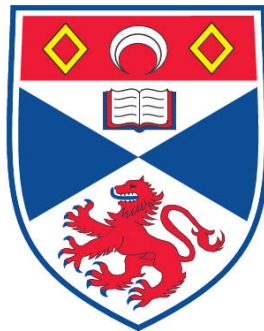


**PUBLIC INFORMATION USE IN NINESPINE STICKLEBACKS
(PUNGITIUS PUNGITIUS): ISOLATING THE MECHANISMS
USING COMPUTER-ANIMATED STIMULI**

Laura Chouinard-Thuly

**A Thesis Submitted for the Degree of MPhil
at the
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UNIVERSITY OF ST ANDREWS
INSTITUTE OF BEHAVIOURAL AND NEURAL SCIENCES

**PUBLIC INFORMATION USE IN
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PUNGITIUS): ISOLATING THE
MECHANISMS USING COMPUTER-
ANIMATED STIMULI**

BY LAURA CHOUINARD-THULY

FOR THE DEGREE OF MASTERS OF PHILOSOPHY

JUNE 2012

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I *Laura Chouinard-Thuly*, hereby certify that this thesis, which is approximately 11 000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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Abstract

Many studies demonstrated the use, and strategies of use, of public information -or the ability of an observer to assess a resource's quality by watching inadvertent behavioural cues- in the ninespine stickleback (*Pungitius pungitius*) in a foraging patch assessment problem. Many aspects of behaviour were seen to vary with an increased feeding rate and identifying the one responsible for transmission of information is difficult with live demonstrators. This project will create and utilize computer-animated ninespine sticklebacks to isolate behaviours and test which ones are used by observers to gain information. We predicted and found that out of six different behaviours associated with an increase in feeding rate, strike rate is the one used to assess foraging patches' quality. Observer ninespine sticklebacks preferred to associate with sides that were formerly associated with an animated shoal of conspecifics different only in the amount of strikes per demonstration period, in a ratio of six versus two.

Introduction

Social Learning

When trying to learn about the quality of a constantly changing environment, animals have the option of using different sources of information. One source would be personal, or private information, where an individual assesses the quality of a resource by investigating the said resource. If this option is not available, they can use social information, or information produced by other individuals.

Social learning can be broadly defined as the learning that is facilitated by observation of, or interaction with, another animal or its products (Hoppitt and Laland, in press). Social learning is used as an alternative to individual learning (or asocial learning) as a means to gather knowledge when this information is not sufficient, or is absent. Any information that is acquired from, or as a consequence of, observation, or interaction with other animals is termed social information (Kendal et al., 2004). Typically, the users of this information are referred to as “observers” while the producers of this information are called “demonstrators” (Heyes and Galef, 1996; Hoppitt and Laland, in press). Social learning, according to the definition, can also act on a simpler level, where individuals only serve to facilitate individual learning. For example, a fish in a school could be exposed to a resource of food simply by following other individuals, and then discovering and sampling the patch personally. In this case, learning is facilitated by the presence of individuals in a mechanism called social facilitation, but the information about the resource is still personal (Hoppitt and Laland, in press).

It is also interesting to note that although social learning has a broad and encompassing definition, if the propagation of a novel behaviour through social learning process results in homogeneity of behaviour that extends beyond the period of interaction, it is referred to as social transmission (Hoppitt and Laland, in press). The term social transmission is used to

define more restricted instances where social information spreads through groups of animals creating a match between the observers' and demonstrators' behaviour. Further, it is a mechanism that accounts for animal traditions, a distinctive behaviour shared by two or more individuals in a social unit that has a maintained propagation and spreads further through social processes (Hoppitt and Laland, in press). These behaviours then become characteristic of that group of animals.

Individuals rely on social information according to various strategies, defined as “when” and “who” strategies, and which are not mutually exclusive (Laland, 2004). The “when” strategies refer to the decision to go along with social learning depending on circumstances, while the “who” strategies define the cases where observers use social learning depending on the characteristics of the demonstrator. For example, observers could use social learning when uncertain of their own knowledge, when gaining private information is too costly, or when they are dissatisfied with their own behaviour. They can also use information from the majority, kin, “friends”, etc (Laland, 2004).

Social information can be transferred from the demonstrator to the observer by signals or traits specifically selected to transmit information (Danchin et al., 2004). This can be seen in the case of teaching, for example in wild meerkats, where experienced individuals changed their behaviour at a cost to themselves in order to stimulate learning of prey handling in young pups (Thornton and McAuliffe, 2006). In this case, the transmission of information definitely occurs through a directed and intentional process of communication.

