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ORIGINAL PAPER

Current predation risk has opposing effects on social learning of foraging locations across two guppy populations

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Abstract
Social learning, where animals learn from other individuals, occurs in many diverse species. The influential but debated 'costly information' hypothesis posits that animals will rely more on social information in high-risk contexts, such as under increased predation risk. We examined and compared the effects of perceived predation risk on social learning of foraging sites in female Trinidadian guppies from wild and domestic populations raised in common-garden environments. We used a demonstrator-observer pairing where a subject could observe conspecific 'demonstrators' feeding from one of two feeders, and measured whether the observer subsequently spent more time at a demonstrated or non-demonstrated feeder. We manipulated perceived predation risk using alarm cue (conspecific skin extract). Stress responses and social learning differed between the two populations. Most notably, high predation risk enhanced social learning in the wild-type guppies, but depressed it in the domestic guppies. Thus, fish from both populations were able to socially learn, but under opposing contexts. These results suggest social learning propensities are the product of multiple interacting systems, and biases to favour social learning can emerge dependent on evolutionary history and current conditions.

Keywords Social learning · Stress · Risk · Anti-predator behaviour · Comparative study · Fish

Introduction

Animals can gain low-cost, pre-tested knowledge from others ('social learning'; Hoppitt and Laland 2013; Olsson et al. 2020), instead of learning from their personal experiences with the world. However, social learning also carries costs, such as increased competition for the same resources or acquisition of outdated, irrelevant or suboptimal behaviour patterns (Seppänen et al. 2007; Rieucau and Giraldeau 2011). Thus, we expect individual, population and species differences in social learning propensities, differences that could emerge from evolved psychological rules that optimize social learning ('social learning strategies') and/or from past individual experience with social cues (Laland 2004; Kendal et al. 2009; Heyes and Pearce 2015; Reader 2016; Leadbeater and Dawson 2017).

An influential, but relatively untested, 'costly information' hypothesis posits that animals will learn from others when the costs of learning for oneself are high—a hypothesis now also termed 'copy when asocial learning is costly' (Boyd and Richerson 1985; Laland 2004; Kendal et al. 2018). While these costs could take a number of forms (Rieucau and Giraldeau 2011), often costly information is operationalized as the risks of individual exploration. For example, under intense predator pressure the risks of individual exploration for food may be greater, leading to the prediction that reliance on social learning is increased. Moreover, in such situations the benefits of group foraging may be increased, because being in a group can reduce individual predation risk (Krause and Ruxton 2002), leading to an additional reason to copy others. Similar predictions are made by social foraging and producer-scrounger models, where individuals under risk benefit by joining the foraging discoveries of others (Lendvai et al. 2004; Mathot and Giraldeau 2008).

The prediction that predation risk increases social learning propensities has been addressed with both experimental manipulations of current risk and comparative studies, but has received mixed support. For example, experimental manipulations of risk provided support for the prediction in fish, but not in two rodent studies (Galef and Whiskin 2006;

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Webster and Laland 2008; Galef and Yarkovsky 2009). Comparative work on stickleback fish (Gasterosteidae) has provided evidence for species differences in social learning propensities that are replicated across populations, but neither population or species variation in predation risk consistently predicted social learning propensities (Coolen et al. 2003; Webster et al. 2019; Keagy et al. 2023). Thus, the impact of predation risk on social learning is unclear. Furthermore, there is considerable debate over whether differences in social learning propensities are best explained as products of domain-specific adaptive specializations or as domain-general associative learning processes (Heyes and Pearce 2015; Reader 2016; Leadbeater and Dawson 2017; Kendal et al. 2018). That is, are social learning propensities best explained as the result of derived processes that can evolve and develop somewhat independently from other traits (the 'adaptive specialization' account), or as the result of general processes that have not evolved specifically to maximize the benefits of social learning (the 'general process' or 'associative' account)?

Relevant to the costly information hypothesis are impacts of stress on social learning propensities. Studies manipulating stress and measuring social learning in birds (zebra finches *Taeniopygia guttata* and Japanese quail *Coturnix japonica*) paint a complicated picture, with stress having opposing effects on social learning propensities depending on timing and circumstances (Boogert et al. 2013; 2018). Such studies, although they can be interpreted as adaptive responses to stress, raise the possibility that some impacts on social learning may be pathological, maladaptive or a byproduct of other processes. Moreover, they bring into question the extent to which social learning propensities vary independently of other traits (Heyes and Pearce 2015).

