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The Learning Mechanism Underlying Public Information Use in Ninespine Sticklebacks (*Pungitius pungitius*)

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Elucidating the mechanisms by which animals learn from others is central to understanding the evolution of behavioral adaptations and the constraints that limit options when gathering information about the environment. Here we present findings from three experiments that investigated the psychological mechanisms underlying public-information use in ninespine sticklebacks (*Pungitius pungitius*). Using a prey patch choice assay we compared two candidate processes, local enhancement and stimulus enhancement. These experiments revealed (a) that fish only selected socially demonstrated prey patches via local enhancement, (b) that even in the absence of any confounding influence of local enhancement there was no evidence for stimulus enhancement in patch choice, and (c) sensitization rather than associative learning underlies the observed public information use. Our findings suggest that local and stimulus enhancement are distinct processes, and that local enhancement is not merely a subcategory of stimulus enhancement, as has previously been argued in the literature. We offer several reasons why learning via stimulus enhancement may not have arisen in ninespine sticklebacks, and speculate that the evolution of this learning mechanism may be favored by specific properties of social structure.

Keywords: diffusion, producer-scrounger, social learning, social information, social transmission

Animals from a broad range of species gather and exploit information generated by others. Doing so potentially allows them to overcome many of the costs of sampling the environment directly (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Danchin, Giraldeau, Valone, & Wagner, 2004; Galef & Giraldeau, 2001; Heyes & Galef, 1996; Valone & Templeton, 2002). Given the widespread use of social information and the apparent adaptive advantages of social learning, there is currently significant research interest in the costs and benefits of social information use, the conditions that determine when and whom individuals should copy (Giraldeau, Valone, & Templeton, 2002; Kendal, Coolen, & Laland, 2004; Kendal, Coolen, van Bergen, & Laland, 2005; Laland, 2004; Laland, Atton, & Webster, 2011; Webster & Ward, 2011) and the mechanisms by which they achieve this (Galef & Giraldeau, 2001; Heyes, 1994; Hoppitt & Laland, 2008).

Ninespine sticklebacks (*Pungitius pungitius*) have been used in recent years to investigate functional aspects of social learning, and in particular public information use. Public information use is a specific form of social learning through which observing individuals are able to gauge the relative quality of resources by monitoring the success with which others, termed “demonstrators,” exploit them (Coolen, van Bergen, Day, & Laland, 2003).

This work, reviewed by Laland, Atton, and Webster (2011), has used a social foraging binary choice paradigm in which observer fish are allowed to observe two groups of demonstrators feeding at different rates from artificial feeder units. The observer cannot see the food but can estimate prey patch quality based upon the feeding rate of the demonstrators. Subjects are then allowed to select a prey patch in the absence of the demonstrators. Typically, the fish move to the location where they have previously observed the demonstrator group feeding at the greater rate, indicative of prey patch selection via public information about its quality. While we have made progress toward understanding the conditions that determine when individuals are likely to copy in this way (Kendal, Rendell, Pike, & Laland, 2009; Pike, Kendal, Rendell, & Laland, 2010; Pike & Laland, 2010; van Bergen, Coolen, & Laland, 2004; Webster & Laland, 2011), little is known about the mechanisms underlying the transmission of public information in the ninespine stickleback system. Here we investigate the psychological processes that may underpin this form of social learning, initially exploring whether the fish are learning about a location or the feeder (e.g., local vs. stimulus enhancement), and then considering whether this is the product of single-stimulus or associative learning.

Local enhancement describes the process by which an observing animal becomes more likely to approach a location, or interact with objects at that location, during or after it has detected the presence, or behavior, of others at that location (Thorpe, 1956). Thorpe (1956) described local enhancement as “apparent imitation resulting from directing the animal’s attention to a particular object or to a particular part of the environment” (Thorpe, 1963, p. 134), a definition that contains both ambiguous (“apparent imitation”) and arbitrary (“attention”) elements. Galef (1988) broadened the concept to include cases in which animals interact indirectly, via residual products, such as scent marks and feces. Both Galef

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(1988), and Heyes (1994), further suggest that local enhancement be considered a subset of stimulus enhancement (described below). Here we deploy the more inclusive definition of local enhancement offered by Hoppitt and Laland (2008), which does not necessarily require (but does not exclude) subsequent learning on the part of the observer. Here, local enhancement can result from socially mediated learning about a specific location, aggregation, a tendency to move in groups, or through the demonstrator's products. See Hoppitt and Laland (2008) for a more detailed discussion. In the case of our ninespine stickleback public information use experiments learning *is* known to be involved, because the observers visit the patches after the demonstrators have been removed and because residual cues have been controlled for (Coolen et al., 2003) or excluded (Webster & Laland, 2011, 2012) by the experimental design. In cases where the observer visits the demonstrated location when demonstrators are no longer present this process is sometimes referred to as "delayed local enhancement" (Coolen et al., 2003).

Stimulus enhancement occurs when perception of a demonstrator animal in close proximity to, or interacting with, a stimulus in the environment (rather than a discrete spatial location) causes the observer to subsequently become more likely to interact with similar stimuli. By this definition, the means by which the demonstrator leads the observer to interact with the stimulus is not important (Heyes, 1994; Hoppitt & Laland, 2008). A crucial component of stimulus enhancement is stimulus generalization, with the observer becoming more likely to interact with, or be attracted to, any of a class of similar stimuli in other locations (Hoppitt & Laland, 2008), rather than the specific stimulus with which the demonstrator interacted. Stimulus enhancement could potentially facilitate public information use by drawing the attention of the observer to an object in the demonstrated prey patch, such as the characteristics of the artificial feeders employed in such studies.

In addition to examining the relative importance of learning about spatial locations or objects in public information use, we also sought to determine how the fish came to learn about these factors. This might occur through an associative process (e.g., observational conditioning), or through a nonassociative process, such as single-stimulus learning (e.g., sensitization). Observational conditioning takes place when the behavior of a demonstrator toward a stimulus acts in itself as a conditioned stimulus to an observer, which will subsequently behave in the same way when encountering the same or similar type of stimuli. Exposure of the observer to the relationship between these stimuli at one point in time leads it to respond in a similar manner as the demonstrator did when encountering such an object or cue in the future (Heyes, 1994; Hoppitt & Laland, 2008). Thus, observational conditioning can be regarded as a special case of Pavlovian conditioning, where the association is learned through observation of other individual's behavior (Heyes, 1994). In the context of public information use, we might expect that if observational conditioning is operating, the observer, having witnessed the feeding behavior of the demonstrators and subsequently becoming more likely to adopt foraging behavior in the same location itself, should only visit the demonstrated location in a foraging context. Conversely, if its priorities were to change, for example from foraging to seeking refuge, the observer might not be expected to be as likely to visit the demonstrated patch.

A second possibility is that any learning that takes place in public-information use is nonassociative, where sensitization is the obvious candidate. Sensitization is a form of single-stimulus learning where demonstrator-mediated exposure to a stimulus is detected in an increase in responsiveness to that stimulus (Heyes, 1994). In this case the stimulus is a particular location. Here, observing demonstrators feeding at a greater rate at one location may lead the observer to be more likely to visit that location subsequently. If public information use occurs through a nonassociative process (that is, without observational conditioning) then we might expect the observer to be more likely to move toward the demonstrated patch even when its behavioral priorities change (e.g., from the foraging, the demonstrated behavior, to sheltering).

