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Public information use by foraging ninespine sticklebacks: Social learning or an unlearned social influence on travel direction?

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Abstract

If we are to understand the cognitive basis and evolutionary origins of a particular behaviour, it is necessary to identify its underlying mechanism. Ninespine sticklebacks (*Pungitius pungitius*) can identify the richer of two prey patches by observing other foragers' success. This may be due to social learning, or an unlearned social effect on travel direction, brought about by the fish being more likely to face and subsequently travel towards areas where they have observed more feeding activity. Here we show that observer orientation does not predict patch choice, and that fish are still more likely to spend more time in richer patches even if they have to take an indirect route to reach them. This suggests that sticklebacks can learn the location of the richer patch through observation, and viewed in conjunction with other published findings, suggests that learned local enhancement lies behind public information use in this species.

1. Introduction

Animals can acquire information about the quality of a resource by monitoring the behaviour of others as they sample or exploit it. Such information, usually produced passively and inadvertently, is known as public information (Valone & Templeton, 2002; Chittka & Leadbeater, 2005; Danchin et al., 2005). Public information may be used in a variety of contexts. Social foragers may monitor the behaviour of group mates so as to identify those that have located food that can be scrounged (Giraldeau & Caraco, 2000),

using cues such as their posture or activity to indirectly locate the food upon which they are feeding (Coolen et al., 2001). The hermit crab (*Coenobita compressus*) uses public information arising from competitive interactions, and is attracted to areas of greater commotion, which can be indicative of higher quality patches of food or high quality shells, a resource necessary for shelter (Laidre, 2013). Some bird species use public information about conspecific breeding success when selecting areas of habitat in which to locate their own nests. In collared flycatchers (*Ficedula albicollis*), breeding pairs are less likely to settle in areas where other pairs are raising fewer young, and residents leave areas at higher rates if the number and quality of other pairs' nestlings there are low (Doligez et al., 2002). Lesser kestrels (*Falco naumanni*) use the reproductive success of other breeders to select breeding sites over successive breeding seasons, with the number of new immigrants to a particular site depending upon the number of successful breeding pairs in the previous year (Aparicio et al., 2007).

Comparative studies focussing on how animals acquire, process and learn from public information, and the conditions under which they are most likely to respond to it, inform research in a diverse range of fields, from behavioural ecology and psychology to anthropology, economics and artificial intelligence (Heyes & Galef, 1996; Laland, 2004; Nehaniv & Dautenhahn, 2007; Galef, 2009; Rendell et al., 2010, 2011; Webster & Ward, 2011; Hoppitt & Laland, 2013; Zentall & Galef, 2013). Understanding the mechanisms that bring about behavioural responses to public information is vital if we wish to infer the cognitive processes that drive them and the evolutionary and developmental forces that have shaped them. This entails, among other things, identifying the stimuli to which the animals are responding, determining how these affect changes in the behaviour of the animal, confirming whether exposure to public information results in learning, and if it does, determining what is learned. In many cases, social influences upon behaviour and learning might plausibly arise via several different mechanisms. It is therefore essential for researchers to discriminate between these, allowing them to rule out those that cannot adequately account for the observed behaviours, and thereby allowing the most likely candidate mechanisms to be identified (Byrne, 2002; Hoppitt & Laland, 2013).

The social foraging behaviour of stickleback fish (Gasterosteidae) has proved to be one of a range of useful model systems for studying how and when animals rely upon public information (reviewed by Laland et al., 2011).

A number of studies using this system have deployed a binary choice assay, in which a subject, 'the observer', is given the opportunity to watch two groups of demonstrator fish feeding from artificial patches that yield prey at different rates. Following an observation period, the demonstrators are removed and the observer is released from its holding unit and allowed to visit the locations of the two prey patches. Statistical models can then be used to infer whether a majority of observers visit the richer patch first, and/or spend more time within it relative to the poorer patch, and whether therefore they are selecting patches under the influence of public information. Ninespine sticklebacks (*Pungitius pungitius*) have been found to be particularly adept at this task (Coolen et al., 2003; Laland et al., 2011; Webster & Laland, 2015). Research into the mechanism underlying public information use in the ninespine stickleback has revealed that ninespines tend to visit the location where they saw demonstrators feeding at the greatest rate, but that they are not able to generalise to other locations with similar physical characteristics or landmarks as the richer patch (Webster & Laland, 2013). In other words, public information use in this species operates via a form of local enhancement, but not stimulus enhancement (Hoppitt & Laland, 2008, 2013).

