details below).

Social associative learning assays, in which focal fish's association with a food reward is facilitated by visual information from a pre-trained demonstrator, were performed in an experimental tank as described above with minor modifications. Each experimental tank consisted of two home compartments and an experimental compartment which were separated by one transparent and one opaque sliding door (Fig. 1). Females (demonstrators and focal individuals, see below) were housed in the home compartments throughout the experiment and were allowed visual contact between the home tanks. The experimental compartment was only accessible during the test trials and was visually isolated to avoid disturbing the fish while the arena was being manipulated.

Experimental procedure

Pre-training phase

All females were initially pre-trained to dislodge a disc by partially covering the hole in the plate with food and reducing the gap in subsequent trials. This training was carried out using green-coloured discs to avoid any association with the colours of the actual tests. All females participated in 30 training trials.

For the social associative learning assays, we initially trained 30 wild-type adult females to dislodge a disc (either red or yellow). These females served as demonstrators for the experimental females. Demonstrator females participated in 30 trials and were only used as demonstrators when they reached at least 80% correct choices over 12 trials (over 2 days).

Cognitive assays

Colour associative learning assay

We trained 72 females (36 control females and 36 polarization-selected females) to dislodge either a red or yellow disc (the different colours divided equally across treatments to control for potential colour biases). For each trial, we first opened the opaque

door to allow females to assess the arrangement of the discs before entering the experimental compartment. We then opened the transparent door to record their choice. We scored the disc the female attempted to dislodge first as either correct or incorrect choice. Each trial lasted for 60 s and was only completed if the food reward was consumed. If the rewarded disc was not dislodged within 60 s, we continued the trials for up to 5 min, after which we opened the rewarded disc and allowed the fish to consume the food. While it was considered a non-choice trial if none of the discs were touched, this allowed all females to experience the same number of positively reinforced trials throughout the experiment. We controlled for any potential colour bias by randomly allocating females to each of the colour treatments. The position of the two discs (right or left side on the plate) was chosen randomly for each trial. We performed between three and six trials every day for a total of 30 trials for each experimental fish. Females in each selection treatment reached at least 80% correct choices over the last day of training with no further significant increase in success rate.

Reversal learning assay

When the females had reached their end performance level, the rewards were then reversed (females previously trained on red would now have to dislodge the yellow disc to access the food reward and vice versa). We followed the same procedure as above, but performed 72 trials for the more challenging reversal learning assay (see Buechel et al., 2018).

Social associative learning assay

We trained another set of 72 experimental females (36 control females and 36 polarization-selected females) to dislodge the disc, but allowed each focal fish to observe a demonstrator perform the correct choice before each trial. This allowed us to test for a potential difference between the control and polarization-selected individuals during an associative learning task where they were aided by social visual information from an informed conspecific. An earlier study has previously demonstrated that this social learning set-up works. In that study, focal fish performance was much better with correct social information than with incorrect social information (Fernlund Isaksson, 2018). Owing to space constraints, these trials were performed over three temporal blocks. In each trial, we first opened the opaque door on both compartments and allowed both the demonstrator and the focal individual to come closer to the doors. We

then opened the transparent door of the demonstrator and scored the first disc the demonstrator attempted to dislodge as either the correct or incorrect first choice. Note that demonstrators were trained to dislodge the colour disc their focal individuals were assigned to as their correct choice and that the success of demonstrators was $91 \pm 0.6\%$ (mean \pm s.e.m.). We completed the demonstration when the demonstrator consumed the food reward. If the focal individual was not facing the experimental compartment, the demonstration was repeated. The demonstrator was then returned to the home compartment. We then opened the doors of the focal individual and scored the choice based on the disc she tried to dislodge first. We used the same criteria for choice as with the individual learning assays. The focal individuals thus solved the associative learning task using social visual information provided by a demonstrator, as well as using personal (trial and error) information on each trial. We performed between four and six trials every day for a total of 30 trials for each experimental fish. The end performance was considered to be reached when focal individuals reached 80% correct choices over at least six consecutive trials within the same day.

