

Experience shapes social information use in foraging fish

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Many species of animal use social information, and in a variety of different contexts, but it is not clear to what degree their ability to do this depends upon their prior experience of the association between the behaviour of others and reward. We addressed this question in an experiment in which two stickleback species (*Gasterosteus aculeatus* and *Pungitius pungitius*) were exposed to a novel feeding task and then tested under a range of conditions. Using a fully factorial training design, fish were fed from either the surface or the bottom of their tank, and at the same time were exposed to conspecifics feeding from the surface or bottom. At test, we showed that in order to be able to use demonstrator behaviour to anticipate the presence of food at the surface, test subjects needed first to have prior experience of both: sticklebacks responded to the behaviour of conspecifics that were feeding at the surface by rising higher in the water column themselves, but, crucially, they only did this if they had prior experience both of finding food at the water surface and of seeing others feed there. Moreover, they only displayed this response in the presence of feeding conspecifics, but not when the demonstrators were not feeding or were absent. The role of prior experience and learning in social information use is surprisingly understudied. We suggest that such work is vital if we are to understand the level at which natural selection operates in shaping social information use and social learning.

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Animals can acquire information about the distribution of resources and hazards in their environment via the behaviour of others. Social information use is well documented in a range of species, with animals paying attention and responding to information from both conspecifics and heterospecifics (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Danchin, Giraldeau, Valone, & Wagner, 2004; Galef & Giraldeau, 2001; Hoppitt & Laland, 2013; Rendell et al., 2011; Valone, 2007; Valone & Templeton, 2002; Ward & Webster, 2016; Webster & Laland, 2017). An important question for researchers interested in the transmission of social information is how an individual's experience shapes its ability to recognize and respond appropriately to social cues that convey relevant information.

Many species form groups for a variety of different reasons (Krause & Ruxton, 2002; Ward & Webster, 2016), and social attraction alone may lead individuals to encounter and learn about the presence or quality of the resources that others are using (Atton, Hoppitt, Webster, Galef, & Laland, 2012). Over time, individuals that have often previously found resources when joining others may become even more likely to join others. In house sparrows, *Passer*

domesticus, birds that had previously found food when foraging alongside others (taxidermy models in these experiments) were more likely to join others when foraging subsequently (Belmaker, Motro, Feldman, & Lotem, 2012; Katsnelson, Motro, Feldman, & Lotem, 2008). Bumblebees, *Bombus terrestris*, can acquire flower colour preferences after joining conspecifics and subsequently find food on novel flowers of a given colour (Avarguès-Weber & Chittka, 2014; Dawson 2013). Through foraging near others, animals may come to form associations between the presence of others and the distribution of resources. Beyond simple social attraction, animals might use further cues when deciding when and whom to join. They may be more strongly attracted to larger or denser groups (Frommen, Hiermes, & Bakker, 2009), with the distribution of such aggregations in turn being shaped by the distribution of resources in the environment. There is increasing evidence that social attraction is plastic and can be affected by social experience both early on in development as juveniles (Boogert, Farine, & Spencer, 2014; Chapman, Ward, & Krause, 2008) and in adulthood (Swaney, Kendal, Capon, Brown, & Laland, 2001). Animals may also be more attracted to groups containing active compared to inactive individuals, or those containing individuals exhibiting cues such as postures or movements associated with feeding or competing (Coolen, Giraldeau, & Lavoie, 2001), behavioural biases that may well be affected by experience.

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In this study we explored the importance of both exposure to conspecific feeding-specific behaviour and personal experience of finding food in the tendency of fish (three- and nine-spined sticklebacks, *Gasterosteus aculeatus* and *Pungitius pungitius*) to subsequently respond to social cues indicating the presence of food at the surface of the water. We have used these species as model organisms for investigating social information use and learning for a number of years, finding that both are capable social information users, but also that they differ in their ability to learn from social cues (Laland, Atton, & Webster, 2011). Both species are generalist foragers, capturing prey from the substrate and water column and feeding from the surfaces of rocks, plants and other structures (Bell & Foster, 1994). While neither species generally feeds from the surface of the water, we show here that both can be trained to do so, in this case from the underside of a floating tile.

In the experiment described here we controlled the exposure of test subjects to both the presence of food at the surface and the social cues provided by others feeding there, such that at the end of the exposure period, each fish had been exposed to one of four conditions: (1) the test subject had experience of both feeding at the surface and of seeing conspecifics do so too; (2) it had experience of feeding from the surface, but had only ever seen conspecifics feed from the substrate material at the bottom of its housing tank; (3) it had no experience of feeding from the surface but had seen conspecifics do so; (4) it had neither fed from the surface nor seen conspecifics do so. We tested the hypothesis that the ability to use social information about the presence of food at the surface would depend upon test subjects having experience of both finding food there themselves and of previously seeing others feed there. We predicted that, when tested, subjects would rise higher in the water column only if they had this joint experience (condition 1) and only if demonstrators were present and feeding at the surface too.