Building upon this work on the cognitive mechanisms of public information use, in this study, we sought to determine whether the observers' patch selection was based upon social learning or whether it arose from an unlearned social influence upon travel direction. It is possible that if, at the end of the demonstration phase, the observer is more likely to be facing towards the rich patch, to which its attention has been drawn by the more frequent or intense feeding-related behaviours of the demonstrators at that location, then it may simply be more likely to travel in that direction when released. This might cause it to become more likely to encounter the rich patch first, and perhaps once there to spend more time within it, without having necessarily learning anything about patch quality. This means of patch selection seems plausible in light of recent studies of social foraging that have employed diffusion analyses to infer the spread of foraging-related information through freely-moving shoals. These have shown that indirect social effects on foraging patch detection are an important means by which group members locate hidden prey patches (Atton et al., 2012, 2014; Webster et al., 2013). Indirect social effects occur, for example, when searching individuals travel together and influence each other's directions of heading, and therefore encounter and

learn about resources at the same time, or when naïve individuals discover resources simply because they happen to be following experienced individuals that have already found them for themselves.

In order to distinguish between these mechanisms, we carried out two experiments. Our first experiment tested whether the direction that the observer fish were facing at the moment that they were released was related to whether the rich or poor patch was entered first. Finding that fish were more likely to enter first the patch that they were facing would not necessarily rule out social learning. However finding that the majority of fish first entered the richer patch, even if they were not facing towards it when released, would strongly suggest that an unlearned social effect on travel direct was unlikely to account for such a patch choice bias. Our second experiment asked whether fish were still able to select the richer patch if they were forced to swim through a chicane, causing them to change travel direction, before they were able to approach the prey patches. If the fish were still more likely to enter the rich patch first, even after orientating away from it, then an unlearned social effect on travel direct could be ruled out, leaving social learning of rich patch location as the most plausible explanation.

2. Materials and methods

2.1. Collection and housing

Sticklebacks were collected from Melton Brook, Leicestershire, UK (GRID REF: SP 602075) in October 2009 with testing taking place between February and April 2010. In the laboratory they were held in groups of 40 to 50 in 90-l aquaria. Each aquarium contained a layer of coarse sand, an external filter, and artificial vegetation for cover. The light/dark regime was held at 14:10 h and the temperature was maintained at 8°C. They were fed daily with frozen bloodworms.

2.2. Overview

The experimental set up used in these experiments is derived from that of Coolen et al. (2003). Initially restrained observers were allowed to watch two groups of demonstrators feed from artificial patches that yielded prey at different rates. They were then released and allowed to enter goal zones located next to the prey patches. Previously published experiments that have used this set up have typically found that ninespine sticklebacks exhibit a

bias towards approaching the patch where they saw demonstrators feeding at the higher rate (Laland et al., 2011). In Experiment 1 we sought to determine whether the first patch that the observer entered was affected by the direction that it was facing at the moment that it was released. In Experiment 2 we asked whether the observer showed a bias towards the rich patch if it had to navigate a chicane, briefly turning away from it, after it was released.

2.3. Experiment 1

We established a binary choice test tank consisting of a glass aquarium measuring 90 × 30 × 30 cm (Figure 1). Abutting this we placed two 30 × 15 × 15 cm glass demonstrator tanks. The three tanks were separated by 5 mm. The sides of the tanks that faced each other were left uncovered, while the other sides were covered in black plastic sheeting. Each tank contained a 1-cm layer of sand. The water depth in all tanks was 12 cm. The central aquarium housed the observer, initially within a 10 × 10 cm base, 15 cm tall holding unit constructed from clear Perspex. This was attached via a monofilament line to an arm at the top of the tank, allowing it to be raised via a pulley. The holding unit was placed in the centre of the larger aquarium. The rich and poor patch goal zones were located within the 15-cm-wide section at each end of the observer tank, next to the demonstrator tanks. They were indicated using a yellow plastic bar across placed across the width of the tank and set within the sand substrate, so that the surface of the bar was level with the surface of the sand. The goal zones were used to determine prey patch preferences, as described below. During the test phase, described below, the movement of the observer was recorded via a high-definition webcam fixed above the tank and connected to a laptop.