In order to investigate the roles of local and stimulus enhancement, observational conditioning and sensitization in public-information use in foraging ninespine sticklebacks, we conducted three experiments. In the first, we investigated public-information use when location and stimulus cues were either in agreement or conflict. We achieved this by giving focal fish a binary choice between two prey patches at which they observed demonstrators feeding at different rates. In one set of trials, only one demonstrator group fed, and only one feeder unit was present. In another set of trials, both groups fed, with two differently colored feeders simulating rich and poor patches. The rationale behind this experimental design was to determine whether fish varied in their ability to use local or stimulus enhancement when discriminating between absolute and relative differences in stimulus intensity. After the demonstration phase the feeders were either retained in their original position, or swapped between demonstrator tanks. We predicted that if local enhancement were more important than stimulus enhancement, then when the feeders were swapped the focal fish should prefer the location where they saw the demonstrator group feeding at a higher rate, while if stimulus enhancement were more important they should move to the new location of the feeder. If both mechanisms contribute to public information use then we might expect to see an additive effect in terms of greater time allocation by focal fish when local and stimulus enhancement cues were in agreement compared to when they were in conflict.

In the second experiment, we investigated the role of stimulus enhancement in prey patch selection, while controlling for any confounding effects of local enhancement. We used a four-armed, cross-shaped binary choice apparatus in which the focal fish received a demonstration of two prey patches yielding prey at different rates, with associated stimulus landmarks along one axis of arms, while the other two arms were closed off with opaque barriers. Depending upon the condition, we used either differently colored feeders as landmarks, or more naturally realistic markers such as rocks and plants; the closely related threespine stickleback (*Gasterosteus aculeatus*) is able to differentiate sand and gravel substrates (Webster & Hart, 2004, 2006) and discriminate between rocks and artificial plants (Girvan & Braithwaite, 1998, 2000; Odling-Smee & Braithwaite, 2003; Odling-Smee, Boughman, & Braithwaite, 2008) when navigating. Following the demonstration, the arms in which the demonstrators had been housed were closed off and the barriers to the other arms were removed, to reveal identical sets of landmarks. We predicted that if stimulus enhancement were operating, that the fish would generalize between land-

marks and select the goal zone containing the landmark associated with the rich prey patch in the demonstrated arm of the arena.

In a third experiment, we aimed to determine whether the selection of prey patches demonstrated in the preceding experiments was based upon associative or nonassociative processes. We achieved this by giving subjects a demonstration of a rich and a poor prey patch, as previously, before inducing sheltering behavior (rather than foraging behavior) in half of the trials. If observational conditioning underlies public information use, then we would expect the fish to form an association between the feeding behavior of the demonstrators and the presence of food at the feeder or location of the demonstration. We would then expect to see the fish move to that area when foraging, but not in other behavioral contexts, such as sheltering. Conversely, we reasoned that if sensitization underlies public information use then we should expect to see the fish spend more time in the rich goal zone irrespective of the behavioral context, as it will only have learned about a single stimulus.

Method and Results

Fish Collection and Housing

Ninespine sticklebacks were collected from Melton Brook, Leicestershire, U.K. (GRID REF: SP 602075) in October, 2010 for use in Experiment 1, with testing taking place between March and May, 2011. A second stock of fish were collected from the same location in April, 2011 for use in Experiments 2 and 3, with testing occurring between October, 2011 and January, 2012. In the laboratory they were held in groups of 40 to 50 in 90L 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 hours and the temperature was maintained at 8 °C. They were fed daily with frozen bloodworms.

Experiment 1: Local Enhancement Versus Stimulus Enhancement

Experiment 1 Method

Test Arena

In this experiment we used 80 fish as test subjects and an additional pool of approximately 100 fish as demonstrators. We established a binary choice test arena similar to that described in Coolen, van Bergen, Day, and Laland (2003, Figure 1a). This consisted of an aquarium measuring 45 cm long by 30 cm wide and 30 cm tall. At each end of the test tank we placed a 15 cm long, 30 cm wide, and 15 cm tall tank. 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 fine sand. The water depth in all tanks was 12 cm. The large, central aquarium housed the test subject, termed the observer. The observer was initially held in a 10 by 10 cm base, 15 cm tall holding unit constructed from clear Perspex. This was attached via a monofilament line to a 10 cm long arm at the top of the tank, allowing it to be raised via a simple pulley mechanism. The holding unit was placed against one the side walls of the aquarium, in its center. Eight cm from

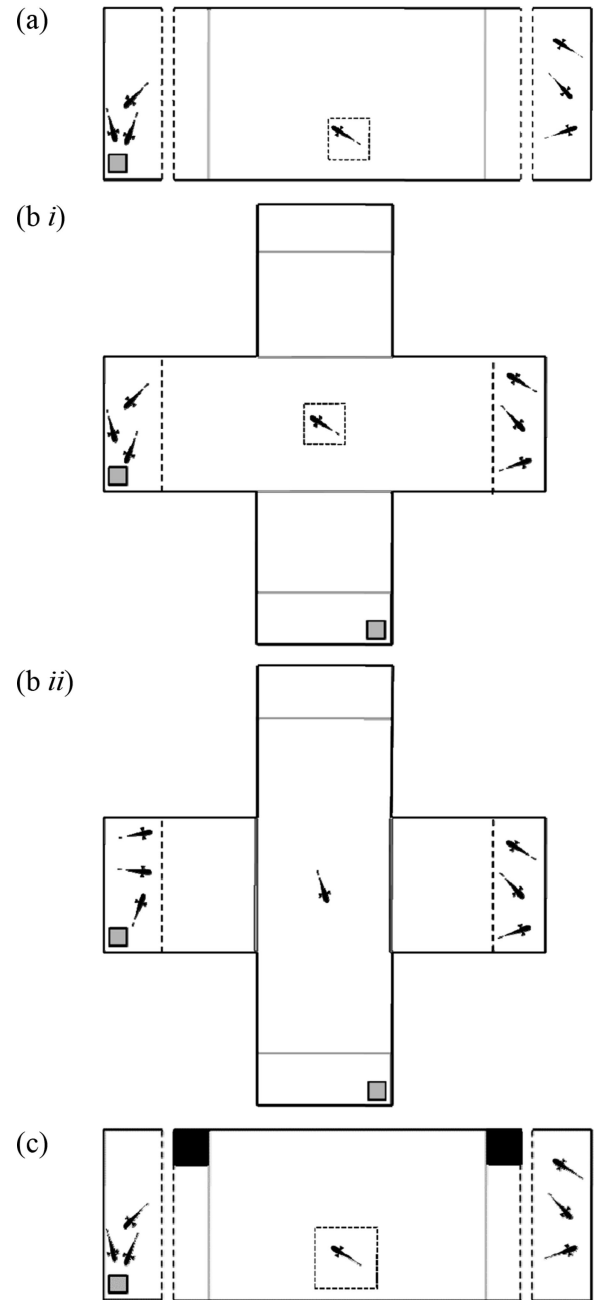


Figure 1. Experimental arenas. (a) The binary choice arena used in Experiment 1, consisting of a larger central choice tank housing the test subject and two smaller demonstration tanks, holding the demonstrators and feeder units. (b) The cross-shaped binary choice tank used in Experiment 2. This tank was designed to test for evidence of stimulus enhancement, while controlling for confounding effects of local enhancement. Fish received a demonstration of two feeding patches (indicated by the presence of different colored feeders or other landmarks, depending upon the treatment) in one axis test arena (b i) before being allowed to visit different patches containing identical landmarks in the opposite axis (b ii). Solid black lines indicate opaque walls, broken black lines indicate colorless, transparent walls and solid gray lines delineate the goal zones. (c) The binary choice arena used in Experiment 3, a modified version of that used in Experiment 1, incorporating two shelters (black squares). The number and color of feeder units (gray squares) in the experimental arenas varied, depending upon the treatment. Please see the main text for further details. Diagrams are not drawn to scale.