Individual and collective spatial associative learning assay

We trained another set of females either individually ($N=48$ control, 48 polarization selected) or in groups of three (48 groups of control=144 females, 48 groups of polarization-selected females=144 females) to dislodge yellow discs over four blocks. Individuals in this test were trained to associate one side of the tank (either left or right) with a food reward. They were housed in their home compartments either individually or in groups of three. When housed individually, a yellow disc was placed at either the right or the left. When three individuals were used in the assay, three yellow discs were placed at the right and three yellow discs at the left end of the plate. One side was considered the rewarded side (i.e. discs that could be dislodged), while the other side contained the unrewarded stimulus (glued-on knob discs). In each trial, the opaque door was opened first, followed by the opening of the transparent door. We then scored the first disc (i.e. side) the focal individual attempted to dislodge first as either the correct or incorrect choice. During the group treatment, we scored the first choice the first female made (i.e. scored $N=48$ choices per selection treatment). We also recorded latency (time in seconds) until the correct choice was performed. Each trial lasted for 2 min and was only completed if the food reward was consumed. If the rewarded disc was not dislodged within 2 min, we continued the trials for up to 5 min, after which we opened the rewarded disc and allowed the fish to consume the food. We performed six trials every day for a total of 24 trials. In order to also test all fish individually, females in groups were placed in an individual experimental tank after the group assay, and females that had been tested individually were moved to another tank to experience the same manipulation. We then performed a one-test trial where we tested their association to the left or the right by recording the first disc each individual tried to dislodge and the time she took to make the correct choice.

We considered fish to have learned the task if they reached a learning criterion of 7 out of 7 correct choices (e.g. Damas-Moreira et al., 2018), significant according a binomial probability in all assays (except for the one-test trial). For all assays, females that failed to push the disc or eat, or showed signs of stress by remaining in a corner of the tank, were returned to stock tanks and excluded from further analyses ($n=1, 4, 7, 4$ for each assay, respectively). All females were tested in a randomized order, with trials typically running between 08:30 h and 17:00 h, after which females were deprived of food.

Statistical analyses

To analyse the effect of artificial selection on schooling behaviour in the probability of success per trial, we used generalized linear mixed models (GLMMs) with a logit link function using the lme4 package (Bates et al., 2015) in R (v. 3.6.1, <https://www.r-project.org/>). We fitted individual binary outcome variables based on correct or incorrect first choices.

For the colour, reversal and social associative learning assays, we included treatment (control and polarization-selected), colour (red and yellow) and trial as fixed effects. This analysis tests for differences between 'learning curves' between the treatments. We additionally included block for the social learning assay as a fixed factor. We also included side as a fixed factor, but removed it if it was not significant. We included the interactions between treatment, colour and trial, as well as fish identity nested in trial (trial|female ID), as a random effect. See details for the inclusion of random effects below.

To test for differences between individual and collective spatial learning, we first tested the success of each fish based on correct or incorrect first choices by including treatment and regime (control individual, control collective, polarization-selected individual and polarization-selected collective), side, trial and block as fixed factors. We included the interactions between treatment, learning regime, side and trial as well as fish identity nested in trial (trial|female ID) as a random effect. We then tested whether time until the correct choice had an effect on learning rates by running the same model, but including time until the correct choice as a response variable. Finally, to test individual learning performance, we tested females both correct and incorrect first choices and time until the correct choice when they performed a one-test trial in two separate generalized linear models (GLMs). We included treatment and regime as above, and side and block as fixed factors.

To analyse the effect of artificial selection on schooling behaviour on whether fish reached our learning criterion (1=learnt, 0=failed), we used GLMs with a binomial distribution. For the colour, reversal and social associative learning assays, we included treatment and colour as fixed effects. For the social learning assay, we additionally included block as a fixed effect. For the individual and collective spatial associative learning assay, we included treatment, side and block as fixed effects. Finally, to test whether there was a difference in how fast fish took to reach our learning criterion between treatments, we ran similar models as for the learning criterion, but used the number of trials as a response variable and a Poisson distribution. Note that these models only included fish that reached the learning criterion.

Initially, all models included replicate (three levels), and replicate nested in the treatment (1|treatment: replicate), but replicate returned a zero variance that caused singular fit. Note that replicate refers to the origin of fish from each of the lines (three control and three polarization selected). To control for a potential effect of replicate, we included it as a fixed effect in all models, and excluded it when it was not significant (see code for details; <https://osf.io/e7dnh>). Plots of the learning trajectories revealed in some assays to be non-logit linear. Accordingly, we log transformed time (i.e. trial) which improved the fit in some cases (see supplementary material available at <https://osf.io/e7dnh>). We also tested the significance of the random effect in our models (trial|fish) by comparing our final model against a model with either a fixed intercept (1|fish) or a fixed slope (0+trial|fish) using a log-likelihood ratio test. If this was not significant, we used a fixed intercept for simplicity. All model terms were tested for significance using the ANOVA function in the car package (Fox and Weisberg, 2011) specifying Type III Wald

chi-square tests. We ran all models with and without interaction terms and compared the model fit of the reduced and full models using a log-likelihood ratio test. If removal of the interaction terms did not affect the model fit, we interpret the main effects from the reduced model. The model results and code are available from <https://osf.io/e7dnh>.