Each of the smaller aquaria held a group of three conspecific demonstrators, and a feeder which was used to deliver prey to the demonstrators during the experiment. The feeders consisted of a 4 × 4 cm base, 30-cm-tall tower. The front wall, facing the demonstrators, and angled 90° away from the observer holding unit, was transparent so that the demonstrators could see the prey as it was delivered. The rear wall was white to contrast with the prey. The side walls were opaque, so that the observer in the central aquarium could not see the prey. Demonstrators were unable to reach the prey until it sank to the bottom of the feeder, but nonetheless attempted to do so by striking at the transparent wall as the prey item fell. The front wall of the feeder stopped 1 cm short of the floor of the tank, allowing the demonstrators to eat the prey once it had reached the bottom of the feeder. Prey
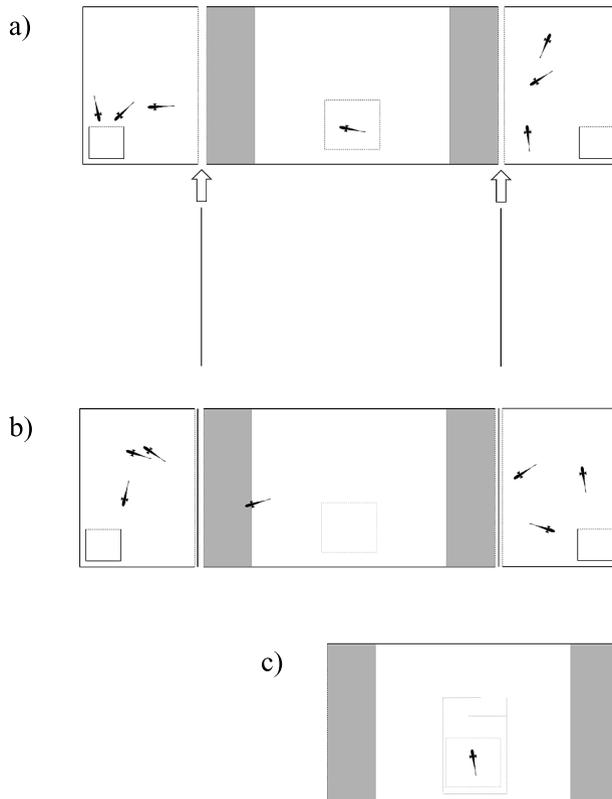
Figure 1. The public information binary choice tank used in Experiments 1 and 2, consisting of a larger central choice tank housing the test subject and two smaller demonstration tanks, holding the demonstrators and feeder units. Solid and broken lines indicate opaque and transparent barriers respectively. The grey shaded areas indicate the goal zones. (a) The layout of the tank during the demonstration phase; (b) the layout during the test phase, with opaque barriers now in place between the central and demonstrator tanks, and the focal fish released from the raised holding unit. (c) The chicane used in Experiment 2. The fish, once released from the inner holding unit is forced to swim out through the chicane, before it can enter the wider arena and enter either goal zone.

consisted of 3-mm-long pieces of thawed frozen bloodworm, small enough to be consumed with minimal handling by the demonstrators, ensuring that the observer could see the feeding behaviour of the demonstrators, but not the prey itself. Using separate tanks to hold the demonstrators prevented the observer from using prey chemical cues to acquire private information about prey distribution (Webster et al., 2007).

We used 38 fish as observers, with an additional pool of approximately 200 fish as demonstrators. Observers, the test subjects, were only used once. Some demonstrators were used more than once, but not within the same 72-h period. Fish showing signs of having entered reproductive state were excluded, since this has been shown to influence public information use in the species (Webster & Laland, 2011). The demonstrators and observers were deprived of food for 24 h before testing. Before the start of each trial one of the two feeders was randomly selected to be the rich feeder, yielding three times more prey than the poor feeder. Three demonstrators were added to each demonstrator chamber and allowed to settle for 10 min before the observer was added to the holding unit and allowed to settle for a further 10 min.

The demonstration phase lasted for 6 min and ran as follows. At the beginning of the first, third and fifth minute, 2 pieces of prey suspended in 1 ml tank water were added to the rich feeder, using a pipette. The poor feeders received no prey during the first and third minute, but were given 'blank' consisting of 1 ml tank water at the same time that the rich feeder received prey. During the fifth minute of the two-feeder treatments the poor feeder also received prey. This ensured that while prey were delivered at a 3:1 ratio, the observer was unable to select a prey patch simply on the basis of it being the last place it saw fish feeding. After six minutes opaque black plastic walls were inserted into the 5-mm gaps between the central tank and the two demonstrator aquaria. The observer was allowed to settle for sixty seconds, then the holding unit was raised 5 cm using the pulley. In raising the holding unit we were careful not to disturb the surface of the water, as this can startle the fish. It took less than 1 s to raise the holding unit, and none of the fish displayed any fright response, such as darting away immediately, erecting the pelvic spines or attempting to hide on the bottom of the tank. Raising the holding unit commenced the test phase of the trial.

