



Familiarity facilitates social learning of foraging behaviour in the guppy

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Previous studies have shown that guppies, *Poecilia reticulata*, can learn the route to a food source by shoaling with knowledgeable conspecifics, and prefer to shoal with experienced foragers and familiar fish. We tested the hypothesis that guppies would learn more effectively from (1) familiar than unfamiliar demonstrators and (2) well-trained than poorly trained demonstrators. Demonstrator fish were given experience in swimming a route to a food source and then introduced into shoals of untrained observer guppies; the spread of this foraging skill was recorded over 15 trials. The demonstrators were either familiar or unfamiliar to the observers and either well trained or poorly trained. Observers performed significantly better when the demonstrators were familiar. The training of the demonstrators made no overall difference to the performance of naïve observers. However, whilst observers in shoals exposed to well-trained demonstrators did better initially than those with poorly trained ones, the latter learned the route to the feeder faster. Our results suggest that familiarity may generate a form of directed social learning in guppy shoals, in which fish learn more effectively from familiar conspecifics. An analysis of who follows whom suggests that well-trained demonstrators can provide a 'tip-off' as to the location of the hole but poorly trained demonstrators were more likely to be followed. The results suggest that while observers are able to shoal with poorly trained demonstrators, well-trained demonstrators swim the maze route too quickly to be followed, but may attract attention to the maze route.

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Social learning refers to learning that is influenced by observation of, or interaction with, other individuals (Galef & Giraldeau 2001). It is thought to be adaptive because it allows individuals to acquire pertinent information by exploiting the experience and knowledge of conspecifics, without incurring risks that might be associated with asocial learning or having to devise novel behaviour. Social learning processes may result in behavioural innovations spreading rapidly within populations, as the cost of acquisition of a socially learned behaviour for each individual is relatively low.

Laboratory studies have established several ways that animals can learn socially, only some of which rely on complex cognitive abilities (Galef 1988; Whiten & Ham 1992; Heyes 1994). Most cases of social learning in animals appear to result from very simple processes (Galef 1988) such as 'local enhancement' (Thorpe 1956) and stimulus enhancement (Spence 1937), when the behaviour of one animal draws the attention of a second to a particular locality or stimulus in the environment (Spence 1937). Often what is transmitted between

demonstrator and observer amounts to little more than a tip-off, but experimental studies have found that this can frequently lead to learning in the observer, and to the diffusion of a behaviour through a population (Galef 1988). Galef (1988) has suggested that local enhancement may result from a propensity on the part of naïve individuals to approach conspecifics, or alterations they have made in the environment. Shoaling in fish represents such a tendency, and may instigate the transmission of adaptive information between individuals (for example forage patch copying). Local enhancement may be responsible for the shoaling traditions of reef fish (Helfman & Schultz 1984; Warner 1988), as well as the findings of experimental studies of social learning in fish (Laland & Williams 1998).

Several studies on social learning have been carried out with the guppy, *Poecilia reticulata*, principally because of the ease of maintaining aquarium populations, and the practical advantages of fish for population-level analyses where many populations are required. In the guppy, social transmission of information influences female mate choice (Dugatkin & Godin 1992, 1993), avoidance task learning (Sugita 1980) and foraging behaviour (Laland & Williams 1997, 1998; Lachlan et al. 1998).

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In the wild, guppies typically forage in small, loosely organized shoals, on a variety of food sources, such as benthic algae, aquatic insect larvae and diatoms (Dussault & Kramer 1981; Magurran et al. 1995). Shoaling appears to be a response to predation pressure (Seghers 1974), but may have other functions (Pitcher & Parrish 1993; Magurran et al. 1995), including the transmission of foraging information between fish (Laland & Williams 1997). Guppy shoals are not random aggregations, and numerous factors influence the choice of shoaling partners, including shoal size (Lindström & Ranta 1993; Lachlan et al. 1998), fish size (Lachlan et al. 1998), sex (Lindström & Ranta 1993), demonstrator experience (Lachlan et al. 1998) and familiarity (Magurran et al. 1994). Lachlan et al. (1998) suggested that, given the importance of shoaling to social learning in guppies, factors affecting shoaling preferences might also affect the transmission of novel behaviour within shoals. There is evidence that familiar fish form more cohesive shoals (Chivers et al. 1995), and while this has antipredator benefits, Lachlan et al. (1998) suggested that familiarity might also provide greater opportunities for social learning. If this is the case, familiarity could affect the transmission of foraging information in shoals, and social learning may play a role in guppies' shoaling preferences for familiar conspecifics.

A key assumption behind theoretical models of social learning is that social interactions occur at random within the population. Recently however, Coussi-Korbel & Frigaszy (1995) discussed the possibility of 'directed social learning', in which transmitted information is restricted to, or directed through, a subset of individuals as a result of various processes influencing social interaction. Reader & Laland (1999) implicated directed social learning in a study of social foraging in the guppy, which found that sex, age and hunger level strongly affected the foraging performance of fish. Therefore if the knowledgeable members of a group are not of uniform foraging ability, naïve individuals may learn at different rates from differentially skilled individuals.