In other cases, the transfer of information happens through undirected signalling. When this happens, the transmission is said to occur through public information. Public information is the gathering of information on a resource's quality through observation of other individuals performance or activities with that specific resource (Valone, 2007; Valone and Templeton, 2002). The key points here are that the cues are behavioural and inadvertent, making this information available to anyone who monitors the activities.

Public information is now thought to be a prevalent phenomenon, and has been described in many different taxonomic groups (Danchin et al., 2004). It happens in many different contexts in relation to various resources, or states of the environment.

Public Information

Public information is used to assess different situations, such as foraging, mate choice, habitat selection, eavesdropping, opponent assessment, and level of danger by using inadvertently produced behavioural cues (Danchin et al., 2004; Valone and Templeton, 2002). The main advantage of using public information is that because the process is unintentional, the demonstrators are watched while they aim to perform at their best (Danchin et al., 2004). A brief overview and description of these contexts will be given in the following pages.

Foraging

In this case, the information gained relates to the quality and characteristics of a food patch. There are many instances in which private information could be insufficient; amongst many reasons, personal knowledge could be outdated due to a changing environment, or too hard to obtain in a high predation risk, pressuring individuals to utilize an alternative source of knowledge. In cases of patch assessment, the behaviours that are being monitored are foraging activities and success of other individuals. Templeton and Giraldeau (1995) demonstrated the use of public information in a foraging context in a group of European starlings (*Sturnus vulgaris*). They showed that starlings used probing rate of other individuals as public information on patch quality when it was easily available. This provided the first empirical evidence of public information use in a patch assessment problem.

Mate Quality Assessment

Choosing a mate is always a crucial decision in terms of fitness, directly responsible for offspring quality. Most often, individual sampling and discriminating between potential partners is not possible, or would be too costly. In these cases, once again, other individuals'

activities are monitored. Two kinds of activities can be monitored that instruct the choosy partner.

First, the quality of potential mates can be assessed by watching others mating decisions and interactions to allow a more enlightened decision (Danchin et al., 2004; Dall et al., 2005). When the sexual interactions are monitored, this form of public information use is referred to as mate-choice copying (Witte and Nöbel, 2011). This can be based directly upon mating decisions of others, or upon watching the courtship behaviour of a potential mate to another individual (Valone and Templeton, 2002).

Information about the quality of potential mates can also be obtained by eavesdropping. This way of gaining information is based on the observation of the outcomes of interactions, or on interception of signals meant for others. This bystander attitude allows the eavesdropper to avoid exposure to risky situations and enables access to information at a low risk and cost (McGregor and Peake, 2000). It also guarantees access to reliable information since interactions between two individuals are assumed to be devoid of cheating (Witte and Nöbel, 2011). The female fighting fish will mate preferentially with winners of male-male interactions (Doutrelant and McGregor, 2000).

Habitat Choice

In a case where an individual has to assess the suitability of a habitat for breeding, the breeding success of other individuals can be used as public information. It was first demonstrated in a species of bird, the Black-Legged Kittiwake (*Rissa tridactyla*). Indeed, they breed in a patchy and variable nesting environment where quality varies over the years. The birds were shown, providing the first evidence for this type of public information use, to base their nesting site choice on the previous year's breeding success of conspecifics (Danchin et al., 1998). Other species of birds, the Pied Flycatcher (*Ficedula hypoleuca*) and the Collared Flycatcher (*Ficedula albicollis*), have been demonstrated to use the reproductive success of both conspecifics and Great Tits (*Parus Major*) heterospecifics, to assess habitat quality (Forsman, 2008; Doligez et al.,

2004a, 2004b). This assessment is thought to be conveyed through the frequent visits of male Flycatchers, responsible for choosing the nesting site, to the other individuals' nest boxes.

The prevalence of public information use throughout the animal kingdom shows that it does not necessarily require highly developed cognitive function. It is instead utilised as an evolutionarily adapted alternative for private information, which can be costly to gather. Indeed, public information, in a foraging context, was demonstrated to be present in a species of fish, the ninespine stickleback (*Pungitius pungitius*) previously thought to be a simple organism (Coolen et al., 2003).

Public Information Use in Sticklebacks

The ninespine sticklebacks are a species of fish of the Gasterosteidae family, living in freshwater of temperate climates through the Northern Hemisphere.