RESULTS

Colour associative learning assay

We obtained data from 71 females (36 control and 35 polarization selected females). While females from both selection treatments learned to associate colour stimulus with the food reward, learning rate was not affected by polarization selection (Fig. 2A, Table 1). Females trained on the yellow stimulus learned to associate the stimulus colour with the reward at a faster rate than females trained on the red stimulus (Table 1; Suppl. 1.1 at <https://osf.io/e7dnh>). Given we found a significant interaction between colour and trial (Table 1; Suppl. 1.1 at <https://osf.io/e7dnh>), we analysed each colour separately, but found no difference in learning rates between the control and polarization-selected females when trained on either yellow or red (Suppl. 1.2.1 and 1.2.2 at <https://osf.io/e7dnh>). There was no difference between control and polarization females in whether they reached the learning criterion (Suppl. 1.3.1 at <https://osf.io/e7dnh>), but control females reached the learning criterion faster (Fig. 3A; Suppl. 1.3.2 at <https://osf.io/e7dnh>).

Reversal learning assay

Based on data from 68 females (35 control and 33 polarization-selected females), learning rate was not different between the lines, and females from both lines were able to perform reversal learning (Fig. 2B, Table 1). In this experiment, we detected a side bias in female learning performance, such that when the reward was on the right side, females learned at a faster rate (Table 1). There was no difference between control and polarization females in whether they reached the learning criterion (Suppl. 2.1.1 at <https://osf.io/e7dnh>), nor in the number of trials that they took to reach such criterion (Fig. 3B; Suppl. 2.1.2 at <https://osf.io/e7dnh>).

Social associative learning assay

Selection regime had no impact on female learning rates ($n=65$ experimental females, 31 control and 34 polarization selected) (Fig. 2C, Table 1). Both control and polarization-selected female guppies learned to associate the colour stimulus with the food reward, albeit faster when the food reward was associated with the red colour (Table 1). Note that there was no difference in the success of demonstrator females by the colour or treatment they were showing (Suppl. 3.3 at <https://osf.io/e7dnh>). Selection regime had no impact on whether fish reached the learning criterion (Suppl. 3.2.1 at <https://osf.io/e7dnh>), nor in the number of trials that they took to reach it (Fig. 3C; Suppl. 3.2.2 at <https://osf.io/e7dnh>).

Individual and collective spatial associative learning assay

Based on data from 188 females, neither polarization selection nor learning regime (individual or collective) affected learning success rates, but learning regime had an effect on how fast correct choices were made (Fig. 4A,B, Table 1). That is, females from all social and learning regime combinations learned to associate the side stimulus with the food reward, albeit faster when the food reward was on the left side (Table 1; Suppl. 4.1 at <https://osf.io/e7dnh>). However, although social regime did not affect the time females took to make the correct choice, females in groups took on average less time in each trial to find the food reward (Fig. 4B, Table 1). Females from