Lachlan et al. (1998) suggested that if certain guppies within a shoal were knowledgeable about local foraging opportunities, naïve fish that chose to shoal with them would increase their own foraging success through social learning about food sources. This might imply that individuals are likely to learn more effectively from skilled demonstrators. However, several studies in birds have produced the counterintuitive opposite result, with nonproficient demonstrators being better tutors than proficient ones. Biederman & Vanayan (1988) showed that pigeons, *Columba livia*, learned discrimination tasks better from nonproficient tutors and Beauchamp & Kacelnik (1991) found that in zebra finches, *Taeniopygia guttata*, observers learned faster if their demonstrator was less knowledgeable.

We investigated whether the learning of a foraging task in shoals of guppies is affected by the demonstrator's (1) level of performance and (2) familiarity to the observers. We adopted a diffusion study design, establishing shoals composed of both skilled demonstrator and naïve observer fish. In half of the shoals the demonstrators were

proficient, and in the other half they were less proficient. In addition, the shoals of naïve and trained fish were composed of either familiar or unfamiliar fish.

METHODS

We investigated the rate of learning of a food-finding behaviour in 16 shoals of eight fish, each composed of four observer subjects and four demonstrators. The trained demonstrators were in one of four conditions: well-trained fish that were familiar to the observers; poorly trained familiar fish; well-trained unfamiliar fish; or poorly trained unfamiliar fish. The food-finding task required fish to swim through a maze partition to reach a food source and we recorded the time taken for each fish to complete the maze over 15 trials.

Subjects and Apparatus

We used 112 female guppies: 64 as subjects, and a further 48 as demonstrators, from which we selected those of the most suitable quality. We conducted the experiment in four replicate blocks of four populations, each block composed of one population of each of the four conditions. Suitable demonstrators were reused in replicate blocks. All fish were purchased from Neil Hardy Aquatica, London, U.K. We used a domestic strain of guppy, rather than the wild-type, as this allowed us to identify individual fish from natural colour markings, avoiding stressful marking procedures. Each fish that took part in the experiment could be identified by its size, shape and colour markings. The guppies varied in size, and, as previous experiments have shown that fish size is a factor in shoaling preferences (Lachlan et al. 1998), we ensured each shoal consisted of a broad cross-section of different-sized guppies. We used female guppies because previous experiments have found greater evidence for social learning in this sex (Dugatkin & Godin 1993; Laland & Williams 1997).

All populations were housed and tested in glass aquarium tanks (61 × 39 cm and 30 cm high), containing filtered and oxygenated water at 25 °C, to a depth of 33 cm. At the end of each day, the fish were fed on standard tropical fish flake food. An opaque, white PVC dividing partition (36 × 30 cm) was used to divide the tanks transversely and segregate the fish to the starting side of the tank. A test partition, identical to the dividing partition except for a hole of 3 × 4 cm located centrally at its base and positioned ca. 10 cm from the end of the tank, was used as the maze during training and testing. It formed a barrier through which the fish had to pass to reach the target zone of the tank containing food. To aid the fish in locating the hole, we marked the section of the partition surrounding the hole with red nontoxic wax crayon. A red plastic ring 3 cm in diameter and 0.5 cm thick was used as a floating feeder, into which freeze-dried bloodworm (*Chironomus* spp.) was placed. The feeder was positioned centrally on the water surface in the target zone of the tank and was secured to the long sides of the tank, keeping it in the centre of this zone.

Experimental Procedure

The procedure for fish in conditions with familiar and unfamiliar demonstrators differed in important respects. For the eight shoals allocated to the familiar demonstrator condition, we created populations consisting of six future demonstrator and four future observer fish 12 days before testing, and 6 days before demonstrator training. Twelve days would appear to be the minimal period necessary for familiarity to develop among guppies (Griffiths & Magurran 1997), as supported by differences in their performance during training. Demonstrator fish in the four populations allocated to the well-trained familiar condition commenced training 6 days prior to testing, and were given training trials three times daily for 6 days. Demonstrator fish in the four populations allocated to the poorly trained familiar condition commenced training 3 days prior to testing, and were given training trials three times daily for 3 days. After demonstrator training, we selected the four most suitable demonstrators, and removed the remaining two from the experiment. Well-trained demonstrators were the four fish in each population of demonstrators with the fastest times to complete the maze during training. Poorly trained demonstrators were the slowest four fish. Any fish that appeared sick or never completed the maze were not used as demonstrators.