METHODS

Subjects and Housing

Several hundred three- and nine-spined sticklebacks were collected from Melton Brook in Leicester, U.K. in October 2008. They were captured using dip nets and transported to our laboratory at the University of St Andrews. Fish were held in single-species groups of 50 fish in 90-litre aquaria. Each aquarium contained a layer of gravel and artificial plants and was equipped with an internal filter. Water temperature was held at 8 °C, and the light regime was 12:12, with the room illuminated between 0700 and 1900 hours. The fish were fed daily to satiation with frozen bloodworms and *Artemia*. They were held under these conditions for several weeks until the experiment began. All fish used in the experiment described below were adults measuring 35–40 mm in length. We did not use fish displaying signs of being in reproductive condition, since this has been shown to affect social information use in other contexts (Webster & Laland, 2011). The experiments described below took place between November 2008 and May 2009.

Design Overview

Fish were trained and tested in aquaria that were divided into two sections, one containing the test subject and the other the demonstrators (Fig. 1). In the training phase of the experiment individual test subjects were presented with food either at the surface of their half of the tank or on the floor and were also given the opportunity to watch conspecific demonstrators feed from the surface or floor in the other half of the tank, as specified by

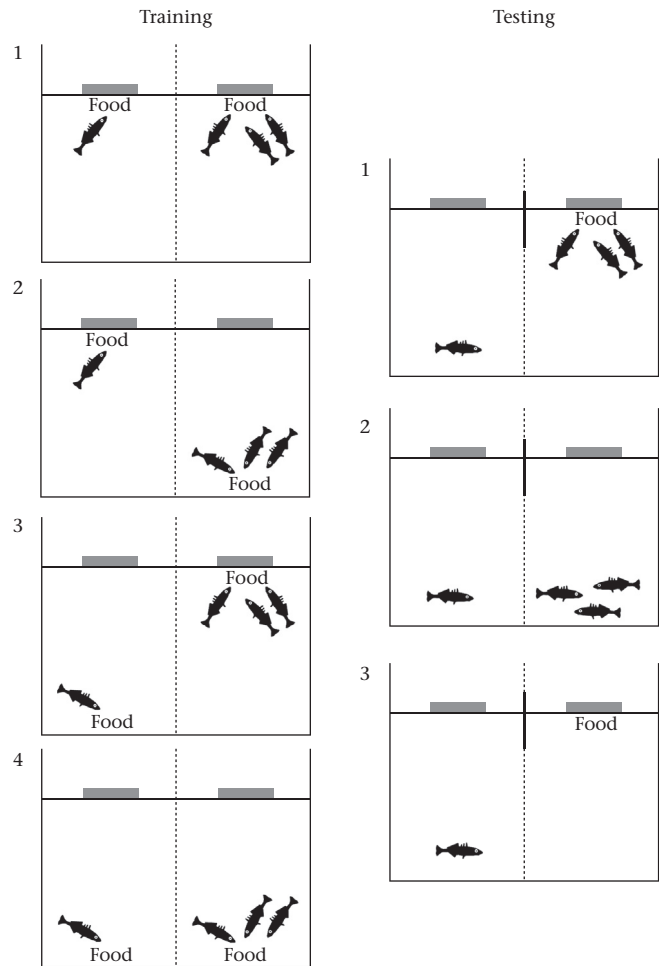


Figure 1. Training and testing regimes. Fish were trained in one of four treatments: 1: test subjects and demonstrators both fed from floating tile (grey block in figure); 2: test subjects fed from tile, demonstrators fed from substrate; 3: test subjects fed from substrate, demonstrators fed from tile; 4: test subjects and demonstrators both fed from substrate. Fish from each training regime were then tested in one of three treatments: 1: demonstrators present and feeding; 2: demonstrators present but not feeding; 3: no demonstrators present.

conditions 1–4 described below. In the test phase they were exposed to conspecifics that were either feeding at the surface or that were not feeding, or they were tested alone. To ensure that subjects' behaviour at test was not biased by the presence of food, no food was present in the test subject's half of the test tank. We used the height of the fish above the substrate as the response variable. Both species tend to remain close to the substrate when not feeding. We therefore expected fish to rise close to the surface only when feeding or when expecting food, making this a reliable indicator of food anticipatory behaviour.

