



## Age and early social environment influence guppy social learning propensities



Ioannis Leris <sup>a, b, \*</sup>, Simon M. Reader <sup>a, b</sup>

<sup>a</sup> Department of Biology and Helmholtz Institute, Utrecht University, Utrecht, The Netherlands

<sup>b</sup> Department of Biology, McGill University, Montreal, Quebec, Canada

### ARTICLE INFO

#### Article history:

Received 29 February 2016

Initial acceptance 6 April 2016

Final acceptance 17 June 2016

MS. number: 16-00178

#### Keywords:

developmental plasticity

early experience

rearing environment

social behaviour

social information

social learning

Social learning, learning from others, allows animals to quickly and adaptively adjust to changing environments, but only if social learning provides reliable, useful information in that environment. Early life conditions provide a potential cue to the reliability of social information later in life. Here, we addressed whether direct early life experience of the utility of social learning influences later social learning propensities. We reared guppy, *Poecilia reticulata*, fry for 45 days in three different social conditions which involved the presence of adult demonstrators providing cues about feeding locations in the tanks ('follow adults' and 'avoid adults' treatments), or their absence ('no adults' treatment). In the 'follow adults' treatment, juveniles that swam in the same direction as the adult demonstrators found food, whereas in the 'avoid adults' treatment, subjects that swam in the opposite direction to the demonstrators found food. We then tested the fish with a social learning task, to examine whether prior experience had influenced the social learning tendencies of the juveniles. After another 45 days of rearing under common-garden conditions with no adult fish present in the tanks, subjects were retested with the same social learning task, to investigate whether early experiences had effects persisting into adulthood. After 45 days of rearing we found no evidence for social learning in any of the experimental groups. However, after 90 days of rearing, we found evidence of social learning, but only in the 'follow adults' treatment. These results suggest that social learning propensities may develop over life, and that prior exposure to conspecifics providing useful foraging information during early life can shape the degree of reliance on social learning in adulthood.

© 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Social learning, learning facilitated by observation of or interaction with other individuals or their products (Heyes, 1994; Hoppitt & Laland, 2013), is widespread across the animal kingdom, with examples from insects, cephalopods, fish, reptiles, amphibians, mammals and birds in numerous contexts, such as learning about predators, mates, nesting sites, foraging techniques, food preferences and locations, grouping and travel routes, and communicative signals (Danchin, Giraldeau, Valone, & Wagner, 2004; Heyes & Galef, 1996; Hoppitt & Laland, 2013; Reader & Biro, 2010; Whiten, Caldwell, & Mesoudi, 2016). While social learning has intuitive benefits, such as rapid learning about a changing environment with minimal personal risk, there is a growing realization that its costs and benefits will vary between individuals and circumstances, leading to the prediction that

animals will employ social learning discriminatorily, following so-called 'social learning strategies' to maximize net benefits (Boyd & Richerson, 1985; Rendell et al., 2011). Variation in such costs and benefits could potentially explain the observed diversity within and between species in their apparent reliance on social information and social learning (Efferson, Lalive, Richerson, McElreath, & Lubell, 2008; Lefebvre & Palameta, 1988; McCabe, Reader, & Nunn, 2015; Reader, Hager, & Laland, 2011; Toelch, Bruce, Newson, Richerson, & Reader, 2014; Webster & Laland, 2011). However, as several researchers have noted, an important question is whether an individual's tendency to seek out and rely on social information is plastic, and to what degree it can be shaped by past experience (Heyes, 2012; Leadbeater, 2015; Mesoudi, Chang, Dall, & Thornton, 2016; Reader, in press).

Behavioural plasticity, a type of phenotypic plasticity, is the capacity of an individual to change its behaviour as a response to varying environments (Bateson, 1983; Pigliucci, Murren, & Schlichting, 2006). Social learning can thus be considered as a process underlying behavioural plasticity, and may itself be plastic.

\* Correspondence: I. Leris, Department of Biology and Helmholtz Institute, Utrecht University, Padualaan 8, 3584 CH, Utrecht, The Netherlands.

E-mail address: [leris.ioannis@gmail.com](mailto:leris.ioannis@gmail.com) (I. Leris).

Behavioural plasticity can be further classified in two categories, 'activation', where the organism exhibits different behaviours in different environmental conditions or as a response to changes in the environment, and 'developmental', where different prenatal or early environments lead to different developmental trajectories and different behavioural phenotypes (Snell-Rood, 2013). While multiple examples of activation plasticity in social learning propensities exist (see e.g. Rendell et al., 2011), as do examples of developmental plasticity in social behaviour (e.g. Adkins-Regan & Krakauer, 2000; D'Andrea, Alleva, & Branchi, 2007; Sundström, Löhmus, & Johnsson, 2003), there are relatively few investigations of the developmental plasticity of social learning or social information use.

Such investigations of developmental plasticity and social information use typically manipulate or measure conditions confined specifically to early life. For example, developmental stressors shape the use of social information in Japanese quail, *Coturnix japonica*, and zebra finches, *Taeniopygia guttata* (Boogert, Zimmer, & Spencer, 2013; Farine, Spencer, & Boogert, 2015); while in rats, *Rattus norvegicus*, maternal care influences social learning propensities later in life (Levy, Melo, Galef, Madden, & Fleming, 2003; Lindeyer, Meaney, & Reader, 2013; Melo et al., 2006). To our knowledge, however, only one study has directly manipulated the value of social information early in life and investigated how this affects the development of social information use. Katsnelson, Motro, Feldman, and Lotem (2008) hand-reared house sparrows, *Passer domesticus*, in the presence of an artificial parent that either reliably indicated food locations or did not. Later in life, the sparrows previously exposed to the 'reliable' parent were more likely to use social information by joining others at a food patch than sparrows previously exposed to an 'unreliable' parent. However, the sparrows were exposed to the artificial parents until immediately prior to test, making it difficult to ascertain whether the findings were the result of early or recent experience. Here, we used guppies, *Poecilia reticulata*, to investigate whether experimental manipulations of the value of social information restricted to early life can shape adult social learning propensities. We focused specifically on social learning, a subcategory of social information use where social information is acquired and has a subsequent influence on behaviour (Reader & Biro, 2010).

The Trinidadian guppy in particular and poeciliid fish in general provide useful study systems for studies of developmental influences on social behaviour and social learning, because of the large background knowledge on their evolutionary and behavioural ecology (Brown, Laland, & Krause, 2011; Evans, Pilastro, & Schlupp, 2011; Magurran, 2005), the ease of experimentally manipulating rearing conditions in the laboratory, and evidence for social learning in both the wild and captivity. For example, guppies have been demonstrated to learn foraging and antipredator behaviour in the laboratory (Brown & Laland, 2002; Lachlan, Crooks, & Laland, 1998) and in the wild (Reader, Kendal, & Laland, 2003). Different aspects of developmental phenotypic plasticity have been examined in a variety of different contexts using the guppy. For instance, early social environment specifically, and interactions with adults in particular, has been shown to inhibit sexual maturity (Magellan & Magurran, 2009), shape sexual behaviour (Guevara-Fiore, 2012) and promote the development of antipredator defences (Chapman, Morrell, Benton, & Krause, 2008). Particularly relevant to our current study, Chapman, Ward, and Krause (2008) manipulated rearing density until giving tests of grouping and social learning propensities. Guppies reared at low densities were more likely to group with others and to socially learn a task involving following others through a maze, compared to fish reared at high densities.