Observer fish were able to shoal with demonstrator fish at all times except during training trials. During training of the demonstrators in the familiar shoals, the observer fish were confined to one end of the tank by a dividing partition, so they could not see the demonstrators or the test partition during each training session. During each training trial, after the observers had been partitioned off, we used a second dividing partition to confine the demonstrators to the centre of the tank, and introduced the test partition behind this. The floating feeder was secured in the target zone, and baited with a small amount of freeze-dried bloodworm. The training trial began with the removal of the dividing partition separating the demonstrators from the test partition. The time taken by each fish to enter the goal zone was recorded by the experimenter sitting beside the tank. It appeared from the training sessions that the presence of the experimenter did not distract the fish. Each trial ended after 10 min had elapsed, when we removed the test partition and feeder. Training was repeated three times a day, at 0900, 1300 and 1700 hours.

For the eight shoals allocated to the unfamiliar demonstrator condition, we created four populations consisting of 12 demonstrator fish and four of eight observer fish 6 days prior to testing. Two of the populations of demonstrators commenced training 6 days prior to testing, and were given training trials three times daily for 6 days. The other two populations of demonstrators commenced training 3 days prior to testing, and were given training trials three times daily for 3 days. After demonstrator training, we selected the eight fastest demonstrators as being well trained, the eight slowest as being poorly trained, and removed the remaining eight from the experiment. Once again, we did not use demonstrators

that were sick, or that had not completed the task, and such fish were replaced with fish that would not otherwise have been used. Furthermore, if the fish that were trained for only 3 days showed exceptionally fast times, they were selected as well-trained demonstrators, and vice versa. Thus, demonstrators were selected not on amount of training but on performance during training. (We were unable to do this with the familiar fish, as it would have broken up the shoals, which would no longer have consisted of familiar fish.)

The procedure for the training of the unfamiliar demonstrator fish was identical to that for the familiar demonstrator fish. After training was completed, we created eight shoals each composed of four demonstrators and four observers, with four tanks containing well-trained demonstrators and four containing poorly trained demonstrators.

Test Procedure

The procedure during testing was identical to that used in training. Testing was performed three times a day, for 5 days, so that the performance of each fish was recorded over 15 trials. A fish was recorded as having completed the maze when its entire body had passed through the partition.

Statistical Analysis

Although guppies are loose shoalers and not schooling fish with coordinated movements, each fish cannot be treated as independent, since fish within a shoal do influence each other's movements to some degree, and shoaling reduces the real number of degrees of freedom. Consequently, in our analysis we adopted a hierarchically structured ANOVA design that included a 'tank' factor, by using the difference from the variance between tanks and that taken up by the tested independent variables as the residual variance. This factor partials out any between-tank variance caused by following, as well as accounting for differences between populations resulting from the alternative maze tasks. Where appropriate, data were log transformed to meet required assumptions of homogeneity of variance and normality of residuals.

RESULTS

Demonstrator Performance

The time taken to enter the goal zone differed significantly between well- and poorly trained demonstrators (ANOVA: $F_{1,12}=5.10$, $P<0.05$) but there was no significant difference with respect to familiarity (ANOVA: $F_{1,12}=1.66$, NS) or the demonstrator training \times familiarity interaction (ANOVA: $F_{1,12}=0.92$, NS). A significant difference in demonstrator training was present within the familiar demonstrators (simple effect: $F_{1,12}=5.16$, $P<0.05$), but not within the unfamiliar demonstrators (simple effect: $F_{1,12}=0.85$, NS), although the well-trained demonstrators still strongly outperformed the poorly

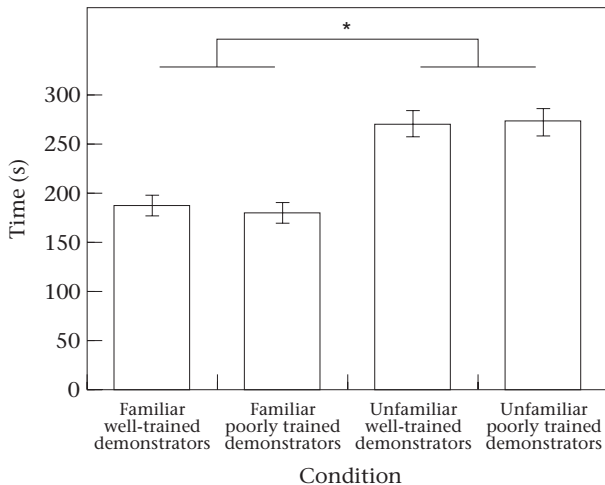


Figure 1. Latency to complete the foraging task by observers with well-trained familiar, poorly trained familiar, well-trained unfamiliar, and poorly trained unfamiliar demonstrators. * $P < 0.025$.

trained ones. The nonsignificant yet lower mean time for familiar demonstrators was largely dependent upon the effect of familiarity within well-trained demonstrators (simple effect: $F_{1,12} = 2.52$, NS). The results suggest that it was legitimate to test the effect of demonstrator quality upon the observers but not the effect of familiarity within demonstrators.