each end of the large central aquarium we placed a yellow plastic bar across its width, set within the sand substrate, so that the surface of the bar was level with the surface of the sand. The areas beyond the bars, immediately adjacent to the two small aquaria, were designated “goal zones” and were used to determine prey patch preferences, as described below.

Within each of the smaller aquaria we placed a group of three “demonstrator” ninespine sticklebacks (35–40 mm standard length). To one (chosen at random) or both of the smaller aquaria, depending upon the experimental condition described below, we added a feeder, which was used to deliver prey to the demonstrators during the experiment. The feeder was placed in the far corner of the demonstrator tank (see Figure 1a). The feeders consisted of a 4 by 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 and, therefore maximize visibility of the prey. The side walls were opaque, and either blue or white, depending upon the experimental condition described below, so that the observer in the central aquarium could not see the prey, but could see the colored feeder. Demonstrators were unable to reach the prey until it sank to the bottom of the feeder, but nonetheless attempted to do so by attacking (i.e., pecking 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 deliveries consisted of two 3 mm long pieces of thawed frozen bloodworm. These were small enough to be consumed with minimal handling by the demonstrators, ensuring that the observing focal fish could see the feeding behavior of the demonstrators, but not the prey itself. The screening on the outside of the test tank prevented the fish from seeing the experimenter as the prey were delivered. Housing the demonstrators in separate aquaria ensured that no chemical cues originating from the prey were available to focal fish, since these may provide direct information about feeder location and prey density (Webster, Atton, Ward, & Hart, 2007). This ensured that focal fish could only base their patch choices upon visual cues derived solely from the demonstrators’ feeding behavior received during the demonstration phase. During the test phase, described below, the focal fish was observed via a high-definition camera (Canon HG20) fixed 120 cm above the tank and connected to a monitor (Powervision waterproof LCD-TV).

The entire experimental arena was surrounded by a shelter constructed from matt black plastic sheeting with the ceiling constructed from diffusion filter paper (white diffusion 216, Lee Filters, Andover, U.K.). Illumination was provided by a ceiling-mounted strip light directly above the test arena. A camera (Canon HG20 high resolution) was placed above the arena, and filmed it through a small aperture in the diffusion filter ceiling of the shelter. The diffusion filter ensured an even distribution of light over the surface of the test arena. Square access holes were constructed in the front of the shelter, in order to allow prey items to be added, the visual barriers to be set in place, and the holding unit to be raised, as described below. The access holes were covered with matt black plastic screens during the test phase of the trial. This ensured that extraapparatus visual cues were unavailable to the test fish during the test phase of the trial.

Experimental Conditions

We investigated four experimental conditions, using either one or two feeders and where location and stimulus (i.e., feeder) cues were set either in agreement or in conflict. In the one-feeder conditions, observers saw one group of demonstrators feed three times from a feeder, while the other group did not feed. No feeder unit was present with the nonfeeding demonstrator group. After the demonstration phase and the removal of the demonstrators (see below), the feeder was either retained in its original position (location and stimulus cues in agreement) or it was removed, and placed in the other demonstrator tank (location and stimulus cues in conflict). In each condition we used white feeders in one half of the trials, and blue feeders in the other half, allocated in a random-systematic fashion (in that half of the trials were assigned one color feeder and one half the other, with the feeder color being randomly predetermined within these boundaries). Fish of a number of species have been shown to discriminate between different colored stimuli in experiments, including ninespine sticklebacks (Duffy, Pike, & Laland, 2009; Pike et al., 2010). The location of the rich patch (either left or right) was randomized. In the two-feeder trials, observers saw one group of demonstrators feed three times from their feeder, while the other group fed only once, demonstrating “rich” and “poor” patches, a configuration and ratio used in previous studies of public-information use in this species and context (Coolen et al., 2003; Coolen, Ward, Hart, & Laland, 2005; Webster & Laland, 2011). Again, the location of the rich patch was randomized. The two feeders within each trial were different colors, either white or blue, with each color being used as the rich or poor feeder an equal number of times, allocated in a random-systematic fashion. After the demonstration phase and the removal of the demonstrators, the feeders were either retained in their original positions or they were swapped between the demonstrator tanks. For each of the four conditions we tested 20 fish. No focal fish was tested more than once. Care was taken to ensure that no demonstrator was used more than once in any 48 hour period. All fish measured 35–40 mm standard length, and within trials all fish were size matched to within 2 mm.

Test Procedure

The demonstrators and focal fish were deprived of food for 24 hr before testing in order to ensure that they were motivated to feed. Then three demonstrators were added to each demonstrator chamber and allowed to settle for 10 minutes before the focal fish was added to the central holding unit and allowed to settle for a further 10 minutes. The demonstration phase lasted for 6 minutes and ran as follows. At the beginning of the first, third, and fifth minute, prey suspended in 1 cm³ of tank water were added to the feeder in the designated rich patch, using a pipette. This was the case for the rich patch on both the one- and two-feeder treatments. In the two-feeder treatments the poor feeders received no prey during the first and third minute, but were given “blank” consisting of 1 cm³ of tank water at the same time that the rich feeder received prey. In the one feeder treatment, the experimenter added no blank of water, but instead simulated the delivery of water with an empty pipette. This served to control for the appearance of the pipette over the demonstrator tank, which by itself conceivably might have had some effect upon the behavior of the demonstrators. 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 focal fish 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 large central tank and the two smaller aquaria housing the demonstrators. The demonstrators were then carefully removed from the smaller tanks. This took approximately 30 seconds. Immediately after this the opaque black plastic walls were removed and the focal fish was allowed to settle for five further minutes. Following this period the holding unit was raised 5 cm using the pulley mechanism. The base of the holding unit was left suspended beneath the water surface, so as not to disturb the surface and startle the test fish. This commenced the trial, and we recorded the following behavior patterns for three minutes: the location of the focal fish location every six seconds (whether within either goal zone or the central “neutral” zone), yielding a total of 30 data points, its latency to enter either goal zone, and the identity of the first goal zone it entered (either the rich zone, adjacent to where the demonstrators had fed at the higher rate, or the poor zone, adjacent to where they had fed at the lower rate, in the two feeder treatment, or not at all in the one feeder treatment). No prey were present in the arena during the test phase.