In the present study, we constrained our experimental manipulations to early life, to examine the effects of early social

environment. We reared juvenile guppies in the presence or absence of adult demonstrator fish that provided differing information about feeding locations, subsequently testing them at two different time points (once immediately after the manipulation and once after a period of time in common-garden conditions) to assess their propensity to socially learn a foraging task. We manipulated the value of social information such that the adult demonstrators either swam towards or away from a feeding location. In our study, food was only provided at one of two locations, and thus both demonstrator groups provided reliable cues, but in the former group subjects had to swim in the demonstrated direction to locate food, while in the latter group they had to swim in the opposite direction. This latter treatment could be considered akin to a situation where competitors exploit and deplete a food source, and thus provide a reliable cue to food absence. We predicted that differing early experience with how social cues indicate food would lead to fish utilizing these social cues differently, and for these differences to weaken but persist to adulthood.

## METHODS

### Overview

We raised guppy fry for 45 days, delivering food in two locations for 96 feeding bouts. The fry were exposed to three different social conditions: (1) adult 'demonstrators' that reliably swam to the same location that food would be delivered to the fry; (2) adult demonstrators that reliably swam to the opposite location of food delivery to the fry; (3) no adults. After these 45 days, we measured subjects' social learning propensities. We then reared subjects in common-garden conditions without any demonstrators for another 45 days, and then retested subjects with an identical social learning test. This procedure allowed us to establish whether experiences confined to early life influenced social learning propensities when adult.

### Subjects and Housing Conditions

Subjects were fry born to domestic guppies that had been reared in 150-litre glass aquaria (120 cm × 40 cm, water depth: 30 cm) in mixed-sex and mixed-age conditions. These domestic guppies were a mixed strain population of approximately 1400 fish, first established in 2003 within the Utrecht University Biology aquarium and based on a founder population of approximately 480 guppies purchased from two commercial suppliers (Ruinemans, Montfoort and Ruisbroek, Maassluis, both The Netherlands). Demonstrators for the social learning test came from the same population, and were housed separately in a 70-litre glass tank (90 cm × 40 cm, water depth: 20 cm) divided in half with a transparent PVC barrier to form two demonstrator groups. All housing tanks were equipped with external canister filters (Eheim, Germany) and thermostat-controlled heaters and were enriched with gravel, artificial plants and ceramic pots. Water quality was closely monitored (nitrates, nitrites, hardness and pH were measured weekly, dissolved oxygen and conductivity biweekly). Water temperature was maintained at 26.5 ± 0.5 °C. Every 15 days 30% of the water was replaced with fresh dechlorinated and copper-free 26.5 °C water.

### Rearing Tanks

Newborn guppy fry (<10 mm total length [TL]) were taken from four 150-litre tanks with dip nets and were placed together in a transparent plastic container. Body size was visually assessed by a 10 mm grid under the container. Fry larger or considerably smaller than 10 mm were returned to the housing tanks. The remaining fry

were randomly allocated to groups of 14 fry and transferred to the experimental rearing tanks. We thus randomized any housing tank effects. A total of 168 fry were subjects.

Fry were reared in six 70-litre glass tanks (90 cm × 40 cm, water depth: 20 cm). Each tank was divided into three compartments with two clear PVC partitions (Fig. 1a), with one group of subjects in each of the two outer compartments. The 20 cm wide central compartment held six male adult guppies (Fig. 1b), except in the ‘no

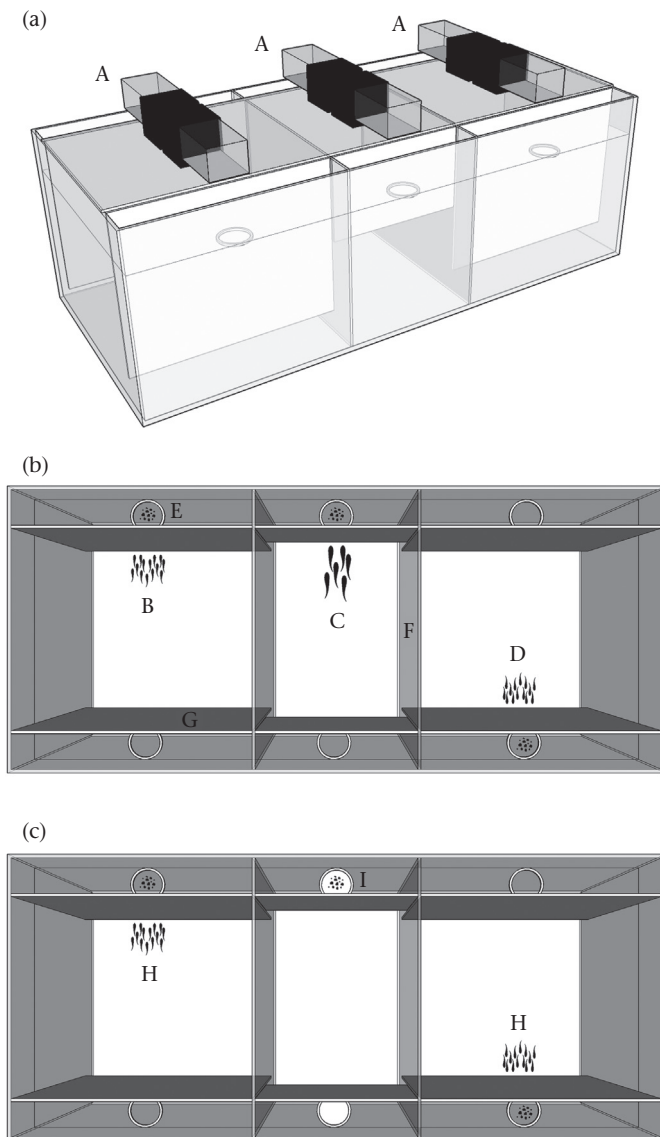
adults’ condition (Fig. 1c). Male demonstrators were used to avoid births during the study. The compartments were not sealed, thus allowing olfactory cues to pass between them. All tanks were equipped with thermostat-controlled heaters and air-driven sponge filters in the fry compartments.

#### Feeding Regime and Experimental Treatments

Crushed flake food (TetraPhyll, Tetra, Germany) was delivered to floating feeders (Fig. 1) by automatic feeders (fry: Eheim 3581; adult demonstrators: Eheim 3582; Eheim, Germany). Fry were fed 60 s after the demonstrators. For the first 3 days of rearing, demonstrators and fry were fed four times per day, twice at a random time between 0800 and 1100 hours (‘morning’) and twice between 1500 and 1800 hours (‘afternoon’). Random feeding times were produced using a pseudorandom number generator function in MatLab (function ‘randi’, MatLab, v. R2011b, Mathworks, Natick, MA, U.S.A.). After this period of habituation to the feeders, feeding was conducted twice a day at a random time in the morning and in the afternoon. Every 5 days, new random feeding times were generated, to avoid any habituation to specific feeding times.