Observer Performance

Observers with familiar demonstrators completed the task significantly faster than those with unfamiliar demonstrators (ANOVA: $F_{1,12} = 9.16$, $P < 0.025$), but there was no effect of demonstrator training (ANOVA: $F_{1,12} = 0.01$, NS), nor any demonstrator training \times familiarity interaction (ANOVA: $F_{1,12} = 0.03$, NS; Fig. 1). The effect of familiarity on observers was significant within the poorly trained demonstrator condition (simple effect: $F_{1,12} = 5.08$, $P < 0.05$) and approached significance under the well-trained demonstrator condition (simple effect: $F_{1,12} = 4.11$, $P < 0.1$).

This result suggests that familiarity between demonstrator and observer was an effective social influence. However, the result could also be explained by familiarity between observers instead of between observers and demonstrators. A comparison of the performance of familiar and unfamiliar demonstrators during their training found no difference in their rate of learning (ANOVA: $F_{1,12} = 2.369$, NS). However, in this case the familiar fish had been together for only 6 days before training, which is not thought long enough for familiarity effects to emerge in the guppy (Griffiths & Magurran 1997).

Change in Performance Over Trials

Among demonstrators a significant demonstrator training \times trial interaction was found (ANOVA: $F_{14,168} = 2.22$, $P < 0.025$), which reflects the observation that well-trained demonstrators initially performed better

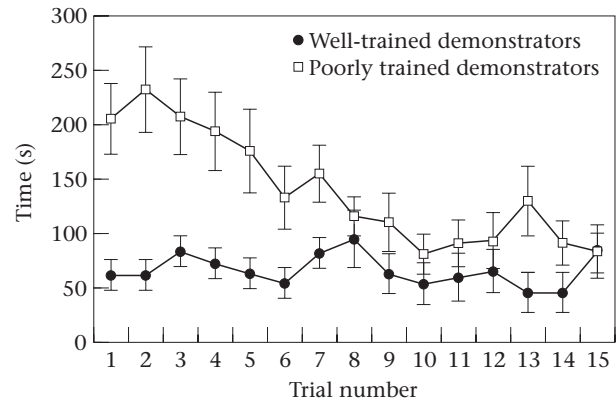


Figure 2. Latency to complete the foraging task by well- and poorly trained demonstrators over the trials.

than poorly trained counterparts, but that this difference diminished over trials, as the poorly trained demonstrators showed the greater improvement. There was thus a significant difference between the performance of well- and poorly trained demonstrators only over the first few trials (e.g. trials 1–3: ANOVA: $F_{1,12} = 13.45$, $P < 0.005$; trials 4–15: ANOVA: $F_{1,12} = 2.19$, NS; Fig. 2).

To examine the demonstrator training \times trial interaction further we carried out trend tests, where a trend of decreasing latency to complete the task over trials would suggest learning. A significant downward trend in latency was found within both poorly trained, familiar demonstrators ($F_{1,210} = 67.9$, $P < 0.001$; Fig. 3c) and poorly trained, unfamiliar demonstrators ($F_{1,210} = 7.70$, $P < 0.01$; Fig. 3d) but not within well trained, familiar ($F_{1,210} = 1.40$, NS; Fig. 3a) or well trained, unfamiliar ($F_{1,210} = 1.02$, NS; Fig. 3b) demonstrators. It would seem that only the poorly trained demonstrators showed a significant improvement in performance through learning, and that the performance of the well-trained demonstrators had reached an asymptote prior to testing. There were no significant familiarity \times trial (ANOVA: $F_{14,168} = 1.20$, NS) or demonstrator training \times familiarity \times trial interactions (ANOVA: $F_{14,168} = 1.02$, NS).

Observers also showed a significant demonstrator training \times trial interaction (ANOVA: $F_{14,168} = 3.67$, $P < 0.001$; Fig. 4), which reflects the observation that observers with well-trained demonstrators were initially faster than observers with poorly trained demonstrators, but this difference disappeared after the first few trials. The familiarity \times trial interaction was not significant (ANOVA: $F_{14,168} = 1.85$, NS), and there was no significant demonstrator training \times familiarity \times trial interaction (ANOVA: $F_{14,168} = 0.85$, NS).