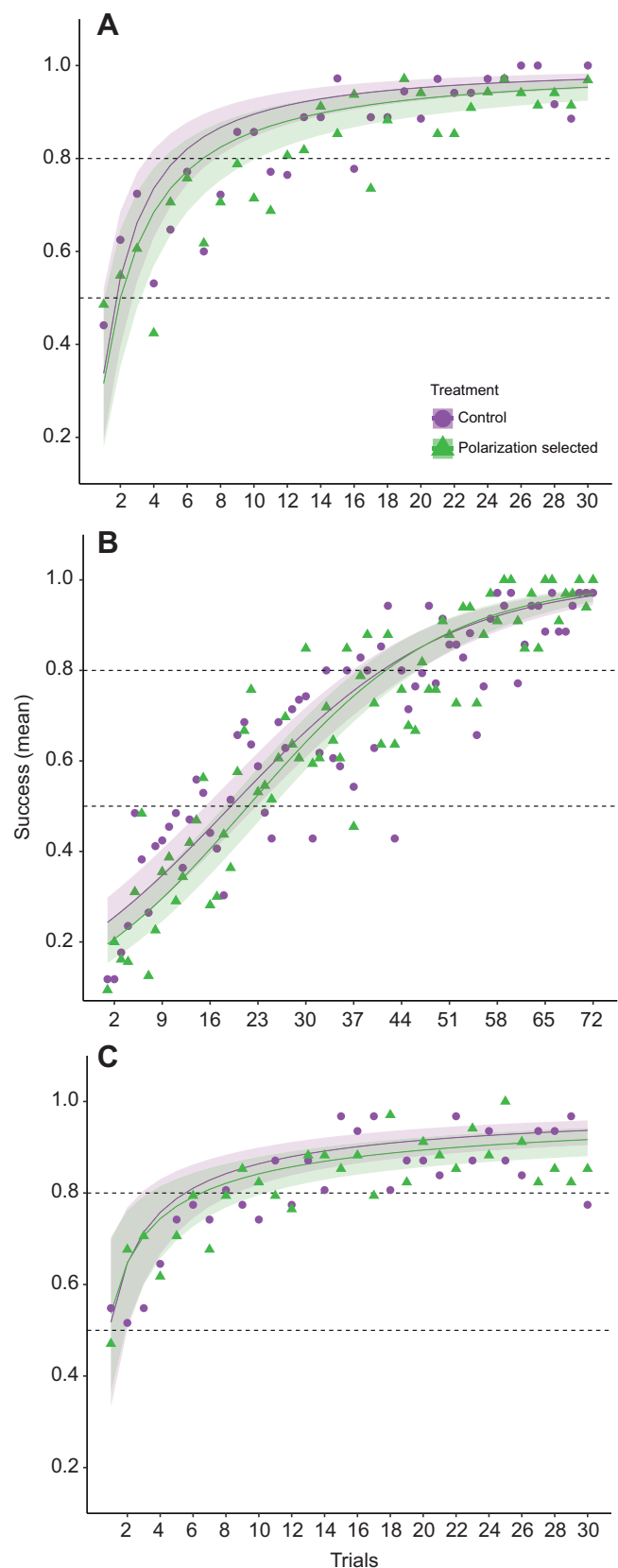


Fig. 2. Proportion of correct choices by control (purple circles) and polarization-selected females (green triangles) in a two-choice colour associative learning test. (A) Colour associative learning assay over 30 trials. (B) Reversal learning assay over 72 trials. (C) Social associative learning assay over 30 trials. Lines are based on model predictions. Shading represents 95% confidence intervals. Dashed lines indicate 50% and 80% end performance levels.

Table 1. Results from linear mixed models with parameter estimates and chi-square (χ^2) tests for different learning assays comparing control and polarization-selected females for their probability of success per trial

Response variable	χ^2	<i>P</i>
Colour associative learning assay		
Intercept	60.7471	<0.001
Selection	0.032	0.858
Trial (log)	137.1394	<0.001
Colour	110.2555	<0.001
Selection×Trial (log)	0.3187	0.572
Colour×Trial (log)	62.3451	<0.001
Reversal learning assay		
Intercept	40.748	<0.001
Selection	1.908	0.167
Trial	222.708	<0.001
Colour	3.094	0.079
Replicate	13.165	<0.001
Side	5.077	0.079
Selection×Trial	1.026	0.311
Social associative learning assay		
Intercept	12.923	<0.001
Selection	0.024	0.877
Trial (log)	2.940	0.086
Colour	40.888	<0.001
Block	4.848	0.089
Selection×Trial (log)	0.336	0.562
Colour×Trial (log)	18.263	<0.001
Individual versus collective spatial learning assay		
Success		
Intercept	0.765	0.382
Treatment	2.1872	0.534
Trial (log)	24.558	<0.001
Side	1.6375	0.201
Block	13.690	0.003
Treatment×Trial (log)	1.997	0.573
Side×Trial (log)	10.833	0.001
Time		
Intercept	84.927	<0.001
Treatment	25.459	<0.001
Trial	111.762	<0.001
Side	6.562	0.010
Block	5.941	0.115
Treatment×Trial	19.321	<0.001

Colour is included for the colour associative learning, reversal learning and social associative learning assays, whereas side is included for the individual versus collective spatial learning assay. Treatment in the individual versus collective spatial learning assay represents control and polarization-selected females tested individually or in groups. *P*-values in bold indicate significant values. Note that we interpret the main effects from the reduced model. The full model (including interactions) and the parameter estimates are provided in the supplementary material at <https://osf.io/e7dnh/>.

the control individual treatment were less likely to reach the learning criterion (Suppl. 4.3.1 at <https://osf.io/e7dnh/>), but neither polarization selection nor learning regime affected how fast they reached the learning criterion (Fig. 3D; Suppl. 4.3.2 at <https://osf.io/e7dnh/>). When tested individually (individual control: 33, individual polarized: 34, collective control: 83, collective polarized: 83), we found a side bias towards the right, but no difference in learning rates between control and polarization-selected females (Suppl. 4.4.1 at <https://osf.io/e7dnh/>). When examining how long fish took to make the right choice when tested individually (individual control: 30, individual polarized: 33, collective control: 73, collective polarized: 71), we did not find any differences due to social regime, but differences due to their learning regime. Unlike the results of when fish were tested in groups, when tested

individually, females that were previously housed in groups took on average longer in each trial to make the correct choice than fish that had been housed individually (Suppl. 4.4.2 at <https://osf.io/e7dnh/>).