Here, we address the above issues in studies of the Trinidadian guppy (*Poecilia reticulata*), a small tropical fish that has become a model system in ecology and evolution (Magurran 2005). Social learning is well established in guppies (Brown et al. 2011). Moreover, guppies show evolved, developmental and immediate responses to prevailing predation risk, which varies considerably across guppy populations (Brown and Godin 1999; Magurran 2005; Reddon et al. 2018; Feyten et al. 2021; Fox et al. 2024). Population comparisons of social learning are rare and have focused on wild animals (Carlier and Lefebvre 1997; Webster et al. 2019; Heinen et al. 2021; Keagy et al. 2023). However, when individuals are raised over generations under common-garden conditions, population comparisons provide an opportunity to investigate evolved changes in social learning propensities. Here, we take such an approach and compare social learning of food locations in two populations, a wild-type ('Paria': see Methods) and a domestic population, under high or low perceived current predation risk. Our aim was not to determine the causal factors underpinning any population difference, which would require replicate population pairs, but instead to establish whether population differences in social learning propensities exist and how perceived predation risk impacts any such differences.

In the current study, subjects viewed conspecific 'demonstrators' feeding at one of two feeders, then demonstrators were removed. If subjects socially learned, we expected them to learn from the demonstrators and subsequently prefer or avoid the demonstrated feeder. To manipulate perceived predation risk, we used chemical alarm cue, a skin extract that in the wild would be released by mechanical damage to the skin of conspecifics (e.g. by a predation event), thus providing a reliable cue of risk. Guppies respond to alarm substance with anti-predator behaviour (Brown and Godin 1999). We thus examined social learning under risk, rather than social learning about risks (Brown 2003; Leadbeater and Dawson 2017; Olsson et al. 2020; Fan et al. 2022). The manipulation of perceived predation risk began shortly before subjects observed demonstrators and continued to the choice phase when subjects could express their feeder preference. We expected the two populations to show different responses to predation risk, allowing us to determine whether the impacts of stress on social learning are generalizable as the costly information hypothesis might predict.

Methods

Guppy populations and experimental groups

We used laboratory bred wild-type and domestic Trinidadian guppies, both gifts of the Rodd Laboratory (University of Toronto, Canada). The wild-type guppies were descendants of guppies captured from a tributary of the Paria river in Trinidad in 2008, supplemented with guppies from the same location in 2016 (the "Houde" tributary; Trinidad National Grid System: PS 896 886). For other work on this population see e.g. Guerrera et al. (2022) and Li et al. (2022). Their capture site is considered a low-predation locality (Houde 1997; Magurran 2005; Li et al. 2022). The domesticated guppies were descendants of fish originating from a mix of commercial suppliers brought into the Rodd Laboratory in 2015. Both populations had thus been bred under standardized laboratory conditions for several generations, allowing us to ascribe any observed population difference to inherited differences. Wild Paria guppies are aggressive to conspecifics and are typically observed alone (Magurran and Seghers 1991), while domestic guppies readily shoal (Swaney et al. 2015), thus we expected considerable social learning differences between the populations.

We housed and bred the guppies in our laboratory in 120 L tanks, separated by population. Tanks had gravel substrate, artificial plants, and were maintained at 25 ± 1 °C. Each tank had its own external water filter (Eheim Professionel 3, Germany). The photoperiod was a 7:00–19:00 h light:dark cycle, mimicking guppies' natural environment, with no natural light. Individuals from each population (Paria or domestic) were exposed as detailed below to either alarm cue or a control (water), thus creating four experimental groups in a 2 × 2 factorial design. We did not investigate domestication per se. Rather, we chose these two populations of very different evolutionary histories because we hypothesized their behaviour would vary considerably, and anecdotally, we had noted problems replicating social learning paradigms in our laboratory and wondered if population origin could be an explanation.

Training and testing tank

Approximately one week before testing, one female and one male were transferred from group housing to each testing tank, a 20 L glass tank filled with 14 L of water (Fig. 1). Only females were used as subjects, with males present to minimize isolation stress. At this stage of investigation, we tested a single sex to avoid any potential confounding effects of sex on our results. We chose females because female guppies have been shown to forage longer, be more explorative, have stronger shoal fidelity and be more responsive to predator cues than males (Magurran and Garcia 2000; Reader and Laland 2000; Magurran 2005; Brusseau et al. 2023). A plastic mesh created two chambers separating the female (occupying 2/3 of tank) and male while allowing visual and olfactory contact. Translucent film on interior long tank walls prevented visual contact between tanks and guppies seeing their own reflection, which we previously found interfered with testing. White corrugated plastic between the two experimental feeders created an obstacle to increase the cost of switching from one feeder to the other, in an attempt to make a feeder decision more meaningful. Sandy-coloured course gravel (~5–10 mm) covered the tank bottom. Tank temperatures and photoperiod were identical to the housing tanks, with the male chamber containing a 50W water heater and a sponge filter. Training and testing occurred between 9:00–17:00 h.