Training Tank and Procedure

Individual test subjects were trained, or otherwise exposed to the floating tile and demonstrators, in cube-shaped aquaria measuring 30 cm along each axis. Each aquarium was divided into two sections using a clear plastic tank divider (Penn Plax brand), with five 2 mm diameter holes per square cm. A layer of sand, 1 cm deep, was added to each aquarium and each was filled with water to a depth of 27 cm. An airstone was added to each side of the aquarium to aerate the water. On the surface of each half of the aquarium a 10 cm square sheet of white polystyrene was floated.

Each aquarium was surrounded with black paper to prevent the test subjects from receiving cues from other fish in adjoining aquaria. The test subject was added to one half of the aquarium, while a group of three conspecific demonstrators were added to the other half. The test subject and demonstrators were held in these tanks for 2 weeks until the test subjects were used in the experiment. They were fed twice per day, five times per week, from Monday to Friday. Subjects were not fed at the weekends. The provision of food to the test subjects and demonstrators varied between the four experimental treatments as follows (see also Fig. 1):

(1) Test subjects and demonstrators both fed from the tile. The polystyrene tiles were removed from the aquaria and dried using paper towels. To each tile a small amount of Vaseline was applied. This was used to stick thawed bloodworms to the underside of the tiles, five for the test subject and 15 for demonstrators. The tiles were then placed back in the aquaria, bloodworms facing down, and the fish were allowed to feed from them. After 1 h the tiles were removed and replaced with clean ones, containing no Vaseline or food. Fish were initially reluctant to feed from the underside of the tiles during the first few days of the training, although most fish did feed within the hour. Within a week or so all the fish readily fed from the tiles consuming most of the food within the first few minutes.

(2) Test subjects fed from the tile, demonstrators fed from the substrate. The polystyrene tiles were removed, and Vaseline was applied to them as described above, but bloodworms were only added to the tile of the test subject. When the tiles were returned to the aquaria, the demonstrators were provided with 15 bloodworms on the surface of the sand substrate. These were applied using a large pipette, with the food contained within 2 cm³ of tank water.

(3) Test subjects fed from the substrate, demonstrators fed from the tile. Feeding was performed as in treatment 2, above, except here it was the test subject that received five bloodworms delivered to the sand substrate, while the demonstrators' food was provided on the underside of the tile.

(4) Test subjects and demonstrators both fed from the substrate. The tiles were removed, and Vaseline was applied to them as above, but both the test subjects and the demonstrators received their food via pipette to the sand substrate, five and 15 bloodworms, respectively.

In total, 360 test subjects (180 of each species) were trained, 45 in each of these training conditions. These in turn were tested in the three experimental treatments described below. Thirty training tanks were established and arranged into six blocks of five tanks each. Within each block five fish of the same species received the same training (in one of the four training conditions described below) and were then tested in one of the three test conditions described below. This was repeated over 12 cycles until 360 fish had been trained and tested. The training and testing schedule is presented in [Appendix Table A1](#).

Test Tank and Procedure

The test tank was similar to the training tank, except that a transparent Perspex container, 30 cm tall with a 12 cm base, was present in the demonstrator half of the aquarium. This was watertight and was used to prevent the test subject from being able to detect chemical cues from the bloodworms that were present in two of the treatments described below. The top 2 cm of the container was covered with black PVC tape. This prevented the test subject from being able to see any bloodworms that were attached to the underside of the demonstrators' tile, but still allowed them to see the demonstrators feeding. Three sides of the

test tank were covered with black paper to prevent outside disturbance. One side was left uncovered to allow us to film through the side of the tank using a digital video camera. The test tank was filled with water to a depth of 27 cm. Horizontal lines 1 cm apart were drawn on the side of the tank facing the camera. These allowed us to record the height in the water column of the test subject, our response variable, as described below. In cases where the test subject was level with one of the lines we used the height of the fish's eye relative to the line as a guide: if the eye was above or below the line then the fish was recorded as above or below. If the eye was level with the line the fish was always recorded as below. In all treatments a tile with Vaseline on it was present in the test subject's half of the tank, but this never contained food. We performed three experimental treatments, testing 15 fish per species from each of the four training conditions. (1) Demonstrators present and feeding: three conspecific demonstrators were present and allowed to feed from 15 bloodworms stuck with Vaseline to the underside of the polystyrene tile. (2) Demonstrators present but not feeding: three demonstrators were again present, but this time no food was provided on the tile. (3) No demonstrators present: no demonstrators were present, but food was provided on the tile. Although the design of the experiment prevented the fish from being able to see or smell the food, including food in the 'no demonstrators' condition allowed us to rule out the use of other cues, such as discoloration of the water that might have been caused by the food.