We reared fry in three experimental treatments. In the ‘follow adults’ treatment, six adult males were present in the central compartment of the tank and were fed on the same side of the tank that food would be delivered to the juveniles. Thus demonstrator movement predicted where the food would be administered, and subjects that utilized this cue would be able to locate the food more rapidly than other fish. The second ‘avoid adults’ treatment was identical to ‘follow adults’, except that fry were fed in the opposite direction to the adults would be able to locate the food more rapidly than other fish. We set up four replicate tanks, and within each tank paired subjects in the ‘follow’ and ‘avoid adults’ treatments: one group of fry per tank were in the ‘follow adults’ treatment, the other group in the ‘avoid adults’ treatment. Thus subjects were exposed to matched demonstrator and feeding conditions, apart from the fact that demonstrator behaviour predicted either the presence or absence of food. In the third ‘no adults’ treatment, there were two replicate tanks each with two groups of subjects, and no adults present. In this treatment, demonstrator feeding rings were replaced with perforated opaque plastic cups suspended from the tank walls, where food was delivered as in the other two treatments. This ensured that food odour was present in the central compartment during feeding time as in the other two treatments. The apparatus was designed so that subjects did not see the food itself being administered in any of the experimental treatments (Fig. 1b). Ramshorn snails, *Planorbis* spp., were present in all tanks to consume any leftover food, and in the ‘no adult’ treatment they were also placed in the cups since uneaten food would result in deterioration of water quality.

After 45 days of rearing under the aforementioned developmental conditions, the juvenile fish were presented with a social learning test (described below). At the end of this test, fish were returned to their housing tanks (now divided into two compartments with a single clear PVC partition) and were reared for another period of 45 days in common-garden conditions, with no other partitions and no adult demonstrators present. During this second rearing period, the floating feeders were removed and crushed flake food was delivered by automatic feeders as before in the centre of each compartment twice per day. This ensured that no further learning regarding foraging locations could occur during this period. At day 90 the fish were retested with the same social learning test.



**Figure 1.** Rearing tanks: three-dimensional (a) side view and (b) top view of the ‘follow adults’/‘avoid adults’ tanks and (c) the ‘no adults’ tanks. The tanks were split by transparent dividers into three compartments, each with two automatic feeders (A). Each compartment contained two floating ring feeders made of 5 mm air tubing. Two longitudinal opaque PVC partitions with a 5 cm gap prevented subjects from seeing the feeders but allowed them to swim underneath to access them. B: ‘follow adults’ fry in their compartment, fed in the same location as the adult demonstrators; C: adult male demonstrators located in the central compartment of the tank; D: ‘avoid adults’ fry in the second outer compartment, fed in the opposite location to the adult demonstrators; E: feeder; F: transparent PVC partition separating the compartments; G: opaque partition that allowed feeder access; H: ‘no adults’ fry in both outer compartments of the tank; I: perforated opaque plastic cup used to collect the food delivered in the empty demonstrator compartment and thus ensure food odour cues were present in all experimental conditions.

### Social Learning Test

Tests were conducted in a 25-litre glass tank (40 cm × 25 cm, water depth: 10 cm) divided into four compartments with clear PVC partitions (Fig. 2). A subject was placed in an observation compartment, where, during a demonstration phase, it could observe demonstrators choose between one of two feeders in two feeding compartments. After demonstration, subjects could choose a feeding compartment in a similar manner to the rearing period by swimming through a 2 cm gap under clear PVC transparent partitions. Coloured plastic tape (left: green stripes; right: blue squares) was used to make the partitions visually distinctive. A heater in the observation compartment maintained water temperature. No gravel was present to aid visibility from above.

Demonstrators (mean body mass ± SE: 0.21 ± 0.05 g) were selected each day from a pool of 16 adult male guppies trained to the 'left/green' side and a pool of 13 trained to the 'right/blue' side. Demonstrators had been trained for 2 weeks prior to the experiment to enter their respective feeding area and feed from a floating ring feeder within 60 s. They were also habituated to being caught by a net and being transferred to the experimental tank in a transparent plastic cup. Each group was used maximally twice per day to ensure that demonstrators were not satiated and reliably fed from the feeder.

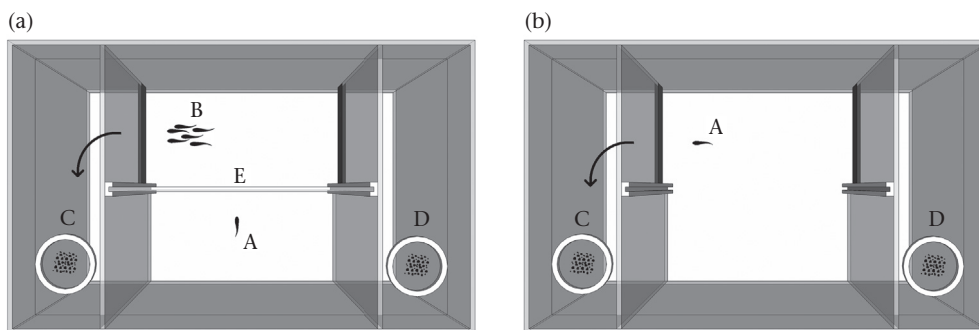
Every day before testing, the experimental tank was filled with water from the demonstrator housing tank to standardize olfactory cues present in the water. A subject fish was selected at random, caught by net and transferred in a transparent plastic cup to the observation compartment of the experimental tank. Crushed flake food was added to the two floating feeders in the choice compartments and a group of six demonstrators transferred to the demonstrator compartment. After allowing 2 min for acclimation, the subject's cup was slowly tilted until it swam out into the observation compartment. Sixty seconds later, the demonstrators' cup was tilted and they were released. In all trials the demonstrators reliably swam to the feeding compartment they had been trained to and fed. The demonstration lasted 3 min, after which we placed three opaque partitions around the observation compartment, blocking the subject's view for 5 min. The demonstrators were shepherded back to their start compartment and removed, all food was removed with a siphon, then new food was added to both feeders. After the 5 min, the opaque partitions were removed and the transparent divider was slowly lifted using a string/pulley system, allowing the subject to swim freely and choose a feeder compartment. Behaviour was recorded for 5 min. One fish did not leave the observation compartment within 5 min after the divider was lifted and thus no measurements were taken. Four additional trials were compromised by apparatus failure and thus were also removed from the data set. Between trials, uneaten food was

removed, a portion of water was replaced with fresh water, and the water was mixed to mix any remaining olfactory cues. Identical social learning tests were run at days 46–48 and days 91–93. On days 46–48 (henceforth 'Day 45') 96 subjects were tested, and at days 91–93 (henceforth 'Day 90') 87 subjects were tested. All fish that left the observation compartment entered a feeder compartment. Few fish had reached sexual maturity at Day 45, and thus subject sex was not analysed then. Given the small size of the fish at Day 45 it was not possible to use elastomer tags or other methods to identify individuals, and thus we did not track individual identity across time points.

### Behavioural Measures and Data Analysis

Fish movement and behaviour was recorded during the trial using JWatcher (v1.0, Blumstein, Evans, & Daniel, 2006). Trials were also recorded with a high resolution webcam (QuickCam Pro 9000, Logitech, Newark, CA, U.S.A.) suspended above the experimental tank. For the social learning test we measured the time spent in the demonstrated and nondemonstrated areas and the latency to enter the demonstrated and nondemonstrated compartments. We recorded the time spent motionless and the total number of dashing events (i.e. rapid darting movements) as measures of stress (Budaev, 1997; Elvidge & Brown, 2015), but such events were infrequent and were thus not analysed further. Data are archived online in the Dryad repository (<https://datadryad.org/resource/doi:10.5061/dryad.8538d>).