Training

To familiarize the subjects with the experimental feeders, we fed them from these feeders for the entirety of the training session (12 trials presented to each subject over three consecutive days, with four trials per day). Training trials began with the removal of the artificial vegetation from the female chamber, allowing the subject to freely swim throughout the chamber. Both feeders were then placed at their respective sides of the tank (left and right) in full view of the subject. Assignment of food to one feeder per trial was pseudorandomized, so that each feeder contained food for half the training trials. Hence, subjects should not have acquired a preference for a specific feeder by the time testing began. A small (~0.2 mg) amount of food flakes (Tetramin flakes, Tetra®; Melle, Germany) was placed in the chosen feeder with tweezers to prevent satiation between trials. We pretended to add food with tweezers in the empty feeder to prevent an association between the tweezers and reward. The floating feeders were designed to be visually and spatially distinct, one with vertical blue and yellow stripes always being placed to the left of the tank (from the experimenter's perspective) and the other with horizontal blue and yellow stripes always placed to the right. We choose these colours because guppies can distinguish blue and yellow from other colours and blue and yellow are not strongly preferred colours (Rodd et al. 2002; Lucon-Xiccato et al. 2019; Toure and Reader 2022). If the subject fed before 30 min, the trial was deemed successful, the time of feeding was recorded to the nearest 5 s, and the subject was allowed to feed for 3 min before the trial ended. If after 30 min the subject did not feed, the trial ended and was deemed unsuccessful and the fish was awarded the maximum possible time for completion. After the trial, feeders were removed and rinsed of any remaining food particles, and any unconsumed food was removed from the tank.

The third day of training was slightly modified to more closely resemble the social learning test: three artificial leaves were placed in both feeders to slightly obscure the food, requiring close approach to determine whether food was present. Leaves were not present during the initial training to ease familiarization to the feeders.

We could not train all subjects on one day, so we trained fish in batches or 'cohorts', completing training and testing for one cohort before moving on to the next. 66 of 100 guppies from 14 cohorts successfully completed 8 to 12 training trials (our training criterion) and were moved on to the social learning test. Sample sizes before training were balanced between populations, treatments, and cohorts, and the final sample of guppies that passed the training phase was also balanced. The probability of success did not significantly differ between populations (chi-square test—domestic: 34/53 versus Paria: 32/47; $\chi_1^2 = 0.17$, $p = 0.68$). We examined whether the training performance of the 66 subjects that passed the training phase differed between populations using a general linear model. We analysed the time to feed on the first and last training trial, including in the model population, trial (first or last), and the interaction between population and trial. We found no significant difference between populations ($F_{1,64} = 1.55$, $p = 0.22$) and no significant population by trial interaction effect ($F_{1,64} = 1.15$, $p = 0.29$). However, time to feed decreased from the first to last training trial (from a mean ± SE of 484.32 ± 56.32 s to 118.94 ± 38.20 s; $F_{1,64} = 29.31$,