We examined these results further with trend tests. Observers with poorly trained demonstrators were slower in the first trial than those with well-trained demonstrators, yet observers within both poorly trained demonstrator conditions showed a significant decrease in times over trials, indicative of learning (poorly trained, unfamiliar demonstrators: $F_{1,210} = 32.57$, $P < 0.001$; poorly trained, familiar demonstrators: $F_{1,210} = 94.65$, $P < 0.001$; Fig. 3). Observers with well-trained demonstrators

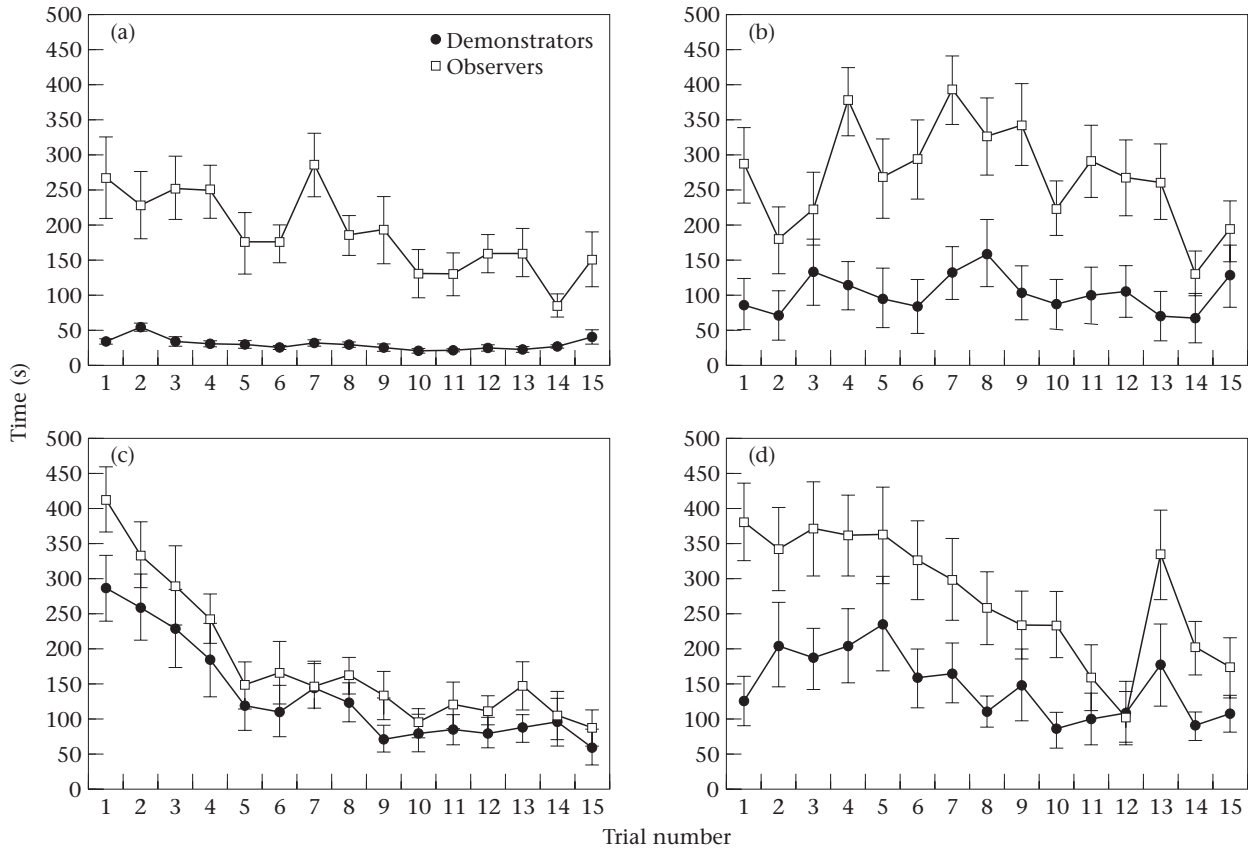


Figure 3. Latency to complete the foraging task by both observers and demonstrators over trials, split into the four groups. Observers had (a) well-trained, familiar demonstrators, (b) well-trained, unfamiliar demonstrators, (c) poorly trained, familiar demonstrators and (d) poorly trained, unfamiliar demonstrators.

differed in that only those observers with familiar demonstrators showed evidence of learning (well-trained, familiar demonstrators: $F_{1,210}=26.17$, $P<0.001$; well-trained, unfamiliar demonstrators: $F_{1,210}=3.17$, NS; Fig. 3). While familiarity enhanced overall observer performance, it was associated with evidence for learning only in observers with poorly trained demonstrators. In contrast, demonstrator training did not enhance overall

observer performance, but did affect the rate of change in performance, with observers with poorly trained demonstrators showing signs of learning.