Statistical Analysis

We used Cox regression survival analysis to investigate the effects of the experimental treatments (one feeder or two feeders; cues in agreement or cues in conflict) upon latency to enter either goal zone. We used binary logistic regression to investigate the first goal zone choice of focal fish. Experimental treatments were included as fixed factors.

We used general linear models (GLMs) to compare the difference in time allocation to the goal zones. Experimental treatments were included as fixed factors, Latency to enter either prey patch included as a covariate and the color of the rich feeder and its location (left or right) were included as random factors. Proportional data on time allocation to goal zones were normalized by arcsine transformation. The difference in time allocation was calculated by subtracting the proportion of time spent in the poor quality goal zone from that spent in the rich goal zone. Within each treatment group we performed further paired sample t tests, comparing time in the rich patch to time in the poor patch.

Effect sizes were estimated using Cohen’s d for the t tests and partial η^2 scores (ηp^2) for each variable in the GLMs. For Binary data we used Nagelkerke’s pseudo r^2 to estimate association strength.

Experiment 1 Results

Latency to Enter Goal Zone

We found no effects of either feeder number (Cox regression survival analysis, Wald = 0.04, $df = 1$, $p = .95$), agreement or conflict between location and stimulus cues (Wald = 0.96, $df = 1$, $p = .33$) nor any interaction effect between these (Wald = 0.21, $df = 1$, $p = .65$) upon latency to enter either goal zone (Figure 2a).

First Choice

One fish (in the two feeders, cues in conflict treatment) failed to enter either goal zone and was excluded from the analysis of first

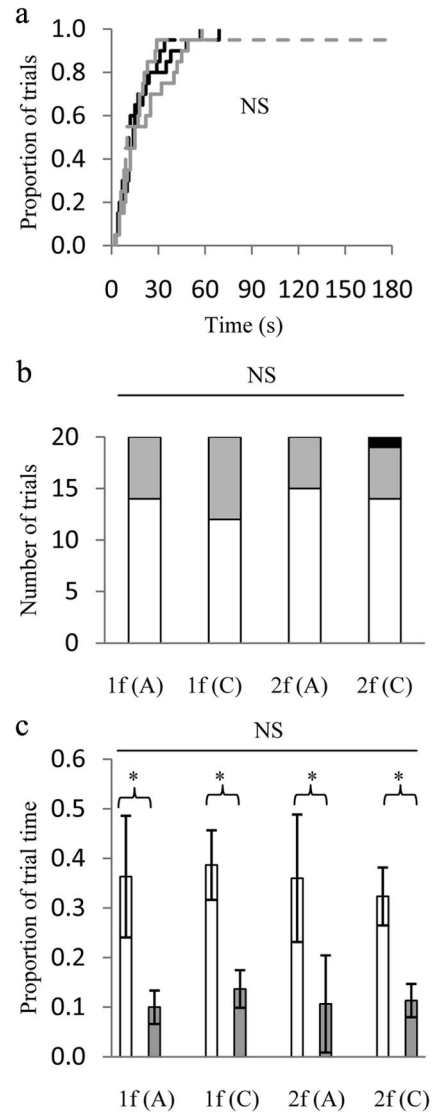


Figure 2. (a) Survival plot showing latency to enter either goal zone. (Solid black line: one feeder, local enhancement and stimulus enhancement cues in agreement; broken black line: one feeder, local enhancement and stimulus enhancement cues in conflict; solid gray line: local enhancement and stimulus enhancement cues in agreement; broken gray line: local enhancement and stimulus enhancement cues in conflict). (b) The number of trials in which the fish first entered the goal zone corresponding to the location of the demonstrated rich patch (\square), the demonstrated poor patch (\blacksquare) or in which they failed to enter either patch (\blacksquare). (c) The proportion of trial time (mean \pm 95% confidence interval) spent in the demonstrated rich (\square) and poor patches (\blacksquare). 1f (A), 1f (C), 2f (A) and 2f (C), respectively, indicate one feeder, local enhancement and stimulus enhancement cues in agreement; one feeder, local enhancement and stimulus enhancement cues in conflict; two feeders, local enhancement and stimulus enhancement cues in agreement; two feeders, local enhancement and stimulus enhancement cues in conflict. * Indicates $p < 0.5$, NS indicates no significant difference.

choice (Figure 2b). Binomial logistic regression revealed that the first goal zone entered by the focal fish was not affected by either the number of feeders or whether the location and stimulus cues were in agreement or conflict ($z = 0.80$, $df = 1$, $p = .37$; $z = 0.31$, $df = 1$, $p = .58$; $r^2 = 0.02$).

Time Allocation

Within-treatment paired t tests revealed that the fish spent more time in the rich than in the poor patch in all four groups (one feeder, cues in agreement; one feeder, cues in conflict; two feeders, cues in agreement; two feeders, cues in conflict, respectively: $t = 3.84$, $df = 19$, $d = 0.69$, $p = .001$; $t = 5.81$, $df = 19$, $d = 1.90$, $p < .001$; $t = 2.95$, $df = 19$, $d = 0.84$, $p = .036$; $t = 5.79$, $df = 19$, $d = 2.02$, $p < .001$, Figure 2c).

A GLM indicated no effects of either feeder number ($F_{(1, 63)} = 0.49$, $\eta^2 = 0.35$, $p = .62$), cue agreement or conflict ($F_{(1, 63)} = 0.08$, $\eta^2 = 0.11$, $p = .84$) or latency ($F_{(1, 63)} = 0.94$, $\eta^2 = 0.02$, $p = .38$) on the difference between time spent in the rich patch versus the poor patch. Neither feeder color ($F_{(1, 63)} = 0.04$, $\eta^2 = 0.01$, $p = .96$) nor the side of the richer patch (left or right, $F_{(1, 63)} = 0.17$, $\eta^2 = 0.10$, $p = .73$) had any effect upon relative time allocation either. Rerunning the GLM with the random factors omitted, and without three-way interactions between variables also failed to identify any effect of either feeder number ($F_{(1, 75)} = 0.58$, $\eta^2 = 0.01$, $p = .54$), cue agreement or conflict ($F_{(1, 75)} = 0.09$, $\eta^2 = 0.01$, $p = .77$) or latency ($F_{(1, 75)} = 1.71$, $\eta^2 = 0.02$, $p = .20$) upon relative time allocation.

Experiment 1 Discussion

In this experiment we gave fish the opportunity to observe two demonstrator groups at different prey patches. The demonstrator groups were fed at different rates, such that either one group was feeding and one was not, an absolute difference, or one group was feeding at a greater rate than the other, a relative difference. The test fish was then allowed to move toward the prey patches, in the absence of the demonstrators. We manipulated both location and stimulus (feeder color) cues during the choice phase by retaining or switching the feeders, such that these cues were set up either in opposition or in accordance. We saw that the test fish exhibited behavior consistent with their learning about patch location when the cues conflicted, while there was no additive effect upon patch selection that could be attributed to stimulus enhancement when the cues were in agreement. This finding could be explained either by overshadowing, in which the spatial or location cues override the visual stimulus (feeder color) cues, or it could imply that ninespine sticklebacks learn through local enhancement but are incapable of learning via stimulus enhancement. We, therefore, devised a second experiment to determine whether ninespine sticklebacks were capable of learning via stimulus enhancement when any confounding effects of local enhancement were controlled for.