DISCUSSION

Based on known differences in group-level behaviour, we tested for potential differences in individual cognitive performance between control and polarization-selected females using a range of assays based on the associative learning paradigm. Control females did not outperform polarization-selected females in the colour associative learning test, nor when the association was reversed. When visual social information was available, there was also no difference between control and polarization-selected females. We found no difference in spatial associative learning performance when fish were tested by themselves or in groups, albeit fish in groups took less time to make the correct choice regardless of which selection regime they belonged to. Finally, we found somewhat contradictory differences between control and polarization-selected females in different learning assays, which should be interpreted with caution. Control females reached the learning criterion faster in the colour associative learning test. However, control females tested individually in the spatial learning assay were less successful in reaching the learning criterion. As such, our results may weakly support the distributed cognition hypothesis, but more prominently suggest that associative learning is not tightly linked with the evolution of collective motion.

Contrary to our expectations, we did not find strong evidence in support of the distributed cognition hypothesis. That is, we did not find a robust reduction of associative learning abilities in polarization-selected females as a result of a reduction in cognitive load in each group member (Theiner, 2018), but there was some indication of control females outperforming polarization-selected females in how fast they reached the learning criterion in only one test (colour associative learning test). In group-living animals, information can be costly to acquire owing to energetic investments required to detect environmental cues, which may lead to individuals relying more on social interactions, and result in individuals that are highly socially responsive (Guttal and Couzin, 2011; Herbert-Read, 2016). However, our results did not detect any differences in individual associative learning among individuals that vary in their ability to associate with group members in a schooling behaviour context. Previous studies supporting the distributed cognition hypothesis have been based on different aspects of social complexity. For instance, O'Donnell et al. (2015) found a higher brain investment in solitary than in social species of wasps associated with the structure of family groups and labour specialization among group members. Similar results were found in mole rats, where solitary species had a higher neuron density than social species (Kverkova et al., 2018), and in woodpeckers, where species living in groups showed a reduction in brain size, potentially as a result of cooperative breeding allowing disinvestment in expensive brain tissue (Fedorova et al., 2017). In these studies, the driver of social complexity was compared across species and associated with cooperative systems. As such, it seems like the distributed cognition hypothesis is associated with species with stable social organizations, and therefore relatively general. Social behaviours can be regarded as being demanding in terms of reciprocal cooperation, deception and forming coalitions (Ioannou, 2017), meaning there could also be selection for increased cognitive abilities at the individual level (see the 'social brain' hypothesis; Dunbar, 1998; Humphrey, 1976; Jolly, 1966). Because the social brain hypothesis targets highly complex social interactions as the cognitive challenges that select for higher general intelligence