If fish socially learned in the social learning test, demonstrators would influence the subsequent choices of subjects, with subjects either copying or avoiding demonstrated locations. We conducted analyses in two steps, first examining whether there was evidence for social learning in any experimental treatment, and second examining whether the evidence for social learning differed between treatments. We subtracted the time spent in the non-demonstrated compartment from the time spent in the demonstrated compartment (henceforth 'time-in-compartment difference'), and the latency to enter the demonstrated compartment from that to enter the nondemonstrated compartment (henceforth 'latency-to-enter difference'), to examine and illustrate any demonstrator influences. Positive values indicate a preference for the demonstrated location in both measures. We predicted that fish from the 'follow adults' treatment would copy the demonstrators' choice, while fish from the 'avoid adults' treatment would choose the opposite location to that demonstrated, and thus in the two treatments demonstrated location would have a significant but opposite effect. We predicted that fish from the 'no adults' treatment would be minimally influenced by the demonstrators' behaviour.



**Figure 2.** Social learning task: (a) demonstration phase and (b) test phase. A: subject held in the observation compartment; B: group of demonstrators in the demonstrator compartment, in this example trained to swim under the left partition to the left compartment; C and D: floating feeder ring with food in the left and right choice compartments; E: removable transparent PVC partition. In the test phase the PVC partition is lifted by a string and the subject (A) can make a choice by swimming under the left or right partition.

Data were tested for normality with Shapiro–Wilk's  $W$  test and for homoscedasticity with Levene's test. If these assumptions were not met, the data were square root or root 10 log transformed as appropriate so that normality and homoscedasticity were achieved. We used factorial ANOVA, with 'treatment', 'sex' (at Day 90 only), and 'demonstrated location' being fixed factors, while 'tank' was treated as a random blocking factor and 'body mass' was assessed as a covariate. Analyses were conducted with SPSS Statistics 20.0.0 (IBM Inc., Armonk, NY, U.S.A.). Sex was removed from analyses if it had no significant effect ( $P > 0.1$ ).

We also compared behaviour at Day 45 and 90, with sexes and tanks pooled. These data represent repeated measures on the same individuals, but as we were unable to mark individuals we could not include individual identity in the analyses. For these analyses, we examined 'time-in-compartment difference' and 'latency-to-enter difference', as well as the subjects' latency to enter any compartment ('latency-to-choose') using factorial ANOVAs, with 'testing age' (45 or 90 days from the beginning of rearing) and 'treatment' as fixed factors. To partially account for non-independent data, we calculated the  $F$  and  $t$  values as if data were independent and then compared these values to the critical  $F$  and  $t$  value for reduced degrees of freedom represented by our sample size.

#### Ethical Note

All experimental procedures were approved by the Utrecht Ethics and Animal Care and Use Committee (DEC) under protocol number 2011.I.05.050, and conform to ASAB guidelines and Dutch law. At the end of the study all fish were returned to breeding populations at Utrecht University.

## RESULTS

### Day 45

At Day 45, we found no evidence for social learning in any of the three experimental treatments, since the mean 'time-in-compartment difference' did not differ significantly from 0, the value predicted by chance (one-sample  $t$  tests: 'follow adults':  $t_{37} = 0.71$ ,  $P = 0.48$ ; 'avoid adults':  $t_{27} = 0.21$ ,  $P = 0.83$ ; 'no adults':  $t_{29} = 0.19$ ,  $P = 0.85$ ; Fig. 3a). Similarly, the mean 'latency-to-enter difference' did not differ from 0 in any of the experimental treatments (one-sample  $t$  tests: 'follow adults':  $t_{37} = 0.37$ ,  $P = 0.71$ ; 'avoid adults':  $t_{27} = 0.19$ ,  $P = 0.85$ ; 'no adults':  $t_{29} = 0.91$ ,  $P = 0.37$ ; Fig. 3c). Looking across treatments, the three experimental treatments did not differ significantly on either the 'time-in-compartment' measure (ANOVA:  $F_{1,75} = 0.18$ ,  $P = 0.69$ ) or the 'latency-to-enter' measure (ANOVA:  $F_{1,75} = 0.10$ ,  $P = 0.77$ ). There was no evidence for a significant side bias in either measure (ANOVAs examining the effect of demonstrated location: 'time-in-compartment difference':  $F_{1,75} = 4.32$ ,  $P = 0.11$ ; 'latency-to-enter difference':  $F_{1,75} = 3.30$ ,  $P = 0.14$ ; a side bias would be represented by a significant effect of demonstrated location on these measures). 'Tank' had no significant effect (ANOVA: 'time-in-compartment difference':  $F_{4,75} = 0.076$ ,  $P = 0.98$ ; 'latency-to-enter difference':  $F_{4,75} = 0.09$ ,  $P = 0.98$ ) and body mass had no significant effect as a covariate (ANOVA: 'time-in-compartment difference':  $F_{1,75} = 2.74$ ,  $P = 0.10$ ; 'latency-to-enter difference':  $F_{1,75} = 2.19$ ,  $P = 0.14$ ).

### Day 90

At Day 90, we found evidence for social learning in the 'follow adults' treatment, with subjects faster to enter and spending more time in the demonstrated than the nondemonstrated compartment

(Fig. 3b,d; one-sample  $t$  tests: 'time-in-compartment difference':  $t_{31} = 2.42$ ,  $P = 0.022$ ; 'latency-to-enter difference':  $t_{31} = 2.27$ ,  $P = 0.03$ ). However, we found no evidence for social learning in the 'avoid adults' (one-sample  $t$  tests: 'time-in-compartment difference':  $t_{27} = 0.25$ ,  $P = 0.81$ ; 'latency-to-enter difference':  $t_{27} = 0.93$ ,  $P = 0.36$ ) and 'no adults' treatments (one-sample  $t$  tests: 'time-in-compartment difference':  $t_{26} = 0.99$ ,  $P = 0.33$ ; 'latency-to-enter difference':  $t_{26} = 0.78$ ,  $P = 0.44$ ). Looking across treatments, sex did not have a significant effect on the 'time-in-compartment difference' or 'latency-to-enter difference' (ANOVAs:  $F_{1,44} = 3.05$ ,  $P = 0.14$ ;  $F_{1,44} = 0.08$ ,  $P = 0.79$ , respectively) and was thus removed from subsequent analysis. The experimental treatments did not differ significantly on either the 'time-in-compartment difference' or the 'latency-to-enter difference' measures (ANOVAs:  $F_{1,66} = 3.07$ ,  $P = 0.17$ ;  $F_{1,66} = 4.29$ ,  $P = 0.12$ , respectively). There was no evidence for a side bias, i.e. no significant effect of demonstrated location (ANOVAs: 'time-in-compartment difference':  $F_{1,66} = 0.10$ ,  $P = 0.77$ ; 'latency-to-enter difference':  $F_{1,66} = 0.13$ ,  $P = 0.74$ ). 'Tank' had no significant effect (ANOVAs: 'time-in-compartment difference':  $F_{4,66} = 0.79$ ,  $P = 0.60$ ; 'latency-to-enter difference':  $F_{4,66} = 0.61$ ,  $P = 0.68$ ). Body mass was a significant covariate in the case of 'latency-to-enter difference' (ANOVA:  $F_{1,66} = 4.99$ ,  $P = 0.029$ ) but not in the case of 'time-in-compartment difference' (ANOVA:  $F_{1,66} = 1.01$ ,  $P = 0.32$ ).