Experiment 2: A Role for Stimulus Enhancement in Prey Patch Selection?

Experiment 2 Method

In this experiment we used 60 fish as test subjects and an additional pool of approximately 100 fish as demonstrators. Our first experiment revealed that ninespine sticklebacks exhibited behavior consistent with local enhancement when given the choice of selecting prey patches based upon conflicting local or stimulus enhancement cues. It is not clear whether this is because local enhancement cues overshadow stimulus enhancement cues, or

because the fish are simply incapable of learning via stimulus enhancement. This experiment aimed to determine whether stimulus enhancement plays any role in prey patch selection in the absence of any confounding influence of local enhancement in ninespine sticklebacks.

Test Arena

We constructed a cross-shaped binary choice tank (Figure 1b) in which the focal fish received a demonstration of two prey patches with associated stimulus landmarks along one axis of the arena (e.g., along the east and west arms), while the other arms were closed off with opaque barriers. Subsequently the arms in which the demonstrators had been housed were closed off and the barriers to the other arms (e.g., north and south) were removed, to reveal identical landmarks. If the fish were able to exploit public information through learning about patch stimulus characteristics we would expect them to generalize between landmarks and select the goal zone containing the features or landmark associated with the goal prey patch in the demonstrated (but now inaccessible and invisible) arm of the arena.

The test tank was constructed from opaque black plastic. Each arm measured 30 cm long by 23 cm wide by 20 cm tall. In the first and second of the experimental treatments the arena contained a 1 cm layer of fine sand substrate. In the third treatment, described below, different substrates were used. In all treatments the water depth was 15 cm. The test arena was not water tight, and was held within a 120 cm diameter plastic pool. In the center of the central square at the intersection of the arms was a holding unit, attached via a monofilament line to an arm as described in Experiment 1, to house the observer during the demonstration phase of the trial. Eight cm from each end of each arm we placed a yellow plastic bar across its width, set within the substrate, so that the surface of the bar was level with the surface of the sand. The areas behind the bars were designated goal zones and were used to determine prey patch preferences, as described below.

During the demonstration phase, one pair of arms directly opposite each other was selected to hold the demonstrators. The other arms were closed off using black plastic barriers attached across the entrances of the arms using magnetic strips. At the far end of each of the demonstrator arms we placed a 10 cm wide, 23 cm long, and 15 cm tall Perspex aquarium. This housed three demonstrators as described above. A feeder unit was present in one or both of these aquaria, depending upon the experimental treatment, as described below. Also as described below, in the third treatment condition we included other landmarks. During the test phase the focal fish was observed via a high definition camera (Canon HG20) fixed 120 cm above the tank and connected to a monitor (Powervision waterproof LCD-TV). As in Experiment 1, the entire experimental arena was surrounded by a shelter constructed from matt black plastic sheeting with the ceiling constructed from diffusion filter paper (white diffusion 216, Lee Filters, Andover, U.K.). Illumination was provided by a ceiling-mounted strip light directly above the test arena. Access holes constructed in the front of the shelter, allowed access to the apparatus as described above. This ensured that extraapparatus visual cues were unavailable to the test fish during the test phase of the trial.

Experimental Conditions

We investigated three experimental conditions. In the first, the subjects saw one group of demonstrators feed from a feeder while the other group did not feed, and no feeder was present. In the second they saw one group feed three times from one feeder and the other group feed once from a feeder. The feeders were different colors. In the third condition the subjects saw one group of demonstrators feed from a feeder while the other did not feed, with no feeder present, but here we also included naturally realistic landmarks, in the form of different substrates, rocks, and artificial plants.

In the first one-feeder treatment we used white feeders in one half of the trials, and blue feeders in the other half, allocated in a random-systematic fashion and the location of the feeder (either left or right) was also randomized. In one of the closed off arms of the arena we placed a feeder whose color match that used in the demonstrated rich arm, while the other contained no feeder. Again the location of the feeder was determined randomly. The feeders were 20 cm tall, so as not to be visible over the barriers closing off the arms of the test tank, but were otherwise identical to those described in Experiment 1.

In the two-feeder treatment the focal fish was allowed to observe one group of demonstrators feed three times from their feeder, while the other group fed only once, demonstrating “rich” and “poor” patches as in the first experiment. Again, the location of the rich patch was randomized. The two feeders within each trial were different colors, either white or blue, with each color being used as the rich or poor feeder an equal number of times, allocated in a random-systematic fashion. In each of the closed off arms of the arena we placed a feeder, one white and one blue. Again the placement of each feeder was determined randomly.

In the third treatment we used only a single (white) feeder, from which one group of demonstrators was fed three times. The other group did not feed, as in treatment 1. Here however we also included naturally realistic landmarks. Although many fishes readily discriminate between artificial, differently colored landmarks (Duffy et al., 2009; Pike et al., 2010; Webster & Laland, 2008), it is conceivable that these may be less effective than natural features. Recognition of natural features could be selected for in the contexts of orientation, efficient foraging, or territory delineation, for example (Girvan & Braithwaite, 1998, 2000; Odling-Smee & Braithwaite, 2003; Odling-Smee et al., 2008; Webster & Hart, 2004, 2006). We therefore established two sets of landmarks within the arms of the arena. In one we filled the last 20 cm of the arm with a layer of 0.5 cm dark gray gravel. We also placed a 4 cm diameter, 10 cm tall colorless transparent plastic cup filled with the same gravel in the far corner of the demonstrator tank opposite the feeder (when present). In the other arm we retained the sand substrate and placed a 10 cm tall green silk aquarium plant (Marina Eco Scaper, Rolf C. Hagen Group, Montreal, Canada) within an identical plastic cup filled with water in the far corner. The plant was placed within the cup in order to prevent the fish from hiding in it (Coolen et al., 2003; Hart, 2003; Webster, Ward, & Hart, 2009). The location of the feeder (either left or right) and the substrate-landmark with which it was paired was randomized. In one of the closed off arms of the arena we placed a feeder, substrate and landmark whose color matched that used in the demonstrated rich arm, while the other contained no feeder and the

opposite combination of substrate and landmark. Again the location of these was determined randomly. We tested 60 fish as test subjects (20 in each condition) and used an additional pool of approximately 100 fish as demonstrators. No focal fish was tested more than once. Care was taken to ensure that no demonstrator was used more than once in any 48 hour period. All fish measured 35–40 mm standard length, and within trials all fish were size matched to within 2 mm.