They were demonstrated to use public information in a patch assessment problem using a very simple setup (Coolen et al., 2003). Observer fish were constrained in an observer bay in the centre of a tank of 90cm, which contained a shoal of three fish in each of the 30cm extremities. These shoals were fed at different delivery rates; the poor patch received 2-3 bloodworms twice during ten minutes, while the rich patch received 2-3 bloodworms six times during the ten minutes demonstration period (see figure 1).

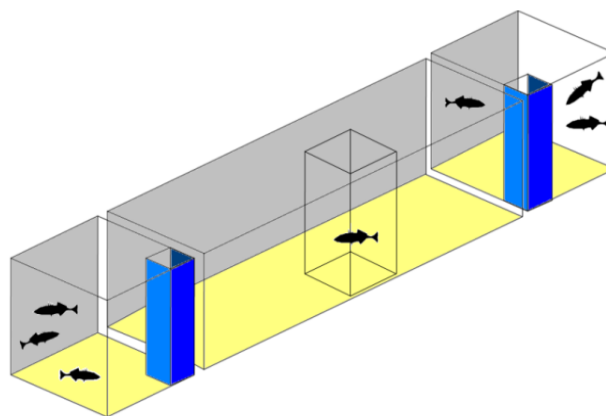


Figure 1: Basic Public Information Setup, with demonstrator shoals and observer

After this period, the demonstrators were removed and the observer released, and the focal fish was free to associate with the patches. The ninespine sticklebacks showed a consistent preference to associate with the formerly rich patch, even when controlling for residual food cues. However, while testing under the same conditions a closely related species, the threespine sticklebacks (*Gasterosteus aculeatus*), these failed to display a preference for either patch, associating with both equally. While this shows that social learning is happening, it does not prove that this transfer of information is made through inadvertent cues. Indeed, at this stage, it could simply result from an intraspecific communication system difference. However, the experimenters repeated the experiment placing a ninespine as the observer, this time using threespines as demonstrators. Once again, the ninespine sticklebacks displayed a consistent preference for the formerly rich patch, showing a computing of inadvertent behavioural cues displayed by the foraging individuals. This was also the first evidence of the use of public information from heterospecifics, in any context or species. The authors also introduce the hypothesis that this species difference could be due to differences in predation risk deriving from the more armoured body of the threespines.

Thus when the ninespine sticklebacks did not have any private information, they relied uniquely on the publicly produced cues. However, when provided with conflicting private and public information, they chose to go along the most reliable source (van Bergen et al., 2004). The experiment highlighted that the ninespine sticklebacks weighted differently public and private information depending on the context, allowing accurate choices of foraging patches. Indeed, ninespine sticklebacks relied on public information when their private information was unreliable or outdated, following expectations for living in a variable environment. When private sampling does not provide consistent information over different samplings, the patch can be considered as highly variable and therefore quality has to be reassessed constantly. In the same way, fish relied more on public information as the time since their last sampling increased. Public information is therefore effectively used in order to make appropriate decisions. Since public information is also produced inadvertently by behaviour, it is a very

reliable, error-free source of information on quality. It is therefore no surprise that ninespine sticklebacks would prefer to use public information over other social cues (Coolen et al., 2005). When fish were provided with a conflict between number of conspecifics and food delivery, they preferred to rely on public information, consistent with other findings. This seems to be a strategy to avoid possible errors that could occur if using other's decisions of foraging patches, i.e. social cues.

In fact, ninespine sticklebacks are using the most reliable source of information to make foraging decisions. From the body of evidence collected it seems that sticklebacks would employ public information in an adaptive way, and that their copying is not unselective. As a matter of fact, individual fish showed a larger tendency to copy large individuals compared to small when these demonstrators presented conflicting public information (Duffy et al., 2009). This is consistent with adaptive strategy hypotheses, as large individuals are more likely to be successful and experienced. It corroborates the idea that copying is structured to lead to high payoffs, and is likely to have evolved with mechanisms to ensure that increase in satisfaction. Indeed, copying conspecifics, to be adaptive, should have a strategy that allows the fish to reach higher payoffs than what is already received, in what is termed a hill-climbing social learning strategy. The ninespine sticklebacks follow such a strategy: copying and choosing public information when the payoff is greater than their own, but sticking to their own when patches are of lower profitability (Kendal et al., 2009). There are many learning strategies where the observers' copying is dependent on the payoff that could explain the previous findings. A further study on how observers would compare and use the payoffs showed that copying is based on a proportional observation strategy (Pike et al., 2010a). The observers copy based on the returned payoff to the demonstrators, as opposed to a proportional reservation strategy or a proportional imitation strategy, where the copying behaviour would be inversely related to their own satisfaction or depending on how much better the demonstrator is doing, respectively (Schlag, 1998, 1999). All these strategies drive populations towards an optimal payoff. In the Pike and Laland study (2010), it was demonstrated that fish switch their feeder preference