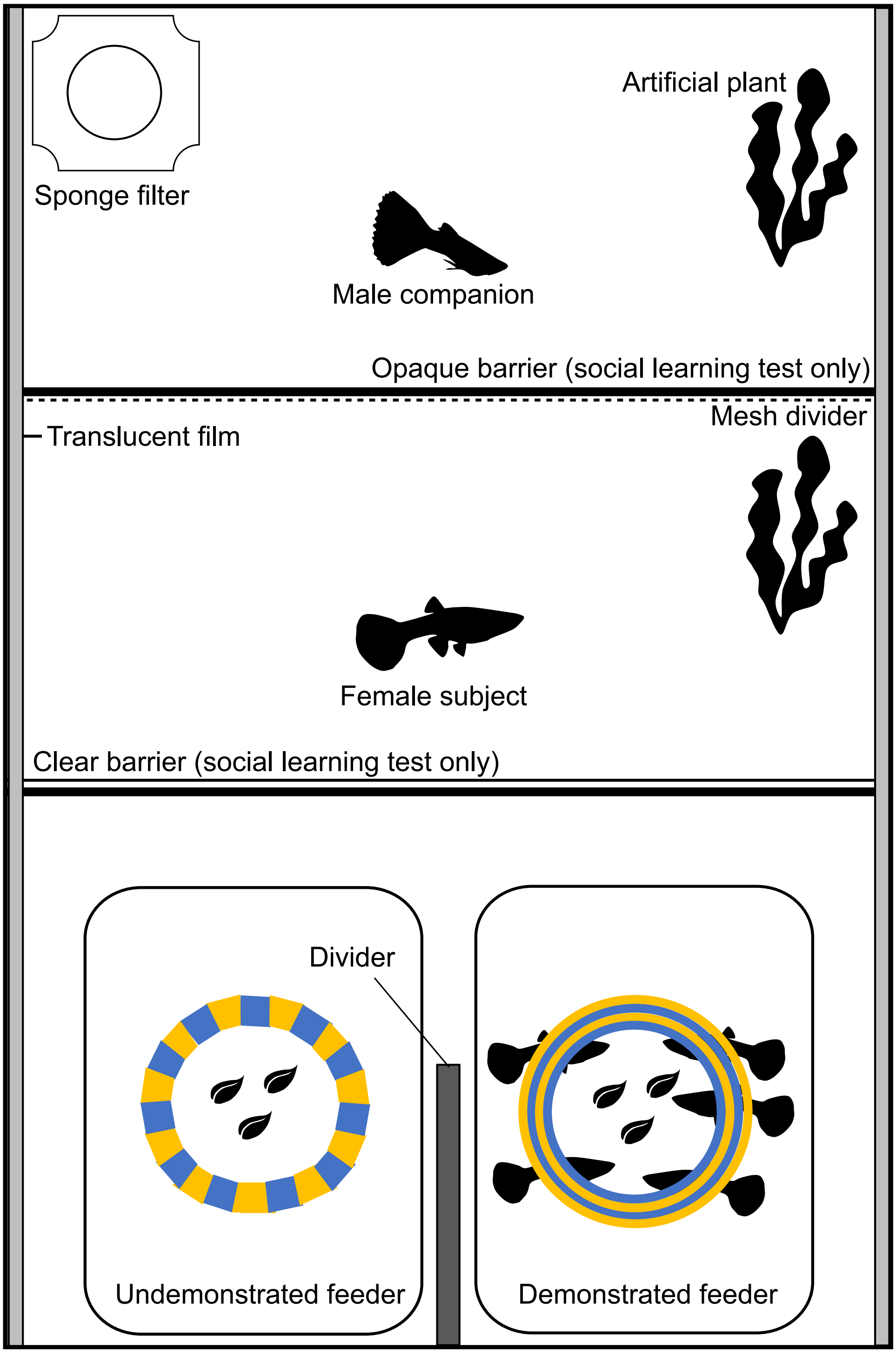

Fig. 1 Experimental tank with female subject, male companion, and demonstrators (social learning test only); top view, not to scale. The same tank was used for housing during the experiment, feeder training, and the social learning test, with barriers, feeders and demonstrators added to the tank according to the experimental stage

$p < 0.0001$), indicating improved performance with training. The analyses of training performance above met relevant statistical assumptions. There were no significant differences between cohorts ($0.38 < p < 0.73$) on our social learning measure (see below) and we thus combined data from all cohorts.

Preparation of alarm cue

We administered an alarm cue solution of conspecific epidermal tissue to the treatment tanks during the social learning test to increase perceived predation risk (Brown and Godin 1999). To prepare the alarm cue, we euthanized guppies in ice water (Wilson et al. 2009), using an equal mix of male and female and Paria and domestic individuals. Following established procedures (Brown and Godin 1999), we prepared an alarm cue solution of 0.1 cm^2 of skin / ml with ultra-distilled water. We prepared enough solution to add 7 ml in each testing tank assigned the alarm cue treatment (control tanks received an equal volume of distilled water), which produced a tank alarm cue concentration similar to Brown & Godin (1999), and was shown in our pilot study in Paria guppies to increase reliance on social cues (unpublished data). We prepared the alarm cue the morning of the social learning test and set it on ice until used. Any leftover alarm cue was discarded at the end of the day.

Social learning test

We based the social learning test on similar designs used successfully in guppies and other fish (Reader et al. 2003; Webster and Laland 2008). We ran the social learning test on the fourth day, immediately following the three consecutive days of feeder training. We removed the artificial vegetation from the female tank chamber, as during training, and removed the sponge filter to prevent alarm cue filtration. We then waited five minutes to allow the subject to habituate to the modified environment. Next, we added barriers to the tank (Fig. 1): an opaque black plastic barrier between the mesh and the male guppy to prevent visual contact with the subject and a second opaque barrier to prevent the subject from seeing the demonstrators enter the tank, placed alongside a transparent barrier for use later on in the test. We waited 30 s and then added the alarm cue or control treatment (water) to the subject's chamber. So that the experimenter (ACF) was blind to the randomly-assigned treatment being administered, alarm cue and control solutions were in syringes covered in black tape by MFG. The experimenter was not blind to the population because the two populations could easily be visually distinguished. The experimenter moved out of the subject's sight for the testing session.

Next, we immediately ran the demonstration phase (Fig. 1). The feeders and plastic leaves were designed to conceal food from the subject but to allow demonstrator feeding activity to be visible. A sealed transparent container with five demonstrator females from the same population as the subject was placed into the tank under one of the feeder locations (randomly chosen). Thus, demonstrators were not exposed to alarm cue. The demonstrators had been housed in the same tanks as subjects prior to the experiment. An identical chamber containing only water was placed under the other feeder location, resulting in an unambiguous difference in social cues between the two feeder locations. Feeders identical to the training feeders, each containing three plastic leaves, were placed in the demonstrator and control containers on the same side as during training (vertical-striped to the left of the tank and horizontal-striped to the right). Thirty seconds after treatment administration we removed the opaque barrier, revealing the transparent barrier and allowing the subject to observe the demonstrators for three minutes. Immediately after the barrier was lifted we added food in the demonstrators' feeder and pretended to add food in the feeder without demonstrators. Demonstrators were used a maximum of three tests to ensure they were motivated to feed.