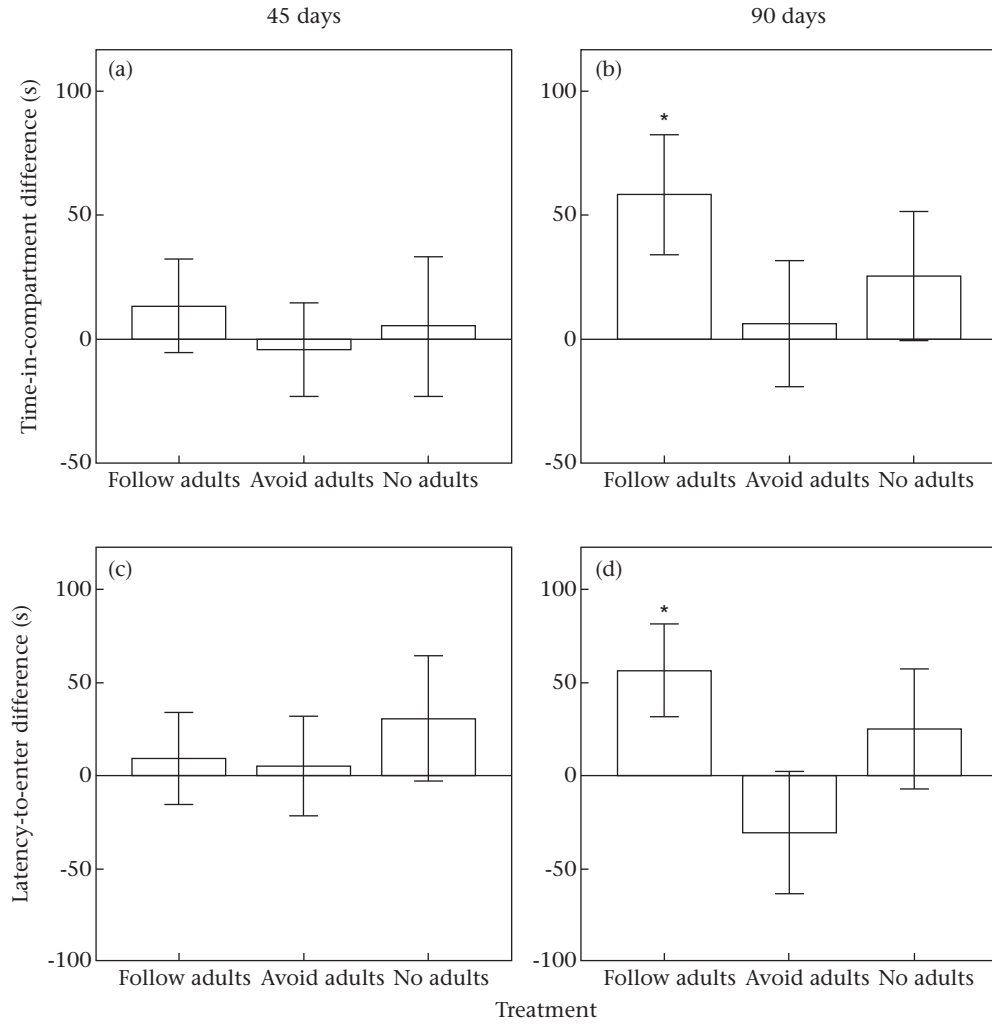
### Comparing Day 45 and 90

Testing age had no significant effect on 'time-in-compartment difference' (ANOVA:  $F_{1,177} = 1.70$ ,  $P$  based on 81 degrees of freedom [henceforth ' $P_{81}$ ']  $> 0.1$ ) or 'latency-to-enter difference' (ANOVA:  $F_{1,177} = 0.01$ ,  $P_{81} > 0.1$ ). However, fish at Day 90 were significantly faster to enter either of the two compartments than they were on Day 45 (ANOVA:  $F_{1,177} = 8.34$ ,  $P_{81} < 0.01$ ). This difference is mainly driven by the subjects in the 'follow adults' treatment, which entered a compartment significantly faster on Day 90 than Day 45 ( $t$  test:  $t_{67} = 2.91$ ,  $P_{30} < 0.01$ ; Fig. 4a), while this effect was not significant in the 'avoid adults' or 'no adults' treatments ( $t$  tests:  $t_{54} = 1.63$ ,  $P_{26} > 0.1$ ;  $t_{55} = 0.87$ ,  $P_{25} > 0.1$ , respectively; Fig. 4a). Overall, however, latency to enter either compartment did not differ between treatments at Day 45 (ANOVA:  $F_{2,93} = 0.23$ ,  $P = 0.80$ ) or Day 90 (ANOVA:  $F_{2,84} = 0.35$ ,  $P = 0.71$ ). Body mass increased significantly from Day 45 to Day 90 (ANOVA:  $F_{1,177} = 164.25$ ,  $P_{81} < 0.001$ ; Fig. 4b), in all three treatments ( $t$  tests: 'follow adults':  $t_{68} = 8.70$ ,  $P_{30} < 0.001$ ; 'avoid adults':  $t_{54} = 7.20$ ,  $P_{26} < 0.001$ ; 'no adults':  $t_{55} = 6.46$ ,  $P_{25} < 0.001$ ). Mass did not differ significantly across treatments at Day 45 (ANOVA:  $F_{2,93} = 0.62$ ,  $P = 0.54$ ). At Day 90, 'follow adults' subjects were 0.03 g or 30% heavier than subjects from the 'avoid adults' treatment and 0.04 g or 36% heavier than subjects from the 'no adults' treatment (principally due to heavier females), but this difference between treatments was not statistically significant (ANOVA:  $F_{2,84} = 2.59$ ,  $P = 0.08$ ).

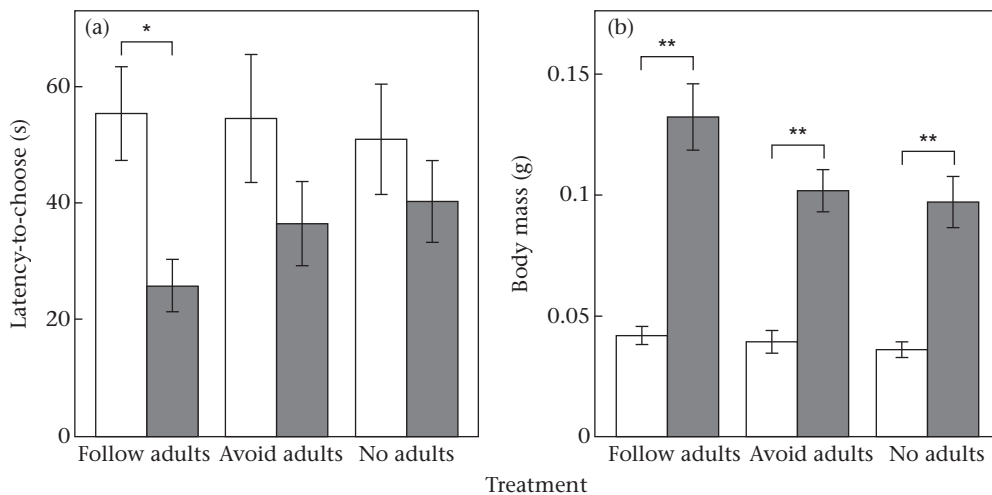
## DISCUSSION

We found no evidence for social learning after 45 days of experimental rearing. After 45 additional days of rearing in standard conditions, we found evidence for social learning on two behavioural measures, but only in those fish that had been exposed to demonstrators that reliably indicated food locations for the first 45 days of life. Our results are consistent with the ideas that performance on this social learning test is dependent upon age and that experience confined to early life affects social learning propensities in later life.