Test Procedure

The demonstration phase was carried out exactly as in Experiment 1, with 3:0 feeding demonstrations performed in treatments 1 and 3 a 3:1 feeding event performed in treatment 2. Immediately after the demonstration phase however, the barriers blocking the previously covered arms were removed and placed over the demonstrator arms. The demonstrators, now hidden, were not removed, a procedure which could have stressed the focal fish unnecessarily. The Perspex demonstrator tanks prevented the exchange of chemicals conspecific or prey cues between demonstrator and observer. Following this the focal fish was allowed to settle for five further minutes, before the holding unit was raised 5 cm using the pulley mechanism. This commenced the trial, and we recorded the following behavior patterns for three minutes: the location of the focal fish location every six seconds (whether within either goal zone or the central “neutral” zone), yielding a total of 30 data points, its latency to enter either goal zone, and the identity of the first goal zone it entered (either the zone containing the same feeder type (and landmarks in treatment 3) as the rich zone, where the demonstrators had fed at the higher rate, or as the poor zone, where the demonstrators had fed at the lower rate, in the two feeder treatment, or not at all in the one feeder treatments). No prey were present in the arena during the test phase.

Statistical Analyses

We performed essentially the same battery of statistical analyses as described in Experiment 1, with the exception of the Cox regression of goal zone selection latencies, which was replaced with a Kaplan-Meier log-rank test. We also performed an addition *t* test, comparing the effectiveness of the different landmarks used in treatment 3.

Experiment 2 Results

Latency to Enter Goal Zone

We saw no differences in latency to enter the goal zone between the three treatment groups (Kaplan-Meier log-rank test: $\chi^2 = 0.29$, $df = 2$, $p = .86$, Figure 3a).

First Choice

Across the three treatments, seven fish failed to enter either goal zone and were excluded from the analysis of first choice (see Figure 3b). Binomial logistic regression revealed that the first goal zone entered by the focal fish did not differ between treatments ($z = 0.02$, $df = 2$, $r^2 < 0.01$; $p = .89$).

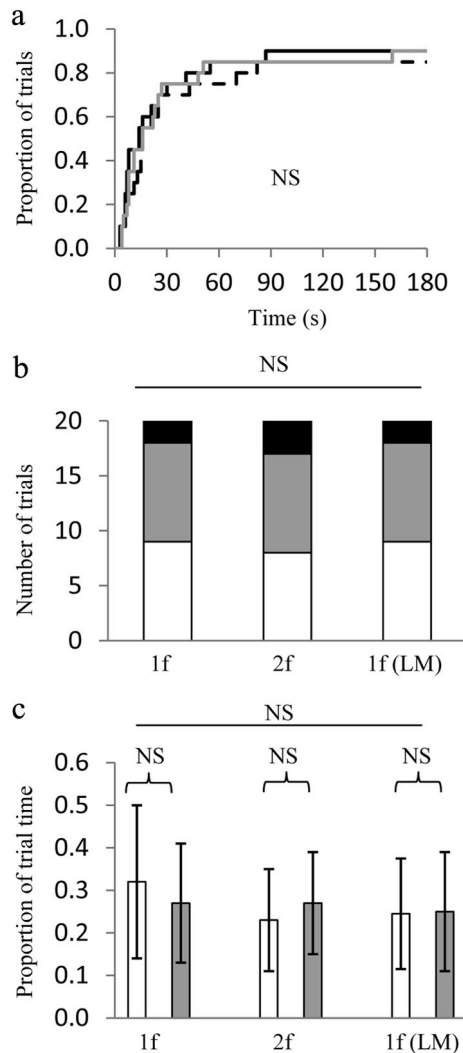


Figure 3. (a) Survival plot showing latency to enter either goal zone. (Solid black line: one feeder; broken black line: two feeders; solid gray line: one feeder plus natural landmarks). (b) The number of trials in which the fish first entered the goal zone whose feeder and/or landmarks corresponded to those associated with the demonstrated rich patch (\square), the demonstrated poor patch (\blacksquare) or in which they failed to enter either patch (\bullet). (c) The proportion of trial time (mean \pm 95% confidence interval) spent in the demonstrated rich (\square) and poor patches (\blacksquare). 1f, 2f and 1f(LM) corresponds to one feeder, two feeders and one feeder plus natural landmarks, respectively. * indicates $P < 0.5$, NS indicates no significant difference.

Time Allocation

Within-treatment paired t tests revealed that fish showed no preference for the goal zone with the feeder colors or landmarks corresponding to the demonstrated rich patch over the goal zone with the markers corresponding to the demonstrated poor patch (one feeder: $t = 0.34$, $df = 19$, $d = 0.14$, $p = .74$; two feeders: $t = -0.38$, $df = 19$, $d = 0.15$, $p = .70$; one feeder plus natural landmarks: $t = -0.09$, $df = 19$, $d = 0.04$, $p = .92$, Figure 3c).

A GLM found no effects of either treatment ($F_{(2, 47)} = 0.12$, $\eta^2 = 0.99$, $p = .88$) or latency to enter either goal zone ($F_{(1, 47)} = 0.05$,

$\eta^2 = 0.01$, $p = .82$) on the difference between time spent in the rich patch versus the poor patch. Neither feeder color ($F_{(1, 47)} = 0.21$, $\eta^2 = 0.03$, $p = .64$) nor the axis of the test tank that the fish was tested in ($F_{(1, 47)} = 0.34$, $\eta^2 = 0.71$, $p = .58$) had any effect upon relative time allocation either. In the third treatment, time allocation was not affected by the landmark paired with the rich patch (t test: $F_{(2, 18)} = 2.28$, $p = .18$).

Experiment 2 Discussion

This experiment looked for evidence of stimulus enhancement in the absence of any confounding influence of location cues, or local enhancement. We saw no evidence that stimulus enhancement was involved in prey patch selection, either when artificial feeders or more naturally realistic landmarks were associated with the prey patches. That is, there was no evidence that the fish were able to generalize their preference for the rich patch to exhibit a preference for other food patches with identical stimulus features, be they color or landmarks. The test apparatus was surrounded by a black plastic shelter, ruling out the possibility of local enhancement via extraapparatus landmarks. Taken with the results of the first experiment, these findings suggest that stimulus enhancement plays no part in social learning via public information use in ninespine sticklebacks.

It is not clear whether learning about prey patch relative quality in this way involves associative learning through observational conditioning, in which the fish forms an association between the feeding behavior of the demonstrators and the presence of food at the location of the goal zone, or whether public information use may be reliant on single-stimulus learning (sensitization), in which the fish, having observed demonstrators feeding in a particular area, become more responsive to, and therefore more likely to move toward, that location, irrespective of the context. We devised a third experiment to investigate this further.

Experiment 3: Associative Verses Nonassociative Learning

Experiment 3 Method

In this experiment we used 64 fish as test subjects and an additional pool of approximately 100 fish as demonstrators. Our aim was to determine whether the fish selected goal zones based upon a process of observation conditioning, or sensitization. If observation conditioning is responsible for the behavior of the observer fish we would predict that the fish would form an association between the feeding behavior of the demonstrators and the presence of food at the location of the goal zone. If this were the case, then we would expect to see the fish move to that area when foraging, but not in other behavioral contexts. If sensitization is responsible, then the fish should become more likely to visit that location subsequently, irrespective of the behavioral context. The following experiment aimed to differentiate between these processes.