We then prepared the tank for the choice phase, which began about 90 s after the demonstration phase. We re-inserted the opaque barrier between the subject and the demonstrator to prevent the subject from seeing the demonstrators and containers being removed. Next, we added new left and right feeders to the tank, each containing three artificial leaves, followed by the removal of the opaque barrier, with the feeders in full view of the subject. These feeders were placed at the end of the tank so that the divider obscured them from one another. New but visually identical feeders were used to prevent the possibility of residual odour cues from the demonstrators or food. No food was placed in the feeders so that prior social information was the only cue available, and not olfactory cues from food.

The choice phase of the test commenced once the transparent barrier between the subject and feeders was removed, giving the subject access to the feeders. The "demonstrated" feeder previously had the demonstrator fish feeding from it during the demonstration phase whereas the "undemonstrated" feeder did not. Testing lasted 10 min and we used a Python keypress-recording program during the test to record time spent near the demonstrated feeder (i.e., inside or within 2 cm of the feeder), time spent near the undemonstrated feeder (inside or within 2 cm), the number of dashing events, and time spent freezing. Trials were also videoed as a backup. Dashing and freezing are types of behaviour indicating stress, used to assess stress responses to the alarm cue, along with the total time spent visiting feeders, given that subjects would be expected to reduce feeding and spend more time at the bottom of the tank when stressed (Brown and Godin 1999). After testing, all feeders, barriers, and artificial leaves were rinsed with aged tap water to remove odour traces that could interfere with subsequent tests.

Statistical analyses

To be included in analyses, fish had to spend at least 10 s visiting feeders during the test, in order to exclude transitory passes unlikely to represent foraging attempts. Except where noted below, this exclusion of four fish had no effects on the pattern of significant results. Data are presented as means ± SE and p-values < 0.05 were considered significant. We analysed four measures: (1) *Total time spent at feeders.* We ran a general linear model in SAS 9.3 (Proc GLM) with treatment, population, and their interaction as fixed effects. Our dependent variable was the sum of time spent near the demonstrated feeder and undemonstrated feeder. Residuals were normally distributed. (2) *Number of dashes.* We ran a Poisson regression model in SAS (Proc GENMOD). We specified a Poisson distribution because the number of dashes were count data. As above, we incorporated treatment, population and their interaction as fixed effects in the model. (3) *Time spent freezing.* We ran a general linear model as for (1). Because analysis of the raw data produced non-normally distributed residuals and contained several zero values, we square-root transformed the data, which improved normality. (4) *Feeder preference.* Because total time spent at feeders differed between treatments and populations (see below), we divided the difference between time spent at the demonstrated feeder and undemonstrated feeder by total time spent at either feeder, which produced a percent time spent at the demonstrated feeder. Positive values indicated that the guppy spent more time at the demonstrated feeder, whereas negative values indicated more time spent at the undemonstrated feeder, with zero indicating no preference. We ran a general linear model as for (1). Residuals were normally distributed. We followed up this analysis with one-sample *t*-tests (means compared to zero) for each cell in our 2 × 2 design to determine whether each population socially learned under the control and alarm cue treatments.

Results

We pretrained subjects to feeders before conducting the social learning test. Of the 66 guppies that successfully completed feeder training, 62 visited the feeders for at least 10 s during the social learning test. Final sample sizes were: Domestic Alarm Cue $n = 13$, Domestic Control $n = 18$, Paria Alarm Cue $n = 14$, Paria Control $n = 17$. During the social learning test, we measured established behavioural indicators of stress (see Methods) alongside social learning performance. All demonstrators fed at every test and none showed dashing or freezing behaviour.

Behavioural indicators of stress

Total time at both feeders. Guppies exposed to alarm cue spent significantly less time at the two feeders compared to guppies exposed to the control cue, water ($F_{1,58} = 4.71$, $p = 0.03$; Fig. 2A). Paria guppies spent less time at the two feeders than domestic guppies ($F_{1,58} = 4.01$, $p = 0.0499$; this difference was non-significant if the four fish visiting the feeders for less than 10 s were included in the analysis: $F_{1,62} = 1.92$, $p = 0.17$). There was no significant interaction between alarm cue treatment and population ($F_{1,58} = 1.66$, $p = 0.20$).

Number of dashing events. Guppies exposed to alarm cue dashed significantly more often than guppies exposed to water ($\chi_1^2 = 14.92$, $p = 0.0001$, Fig. 2B). Paria guppies dashed significantly more often than domestic guppies ($\chi_1^2 = 19.89$, $p < 0.0001$). There was no significant interaction between treatment and population ($\chi_1^2 < 0.01$, $p = 0.99$).