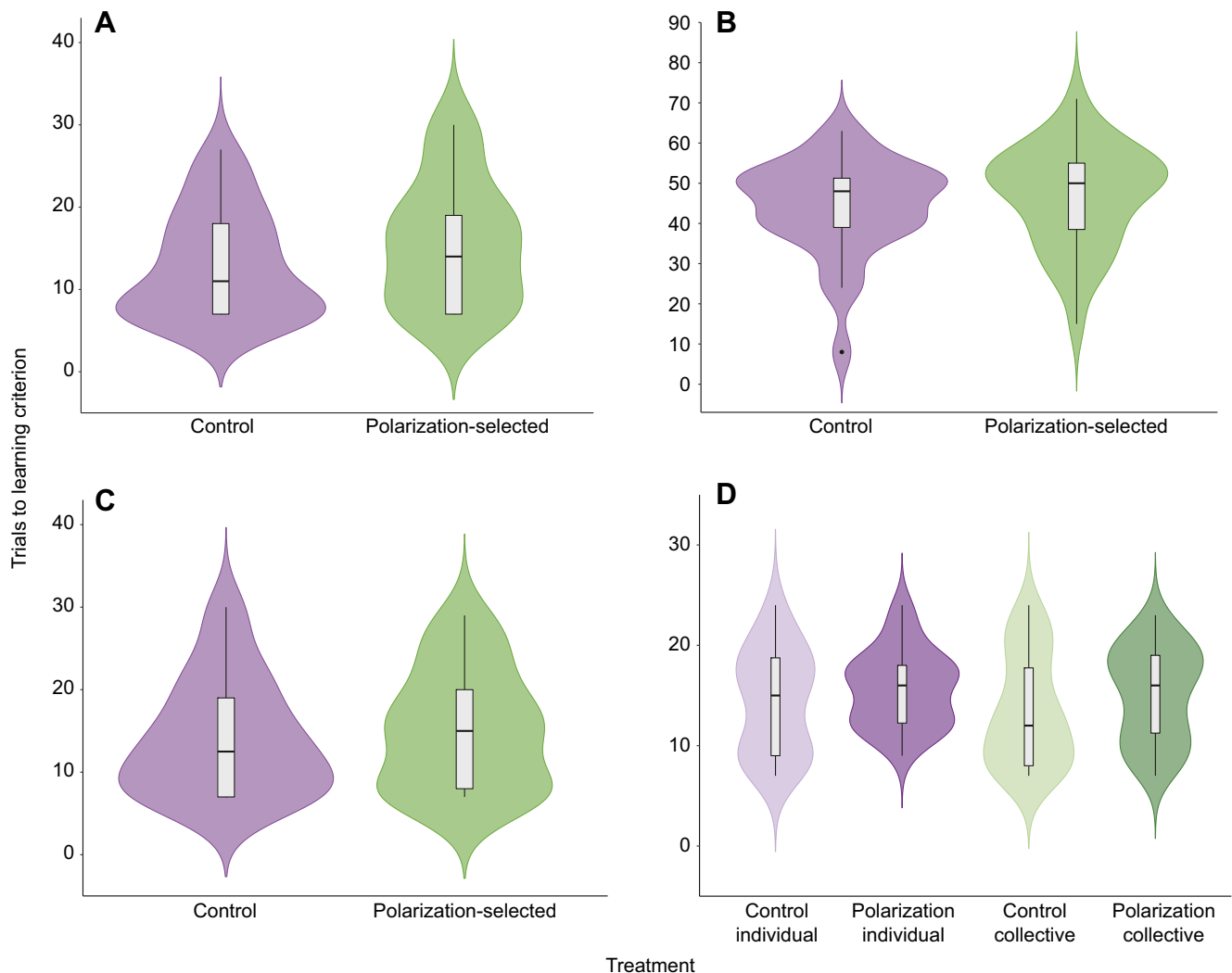


Fig. 3. Performance of female guppies given by the number of trials needed to reach the learning criterion. Violin plots for trials to reach criterion for the (A) colour discrimination assay, (B) reversal learning assay, (C) social learning assay and (D) side-rewarded association for the individual and collective learning assay. Boxplots indicate the median value and interquartile range.

(Humphrey, 1976), it seems unlikely that changes in coordinated movement in schooling behaviour could act as drivers of individual cognitive abilities. Although group cohesion in collective motion demands cognitive abilities associated with the integration of information from multiple individuals (Ioannou, 2017), it is possible that changes driven by changes in direction when schooling do not relax selection for cognition, at least not for associative learning. It is also possible that the cognitive skills required for the associative tasks in our experiments may not be those required to coordinate collective motion. Social cues can drive movement decisions, which lead to shoals being able to solve problems individual fish are not capable of recognizing (Theiner, 2018). For example, single golden shiners perform poorly when tested under different light conditions for their preferred habitat, but the task is solved more easily when in groups as a result of social dynamics (Berdahl et al., 2013). Schooling behaviour may thus represent an alternative evolutionary strategy for solving complex problems compared with developing a more advanced individual cognitive ability (Ioannou et al., 2011). Future cognitive assays on the polarization selection lines will target aspects of cognition that more closely adhere to decision-making in a collective motion context.

Polarization-selected females and control females did not differ, neither in an associative learning task, nor in a socially reinforced associative learning task. This suggests that evolutionary changes in collective motion do not affect social associative learning abilities given polarization-selected females do not tend to use social information more so than control females. Selection pressures associated with aligning close to other individuals during collective motion might thus not be associated with a relaxation in individual cognitive abilities owing to extrinsic differences that underlie schooling behaviour. Individual group members rely on the position and movements of near neighbours for information transfer (Conradt and Roper, 2005; Ioannou, 2017). However, during feeding behaviour, fish schools tend to remain cohesive without being polarized (Calovi et al., 2014). It is likely that within a group, members hold different information about their environment and that some individuals possess relevant experience in solving a particular challenge that other members lack (Webster et al., 2017). Thus, environmental cues associated with food availability and competition for food could explain why individual associative learning abilities are still important when individuals are better at following conspecifics in more cohesive groups. Decision-making