proportionately to how well the demonstrators did. However this tendency to copy is also affected disproportionately by the amount of conspecifics at the feeder, suggesting a conformist learning mechanism (Pike and Laland, 2010). When fish trained to show a preference for a feeder were subjected to conflicting public information in which the number of foraging demonstrators varied, the observer fish displayed an increasing propensity to copy the majority in the test phase. All these evidences seem to point towards a highly structured use of public information, where information about resources is reliably transferred through groups of individuals. These findings are consistent with the hypothesis that these groups should converge towards the optimal scenario, maximizing payoffs and efficiency of information transmission (Laland et al., 2011).

Mechanisms behind public information

The definition of public information is inherently broad, defined to encompass any behaviour that could provide information to observers. It is interesting, once faced with a clear case of public information, to try to elucidate exactly what behaviours are being monitored.

The video analysis of demonstrator shoals feeding showed that some behaviours changed as the feeding rate increased. Indeed, preliminary analysis showed that as the delivery rate increases (2-3 bloodworms, 2 times to 6 times), activity rate and strike rate increased, while distance between individuals and distance to feeder decreased, with no change in aggressiveness (Webster M., pers. comm.). All these cues could be important for a naïve individual when trying to make the best decision on the choice of a food patch. Trying to isolate these cues with live demonstrators proved rather hard, seemingly impossible to control for all confounding factors in the behaviour of the presented shoals. Experiments to manipulate the behaviours included using partitions to change the shoal cohesion, exploiting their red bias to make them strike at pseudo food, raising the water temperature to increase activity rate, etc. Although unclear, the results seem to point towards activity rate and strike rate as a likely clue for the transmission of

information. Indeed, the observer showed a significant preference and associated more with the formerly more active side, and with more strikes per minute (Webster M., pers. comm.).

There was still a need for a system where the behaviour of the demonstrators could be completely controlled, like playback experiments. The use of computer-animated stimuli seemed to fit perfectly with the question asked, and had already been used in many different taxonomic groups.

Computer-Animated Stimuli

The use of repeatable stimuli has increased in the last decade, with techniques ranging from video playbacks to computer generated animations. The advantage of these techniques lies in the fact that the sequence is perfectly repeatable from trial to trial, exempt from variation in the demonstrators' behaviour (Woo and Rieucan, 2011). Within the various alternatives of producing visual stimuli, 3D computer-animated stimuli gives the most accurate and versatile tool (Baldauf et al., 2008). It provides complete control over movements, and thus offers an option absent from still images, or playback sequences (Woo and Rieucan, 2011). It provides complex sequences where many individuals can be simulated.

Three-dimensional animated stimuli are video sequences created from any software allowing movement of objects in three axes. The objects present in the animations are formed inside the software, respecting body dimensions of live animals. The sequences are then usually rendered¹ in advance (although they can be rendered in real-time) and displayed from a 2D apparatus, such as television or computer monitor. (Woo and Rieucan, 2011)

The following pages will present a short review on how computer-animated stimuli have been used to mimic other individuals in animals in general and in fish in particular.

Although computer-animated stimuli have been used in many taxonomic groups, there is only one instance of its use in invertebrates, in jumping spiders (Baldauf et al., 2008; Harland and

¹ A list of definitions is provided in Table 1 on page 16

Jackson, 2002). Three-dimensional lures were used to identify what optical cues influenced the behaviour of the spiders, and it was found that the animated lures were recognized as preys and elicited specific predatory response.

Using a computer-animated Jacky Dragon (*Amphibolurus muricatus*), investigations were made on sexual courting behaviours. It was demonstrated that contrary to what was thought previously, speed is not critical in the display of push-up body rocks; rather, the overall display duration of the demonstration was more important (Woo and Rieucan, 2012). This computer-animated lizard was created by digitally scanning a taxidermic body (Woo, 2007). They also demonstrated that the lizards responded to the animation in a similar way than to real conspecifics, illustrating the success of the presentation.

Another example was done with chimpanzees, where they were presented with yawning computer animations of another individual to try and test contagion (Campbell et al., 2009). It was demonstrated that the chimpanzees showed contagious yawning in response to yawning animated conspecifics and that they did attend and show interest towards the animation.

