



## 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

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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.

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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  $26.5 \pm 0.5$  °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

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