Trials proceeded as follows. First the test subject was added to one half of the tank, and the demonstrators (where present) were added to the container in the centre of the other half. These were allowed to settle for 15 min. A polystyrene tile was then added to each half of the tank, in the case of the demonstrators at the surface of the container. This contained a small amount of Vaseline spread on the downward facing side. Fifteen bloodworms were stuck to the tile in the demonstrators' container in one treatment, as described above; otherwise no food was present. Adding the tiles did not seem to startle the fish. This marked the beginning of the experiment, which lasted for a further 5 min. Each trial was recorded and from the videos we measured the height of the test subject above the substrate to the nearest centimetre every minute, giving a total of five measurements per trial.

Statistical Analysis

We saw no trends for increasing or decreasing height of the test subject above the bottom of the experimental arena during the observation period ([Appendix Figs. A1 and A2](#)). We therefore used the mean height of the test subject as the response variable in our analysis. Data were analysed using a generalized linear model (GLM). Test subject experience, demonstrator cue treatment and species were included as fixed factors, with interactions between all factors also included. Tukey HSD post hoc tests were used to identify differences between test subject experience and demonstrator cue treatments.

Ethical Note

The study adhered to ASAB/ABS guidelines for the use of animals in research and was approved by the University's Animal Welfare and Ethics Committee. No procedures required U.K. Home Office licensing. No animals exhibited signs of stress or illness and at the end of the experiment they were retained in the laboratory for use in other work.

RESULTS

A GLM revealed main effects of demonstrator cue treatment and test subject experience, and an interaction between these. We saw no difference between the two species, but there was an interaction between species and demonstrator cue treatment. There was no interaction between species and test subject experience, nor any three-way interaction between these variables (Table 1, Fig. 2). Among the demonstrator cue treatments, fish swam higher in the water column in the treatment where demonstrators were present and feeding compared to treatments where demonstrators were present but not feeding or when they were absent. We saw no difference between the latter two treatments (Table 2). In terms of test subject experience, fish that had previously both fed from a floating tile and seen conspecifics feed from one swam higher than fish in the other three conditions. We saw no pairwise differences between conditions 2 and 3, conditions 2 and 4 or conditions 3 and 4 (Table 3). These effects explain the interaction observed in the analysis (Fig. 2): across both species, fish only rose high in the water column when they could see others feeding and when they had prior experience of both feeding from a floating tile and seeing conspecifics do the same.

Table 1
Output from a GLM investigating the effects of demonstrator behaviour (Treatment), test subjects' prior training (Experience) and species and the interactions between these on the position of the test subject in the water column

	df	F	P
Treatment	2	65.40	<0.001
Experience	3	112.64	<0.001
Species	1	0.54	0.46
Treatment * Experience	6	49.83	<0.001
Treatment * Species	2	3.07	0.05
Experience * Species	3	2.09	0.10
Treatment * Experience * Species	6	0.56	0.76
Total	360		
Corrected	359		
$R^2=0.70$			

See also Fig. 2 and main text for further details.

Table 2
Tukey HSD post hoc tests comparing the effects of the three demonstrator behaviour treatments

Comparison	P	95% CI lower, upper bounds
P, F vs P, NF	<0.001	1.58, 2.77
P, F vs A	<0.001	2.15, 3.34
P, NF vs A	0.06	-0.03, 1.17

P, F: conspecifics present and feeding; P, NF: conspecifics present but not feeding; A: conspecifics absent. CI: confidence interval. See also Fig. 2 and main text for further details.

Table 3
Tukey HSD post hoc tests comparing the effects of the four observer behaviour treatments

Comparison	P	95% CI lower, upper bounds
1 vs 2	<0.001	3.37, 4.89
1 vs 3	<0.001	3.87, 5.40
1 vs 4	<0.001	3.65, 5.17
2 vs 3	0.31	-0.25, 1.26
2 vs 4	0.78	-0.48, 1.03
3 vs 4	0.87	-0.98, 0.53

1: Experience of feeding from floating tile and seeing others eat from it; 2: experience of feeding from floating tile but not of seeing others eat from it; 3: no experience of feeding from tile, but has seen others feed from it; 4: no experience of feeding from tile or seeing others feed from it. CI: confidence interval. See also Fig. 2 and main text for further details.