Time spent freezing. Guppies exposed to alarm cue spent significantly more time frozen during the social learning test than guppies exposed to water ($F_{1,58} = 4.90$, $p = 0.03$; Fig. 2C). Paria guppies froze longer than domestic guppies ($F_{1,58} = 9.56$, $p = 0.003$). The interaction between population and treatment had a p of 0.051 ($F_{1,58} = 3.96$), with Paria-origin guppies showing higher levels of freezing with alarm cue present.

Social learning performance

There was no significant main effect of alarm-cue treatment ($F_{1,58} = 0.04$, $p = 0.84$) or population ($F_{1,58} = 1.98$, $p = 0.17$) on the guppies' preference for the demonstrated feeder over the undemonstrated feeder during the social learning test (Fig. 3). However, there was a significant treatment by population interaction ($F_{1,58} = 5.51$, $p = 0.02$), with relative preference for the demonstrated feeder increasing when exposed to alarm cue in Paria-origin guppies, but the opposite pattern in the domestic guppies (Fig. 3). When exposed to alarm cue, Paria guppies had a significantly stronger preference for the demonstrated feeder than did domestic guppies ($t_{25} = 2.50$, $p = 0.02$), with no significant difference between the populations when exposed to the control cue ($t_{33} = 0.71$, $p = 0.48$). There was no significant difference in feeder preference between alarm-cue and control treatments within domestic ($t_{29} = 1.79$, $p = 0.08$) or Paria-origin guppies ($t_{29} = 1.53$, $p = 0.13$). There was a significant preference for the demonstrated over the undemonstrated feeder in Paria fish exposed to alarm cue ($t_{13} = 2.68$, $p = 0.02$) and in the domestic fish exposed to the control treatment ($t_{17} = 2.37$, $p = 0.03$), while no significant feeder preference was observed in Paria fish exposed to the control treatment ($t_{16} = 1.28$, $p = 0.22$) or domestic fish exposed to alarm cue ($t_{12} = -0.47$, $p = 0.65$) (comparison of means to zero in Fig. 3). That is, there was evidence for social learning in Paria fish exposed to alarm cue and in domestic fish exposed to the control treatment, and no evidence for social learning in the other population/treatment combinations.

Discussion

We found that two guppy populations reacted differently to manipulations of acute perceived predation risk (i.e., presence or absence of conspecific alarm cue). Predation risk had opposing effects on female social learning propensities