We further analysed the effect of demonstrator training upon observers by comparing the performance of observers with well- and poorly trained demonstrators over trials 1–3, when there was a significant difference in demonstrator training (demonstrators: ANOVA: $F_{1,12}=13.45$, $P<0.005$), and during trials 4–15, when there was not (demonstrators: ANOVA: $F_{1,12}=2.19$, NS). Over trials 1–3, observers in the presence of well-trained demonstrators performed significantly better than those with poorly trained demonstrators (ANOVA: $F_{1,12}=5.76$, $P<0.05$), while there was no significant difference between observers with respect to familiarity over trials 1–3 (ANOVA: $F_{1,12}=0.00$, NS). When well-trained demonstrators were not significantly better than poorly trained demonstrators, over trials 4–15, there was a significant difference in performance with respect to familiarity (ANOVA: $F_{1,12}=14.41$, $P<0.005$), but not demonstrator training (ANOVA: $F_{1,12}=1.21$, NS). In fact, during these trials observers in the presence of poorly trained demonstrators performed slightly better than those with well-trained demonstrators.

To examine the relationship between demonstrator and observer performances in each condition we used

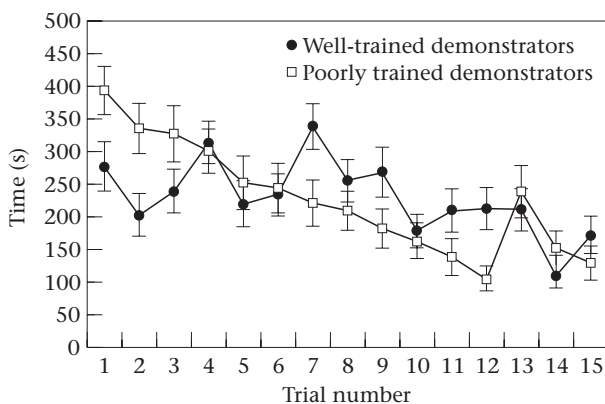


Figure 4. Latency to complete the foraging task by observers with well- and poorly trained demonstrators over the trials.

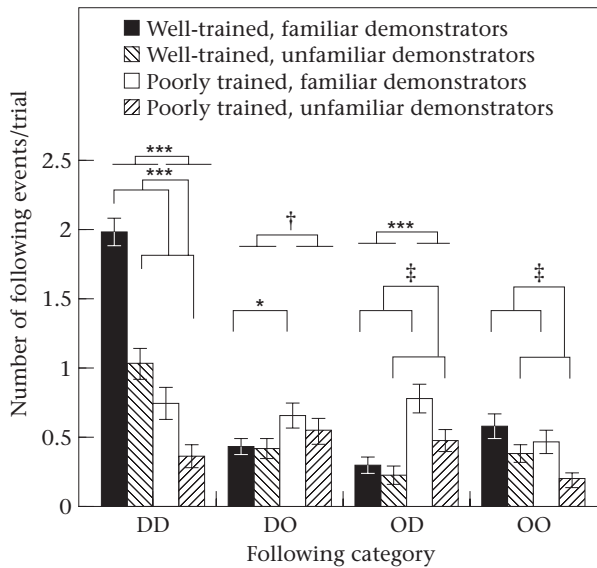


Figure 5. The number of successful completions of the maze that were following events in each of the four conditions, where DD represents a demonstrator followed by a demonstrator, DO a demonstrator followed by an observer, OD an observer followed by a demonstrator, and OO an observer followed by an observer. † $P=0.08$; ‡ $P=0.06$; * $P\leq 0.05$; *** $P\leq 0.01$.

regression analysis. The dependence of observer mean times upon demonstrator mean times in the familiar, well-trained condition approached significance ($F_{1,13}=4.25$, $P=0.06$), reflecting a constant demonstrator and yet decreasing observer performance over the trials. There was no significant regression of demonstrator performance on observers when observers were with well-trained, unfamiliar demonstrators ($F_{1,13}=3.75$, $P=0.08$). In comparison, both poorly trained demonstrator conditions showed strongly significant regressions of demonstrator performance on observers (poorly trained, familiar: $F_{1,13}=232.23$, $P<0.001$; poorly trained, unfamiliar: $F_{1,13}=16.77$, $P=0.001$). This finding raised the counterintuitive possibility that poorly trained demonstrators had a greater effect on the observers over the 15 trials than well-trained demonstrators. However, the regressions did not provide definitive evidence that observers were following or learning from poorly trained demonstrators rather than vice versa.

To address this issue we conducted an analysis of following, where a following event was defined arbitrarily as any occasion when one fish went through the partition within 10 s of another fish. We assumed that each fish followed the fish that preceded it in a linear chain. Analysis of other models of following, and other interindividual intervals, gave similar patterns.