DISCUSSION

This experiment addressed the question of how observer experience of both reward and demonstrator behaviour shapes subsequent social information use. We showed that in order to be able to use demonstrator behaviour to anticipate the presence of food at the surface, the observers needed first to have prior experience of both: sticklebacks that could not see or smell food responded to the behaviour of conspecifics that were feeding close to the surface of the water by rising higher in the water column themselves, but, crucially, they only did this if they themselves had

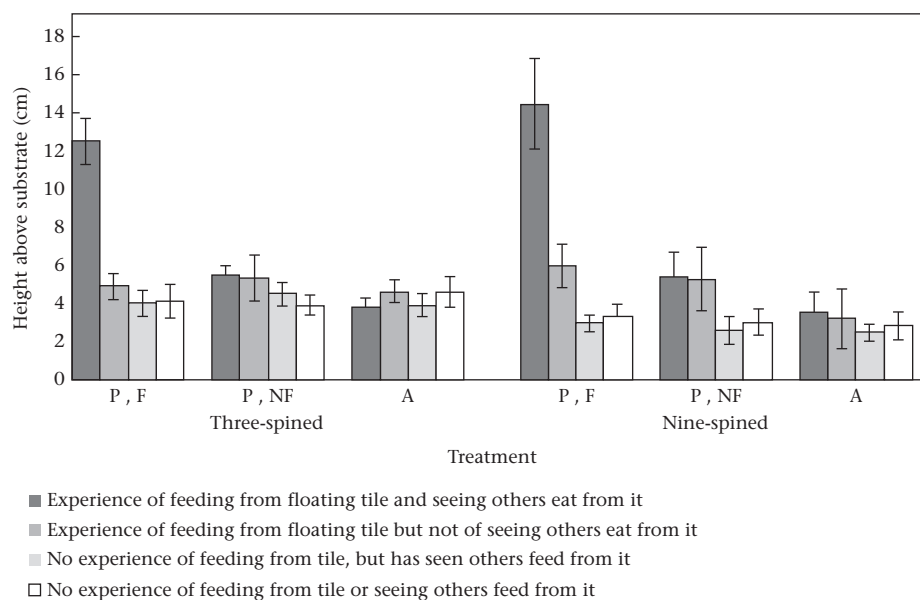


Figure 2. The height (cm) above the base of the tank (mean ± 95% confidence interval, N = 15 trials per data point) seen in test three-spined and nine-spined sticklebacks trained under four different regimes (see key to figure) and tested under one of three treatment conditions (P, F: conspecifics present and feeding; P, NF: conspecifics present but not feeding; A: conspecifics absent). Rising higher above the base of the tank is interpreted as food anticipatory behaviour.

earlier both found food at the water surface and seen others feed there. This suggests that the fish have learned that the presence or some aspect of the behaviour of demonstrators in the upper levels of the water column predicted the arrival of food at the surface. Experienced individuals only displayed this response in the presence of feeding conspecifics, but not when the demonstrators were not feeding (and were not close to the water surface), or when demonstrators were absent. Fish from the other observer experience treatments, those that lacked the double experience of both feeding at the water surface and seeing others feeding there, exhibited no tendency to rise higher in the water column when tested, even when feeding demonstrators were present. This is consistent with associative learning, with the fish having learned an association between the floating feeder and a food reward and demonstrator behaviour and the feeder, leading to an association between demonstrator behaviour and food. Perhaps more simply, the fish may have learned that demonstrators moving towards the surface predict the arrival of food there. Further work is needed to disentangle these effects.

We saw no differences in the behaviour of the two species, although we did see an interaction between species and treatment. The nature and biological significance of this interaction is somewhat unclear, however, with the nine-spined sticklebacks that had not been trained to feed from the tile tending to remain at a lower level above the substrate than did similarly trained three-spined sticklebacks. This may simply reflect fine-scale differences in the habitat preferences of the two species; nine-spined sticklebacks have previously been shown to prefer structured over open environments (Coolen, Bergen, Day, & Laland, 2003; Hart, 2003; Webster, Ward, & Hart, 2009) and in the experimental setting in the absence of other cover, they might have remained closer to the substrate as a form of cover-seeking behaviour. In terms of social information use and experience, however, the responses of the two species did not appear to differ. This contrasts with earlier work examining social information use and social learning in other contexts in these species (Coolen et al., 2003), in which nine-spined sticklebacks, but not three-spined sticklebacks, were shown to be able to use public information transmitted through demonstrator foraging behaviour in order to select the richer of two prey patches.

The role of prior learning of associations in the shaping of subsequent social information use has arguably been understudied compared to other aspects of social information use and learning and warrants further investigation (Leadbeater, 2015; Leadbeater & Dawson, 2017; Reader, 2016).