Test Arena, Procedure, and Analyses

We provided subjects with a social demonstration of two prey patches as previously, and then allowing them to choose be-

tween two goal zones next to the demonstrated areas. However, in half the trials we changed the priority of the test fish from foraging to seeking shelter, by increasing the light levels in the test arena following the demonstration. A pilot experiment (see below) established that under the higher light conditions the fish spent substantially more time under shelter compared to the lower light treatment. A small shelter was included at either end of the test arena. If observational conditioning underlies public information use we should expect the fish to spend more time in the goal zone next to the rich prey patch under lower light conditions, but to be equally likely to visit and spend more time in either shelter, under the higher light conditions. If sensitization is responsible however, we would expect the fish to spend more time in the shelter near the rich patch under both lower and higher light conditions.

We established a test arena identical to that described in Experiment 1, to which we added two shelters (Figure 1c). These were 8 cm by 8 cm black plastic squares, raised 10 cm above the substrate on a 1 cm wide black plastic column.

The entire experimental arena was surrounded by a shelter constructed from matt black plastic sheeting as described above. An additional 60 W strip light was mounted 120 cm above the test apparatus. We placed a triple layer of diffusion filter paper (white diffusion 216, Lee Filters, Andover U.K.) 5 cm beneath this in order to diffuse the light equally across the experimental arena. A camera (Canon HG20 high resolution) was placed above the arena, and filmed it through a small aperture in the diffusion filter ceiling of the shelter. Square access holes were constructed in the front of the shelter, in order to allow access to the apparatus as described above. This ensured that extraapparatus visual cues were unavailable to the test fish during the test phase of the trial. The light intensity in the center of the arena measured 84.0–86.9 lx when the strip light was switched off and 180.1–197.1 lx when it was on. Under the shelters it was 12.2–19.2 lx when it was off and 24.3–30.2 lx when it was switched on. Note that when the strip light was switched off the arena was illuminated by ambient light from ceiling mounted strip lights, as it was in Experiments 1 and 2.

We performed a pilot experiment in order to confirm the efficacy of light in inducing shelter-seeking behavior in the fish. Here there was no social demonstration. The test fish was added to the holding unit and allowed to settle for five minutes, with the strip light switched off. We then either switched the light on, or left it off, and immediately released the fish. We point sampled its behavior for 3 min, recording at 6 s, recording whether it was beneath one of the shelters or in the open. Fish were classed as being beneath the shelter if more than 50% of their body was estimated to be beneath it. We performed 12 trials in each condition. No fish was used more than once.

We performed the main experiment using exactly the same procedure as described in Experiment 1. We used two feeders, and a 3:1 prey delivery ratio. Since previous experiments had shown no effect of feeder color, we used only white feeder units. Demonstrations took place with the strip light switched off. Immediately prior to the release of the focal fish we either switched on the strip light, or left it off. We performed 20 trials in each condition. No fish was used more than once.

Statistical Analyses

For the pilot experiment we performed an independent samples t test, comparing the total time spent under either shelter between the two experimental treatments.

For the main experiment we used two GLMs to compare the difference in time allocation to the goal zones. The first considered total time in the corresponding goal zone, including time spent beneath the shelters within each goal zone time allocation score. Experimental treatment (light intensity) was included as a fixed factor. Latency to first enter either prey patch included as a covariate and the location of the rich patch (left or right) was included as a random factor. Proportional data on time allocation to goal zones were normalized by arcsine transformation. The difference in time allocation was calculated by subtracting the proportion of time spent in the poor quality goal zone from that spent in the rich goal zone. The second GLM, considered the difference in time spent under the shelters only.

Within each treatment group we performed further paired sample t tests, comparing time in the rich patch to time in the poor patch. Finally, we performed an independent samples t test, comparing the total time spent under either shelter between the two experimental treatments.

Effect sizes were estimated using Cohen's d for the t tests and partial η^2 scores (η^2) for each variable in the GLMs.

Experiment 3 Results

Pilot Experiment

Fish spent more time beneath the shelters in the higher light treatment than they did in the lower light treatment, conforming the efficacy of the assay (t test: $n = 12$, $t = 6.60$, $d = 2.71$, $p < .001$, Figure 4a).

Main Experiment

A GLM revealed no effects of experimental (light) treatment ($F_{(1, 36)} = 0.038$, $\eta^2 = 0.03$, $p = .88$), latency to enter either goal zone ($F_{(1, 36)} = 3.27$, $\eta^2 = 0.06$, $p = .09$) or location of the richer patch (left or right, ($F_{(1, 36)} = 0.28$, $\eta^2 = 0.04$, $p = .69$) upon the difference between time spent in the rich or poor prey patches.

Similarly, we saw no effects of experimental (light) treatment ($F_{(1, 36)} = 0.03$, $\eta^2 = 0.05$, $p = .60$), latency to enter either shelter ($F_{(1, 36)} = 3.32$, $\eta^2 = 0.05$, $p = .17$) or location of the richer patch (left or right, ($F_{(1, 36)} = 1.75$, $\eta^2 = 0.06$, $p = .47$) on the difference between time spent in the two shelters alone (Figure 4b).

Paired samples t tests revealed that fish spent more time in the goal zone closer to the rich patch than they did in the goal zone corresponding to the poor patch in both the lighter and darker treatment ($t = 2.98$, $df = 19$, $d = 1.18$, $p = .01$ and $t = 2.18$, $df = 19$, $d = 0.89$, $p = .04$, respectively).

Fish in the higher light treatment spent more time under either shelter than did those in the lower light treatment, in accordance with the pilot experiment (independent samples t tests: $t = 5.56$, $df = 38$, $d = 1.99$, $p < .001$).

Experiment 3 Discussion

The experiment provides no evidence of observation conditioning. If observation conditioning were responsible for the behavior

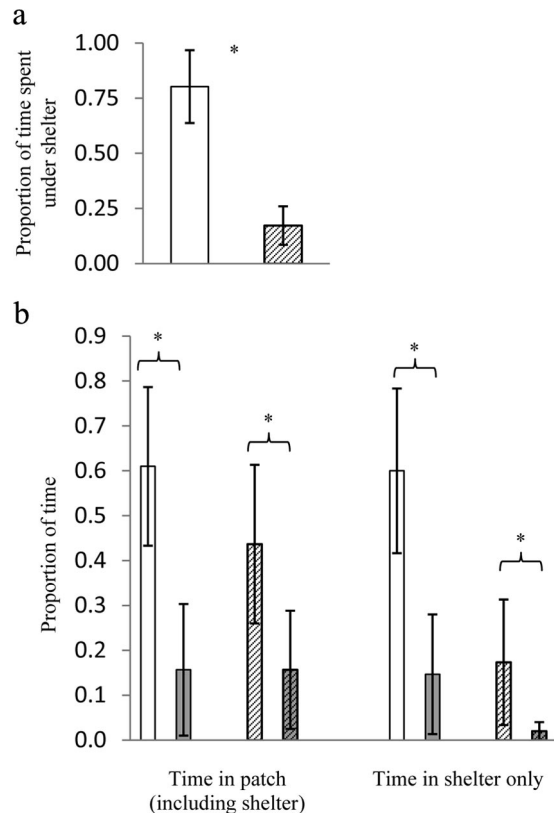


Figure 4. (a) We conducted a pilot experiment in order to determine the efficacy of the light treatment in inducing shelter use. The proportion of trial time (mean \pm 95% confidence interval) spent beneath the shelters in the higher light (open bar) and lower light (hatched bar) treatments. (b) The proportion of trial time (mean \pm 95% confidence interval) spent in the demonstrated rich (\square) and poor patches (\blacksquare) in the higher light (open bar) and lower light (hatched bar) treatments. * Indicates $p < 0.5$.

of the test fish, then we would have expected to see them exhibit a preference for the goal zone corresponding to the rich patch only in a foraging context. Instead, we saw that the test fish were just as likely to visit the location of the demonstrated richer patch when an environmental stimulus (bright light) caused them to seek shelter, as they were under standard lighting conditions, when they were presumably foraging. However, the findings are consistent with single-stimulus learning via sensitization. This implies that observation of the demonstrator group feeding at the greater rate caused the test fish to be sensitized to the location of feeder, leaving them more likely to move toward it irrespective of context.