But computer-generated stimuli also allow the experimenter to present an interactive and responsive environment. All the examples above were done using pre-rendered animations, which were repeated to all subjects. Exploring the more interactive side of these animations, rhesus monkeys were presented with maze task, requiring the focal monkey to explore the maze with a joystick and subsequently find an object (Washburn and Astur, 2003). This task required a higher level of cognition from the subjects, as they were asked to move in a computerised 3D dimension maze through the manipulation of a joystick. Nonetheless, it was demonstrated that with some practice, monkeys were able to navigate these mazes and successfully retrieve a reward.

Computer-animated stimuli use in fish

Computer generated stimuli have been extensively used in experiments with fishes. Most of the experiments have been behavioural, with a large proportion axed towards sexual selection and underpinning the characteristics required for success.

Theo Bakker's lab was certainly a pioneer in the use of these animations, studying sticklebacks' mating preferences. They first started by testing various different stimuli to find preferences, to finally settling on non-interactive tests using computer animations that permit variation of traits relating to colouration, morphology, and also courting behaviours (Künzler and Bakker, 1998). They produced their animated sticklebacks by digitising slices of a fixated body of a male. They then recreated the courtship path, and presented the animations with varying traits to female in a simple preference test. They showed in their first study that females presented with these stimuli were not scared or inhibited, and that they were able to discriminate between the animated displaying males, proving that the system is thus appropriate for this kind of study (Künzler and Bakker, 1998). They further demonstrated that females' preference correlated with their own physical condition by another transformation of the same animation object (Bakker et al., 1999). Using the same set up, this lab also uncovered the first empirical evidence of the preference for a combination of traits of high fitness, compared to contradictory or single variation (Künzler and Bakker, 2001). The use of computerised stimuli in this experiment allowed for combinations of contradictory traits, impossible to create in live demonstrators. These animations also permitted them to study sperm competition, and how the presence of another courting rival affects ejaculate size. Using the same setup and system as the one which proved appropriate in earlier studies, they showed that males adjust the size of ejaculate depending on the assessed competition (Zbinden et al., 2003). This ejaculate size is also dependant on the body size of their rivals, pointing to precise mechanisms for sperm competition assessment (Zbinden et al., 2004). Further examining the factors that influence female preferences, they used these animations to study symmetry preference, using the tool of animations as a way to create particular phenotypes that would be hard to reproduce in natural

fish. It proved that there is sexual selection of spine symmetry, and especially when inbred females were choosing, using this discrimination to enhance their gene pool quality (Mazzi et al., 2003, 2004).

Suitability of computers animation for behavioural and cognitive studies was demonstrated through a long and varied history. The system has been proven to work, and extensively so with sticklebacks. It does work efficiently or testing on behaviour across many species, and seem to offer exactly the kind of control we are looking for in order to test isolated behavioural cues, and lighten the mechanisms selected to produce this advantageous use of public information in the ninespine sticklebacks.

The Project

Even though these animations have been used extensively to study behaviour, this project will be, as far as we are aware, the first attempt to transmit social information to inform the decision of a live observer by other means than social facilitation. This project deals with the creation of a suitable animation for ninespine sticklebacks, which will mimic conspecific shaped demonstrators closely enough to elicit specific reactions.

The first part of the project deals with the creation of the stimuli and the tests done to ensure that they are perceptible to the subjects. Part I provides in details the methods for building an animation, and deals with technical facts. It also tests the live observers' reaction to the animated fish using shoaling experiments, hopefully producing the expected results.

Once this established, the second part deals with creating and testing animations that differ only in one potential public information cue. The goal is to identify the behaviours that are susceptible to be useful when monitoring activities and gaining public information. It will attempt to highlight the specific mechanisms used by stickleback in the adaptive use of public information.

Part I: The Animation

Introduction

Already proven to be suitable by many studies, computer-generated animations are a useful tool to exclude all confounding variables in behavioural, and in this case, social learning experiments. Moreover, it has been proven to be appropriate in the threespine stickleback, closely related to our focal species, the ninespine stickleback (Künzler and Bakker, 1998). The aim of this project is to build an animation that will be recognized by live observers as other individuals, with a long-term goal of using them to test public information cues, and investigate social learning mechanisms. This part of the project deals with the technical requirements of building 3D computer-generated animations, and testing that the fish are attentive and react to these presented stimuli in a way similar to the way they would with live demonstrators. To investigate their reaction, basic shoaling experiments were used, where fish were presented with two different shoals and their association was recorded.