Figure 5 shows that the well-trained demonstrators followed each other significantly more frequently than poorly trained demonstrators (ANOVA: $F_{1,12}=29.23$, $P<0.001$) and also familiar demonstrators followed each other more frequently than unfamiliar demonstrators (ANOVA: $F_{1,12}=14.39$, $P=0.003$). When observers followed demonstrators the greater following of poor demonstrators than well-trained demonstrators

approached significance (ANOVA: $F_{1,12}=3.65$, $P=0.08$), and was significant within the familiar condition (ANOVA: $F_{1,12}=4.43$, $P<0.05$). There was no difference in the number of times observers followed familiar or unfamiliar demonstrators (ANOVA: $F_{1,12}=1.624$, NS). When demonstrators followed observers, there was significantly more following by poorly trained demonstrators than well-trained demonstrators (ANOVA: $F_{1,12}=16.223$, $P<0.002$), while the greater following by familiar demonstrators than unfamiliar demonstrators approached significance (ANOVA: $F_{1,12}=4.06$, $P=0.06$). When observers followed other observers, the greater following among familiar than unfamiliar fish approached significance (ANOVA: $F_{1,12}=4.276$, $P=0.06$) but the number of observers with well-trained demonstrators following other observers was not significantly more than those with poorly trained demonstrators (ANOVA: $F_{1,12}=1.77$, NS).

DISCUSSION

Our results suggest that demonstrator–observer familiarity enhanced the rate at which guppies learn a foraging task. Chivers et al. (1995) found that familiar shoals are more cohesive than unfamiliar shoals. This may increase the likelihood that observers followed demonstrators or attended to their behaviour. The effect of demonstrator training on observer performance is more complex. Whilst the initial performance of observers with well-trained demonstrators was better than that of observers with poorly trained ones, the latter showed a faster rate of increase in performance and more closely mirror the times of demonstrators. As a result, over 15 trials there was no overall difference in performance of observers with demonstrators that differed in training.

Our findings suggest that well-trained demonstrators facilitated learning in observers in the short term only, perhaps by directing attention to the hole in the partition through a local enhancement process. Well-trained demonstrators, however, tended to travel through the partition too quickly for the observers to follow, resulting in observers following one another. In contrast we have shown using our following analysis that poorly trained demonstrators were more likely to be followed by observers than their well-trained counterparts, since they solved the maze at approximately the same speed. This interpretation is supported by the much stronger regressions of demonstrator performance on observer performance with poorly trained demonstrators than with well-trained ones. This raises the possibility that demonstrators enhanced the performance of observers in two ways: (1) a local-enhancement-type tip-off and (2) following. The tip-off and following mechanisms of social influence are not mutually exclusive as one fish may follow another and in the process have its attention drawn to the hole. The fact that strong evidence for learning was found amongst observers with poorly trained demonstrators suggests that these may be particularly effective in enhancing observer performance over trials. It may be significant that the poorly trained

demonstrators learned at a similar rate to their observers, and consequently continued to perform over the trials at a rate slightly faster than that of the observers. This type of situation, where demonstrators are only slightly superior to observers in performance, may be optimal for social learning to operate.

The mistakes of poorly trained demonstrators may also enhance the rate of change in performance of observers. In particular, we noticed that poorly trained demonstrators appeared to spend more time at the maze entrance, before swimming through the maze. This would increase the probability of attracting the observers to the maze entrance, allowing them both to follow the demonstrators more closely and to spend more time near the maze entrance. Templeton (1998) showed that in starlings, *Sturnus vulgaris*, naïve observers with a tutor that made incorrect selections in a choice test learned faster than those with tutors that made a mixture of correct and incorrect selections, or that only chose correctly. These studies suggest that information transfer may be more efficient if the observer sees mistakes being made by a demonstrator animal, perhaps because this observational experience clarifies the association between the correct behaviour and its consequences. Alternatively, if local enhancement is the key operational process, then the amount of time the demonstrator spends over the task may draw more attention towards the demonstrator and the object it is manipulating (or the location of interest) than would otherwise be the case.

Our findings lead us to the following general predictions, which we anticipate are likely to apply to other species, not just guppies, and in experimental contexts other than foraging.

(1) Novel learned traits will diffuse faster among individuals that are familiar with one another than among unfamiliar individuals. If members of a subsection of the population, for example a kin group, are more familiar with one another, there will be an increased probability of social learning in that subsection compared with the remainder of the population.

(2) If the level of performance among individuals in the population generates a distribution that is strongly bimodal, individuals in the slower-to-learn subsection are more likely to enhance their performance through social learning from individuals in the faster-to-learn subsection via the effects of a tip-off, such as local or stimulus enhancement, than by exposure, following, or guided learning. In contrast, if the level of performance among individuals in the population generates a distribution that is unimodal, the majority of individuals are more likely to learn from individuals of a slightly higher level of performance than themselves, resulting in opportunities for social learning enhanced through exposure, following, or guided learning. The relative utility of the tip-off effect compared with the guided-learning-type effect may depend on patterns of variability in the environment, with the tip-off more effective in comparatively variable environments, generating a bimodal performance distribution, and guided learning more effective in less variable environments, generating a unimodal performance distribution.

(3) We predict faster diffusion in populations with a continuous, unimodal range in performance or ability, where each individual has the opportunity to learn from individuals of a slightly higher level of performance, than in populations with a multimodal distribution or complex substructure, within which discrete differences in performance may be found between subsections.