We recorded the direction that the focal fish was facing at the moment that the holding unit was raised. Since we were only interested in the direction that the fish was facing at the moment that it was allowed to exit the holding unit, we did not collect any data on the direction that it was facing during the demonstration period. Facing direction was scored using six pairs of ordinal category bins of 30 degrees each, such that 0–30 degrees indicated a fish facing towards the rich patch and 151–180 degrees indicated a fish facing towards the poor patch (Figure 2a). We gauged facing direction based
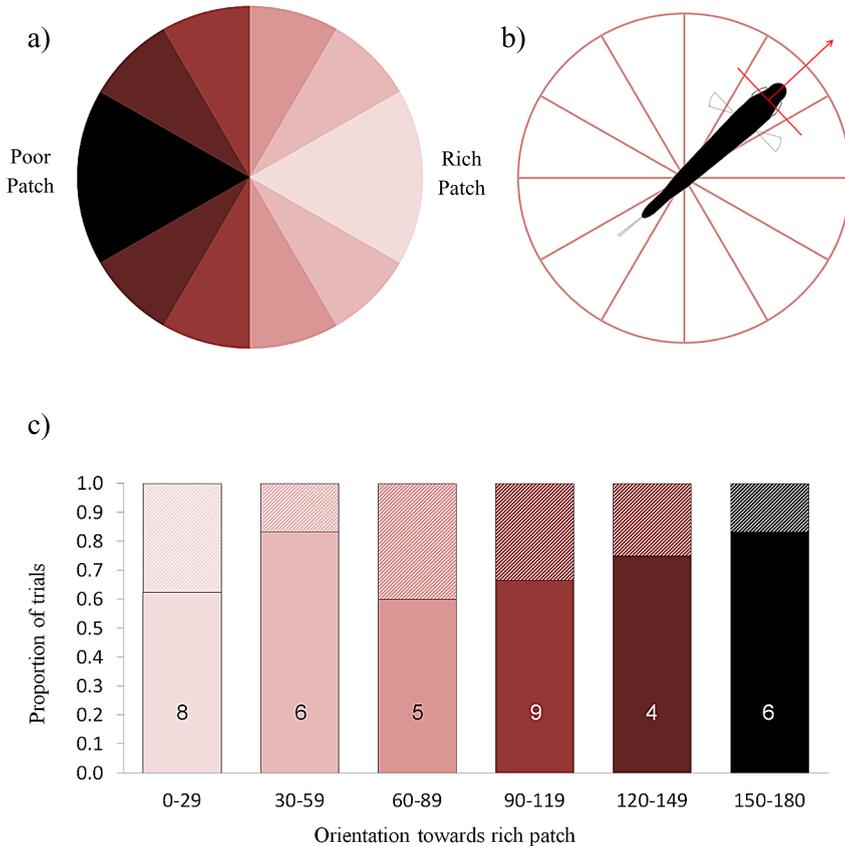
Figure 2. Experiment 1: effect of facing direction at release upon patch choice. (a) Direction of facing at moment of release was placed within six ordinal category bins of 60 degrees each, with fish facing directly towards the rich patch, 0–30 degrees, up to fish facing directly towards the poor patch, 151–180 degrees. (b) The (categorical) angle of orientation was determined using a digital imaging program. Using a still image taken from the video, a straight line was placed between the fish's eyes, and a second line, 90 degrees to the first, was drawn between the point midway between the eyes and the centre of the tip of the snout. A 12-sector circle was superimposed over the frame and centred on the holding unit. The sector that this line passed through was taken as the fish's direction of facing. (c) Count data indicating the first goal zone entered by the fish, grouped by the direction that they were facing at the moment they were released. The colours of the bars correspond to the sectors in (a), and indicate direction of facing. The solid and hatched portions of the bars indicate the number of fish that entered the rich and poor patch goal zone first respectively. The numbers on each bar indicate the number of trials in which the fish was facing in that direction. Direction of facing was not seen to influence first goal zone entered. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