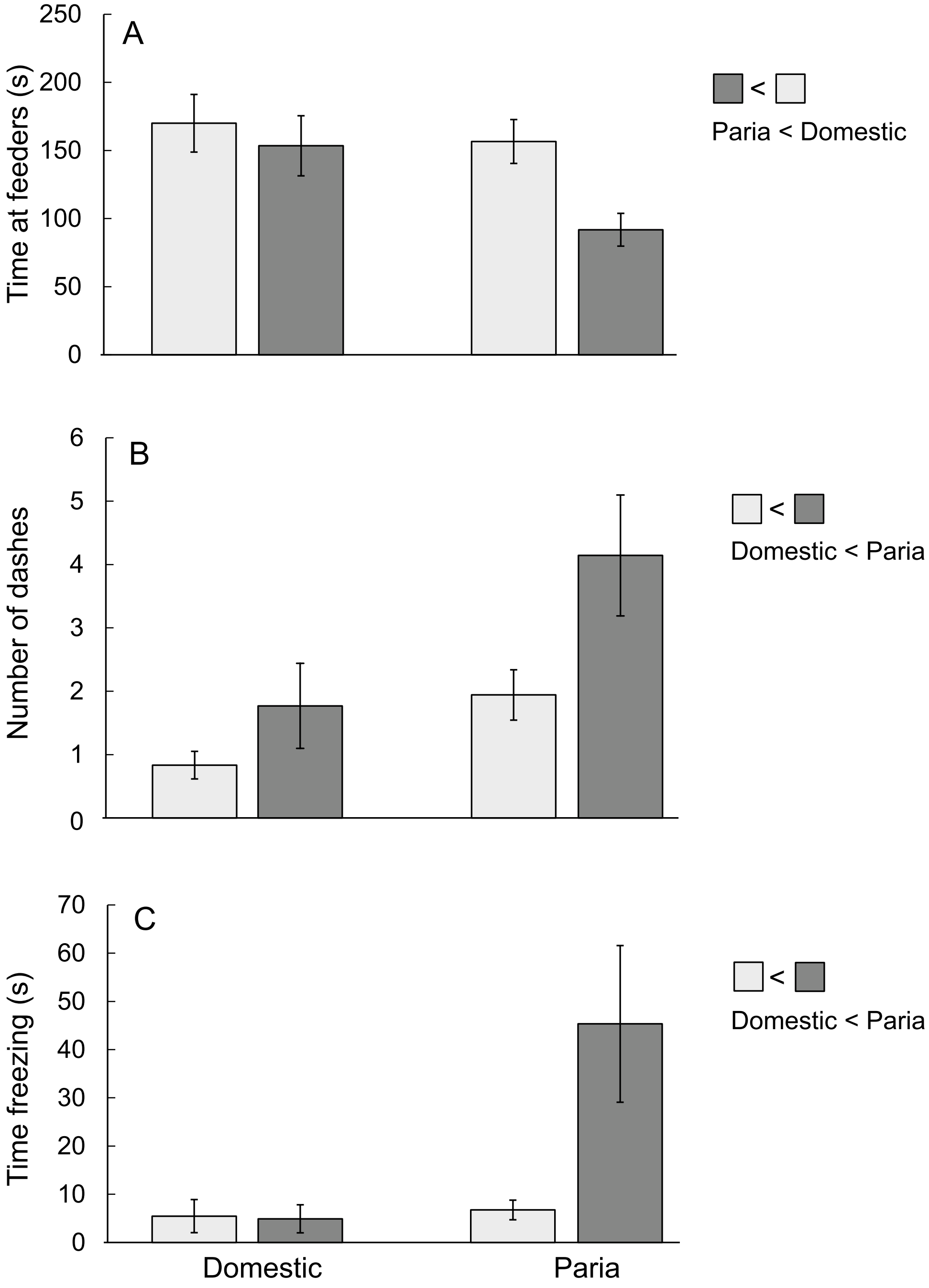

Fig. 2 Stress-related behavioural measures during the 10-min choice phase of the social learning test that followed administration of alarm cue (dark bars) or distilled water (control; light bars) to subjects of two guppy populations (domestic and wild-origin Paria). A: Time subject spent at or near (within 2 cm) both feeders. B: Number of dashing events. C: Time spent freezing. Bars represent means of raw data ± SE, significant differences ($p < 0.05$) are listed in the legend

for foraging sites in domestic versus Paria wild-origin populations. In the wild-origin population, we found evidence for social learning of food locations only under high perceived predation risk (alarm cue), consistent with the predictions of the costly-information hypothesis and an adaptive specialization account. This finding is also consistent with explanations for biases in social learning based on an associative learning framework (an ‘associative’ account; Heyes and Pearce 2015). For example, common contextual cues might favour recall, since acquisition (demonstrator phase) and recall (choice phase) were both under the same predation risk context (alarm cue treatment). Or, conditioned suppression could make social effects more visible (for expanded explanation see Heyes and Pearce 2015; Leadbeater and Dawson 2017), since feeder visits were suppressed under predation risk.

In the domestic population, however, we found evidence for social learning only under low perceived predation risk (water control). Our results thus indicate that population differences in social learning propensities may be context specific. This suggests limits on the generality of the costly information hypothesis, complexity in applying associative

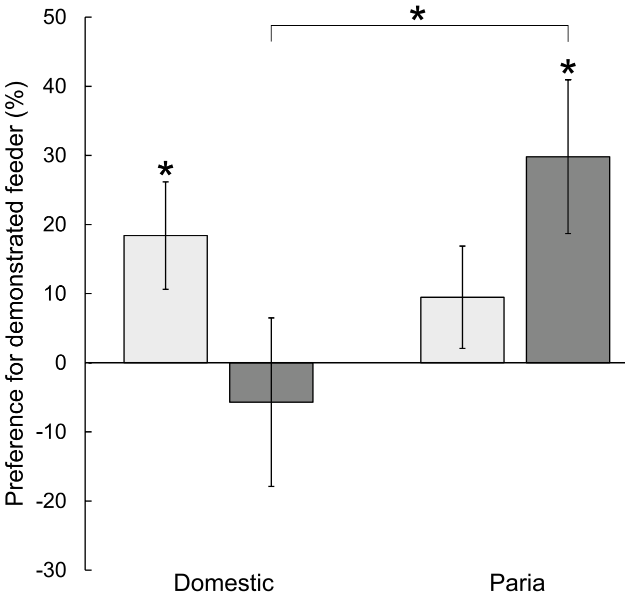

Fig. 3 Socially learned preferences for a demonstrated feeder when alarm cue was present (dark bars) versus absent (light bars) in domestic and Paria wild-origin guppies. Positive preference values indicate that guppies spent more time at the demonstrated feeder whereas negative values indicate they spent more time at the undemonstrated feeder. Bars represent means ± SE, asterisks $p < 0.05$. Asterisks above bars indicate significant differences from zero, the asterisk above the bracket indicates a significant difference between populations under alarm cue administration

accounts, and raises challenges for the comparative study of social learning and for predictions for how information will flow through groups in different conditions. Notably, the population difference in social learning was only detectable under predation risk. Moreover, our results indicate that social learning propensities are not fully independent of phenomena such as stress responses.