We have shown how the rate of acquisition of a behaviour by naïve individuals depends upon the relative performance and familiarity of their demonstrators. We anticipate that eventually it may be possible to describe the relationships between the psychological processes of social influence (e.g. local enhancement, observational learning), the shape of the performance-level distribution in the population, and the diffusion dynamics of socially transmitted traditions.

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References

- Beauchamp, G. & Kacelnik, A. 1991. Effects of the knowledge of partners on learning rates in zebra finches *Taeniopygia guttata*. *Animal Behaviour*, **41**, 247–253.
- Biederman, G. B. & Vanayan, M. 1988. Observational learning in pigeons: the function of quality of observed performance in simultaneous discrimination. *Learning and Motivation*, **19**, 31–43.
- Chivers, D. P., Brown, G. E. & Smith, R. J. F. 1995. Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): implications for antipredator behaviour. *Canadian Journal of Zoology*, **73**, 955–960.
- Coussi-Korbel, S. & Fragaszy, D. M. 1995. On the relation between social dynamics and social learning. *Animal Behaviour*, **50**, 1441–1453.
- Dugatkin, L. A. & Godin, J-G. J. 1992. Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London, Series B*, **249**, 179–184.
- Dugatkin, L. A. & Godin, J-G. J. 1993. Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. *Behavioral Ecology*, **4**, 289–292.
- Dussault, G. V. & Kramer, D. L. 1981. Food and feeding behaviour of the guppy, *Poecilia reticulata* (Pisces: Poeciliidae). *Canadian Journal of Zoology*, **59**, 684–701.
- Galef, B. G., Jr. 1988. Imitation in animals: history, definition and interpretation of data from the psychological laboratory. In: *Social Learning. Psychological and Biological Perspectives* (Ed. by T. Zentall & B. G. Galef Jr), pp. 3–28. Hillsdale, New Jersey: L. Erlbaum.
- Galef, B. G., Jr & Giraldeau, L-A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, **61**, 3–15.
- Griffiths, S. W. & Magurran, A. E. 1997. Familiarity in schooling fish: how long does it take to acquire? *Animal Behaviour*, **53**, 945–949.
- Helfman, G. S. & Schultz, E. T. 1984. Social transmission of behavioural traditions in a coral reef fish. *Animal Behaviour*, **32**, 379–384.

- Heyes, C. M.** 1994. Social learning in animals: categories and mechanisms. *Biological Reviews*, **69**, 207–231.
- 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**, 181–190.
- Laland, K. N. & Williams, K.** 1997. Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, **53**, 1161–1169.
- Laland, K. N. & Williams, K.** 1998. Social transmission of maladaptive information in the guppy. *Behavioral Ecology*, **9**, 493–499.
- Lindström, K. & Ranta, E.** 1993. Social preferences by male guppies, *Poecilia reticulata*, based on shoal size and sex. *Animal Behaviour*, **46**, 1029–1031.
- Magurran, A. E., Seghers, B. H., Shaw, P. W. & Carvalho, G. R.** 1994. Schooling preferences for familiar fish in the guppy, *Poecilia reticulata*. *Journal of Fish Biology*, **45**, 401–406.
- Magurran, A. E., Seghers, B. H., Shaw, P. W. & Carvalho, G. R.** 1995. The behavioural diversity and evolution of guppy, *Poecilia reticulata*, populations in Trinidad. *Advances in the Study of Behavior*, **24**, 155–202.
- Pitcher, T. J. & Parrish, J. K.** 1993. Functions of shoaling behaviour in teleosts. In: *The Behaviour of Teleost Fishes*. 2nd edn (Ed. by T. J. Pitcher), pp. 363–440. London: Chapman & Hall.
- Reader, S. M. & Laland, K. N.** 1999. Foraging innovation in the guppy. *Animal Behaviour*, **57**, 331–340.
- Seghers, B. H.** 1974. Schooling behaviour in the guppy (*Poecilia reticulata*): an evolutionary response to predation. *Evolution*, **28**, 486–489.
- Spence, K. W.** 1937. Experimental studies of learning and higher mental processes in infra-human primates. *Psychological Bulletin*, **34**, 806–850.
- Sugita, Y.** 1980. Imitative choice behaviour in guppies. *Japanese Psychological Research*, **22**, 7–12.
- Templeton, J. J.** 1998. Learning from others' mistakes: a paradox revisited. *Animal Behaviour*, **55**, 79–85.
- Thorpe, W. I.** 1956. *Learning and Instinct in Animals*. London: Methuen.
- Warner, R. R.** 1988. Traditionality of mating-site preferences in a coral reef fish. *Nature*, **335**, 719–721.
- Whiten, A. & Ham, R.** 1992. On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Advances in the Study of Behavior*, **21**, 239–283.