upon the direction that the snout of the fish was pointing. To measure this accurately we took measurements from a still image consisting of the frame of video at the moment from the moment that the holding unit was raised. We used the program TPS digit (Rohlf, 2010) to draw a line running from a position midway between the eyes of the fish, and measured the midpoint of this line. We then drew a second line at 90 degrees to the first, running from the midpoint of the first line out through the centre of the snout of the fish. A circle divided into 12 sectors and aligned as in Figure 2a was superimposed over the frame and centred on the holding unit. The sector through which the second line passed, corresponding to a 30-degree category bin, was taken as the direction of facing (Figure 2b). After the holding unit had been raised we recorded which patch the fish visited first, and how long it took to reach it.

2.4. Experiment 2

Experiment 2 used the same binary choice experimental arena as did Experiment 1, with the exception that half of the trials included a chicane, within which the holding unit was housed (Figure 1c). The chicane measured 15 cm tall, 12 cm wide and 20 cm long. Two 8-cm barriers formed the chicane itself. The inner barrier was positioned on the same side of the chicane wall as the rich patch, and the outer barrier on the opposite side. This forced the fish to perform a switchback, away from the rich patch goal zone, before the fish was able to exit the chicane and access it. Two such chicanes were built so that each could be matched to the location of the rich patch (left or right) which was randomised as in Experiment 1, so that in all trials the fish was forced to turn away from the rich patch before it was able to exit the chicane and enter the main arena, and approach either patch.

We performed 50 trials in total, half with the chicane apparatus and half without it. Thus, half the observers were able to approach the goals directly following release, while the other half were forced to take an indirect route, via the chicane, to get to them. No observer was tested more than once and none of the observers used in Experiment 2 had previously been used as observers or demonstrators in Experiment 1. The set up and procedure during the demonstration phase were otherwise the same as described for Experiment 1. During the test phase, the holding unit was raised as described above, while the chicane (in those trials where it was deployed) remained on the floor of the tank. In this experiment we recorded not only the first goal zone entered by the observer, but also its location every six seconds for five

minutes following the raising of the holding unit, whether within either goal zone or the central 'neutral' zone (including within the chicane), yielding a total of 50 data points.

2.5. Ethical note

All procedures performed in this study were in accordance with the ethical standards of the University of St Andrews, where the study was conducted. No fish died or suffered apparent ill health after being used in this study. Following the completion of this study the fish were retained in our laboratory for use in further studies.

2.6. Statistical analysis

In Experiment 1, the first goal zone that the observers entered was analysed using a binary logistic regression. Direction of facing and latency to enter the goal zone were included as ordinal and continuous covariates respectively, while the location of the rich patch, left or right, was included as a fixed factor.

In Experiment 2, we compared first choice and time allocation to the rich and poor patches within each of the two treatments (chicane or no chicane) using binomial and t-tests. Between treatments, we compared first choice using a binary logistic regression. Time allocation (time in rich patch minus time in poor patch) was compared between treatments using a general linear model. In both models, treatment and the location of the rich patch were included as fixed factors and latency to enter either goal zone was included as a continuous factor.

3. Results

3.1. Experiment 1

Overall, the majority of observers entered the rich patch goal zone first (27 versus 11, binomial test: $N = 38$, $p = 0.014$). A binary logistic regression revealed that direction of facing, latency to enter either patch, and the location of the rich patch did not affect the observers' first goal zone choice (direction of facing: $\chi^2 = 1.45$, df $= 5$, $p = 0.91$, 95% confidence intervals (CI): -0.02, 3.62; location of rich patch: $\chi^2 = 1.83$, df $= 1$, $p = 0.17$, 95% CI: -0.06, 1.66; latency to enter either patch: $\chi^2 = 0.55$, df $= 1$, $p = 0.46$, 95% CI: -0.97, 1.01; Figure 2c).

3.2. Experiment 2

We saw that observers were not more likely to enter the rich patch goal zone first more frequently than would be expected by chance when each of the chicane and no-chicane treatments were considered separately, but that such an effect was apparent when data from the two treatments were pooled, suggesting a weak effect (binomial test, chicane: 16 versus 9, $N = 25$, $p = 0.23$; no chicane: 17 versus 8, $N = 25$, $p = 0.11$; pooled, 33 versus 17, $N = 50$, $p = 0.03$, Figure 3a). Observers did however spend more time in the rich patch goal zone than they did in the poor patch goal zone in both the chicane and no-chicane treatments (paired samples t-test, chicane: $t = 2.64$, df $= 24$, $p = 0.014$; no chicane: $t = 3.20$, df $= 24$, $p = 0.004$, Figure 3b).