Methods

Creating the Animation

The animation was built using a free open source 3D content creation suite called Blender, found at <http://www.blender.org/>. The software works equally well on all operating system and comes with various tutorials online, as well as forum sites where blender “artists” can ask questions and exchange information (<http://www.blenderartists.org/forum/>). A beginner’s book to animation in Blender was also used, providing a step by step guide to required components of an animation (van Gumster, 2009). A list of definitions is provided below.

Term	Definition
Render	Creating a sequence of images from a model
Vertices	Points that create the global form of an object
Edges	Lines that form a connection between two vertices
Face	Polygon formed by at least three vertices
Loop	Series of vertices connected through a path of edges, where the first and the last vertice join
Linking	Joins two objects into a single one
Empties	Objects that are not rendered in the finished process, but serves as guides for position, scale, rotation
Weight	Amount of deformation a specific bone has on the mesh of an object

Table 1: Terms used in Blender.

Creating the Scene

The first step in creating an animation is to create a scene, which means creating a set of object that will be the world into which a specific object (in this case, fish) will move. This includes setting the lights, and cameras.

A five sides cube was used to simulate the tank, and contained a rock and algae objects close to the back “wall” as unmoving size references (the position and size of all objects in the scene is given in table 2).

Object	Dimension			Position			Rotation		
Axis	X	Y	Z	X	Y	Z	X	Y	Z
Tank	17.9	21.811	12,447	-1	0	0	-	-	-
Algae	1.069	1.477	10.594	+/-8.817	+/-5.870	-6.00	-	-	-
Rock	1.217	0.446	0.446	+/-8.774	+/-5.224	-5.632	-	-	-
Camera	-	-	-	95.996	0	0	-	-	-
Key light	-	-	-	-5	-16.891	38.5005	14.776	19.724	-68.704
Fill Light	-	-	-	2.124	-0.638	19.663	0	0	0
Back Light	-	-	-	-0.668	6.237	10.189	0	-90	0
Fish	0.793	2.711	0.833	-	-	-	-	-	-

Table 2: Objects included in the scene of Blender, with dimensions of their bounding box and position of the object pivot point.

The scene was lighted by three sources of light. As the light in blender bounces only once, it is important to place multiple light sources in the scene to illuminate all sides. The usual light

setup is referred to as three-point lighting and consists of placing a key (which is the main light), a fill (which lights the other side to avoid strong shadows) and a back light (which illuminates the object from the back). The key light used in this scene was a spot, set above the top left corner of the tank. The falloff was inverse linear, the distance at which light stopped was 60 units. The fill light was a hemi, with energy set at 0.7. The back light was set as a point type light, with energy at 0.440, and an inverse square falloff of 46.408 units. The rest of the light settings were left to default. The camera used to record the scene was set in perspective with a focal length of 130 mm, clipping starting at 87 and ending as 110. The scene is depicted in figure 2.

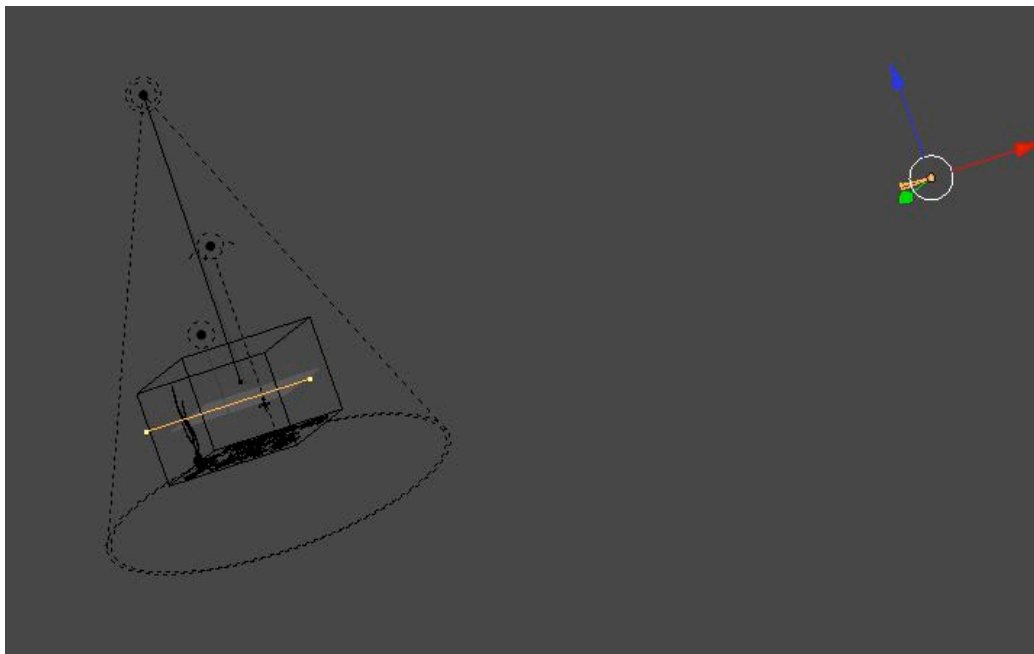


Figure 2: Blender scene with tank, rock, algae, lights, and camera.