An elegant example of one experiment that has directly investigated the processes behind social learning concerns flower preference learning in bumblebees. Dawson, Avarguès-Weber, Chittka, and Leadbeater (2013) showed that social learning of flower colour could be explained by classical conditioning and the integration of two learned associations, first the presence of a conspecific on a flower of a certain colour and second, joining a conspecific and receiving a food reward. This experiment demonstrates that social learning in bumblebees can be explained without the need to invoke adaptively specialized social learning mechanisms. This is an interesting finding since recent debates around social learning and its underlying cognitive mechanisms have questioned the extent to which the distinction between social and nonsocial learning is meaningful or useful. Some researchers have discussed whether, in many cases, social learning might operate through domain-general (i.e. not adaptively specialized) psychological mechanisms, with social learning being an exaptation, that is, an adaptive manifestation of pre-existing adaptations for learning. If this is so then social learning is social only in a functional sense, in

so far as information is channelled through a social source (Heyes & Pearce, 2015; Leadbeater, 2015; Lefebvre & Giraldeau, 1996; Reader, 2016). Work such as Dawson et al.'s (2013) bumblebee experiments, Katsnelson et al.'s (2008) and Belmaker et al.'s (2012) producer–scrounger experiments with sparrows, and our current study demonstrate that experience plays an important role in shaping subsequent social information use. They are consistent with a domain-general, associative basis for these forms of social learning. However, given the relative paucity of empirical work specifically addressing this question, further carefully designed experiments in other species, and exploring social learning in contexts other than foraging, are needed to determine how broadly such findings apply (Reader, 2016; Kendal et al., 2018).

Related work should also investigate biases in the so-called input channels (i.e. perceptual processes) that determine how effectively animals detect, pay attention to and respond to social information, and whether, in some species, these may be biased towards social sources (Heyes, 2012). A basic question and useful starting point for such work concerns whether learning occurs more rapidly or with greater accuracy when information is transmitted via social versus nonsocial channels. In our study, test subjects with the right combination of experience readily responded to feeding conspecifics by displaying food anticipatory behaviour themselves, but it is not clear whether they would have formed this association as quickly, or even at all, had they been exposed to a similarly behaving nonbiological stimulus instead. In principle, the fish could be exposed to the simultaneous presence of both an artificial or abstract stimulus and a food reward and tested using a similar protocol to that deployed in the current study. Similar approaches have been used to study social learning of artificial flower type preferences in bumblebees. Avarguès-Weber and Chittka (2014) found that bumblebees that had previously observed and joined other bumblebees as they fed from artificial flowers learned preferences for artificial flowers of the same colour and visited these both when other bumblebees occupied them and when the flowers were unoccupied. When the test subjects had been allowed to watch and then visit flowers attended by model bumblebees or bumblebee-sized white blocks, however, they learned to 'join' these stimuli when they were present on the flowers but failed to acquire a preference for unoccupied flowers of the demonstrated colour as they did when exposed to live demonstrators. Smolla, Alem, Chittka, and Shultz (2016) reported that when resource distribution was unstable bumblebees copied the flower choices of realistic model bumblebees but that they did not copy the flower choices of an unnatural object, a green rubber cuboid. More research in this area would be useful and such work could provide useful information on whether animals in general learn more readily from social sources or channels, and if so, how and why. Input channel biases may plausibly arise through adaptive specialization, with natural selection favouring the ability to detect, filter and attend to pertinent cues in the behaviour of others, as, for example, appears manifest in the particular sensitivity of rhesus macaques, *Macaca mulatta*, to a snake stimulus in observational conditioning of fears (Mineka & Cook, 1988). However, such biases could also plausibly arise through individual experience as well, and research that attempts to separate and account for the relative contribution of adaptive specialization and learning would be valuable.

In our study we exposed our wild-captured test subjects to an artificial challenge, one we could be reasonably certain they had not encountered before, structuring their opportunity to engage with the task, and to observe others interacting with it, in a controlled manner. It is worth noting that in most studies of social learning,

whether conducted on wild-captured or captive-bred animals, the researchers lack detailed data on the previous experience of their test subjects, experience that may well shape the behaviour exhibited at test. To overcome this potential problem, researchers might in principle use animals that have been bred and raised in a controlled and constantly monitored environment, allowing researchers to compile a complete record of their interactions with their physical and social environment and to quantify their history of exposure to social cues. By studying replicated populations from birth to adulthood under conditions as close as possible to natural, and by collecting physiological and behavioural data and performing appropriate controls, researchers should be able account for the relative importance of development, the opportunity to learn privately and from others and adaptive specialization in shaping social information use and learning. While in practice such a project would be a major undertaking, the means for long-term tracking and collating of such data are now well within the reach of researchers (e.g. Dell et al., 2014; Gernat et al., 2018; Hong et al., 2015; Meikle & Holst, 2015; Peters et al., 2016), as are the statistical techniques for incorporating such information into models that describe how and when individuals acquire novel information and learn new behaviour patterns (Hoppitt & Laland, 2013). Ultimately, such intensive experiments may be necessary if we are to fully grasp the proximate and evolutionary bases of social learning.