To confirm that our alarm cue manipulation impacted perceived risk, we used three behavioural indicators of stress, all anti-predator responses (Fraser and Gilliam 1987; Brown and Godin 1999). On all three measures, fish demonstrated clear stress responses to the alarm cue manipulation. Alarm cue increased dashing, freezing, and reduced time spent at feeders, compared to subjects exposed to the control treatment (water). Paria-origin guppies dashed more, froze more, and spent less time feeding than domestic guppies, with the effect of alarm cue particularly notable in Paria-origin fish. Similar population differences in guppy stress responses have been previously described (e.g. Fraser and Gilliam 1987; Swaney et al. 2015).

Notably, while stress responses to alarm cue in domestic fish were less striking than in the wild-origin fish, particularly for freezing behaviour, alarm cue had an opposing effect on social learning propensity in domestic versus wild-origin fish. Thus, our social learning results are not simply the product of reduced detection or sensitivity to stress in the domestic population, rather, we find the stressor had opposite effects on social learning depending on population origin, with a population difference in social learning propensity only observed under high predation risk. Since fish had been bred and raised in the same laboratory for multiple generations, this strongly suggests an evolved difference that impacts social learning.

A possible alternative interpretation of our social learning test is that fish remembered and returned to the former location of a shoal, rather than to a demonstrated feeder. However, because subjects experienced only a single demonstration (i.e. one trial), our study demonstrates one-trial learning and previous work explicitly examining spatial learning of shoal locations in guppies and other fish suggests this alternative explanation is unlikely (Webster and Laland 2008). For example, there was no evidence that male or female guppies learned the location of a mixed-sex shoal in a T-maze after 10 training trials (Kurvers et al. 2018), male guppies in a two-location task took 15 trials to learn the location of a female shoal (Burns and Rodd 2008), and male but not female guppies were able to learn a route to a mixed-sex shoal over 5 trials (Lucon-Xiccato and Bisazza 2017). These sex differences were ascribed to differences in motivation to seek mating opportunities (Kotrschal et al. 2015; Lucon-Xiccato and Bisazza 2017). Taken together, social learning of a feeder site is the most likely explanation for our results.

Only fish that successfully completed individual training to the feeders went on to the social learning test. This procedure meant that we tested fish for social learning that had similar experiences and individual performance prior to the social learning test. However, around one in three fish did not successfully complete training and we do not know whether our results would generalize to this subset of fish. We found no evidence that one population outperformed the other during training or was more likely to complete training.

In our design, prior to the social demonstration, fish were exposed to personal information that food could appear in one of the two feeders, each with an equal probability, and thus feeder location and appearance did not provide reliable cues for food location. It is possible that alarm cue had effects on acquisition of a feeder preference from demonstrators, on expression of this preference, or both, with two or more processes interacting. For example, perhaps the stressor impacted attention to conspecifics or the recall of food locations differently in the two populations (Clément et al. 2017). The Paria population is unusually aggressive to conspecifics, and the majority of individuals are observed swimming alone in the wild (Magurran and Seghers 1991). Demonstrators were not exposed to alarm cue, but it is possible that the interactive effect on social learning we observed was partly the result of impacts on social affiliation. Stress can impact social affiliations that in turn impact social information use in different ways. For example, familiarity with demonstrators can increase or decrease social learning, and blocking stress responses can facilitate social information use where social affiliation is stressful (Choleris et al. 1998; Swaney et al. 2001; Galef and Whiskin 2008; Martin et al. 2015). Pharmacological manipulations of stress responses (e.g. Boogert et al. 2018) during both acquisition and recall of socially learned information would provide a useful avenue to further explore the role of stress responses on social learning.

Important open questions are whether the population differences we observed are adaptive (i.e., improve fitness), and, if so, under what conditions. Multiple stressors exist. When under stress, the costs and benefits of alternative forms of information gathering and use will vary with the type of stressor, its timing, and its predictability (Taborsky et al. 2021). Moreover, individuals and populations differ in risk sensitivity and stress responses (Taborsky et al. 2021). Given the numerous hypotheses concerning the impacts of stress (Harris 2020), it is important to consider that effects of stress on social learning may be a byproduct of impacts on other systems. Population differences may even be the result of adaptive processes in one population (e.g. our wild-origin population) and a byproduct or maladaptive process in another (e.g. our domestic population). That said, our approach of manipulating perceived risk at a single time point, when information is being gathered and used, is valuable because it illustrates that populations can differ in how a stressor impacts social learning. Messages about how stress and risk impact social learning thus require considerable nuance. The interaction we report between current context (here, high or low perceived predation risk) and evolutionary history (here, population type) provides further illustration of the importance in considering context and individual experience when measuring behaviour, replicating findings across laboratories, and interpreting population and species differences (Webster and Rutz 2020).

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Data availability All data supporting this manuscript are available in the Electronic Supplementary Materials file.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethical approval This study was approved by the McGill University Animal Care and Use Committee (Protocol #7133/7708) and followed guidelines from the Canadian Council on Animal Care and the Animal Behavior Society/Association for the Study of Animal Behaviour (ABS/ASAB). All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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