Creating the Fish Object

The fish object was created from a mesh cube that was subdivided many times to create more vertices and edges, to be later shaped into a fish using a process referred to as box modelling. Playing with the mesh to create the appropriate shapes requires the use of a few functions in Blender, such as Grab, Scale, Rotate, Extrude, Duplicate, all of which move the vertices, edges, and faces in the 3D world.

Half of the cube was deleted, and a mirror on the x axis was created, allowing any change on one side to be perfectly replicated on the other side, for a perfectly symmetrical body. Pictures of an

average stickleback in various angles were displayed in the background and the mesh was formed to fit the shape represented in the pictures. Once the main body was formed, the mesh was subdivided many times, and vertices smoothened with the inbuilt functions of Blender.

To create the eyes of the fish, a ball was inserted at the right position, and then covered with half a sphere. The ball and sphere side vertices were joined to the adjacent vertices of the body mesh. Circular edges and vertices were added in loops patterns for smooth transition, only creating faces with 4 vertices (see figure 3).

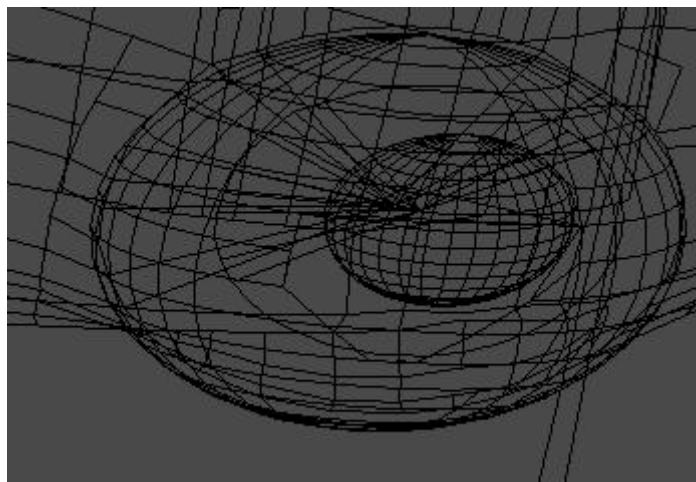


Figure 3: Close-up of the eye of the fish, with two layers of eye.

The two objects (eye and top layer of the eye) were then linked to the main fish body, so that they all move together.

The mouth was created by deleting the front part of the body object. Then multiple loops of faces were extruded and added. They were subsequently shaped into the nose part of a fish body.

The next additions were the pectoral fins, which were created by shaping a subdivided plane into a pectoral fin shape. The vertices on the side were then joined to the vertices on the body. At this point the mirror was still in effect, and actions were recreated on both sides of the body

The main body was complete, with exception of the dorsal, ventral, and caudal fins, as well as the spines. The mirror was then applied, removing the effect on subsequent changes in order to allow the fins to be added and not duplicated.

The ventral, dorsal, and caudal fins as well as the spines were modelled from a mesh plane to allow them to be very thin. The side vertices were then joined to the vertices on the body, and all parts were linked to the main body to create one object (figure 4).