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Appendix

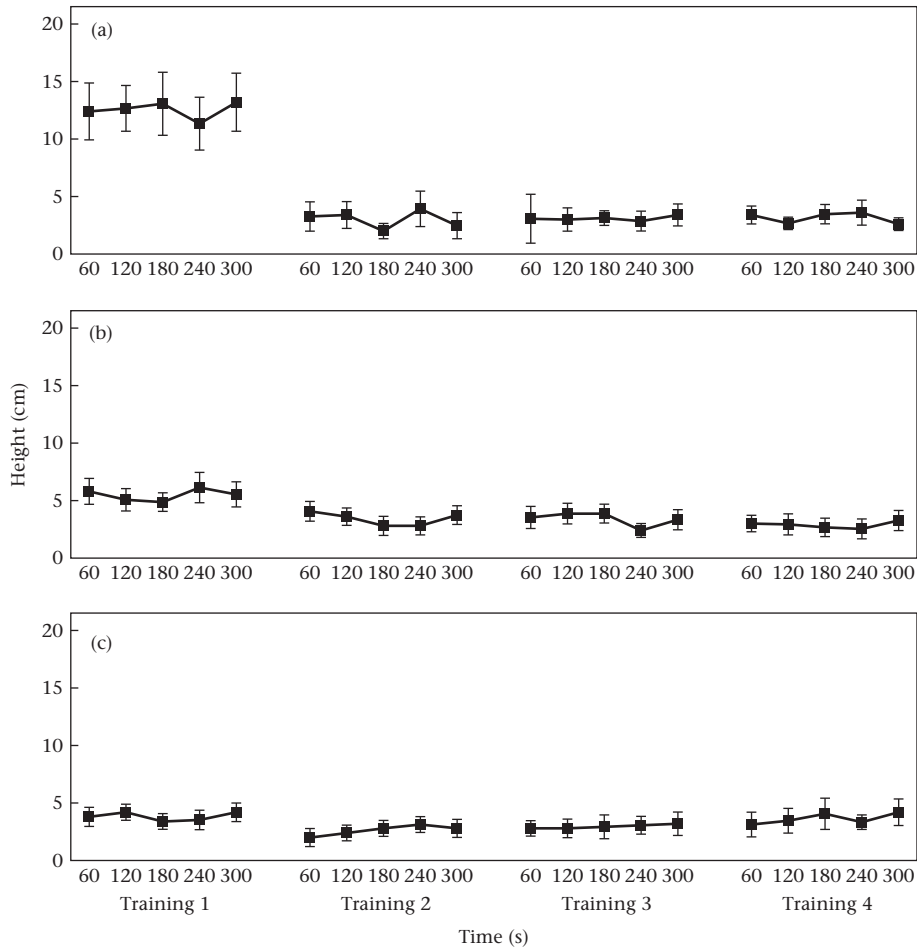


Figure A1. The height (cm) above the base of the tank (mean \pm 95% confidence interval, $N = 15$ trials per data point) seen in three-spined sticklebacks trained under four different regimes (see key to Fig. 2) and tested under one of three treatment conditions: (a) demonstrators present and feeding, (b) demonstrators present but not feeding and (c) no demonstrators present. Rising higher above the base of the tank is interpreted as food anticipatory behaviour. Data show mean height/min during the 5 min tests. Since we saw no major trends over the trial duration we used whole trial means in the analysis presented in the main text and for the data presented in Fig. 2.