Comparing the data for chicane and no-chicane treatments, we saw no differences between the two treatments in either the number of observers first entering the rich patch goal zone (binary logistic regression: treatment: $\chi^2 = 0.13$, df $= 1$, $p = 0.71$, 95% CI: $-0.22, 2.70$; location of rich patch: $\chi^2 = 1.88$, df $= 1$, $p = 0.11$, 95% CI: $0.09, 1.11$; latency to enter either patch: $\chi^2 = 0.29$, df $= 1$, $p = 0.59$, 95% CI: $-0.98, 1.01$). We also saw no difference between the two treatments in the amount of time that the observers spent in the rich compared to the poor goal zone (general linear model: treatment: $F_{1,49} = 0.96$, $p = 0.33$, 95% CI: $-0.79, 5.81$; location of rich patch: $F_{1,49} = 0.01$, $p = 0.91$, 95% CI: $-3.89, 1.49$; latency to enter either goal zone: $F_{1,49} = 2.30$, $p = 0.10$, 95% CI: $-0.07, 3.31$).

4. Discussion

In our first experiment, the direction that the fish were facing at the moment that they were released from the holding unit was not seen to have any effect upon their likelihood of entering the rich or poor patch goal zone first. In Experiment 2, fish spent as much time in the rich patch goal zone if they first had to swim through a chicane forcing them to move in the opposite direction as they did in the condition where they could swim directly towards the goal zone unimpeded, with fish in both treatments spending more time in the rich than the poor goal zone. Taken together, the results of these two experiments provide no support for the hypothesis that patch choice results from an unlearned social influence upon travel direction. To the contrary, the experiments suggest these findings are underpinned by social learning.
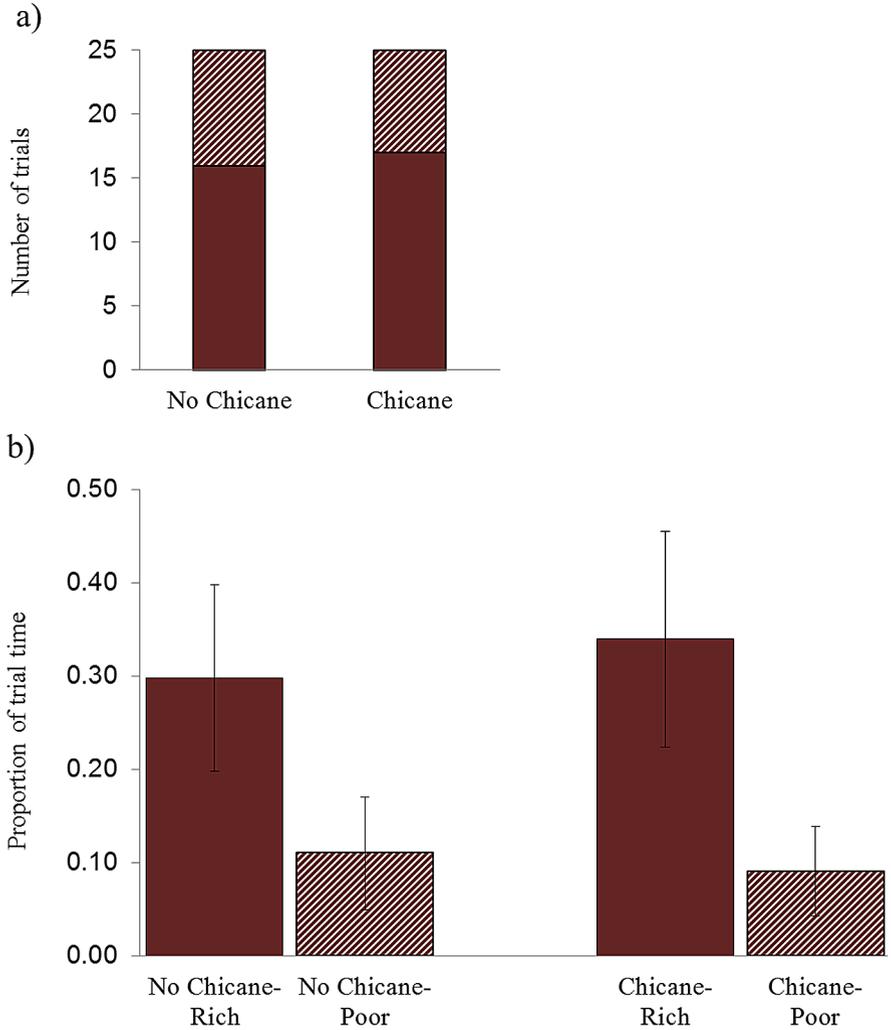
Figure 3. Experiment 2: (a) comparing the first goal zone entered by fish that were either allowed to swim unimpeded following release, or which had to first navigate a simple chicane. The solid and hatched portions of the bars indicate the number of fish that entered the rich and poor patch goal zone first respectively. There was no difference in first goal zone entered between the two treatments. (b) Comparing the time spent in the rich (solid bars) and poor (hatched bars) goal zones for fish tested in the chicane and no chicane conditions. In both treatments, fish spent more time in the rich than the poor goal zones. There was no difference in net time allocation (time in rich patch minus time in poor patch) between the two treatments. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