The most striking aspect of our results is that early life experience had an effect 45 days later, after rearing in common-garden



**Figure 3.** Mean time-in-compartment difference (time spent in the nondemonstrated compartment subtracted from the time spent in the demonstrated compartment) in the social learning test at (a) 45 and (b) 90 days and mean latency-to-enter difference (latency to enter the demonstrated compartment subtracted from the latency to enter the nondemonstrated compartment) at (c) 45 and (d) 90 days. Positive values of both measures indicate a preference for the demonstrated location. \* $P < 0.05$ . Error bars represent the standard error of the mean.



**Figure 4.** (a) Mean latency to choose either feeding compartment (maximum trial length was 300 s) in the social learning test and (b) mean body mass at 45 (□) and 90 (■) days. \* $P < 0.01$ ; \*\* $P < 0.001$ . Error bars represent the standard error of the mean.

conditions. This suggests that early life had long-lasting effects that were not expressed until adulthood. We predicted, in contrast, that the strongest effects on social learning would be observed at 45 days and these effects would be potentially weakened after 45 days in common-garden conditions. Our results therefore suggest that social learning propensities may change over the lifetime of an individual. Similarly, a comparison of different ages of jack mackerel, *Trachurus japonicus*, revealed that social learning tendencies develop in older individuals, together with enhanced schooling behaviour (Takahashi, Masuda, & Yamashita, 2014). A number of explanations could account for the difference in social learning propensities with age that we observed. The social learning task may simply be too challenging or insufficiently motivating for younger fish. For example, younger fish, which are also smaller in body size, may be less motivated to visit locations where large fish were previously present, since larger guppies outcompete smaller guppies in competition for food and may be aggressive towards them (Chapman, Morrell, et al., 2008; Laland & Reader, 1999). Guppies were slower to enter either of the two feeding compartments on Day 45 than Day 90, supporting the idea they were less motivated by the task. Competition was also suggested to underlie age-dependent social learning in male skink lizards, *Eulamprus quoyii*: juveniles socially learned an association task but adults did not, potentially due to greater intermale competition among adults (Noble, Byrne, & Whiting, 2014). The relative age or size of demonstrators and observers has been investigated particularly in fish, and has been shown to influence who-learns-from-whom in both guppies and sticklebacks, *Pungitius pungitius* (Duffy, Pike, & Laland, 2009; Dugatkin & Godin, 1993; Vukomanovic & Rodd, 2007). Directed social learning (Coussi-Korbel & Frigaszy, 1995), in which socially acquired behaviours only flow through a subset of the population, may thus be very common.

In our study, only fish exposed to demonstrators that led them to a food location later used similar social information in the social learning test, entering the demonstrated feeding compartment faster and spending more time there. This finding suggests that early experience with the reliability of social information influences adult social learning propensities, and parallels the results of the similar study of house sparrows (Katsnelson et al., 2008). Our study extends previous work by confining experience of the reliability of social cues to early life, by explicitly varying cue reliability (cf. e.g. Boogert et al., 2013; Lindeyer et al., 2013) and by measuring social learning rather than social information use. Our results thus indicate that the reliability of social cues can shape social learning, supporting the idea that social learning propensities are not simply a by-product of other developmental changes.

In the 'avoid adults' condition, the demonstrators provided equally reliable cues as the 'follow adults condition' in demonstrating the food location, except that demonstrators swam away from, rather than towards, the rewarded location. In our study, food was only available in two locations, and thus the absence of food in one location indicated the presence of food in another. That is, demonstrator behaviour during rearing provided a discriminative cue, with subjects receiving positive reinforcement for following or opposing adults in the 'follow adults' and 'avoid adults' conditions, respectively. However, we saw no indication of social learning in the 'avoid adults' treatment, while we suspect that they would have readily learned to make this discrimination using an asocial cue. Perhaps young guppies have an initial predisposition to follow or attend to others (Magurran & Seghers, 1990; Magurran, 1990a, 1990b), a predisposition that can be strengthened by experience, whereas it is more difficult for guppies to learn to avoid others. Numerous factors may result in such a predisposition, particularly the antipredator and informational benefits of grouping (Krause & Ruxton, 2002).

Moreover, situations where the absence of food reliably indicates exactly where food is present may be rare in nature. However, recent experience has been demonstrated to lead to nonmatching behaviour in several species (Reader, 2014). For example, Dawson, Avarguès-Weber, Chittka, and Leadbeater (2013) showed that bumblebees, *Bombus terrestris*, with experience of conspecifics paired with bitter foods learned to actively avoid conspecific-demonstrated feeders. Interesting open questions are the extent to which any predispositions in social learning tendencies can be altered by experience, and whether specific experiences or developmental stages are particularly impactful in shaping social learning.

We did find clear evidence for social learning in adult fish that had been previously exposed to demonstrators that reliably indicated food. However, the strength of our conclusions is limited by the fact that the comparisons of the three different experimental treatments were not statistically significant (Nieuwenhuis, Forstmann, & Wagenmakers, 2011). Further work would be needed to strengthen our conclusions, for example taking account of the considerable individual variation we observed by using increased sample sizes, a different social learning test, or more extensive training procedures. However, given the limited evidence up to now for developmental effects on social learning, we argue that the present findings offer new evidence that social learning propensities can be shaped by early exposure to social cues, and thus can act as a useful guide and impetus for future work.

Our results have both theoretical and applied implications. If social learning is shaped by both recent and early life experience, this means that observed population and species differences in social learning propensities may at least partially arise from environmental differences, possibly interacting with genetic predispositions (Carlier & Lefebvre 1997; Reader et al., 2011). Developmental plasticity in social learning would allow animals to adjust to variation in the numerous social and ecological characteristics that impact the value of social information. For example, guppy habitats differ in characteristics such as productivity and predation risk, and guppy populations differ in grouping tendencies, intraspecific competition and aggression (Magurran, 2005; Magurran & Seghers, 1991; Reznick, Butler, & Rodd, 2001). All of these characteristics could impact the value of social information and thus the development of social learning propensities. Our results caution against the interpretation of differences in social learning performance as differences in social learning capacity. Flexibility in social learning may be an adaptive feature, vital to maximizing benefits, or alternatively it may reflect constraints on the evolution of predispositions affecting social learning (Reader, in press).

Conservation biologists and agricultural researchers have shown interest in social learning both as a tool to promote the success of individuals reintroduced or released into wild populations and as a consideration in conservation efforts (Brown & Laland, 2001; Reader & Biro, 2010; van Schaik, 2002; Suboski & Templeton, 1989). For example, captive-reared fish typically suffer very high mortality rates when released into the wild (Salvanes & Braithwaite, 2005), and overfishing may not just reduce population numbers but may also eliminate beneficial socially learned behaviours, such as spawning sites in herring, *Clupea harengus* (Corten, 2002). Our results suggest that animals without suitable models to learn from may suffer not just from failing to socially acquire a particular behaviour pattern, but also because social learning fails to develop at all. The take-home message from our study is that social learning propensities may change both over the life span and as a result of differential early-life experience, providing novel routes by which the efficacy of social learning can be fine-tuned.

## Acknowledgments

We thank Henk Schriek, Ko van Rootselaar, Henk Westland and Cor Nijhoff for their assistance with animal care. This project was funded by a Utrecht University Stimulus grant and Natural Sciences and Engineering Research Council Discovery grants #418342–2012 and 429385–2012. We thank Laura Chouinard-Thuly, Pierre-Olivier Montiglio, Adam Reddon, William Swaney and the anonymous referees for useful comments on the manuscript.