General Discussion

Our experiments provide strong evidence that learning about locations facilitates prey patch selection via socially transmitted public information cues in ninespine sticklebacks, but no evidence that the subjects learn generalizable stimulus cues (e.g., feeder color or local landmarks). Experiments 1 and 2 clearly demonstrate that when learning about patch quality through observation of feeding conspecifics ninespine sticklebacks acquire knowledge of the specific rich patch location, but not the general properties of

rich patches. The findings provide clear evidence for local enhancement, but no evidence for stimulus enhancement. A third experiment implies that this results from single-stimulus rather than associative learning, almost certainly through demonstrator-mediated sensitization to the location of the feeder.

The findings of these experiments have implications for the classification of local and stimulus enhancement. Both Galef (1988) and Heyes (1994) have previously suggested that local enhancement be considered a subset of stimulus enhancement, with the location itself acting as a stimulus. However, here we provide evidence for local enhancement but not stimulus enhancement, which might imply that these forms of learning are based on separate rather than identical processes. One difference between learning about a location versus any other stimulus is that the former cannot be generalized (any other location is somewhere else) whereas the latter can (other stimuli can exhibit features in common with the focal stimulus). Our data raise the possibility that while a given species may be capable of learning via local enhancement it may be incapable of learning through stimulus enhancement, or alternatively that they exhibit stimulus enhancement only under restricted circumstances. While dedicated experimentation to address this issue is rare, our findings are consistent with a broad array of data suggestive of extensive local enhancement in animals but little stimulus enhancement (Hoppitt & Laland, 2008). These observations suggest that it is indeed better to consider local and stimulus enhancement as separate processes, rather than categorizing one as a specific subset of the other.

Our third experiment provides evidence that ninespine sticklebacks are capable of demonstrator-mediated single-stimulus learning through sensitization, as Heyes (1994) proposed for stimulus enhancement, but crucially only where the stimulus is a patch spatial location, and without being able to generalize to the properties of other patches. As local enhancement can clearly also occur through other processes (Laland & Plotkin, 1991; Reader, Kendal, & Laland, 2003; Waite, 1981), and can occur without learning, we retain the view that local enhancement is best regarded as a broad umbrella term for a variety of processes mediating location-specific enhancement (Hoppitt & Laland, 2008), rather than a subset of stimulus enhancement.

It is nonetheless unclear why the ninespine sticklebacks used in our study exhibited no evidence of stimulus enhancement, as one might assume that there would be fitness benefits associated with an animal learning through observation of others about food site cues that are potentially reliable general indicators of the presence of the food, including at other locations. One possibility is that learning about the location of a prey patch overshadows learning about its general physical properties. This implies that there are adaptive benefits to being “prepared” by selection to attend to location cues, rather than other features of the prey stimulus; that these fish are attuned by selection to find location cues particularly salient. A prey patches physical location and its physical properties are necessarily linked, both in our experimental apparatus and under natural conditions, and if learning about the two is not possible, then selection may have favored learning about the former, perhaps because the fitness benefits of visiting a location where prey has been seen to be found (by others) outweighs the benefits of visiting similar sites where prey may be found. Another, more ecological explanation for the absence of this type of learning in sticklebacks is that, as ecological generalists utilizing a

broad range of prey found in many habitat components (e.g., benthic, epibenthic, limnetic, and from different substrate types), there has been little evolutionary pressure favoring stimulus enhancement, since prey will usually be available from other sources, and in a variety of very different forms (associated with a range of different cues). The world may be sufficiently noisy to render generalization on the basis of prey patch cues as very hit and miss. Furthermore, unlike stimulus enhancement, local enhancement is reinforced by preexisting basic behavioral processes, including a general tendency to approach conspecifics (Krause & Ruxton, 2002), and a more specific predisposition to move toward others that are feeding (Clarke & Jones, 2001; Krause, 1992; Quenette, Ferron, & Sirois, 1997). The tendency to join groups of conspecifics may have first arisen as an antipredator behavior (Krause & Ruxton, 2002), with the additional benefit of access to social information occurring secondarily, and favoring the evolution of further refinements to the criteria by which prospective groups are appraised by the joiner, such as attention to whether they are feeding or performing behaviors characteristic of feeding.

In the natural setting, local enhancement may also be aided by cues that remain after the demonstrators have moved on. While such cues were excluded from the experimental protocol employed in this study, in nature they could include fecal deposits, actively produced scent marks or other passively produced odors or chemical cues associated with the demonstrators or products arising from their exploitation of resources at the patch, such as prey fragments or damaged substrates (Laland & Plotkin, 1991, 1993; Terkel, 1995). Conversely, stimulus enhancement, in which an observer becomes more likely to visit or interact with features of its environment that are similar to those with which it has previously detected demonstrators interacting, must evolve without this scaffolding.

A number of studies have shown that several species of fishes are, through repeated exposure, capable of learning a socially to distinguish between artificial and natural landscape features (Girvan & Braithwaite, 1998, 2000; Odling-Smee & Braithwaite, 2003; Odling-Smee et al., 2008; Webster & Hart, 2004, 2006; Webster & Laland, 2008). The failure of our experiments to detect evidence of stimulus enhancement then most likely reflects the absence, in ninespine sticklebacks, of a psychological mechanism linking the behavior of conspecifics to specific features (other than particular locations, which constitutes local enhancement), rather than a general inability of the species to learn to discriminate between different physical features within its environment. It may be possible that repeated exposure to social demonstration could induce learning under some circumstances, and this is worthy of further investigation. In nature, in species such as ninespine sticklebacks, individuals observing others feeding would most likely join them directly. It may be that stimulus enhancement is more likely to evolve in species where some individuals are prevented from interacting with certain stimuli in their environment, while having the opportunity to observe others interacting with them. Such circumstances could, for example, be a consequence of social structure, where dominant individuals monopolize certain resources and prevent others from exploiting or directly investigating them, or they could be related to ontogeny, with juveniles watching older groupmates exploiting resources which they are not yet developed enough to tackle themselves. This line of speculation is amenable to direct testing, or to meta-analysis. In principle,

if our reasoning is correct, it should be possible to predict a priori which species will exhibit stimulus enhancement. Finally, stimulus enhancement and/or observational conditioning may be more likely to evolve for social learning in contexts other than foraging, such as predator recognition (Griffin, 2004), where the costs of errors are potentially higher.

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