In a previously published study we showed that ninespine sticklebacks were attracted to the location at which they saw conspecifics feeding, but that they showed no evidence of learning associations between physical cues present at the demonstrated feeding site and the presence of food (Webster & Laland, 2013). The combined findings of this and the present study then point towards learned local enhancement as the mechanism underlying public information use in this species. Useful further work could focus upon the relative importance of social learning in social foraging and producer–scrounger interactions. Other recent studies have documented unlearned social effects on travel direction brought about through attraction to other group members, that explain the rate and order in which individual group members encounter resources as they forage (Atton et al., 2012, 2014; Webster & Laland, 2012; Webster et al., 2013). It would be informative to determine how this form of social learning operates in nature.

Further useful work might also address the relationship between social information use and behavioural lateralisation. Lateralisation research has revealed evidence of left or right-eye bias in some species of fish when monitoring predators or other stimuli (Bisazza et al., 1998). We saw no evidence of a population level bias in direction of facing at release in the sticklebacks tested here. We collected no data on eye use or direction of facing during the demonstration phase of the trial, since determining whether lateralisation exists in this species and context was not an objective of our study. Nonetheless, this is an interesting question that we plan to address in a future study. Individual and/or population level lateralisation should be simple to detect using a binary choice approach such the one used in this study, while in principle it ought to be possible to identify any such biases using information diffusion analyses to in free-ranging fish, under more naturally realistic conditions too (Atton et al., 2012, 2014; Webster et al., 2013).

Building further on this finding, we might ask what are animals actually learning when they select resource patches under the influence of public information? One plausible explanation is that public information use reflects the integration of two learned associations. Such a mechanism was recently found to underlie flower colour-copying behaviour in bumblebees (*Bombus terrestris*). Here, bumblebees visited artificial flowers of the same colour that they had others visit only if they had previously learned to associate the presence of conspecifics with a sucrose solution reward. Similarly, bumblebees

that were trained to associate the present of conspecifics with a bitter, un-palatable stimulus were more likely to avoid flower colours that they had seen others foraging upon (Dawson et al., 2013). In the case of public information using fishes (Webster & Laland, 2008; Laland et al., 2011; this study), such an association might arise from individuals being exposed to some aspect of the foraging behaviour of their group mates, such as their posture or activity levels, while they themselves are feeding. Potentially they could come to learn an association between these behaviours and the presence of food, and by extension, learn that the performance of this behaviour by others at a particular location is predictive of the likelihood of there being food at that location. A topic that is currently interesting researchers interested in the mechanisms, function and evolution of social learning relates to whether such behaviour reflects an adaptive specialisation or whether it is merely asocial learning in which one or more of the learned stimuli happens to be the presence or products of another animal (Lefebvre & Giraldeau, 1996; Sterelny, 2009; Heyes, 2012). This is a fundamental question, and one that is likely to garner more research attention in the coming years. Public information use and social learning more generally are taxonomically widespread and affect behaviour in a variety of different contexts (Valone & Templeton, 2002; Chittka & Leadbeater, 2005; Danchin et al., 2005). Carefully designed experiments that take into account the social environments that animal experience and the potential sources of information that they are exposed to both before and during their participation in experiments or field studies will be necessary if we are to further understand the mechanism or mechanisms that underpin these.

Acknowledgements

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