## References

- Adkins-Regan, E., & Krakauer, A. (2000). Removal of adult males from the rearing environment increases preference for same-sex partners in the zebra finch. *Animal Behaviour*, *60*(1), 47–53. <http://dx.doi.org/10.1006/anbe.2000.1448>.
- Bateson, P. P. G. (1983). Genes, environment and the development of behaviour. In T. R. Halliday, & P. J. B. Slater (Eds.), *Genes, development and learning: Vol. 3. Animal behaviour* (pp. 52–81). Oxford, U.K.: Blackwell.
- Blumstein, D. T., Evans, C. S., & Daniel, J. C. (2006). *JWatcher v. 1.0*. [www.jwatcher.ucla.edu](http://www.jwatcher.ucla.edu).
- Boogert, N. J., Zimmer, C., & Spencer, K. A. (2013). Pre- and post-natal stress have opposing effects on social information use. *Biology Letters*, *9*(2), 20121088. <http://dx.doi.org/10.1098/rsbl.2012.1088>.
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- Brown, C., & Laland, K. N. (2001). Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, *59*(3), 471–493. <http://dx.doi.org/10.1006/jfbi.2001.1689>.
- Brown, C., & Laland, K. N. (2002). Social learning of a novel avoidance task in the guppy: Conformity and social release. *Animal Behaviour*, *64*(1), 41–47. <http://dx.doi.org/10.1006/anbe.2002.3021>.
- Brown, C., Laland, K. N., & Krause, J. (2011). *Fish cognition and behavior* (2nd ed.). Chichester, U.K.: Wiley-Blackwell.
- Budaev, S. V. (1997). "Personality" in the guppy (*Poecilia reticulata*): A correlational study of exploratory behavior and social tendency. *Journal of Comparative Psychology*, *111*(4), 399–411. <http://dx.doi.org/10.1037/0735-7036.111.4.399>.
- Carlier, P., & Lefebvre, L. (1997). Ecological differences in social learning between adjacent, mixing, populations of Zenaida doves. *Ethology*, *103*, 772–784. <http://dx.doi.org/10.1111/j.1439-0310.1997.tb00185.x>.
- Chapman, B. B., Morrell, L. J., Benton, T. G., & Krause, J. (2008). Early interactions with adults mediate the development of predator defenses in guppies. *Behavioral Ecology*, *19*(1), 87–93. <http://dx.doi.org/10.1093/beheco/arm111>.
- Chapman, B. B., Ward, A. J. W., & Krause, J. (2008). Schooling and learning: Early social environment predicts social learning ability in the guppy, *Poecilia reticulata*. *Animal Behaviour*, *76*(3), 923–929. <http://dx.doi.org/10.1016/j.anbehav.2008.03.022>.
- Corten, A. (2002). The role of "conservatism" in herring migrations. *Reviews in Fish Biology and Fisheries*, *11*(4), 339–361. <http://dx.doi.org/10.1023/A:1021347630813>.
- Coussi-Korbel, S., & Frigaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*(6), 1441–1453. [http://dx.doi.org/10.1016/0003-3472\(95\)80001-8](http://dx.doi.org/10.1016/0003-3472(95)80001-8).
- D'Andrea, I., Alleva, E., & Branchi, I. (2007). Communal nesting, an early social enrichment, affects social competences but not learning and memory abilities at adulthood. *Behavioural Brain Research*, *183*(1), 60–66. <http://dx.doi.org/10.1016/j.bbr.2007.05.029>.
- Danchin, E., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science*, *305*(July), 487–491. <http://dx.doi.org/10.1126/science.1098254>.
- Dawson, E. H., Avargues-Weber, A., Chittka, L., & Leadbeater, E. (2013). Learning by observation emerges from simple associations in an insect model. *Current Biology*, *23*(8), 727–730. <http://dx.doi.org/10.1016/j.cub.2013.03.035>.
- Duffy, G. A., Pike, T. W., & Laland, K. N. (2009). Size-dependent directed social learning in nine-spined sticklebacks. *Animal Behaviour*, *78*(2), 371–375. <http://dx.doi.org/10.1016/j.anbehav.2009.05.015>.
- Dugatkin, L. A., & Godin, J. G. J. (1993). Female mate copying in the guppy (*Poecilia reticulata*): Age-dependent effects. *Behavioral Ecology*, *4*(4), 289–292. <http://dx.doi.org/10.1093/beheco/4.4.289>.
- Efferson, C., Lalive, R., Richerson, P. J., McElreath, R., & Lubell, M. (2008). Conformists and mavericks: The empirics of frequency-dependent cultural transmission. *Evolution and Human Behavior*, *29*(1), 56–64. <http://dx.doi.org/10.1016/j.evolhumbehav.2007.08.003>.
- Elvidge, C. K., & Brown, G. E. (2015). Size-based differences determine the contextual value of risky information in heterospecific information use. *Animal Behaviour*, *102*, 7–14. <http://dx.doi.org/10.1016/j.anbehav.2015.01.009>.
- Evans, J. P., Pilastro, A., & Schlupp, I. (2011). *Ecology and evolution of poeciliid fishes*. Chicago: University of Chicago Press.
- Farine, D. R., Spencer, K. A., & Boogert, N. J. (2015). Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Current Biology*, *25*(16), 2184–2188. <http://dx.doi.org/10.1016/j.cub.2015.06.071>.
- Guevara-Fiore, P. (2012). Early social experience significantly affects sexual behaviour in male guppies. *Animal Behaviour*, *84*(1), 191–195. <http://dx.doi.org/10.1016/j.anbehav.2012.04.031>.
- Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, *69*, 207–231. <http://dx.doi.org/10.1111/j.1469-185X.1994.tb01506.x>.
- Heyes, C. M., & Galef, B. G., Jr. (1996). *Social learning in animals: The roots of culture*. San Diego, CA: Academic Press.
- Heyes, C. (2012). What's social about social learning? *Journal of Comparative Psychology*, *126*(2), 193–202. <http://dx.doi.org/10.1037/a0025180>.
- Hoppitt, W., & Laland, K. N. (2013). *Social learning: An introduction to mechanisms, methods, and models*. Princeton, NJ: Princeton University Press.
- Katsnelson, E., Motro, U., Feldman, M. W., & Lotem, A. (2008). Early experience affects producer–scrounger foraging tendencies in the house sparrow. *Animal Behaviour*, *75*(4), 1465–1472. <http://dx.doi.org/10.1016/j.anbehav.2007.09.020>.
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford, U.K.: Oxford University Press.
- Lachlan, R. F., Crooks, L., & Laland, K. N. (1998). Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour*, *56*(1), 181–190. <http://dx.doi.org/10.1006/anbe.1998.0760>.
- Laland, K. N., & Reader, S. M. (1999). Foraging innovation is inversely related to competitive ability in male but not in female guppies. *Behavioral Ecology*, *10*(3), 270–274. <http://dx.doi.org/10.1093/beheco/10.3.270>.
- Leadbeater, E. (2015). What evolves in the evolution of social learning? *Journal of Zoology*, *295*(1), 4–11. <http://dx.doi.org/10.1111/jzo.12197>.
- Lefebvre, L., & Palameta, B. (1988). Mechanisms, ecology, and population diffusion of socially-learned, food-finding behavior in feral pigeons. In T. R. Zentall, & B. G. Galef, Jr. (Eds.), *Social learning: Psychological and biological perspectives* (pp. 141–163). Hillsdale, NJ: Erlbaum.
- Levy, F., Melo, A. I., Galef, B. G., Jr., Madden, M., & Fleming, A. S. (2003). Complete maternal deprivation affects social, but not spatial, learning in adult rats. *Developmental Psychobiology*, *43*, 177–191. <http://dx.doi.org/10.1002/dev.10131>.
- Lindey, C. M., Meaney, M. J., & Reader, S. M. (2013). Early maternal care predicts reliance on social learning about food in adult rats. *Developmental Psychobiology*, *55*(2), 168–175. <http://dx.doi.org/10.1002/dev.21009>.
- Magellan, K., & Magurran, A. E. (2009). The effect of social environment during ontogeny on life history expression in the guppy *Poecilia reticulata*. *Journal of Fish Biology*, *74*(10), 2329–2337. <http://dx.doi.org/10.1111/j.1095-8649.2009.02245.x>.
- Magurran, A. E. (1990a). The adaptive significance of schooling as an anti predator defense in fish. *Annales Zoologici Fennici*, *27*, 51–66.
- Magurran, A. E. (1990b). The inheritance and development of minnow anti-predator behaviour. *Animal Behaviour*, *39*(5), 834–842. [http://dx.doi.org/10.1016/S0003-3472\(05\)80947-9](http://dx.doi.org/10.1016/S0003-3472(05)80947-9).
- Magurran, A. E. (2005). *Evolutionary ecology: The Trinidadian guppy*. New York, NY: Oxford University Press.
- Magurran, A. E., & Seghers, B. H. (1990). Population differences in the schooling behaviour of newborn guppies, *Poecilia reticulata*. *Ethology*, *84*(4), 334–342. <http://dx.doi.org/10.1111/j.1439-0310.1990.tb00807.x>.
- Magurran, A. E., & Seghers, B. H. (1991). Variation in schooling and aggression amongst guppy (*Poecilia reticulata*) populations in Trinidad. *Behaviour*, *118*(3–4), 214–234. <http://dx.doi.org/10.1017/CBO9781107415324.004>.
- McCabe, C. M., Reader, S. M., & Nunn, C. L. (2015). Infectious disease, behavioural flexibility and the evolution of culture in primates. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20140862. <http://dx.doi.org/10.1098/rspb.2014.0862>.
- Melo, A. I., Lovic, V., Gonzalez, A., Madden, M., Sinopoli, K., & Fleming, A. S. (2006). Maternal and littermate deprivation disrupts maternal behavior and social-learning of food preference in adulthood: Tactile stimulation, nest odor, and social rearing prevent these effects. *Developmental Psychobiology*, *48*(3), 209–218. <http://dx.doi.org/10.1002/dev.20130>.
- Mesoudi, A., Chang, L., Dall, S. R. X., & Thornton, A. (2016). The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution*, *31*(3), 215–225. <http://dx.doi.org/10.1016/j.tree.2015.12.012>.
- Nieuwenhuis, S., Forstmann, B. U., & Wagenmakers, E.-J. (2011). Erroneous analyses of interactions in neuroscience: A problem of significance. *Nature Neuroscience*, *14*(9), 1105–1109. <http://dx.doi.org/10.1038/nn.2886>.
- Noble, D. W. A., Byrne, R. W., & Whiting, M. J. (2014). Age-dependent social learning in a lizard. *Biology Letters*, *10*, 10–14.
- Pigliucci, M., Murren, C. J., & Schlichting, C. D. (2006). Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology*, *209*, 2362–2367. <http://dx.doi.org/10.1242/jeb.02070>.
- Reader, S. M. (2014). Experiential effects on mirror systems and social learning: Implications for social intelligence. *Behavioral and Brain Sciences*, *37*(2), 217–218. <http://dx.doi.org/10.1017/S0140525X1300246X>.
- Reader, S. M. (2016). *Animal social learning: Associations and adaptations*. F1000Research (in press).
- Reader, S. M., & Biro, D. (2010). Experimental identification of social learning in wild animals. *Learning & Behavior*, *38*(3), 265–283. <http://dx.doi.org/10.3758/LB.38.3.265>.
- Reader, S. M., Hager, Y., & Laland, K. N. (2011). The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 1017–1027. <http://dx.doi.org/10.1098/rstb.2010.0342>.
- Reader, S. M., Kendal, J. R., & Laland, K. N. (2003). Social learning of foraging sites and escape routes in wild Trinidadian guppies. *Animal Behaviour*, *66*(4), 729–739. <http://dx.doi.org/10.1006/anbe.2003.2252>.



- Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: Theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, 15(2), 68–76. <http://dx.doi.org/10.1016/j.tics.2010.12.002>.
- Reznick, D. N., Butler, M. J., IV, & Rodd, F. H. (2001). Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. *American Naturalist*, 157(2), 126–140. <http://dx.doi.org/10.1086/318627>.
- Salvanes, A. G. V., & Braithwaite, V. A. (2005). Exposure to variable spatial information in the early rearing environment generates asymmetries in social interactions in cod (*Gadus morhua*). *Behavioral Ecology and Sociobiology*, 59, 250–257. <http://dx.doi.org/10.1007/s00265-005-0031-x>.
- van Schaik, C. P. (2002). Fragility of traditions: The disturbance hypothesis for the loss of local traditions in orangutans. *International Journal of Primatology*, 23(3), 527–538. <http://dx.doi.org/10.1023/A:1014965516127>.
- Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, 85(5), 1004–1011. <http://dx.doi.org/10.1016/j.anbehav.2012.12.031>.
- Suboski, M., & Templeton, J. (1989). Life skills training for hatchery fish: Social learning and survival. *Fisheries Research*, 7(4), 343–352. [http://dx.doi.org/10.1016/0165-7836\(89\)90066-0](http://dx.doi.org/10.1016/0165-7836(89)90066-0).
- Sundström, L. F., Löhmus, M., & Johnsson, J. I. (2003). Investment in territorial defence depends on rearing environment in brown trout (*Salmo trutta*). *Behavioral Ecology and Sociobiology*, 54(3), 249–255. <http://dx.doi.org/10.1007/s00265-003-0622-3>.
- Takahashi, K., Masuda, R., & Yamashita, Y. (2014). Development of observational learning during school formation in jack mackerel *Trachurus japonicus* juveniles. *Behavioural Processes*, 103, 52–57. <http://dx.doi.org/10.1016/j.beproc.2013.10.012>.
- Toelch, U., Bruce, M. J., Newson, L., Richerson, P. J., & Reader, S. M. (2014). Individual consistency and flexibility in human social information use. *Proceedings of the Royal Society B: Biological Sciences*, 281, 2–9.
- Vukomanovic, J., & Rodd, F. H. (2007). Size-dependent female mate copying in the guppy (*Poecilia reticulata*): Large females are role models but small ones are not. *Ethology*, 113(6), 579–586. <http://dx.doi.org/10.1111/j.1439-0310.2007.01343.x>.
- Webster, M. M., & Laland, K. N. (2011). Reproductive state affects reliance on public information in sticklebacks. *Proceedings of the Royal Society B: Biological Sciences*, 278, 619–627. <http://dx.doi.org/10.1098/rspb.2010.1562>.
- Whiten, A., Caldwell, C. A., & Mesoudi, A. (2016). Cultural diffusion in humans and other animals. *Current Opinion in Psychology*, 8, 15–21. <http://dx.doi.org/10.1016/j.copsyc.2015.09.002>.