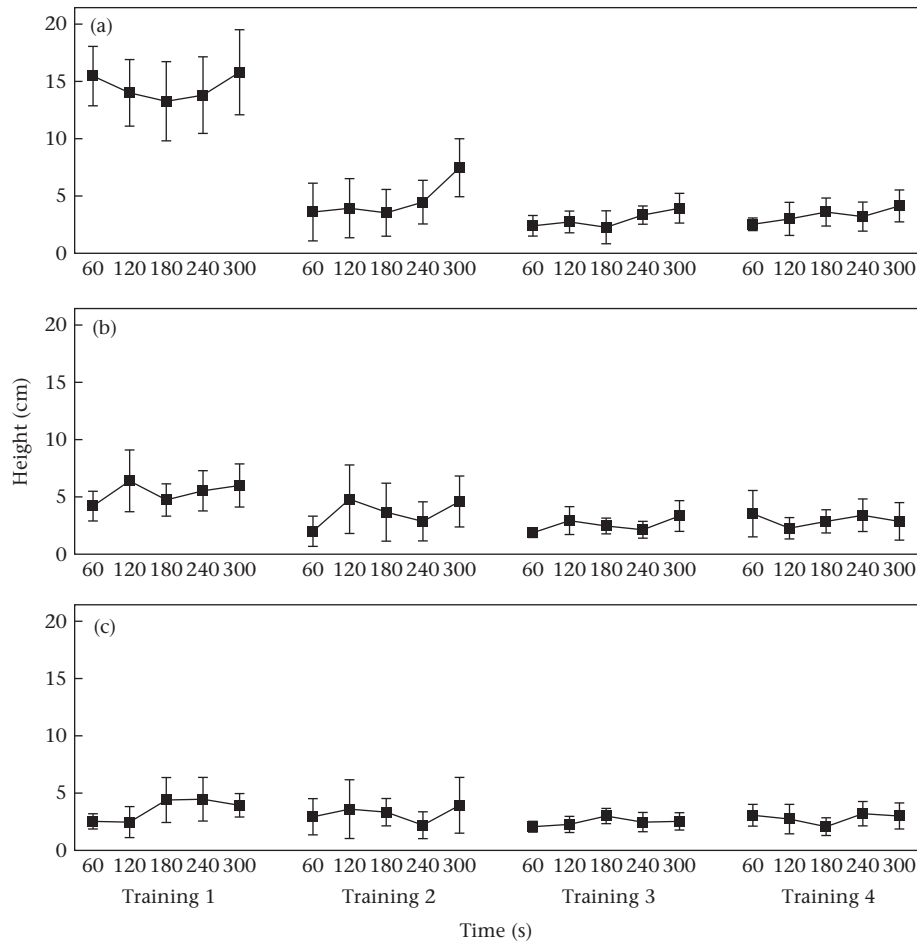


Figure A2. The height (cm) above the base of the tank (mean \pm 95% confidence interval, $N = 15$ trials per data point) seen in nine-spined sticklebacks trained under four different regimes (see key to Fig. 2) and tested under one of three treatment conditions: (a) demonstrators present and feeding, (b) demonstrators present but not feeding and (c) no demonstrators present. Rising higher above the base of the tank is interpreted as food anticipatory behaviour. Data show mean height/min during the 5 min tests. Since we saw no major trends over the trial duration we used whole trial means in the analysis presented in the main text and for the data presented in Fig. 2.

Table A1
Test schedule

Date	Treatment					
	Block A	Block B	Block C	Block D	Block E	Block F
Nov 2008	9ss/1/2	9ss/2/2	3ss/3/2	3ss/1/2	9ss/2/1	3ss/3/1
Nov 2008	3ss/1/1	9ss/4/1	9ss/4/3	9ss/3/1	9ss/1/1	9ss/2/1
Dec 2008	3ss/4/2	9ss/3/2	3ss/1/1	3ss/2/2	3ss/4/3	3ss/3/3
Jan 2009	3ss/3/2	9ss/1/2	3ss/2/1	3ss/2/2	3ss/3/1	3ss/1/3
Jan 2009	9ss/3/1	9ss/1/2	9ss/4/1	9ss/1/1	9ss/2/3	9ss/4/3
Feb 2009	9ss/3/1	9ss/1/3	3ss/1/3	9ss/4/2	3ss/4/1	3ss/2/3
Feb 2009	9ss/3/3	9ss/1/3	9ss/2/3	9ss/2/2	9ss/4/2	9ss/4/3
Mar 2009	9ss/4/2	9ss/1/3	3ss/3/1	3ss/3/3	9ss/3/2	3ss/3/3
Mar 2009	3ss/4/2	3ss/2/3	3ss/4/2	3ss/1/1	3ss/2/1	3ss/2/3
Apr 2009	3ss/2/1	3ss/1/2	3ss/1/2	9ss/1/1	9ss/4/1	3ss/4/3
Apr 2009	9ss/3/3	9ss/3/2	3ss/2/2	3ss/3/2	9ss/3/3	3ss/4/3
May 2009	3ss/4/1	3ss/4/1	9ss/2/1	9ss/2/2	9ss/2/3	3ss/1/3

Thirty training tanks were set up and fish were trained in blocks of five (15 replicates per species per treatment = 5 blocks). See main text for further details. Codes indicate species/training/testing: species: 3ss/9ss = three-spined sticklebacks/nine-spined sticklebacks; training: 1/2/3/4 = test subjects and demonstrators both fed from floating tile/test subjects fed from tile, demonstrators fed from substrate/test subjects fed from substrate, demonstrators fed from tile/test subjects and demonstrators both fed from substrate; testing: 1/2/3 = demonstrators present and feeding/demonstrators present but not feeding/no demonstrators present.