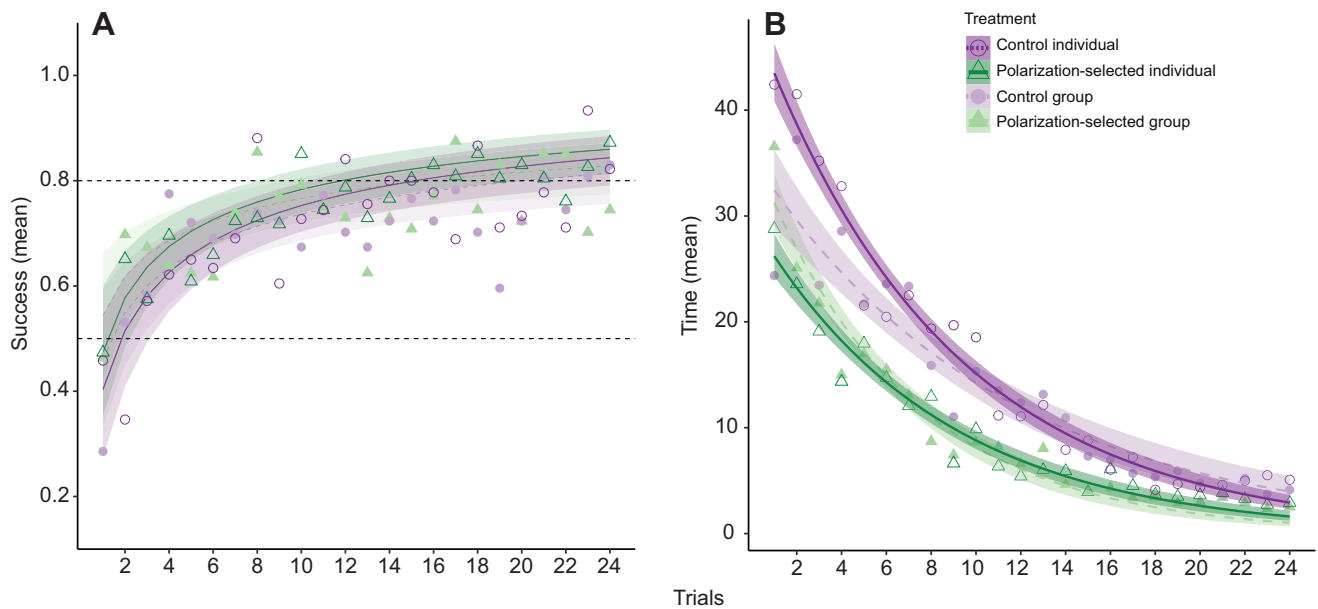


Fig. 4. Individual and collective spatial associative learning assay. (A) Proportion of correct choices and (B) time to make the correct choice by control individuals tested individually and in groups (purple circles dark and light, respectively) and polarization-selected females individually and in groups (green triangles dark and light, respectively) over 24 trials in a side discrimination test. Lines are based on model predictions. Dashed lines correspond to control lines, solid lines correspond to polarization lines. Shading represents 95% confidence intervals. Dashed lines in A indicate 50% and 80% end performance levels.

in shoals may also be influenced by individuals favouring their own self-interest, particularly in many fish species where groups are made up of unrelated individuals that do not form stable bonds (Ioannou, 2017). This variation in social organization again contrasts with studies that have found support for the distributed cognition hypothesis, found in socially cohesive species that form semi-permanent groups (e.g. Fedorova et al., 2017; Kverkova et al., 2018; O'Donnell et al., 2015). Guppy females form temporally stable social networks, where individuals associate with a small number of individuals (Croft et al., 2004). But because guppies are likely to exchange group membership many times over their lifetime (Darden et al., 2020), individuals that tend to polarize more strongly might rely on their own cognitive abilities as equally as those that do not. This was in part supported by the lack of difference in learning rates between control and polarization-selected females when aided by visual information in our social associative learning assay. Although individuals can acquire information by direct sampling, or through observing the behaviour of others (Brown and Laland, 2003), social learning propensities in guppies seem to be influenced by early life experiences and change over their lifespan (Leris and Reader, 2016), constraining the predisposition for social learning.

Cognitive demands and decision-making processes can also change depending on environmental conditions such as predation, and in turn be associated with the structural organization of the group. Individuals in groups with a high degree of fission–fusion dynamics are expected to be good at solving problems that require conditional discrimination (Aureli and Schino, 2019). For instance, when comparing guppies from low and high predation environments, groups of fish from high predation environments switched their positions more often and made movement decisions within the group more frequently, most likely because the costs of group fission are higher in such environments (Herbert-Read et al., 2019). Whether decision-making processes under particular environmental conditions differ between polarization and control females remains to be tested. We did not find any differences between polarization and control females when they were tested in groups or individually. This speaks against any benefit from

being in a group in the polarization-selected fish in associative learning, although this could differ in a predator avoidance context. Positive feedback resulting from copying other individuals can spread information quickly through the group, but can also result in all individuals making the same incorrect choice (Sumpter et al., 2008). By testing the same females individually and in groups, we could test the individual performance in both contexts. Although selection regime did not affect associative learning performance, we did find that those that were tested previously with a group took longer to make the correct choice individually. Although the ‘loss’ of companions could have stressed females previously tested in a group, we believe it is more likely that being in a group can accelerate (i.e. how long) the decision-making process in individuals, given they still performed the test. It has indeed been suggested that as group size increases, individuals tend to make more accurate decisions (Sumpter et al., 2008) and learn faster (e.g. Swain and Fagan, 2019), and the groups are more likely to contain individuals who make better decisions and control collective decisions (Bose et al., 2017; Ioannou, 2017). Consequently, responses to other individuals faster than those that characterize polarization-selected females could still require higher cognitive abilities, but in aspects beyond the associative learning aspects measured here.

Animals associate food with a variety of features such as size, colour, shape and location (Root-Bernstein, 2010). Although colour was counterbalanced and randomly distributed across our treatments to control for any innate preference and colour or side bias, we did find evidence of colour and side biases in our experiments. These biases, however, were not consistent across the learning assays. In the colour associative learning assay, we found an overall preference towards the colour yellow. That is, females made fewer mistakes from early trials when associating the food reward with yellow, so potentially this was not very cognitively challenging from the start for either control or polarization-selected females. Contrary to the colour associative learning assay, we found an overall preference for the colour red in the social associative learning assay. A bias towards red has been shown in other fish such

as sticklebacks, triggerfish (Cheney et al., 2013; Smith et al., 2004) and guppies (Buechel et al., 2018; Cole and Endler, 2015). Guppy females generally prefer to mate with males with orange spots on their body tail and fin (Houde, 1997), a preference that seems to be associated with a feeding preference for orange fruits (Rodd et al., 2002). The hue of orange is in between that of red and yellow. Potentially slightly different lighting conditions in different rooms (the experiments were performed in different rooms) may have made either red or yellow seem closer to orange. We found a side bias for the right in the reversal learning assay, and a side bias for the left side in the spatial learning assay. Although laterality has been shown in poeciliid fish in response to detour tests (Bisazza et al., 1997), our assays emphasize taking preference bias into account when investigating learning rates. Importantly, the colour and side biases did not affect any of the conclusions concerning the comparisons between the selection regimes.

Finally, polarization was selected for in an open field test, i.e. in a risky environment, and may thus have not selected for abilities needed in foraging, which is the reward paradigm used in our cognitive assays. Although high polarization in groups may enable individuals to forage more efficiently through information transfer, it can also result in individuals competing for resources (Couzin and Krause, 2003; Dall et al., 2005). As a result, it is likely that cognitive abilities associated with foraging do not necessarily relate to polarization given individuals could respond spontaneously to other individuals that hold information in a foraging context (Couzin et al., 2005). In guppies, individuals seem to follow the first fish to move when foraging, even when that does not necessarily lead to a successful foraging attempt (Franks and Marshall, 2013). Additionally, evidence from the distributed cognition hypothesis has mainly been found in social insects, where individual foragers can pool information so that the colony exploits resources more efficiently (Dall et al., 2005), which may be dependent on group sex composition in the case of guppies (Snijders et al., 2019).

Understanding and predicting how collective patterns emerge from behaviour and social interactions of individuals is a key goal of collective behaviour research (Jolles et al., 2020). Collective motion studies often fail to account for persistent individual differences (Del Mar Delgado et al., 2018), which can determine the behavioural capacity of individuals, leading to changes in collective behaviour. Although we only found differences between control and polarization lines in one type of learning rate in associative learning, our study provides a starting point towards increased understanding of the underlying patterns that drive collective motion. It remains intriguing which aspects of cognition other than associative learning could be affected, either positively or negatively, by selection on more coordinated movement. Future studies will target additional aspects of cognition, for instance decision-making during predation threat, to provide as complete as possible a picture of the behavioural consequences of evolutionary changes in collective behaviour.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: R.V.-T., A.K., N.K.; Methodology: R.V.-T., A.B., S.D.B., A.K., N.K.; Validation: R.V.-T.; Formal analysis: R.V.-T.; Investigation: R.V.-T., A.B., L.W., E.E.; Resources: A.K., N.K.; Writing - original draft: R.V.-T.; Writing - review & editing:

R.V.-T., A.B., L.W., E.E., S.D.B., A.K., N.K.; Visualization: R.V.-T.; Supervision: R.V.-T., A.B., A.K., N.K.; Funding acquisition: A.K., N.K.

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Data availability

Data have been made publicly available through the Open Science Framework at: <https://osf.io/e7dnh/>.

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