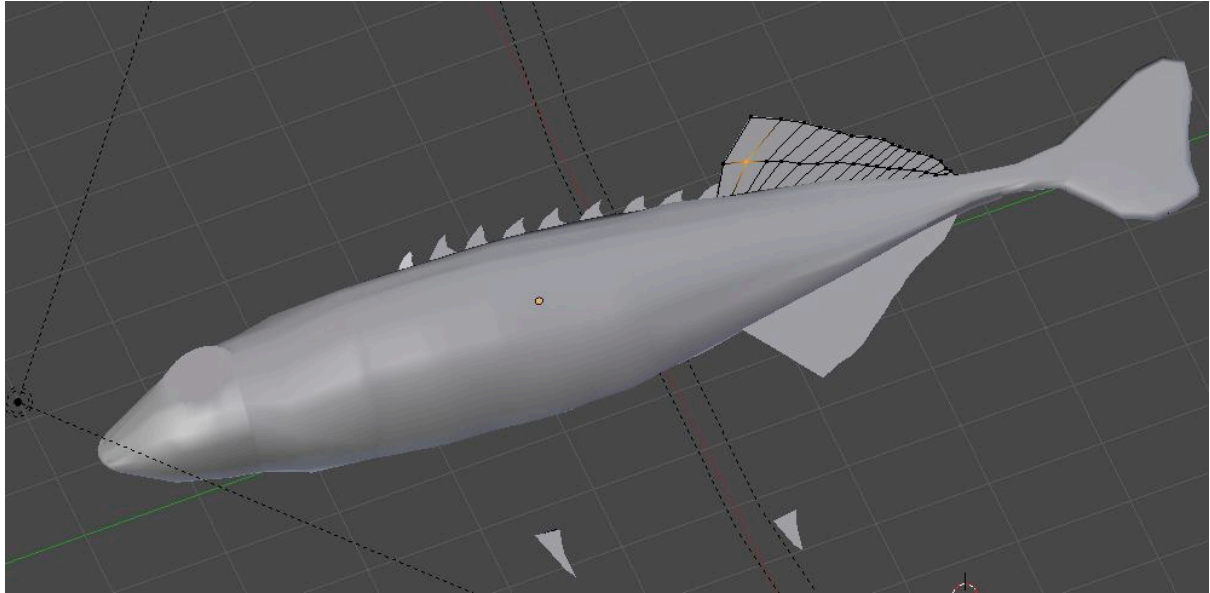


Figure 4: Fish object with spines and fins

All objects were made of mesh, subdivided, and vertices were smoothened to give a natural light reflection. Lastly, the function “remove doubles” was used to insure that no unused duplicate of mesh was left behind.

Applying Bones

According to the literature, motion patterns are very important in the recognition of individuals from an animation and getting the body movements right is crucial (Woo and Rieucan, 2011). Videos of swimming fishes were analysed, to identify and recreate the motion involved in swimming in the ninespine stickleback. Three key movements were identified: the tail bending, the pectoral fin waving, and the caudal fin waving. These movements were controlled by Blender bones, using two different types: the deform bones that modify the mesh of the object, and the control bones that change the position of one or more deform bones.

First, the tail bends whenever the fish changes direction while swimming. To recreate a natural bending of the tail, the fish had to be supplied with a spine, composed of bones linked so that

any movement or rotation in one vertebra would induce the neighbouring ones to bend. To do this, a chain of eight bones was inserted, and constrained to react as a Spline IK. The inbuilt Blender Spline IK function is applied to the last bone of the chain of eight, and assigned a spline fitting of 8. This function constrains the chain of bones to react to the movement of a background Bezier curve, offering predictability and smoothness of a curve movement. This Bezier curve is in turn controlled by the addition of three empty objects placed at each extremity and in the middle. These objects are themselves controlled by control bones, which have no effect on the body. This setup gives a motion pattern similar to what would be seen in a real spine, where each vertebra is connected to the next. The bones were then assigned weight using the automatic weight assignment function in Blender, giving an overlapping gradient of weight to each bone in the spine.

Second, the caudal fin produced a waving motion whenever the fish is moving. To reproduce this specific movement, three bones were extruded from the last bone of the spine, and placed in the caudal fin with 45° between each of them on the z axis. Using the weight paint brushes, a gradient of weight was assigned to each of them, with overlapping edges.

Third, the pectoral fins produce a waving motion constant through movement. To reproduce this effect, three chains of eight bones were extruded from the end of the first bone, using a mirror to obtain a symmetrical skeleton. Using the weight paint brushes, each bone was assigned a gradient of weight on the mesh of the pectoral fin. Once the bones and respective weight were finalised, the mirror was applied, leaving the mirrored changes as is, but allowing further changes to be done on one side only. Then, the bones on one side were assigned constraints called Copy Location, and Copy Rotation. As the name implies, this constricts the bones of one side to copy the movement of the other side. The influence of Copy Location was on the three axes, with the X copying inverted. The influence of Copy Rotation was also on the three axes, but inverting the rotation of the copied bone on the Y and Z axes.

The last step was to assign a parent-of-all empty object, which would be used to change the position of everything comprised in the fish image.

Applying Textures

The default texture and colour of all objects in Blender is a very dull grey. However, each face, or group of faces, can be assigned a chosen colour or texture. These colours and textures can be modified in their diffuse and specular hues, and intensities, as well as in their transparency and reflection. Table 3 gives the details of the material used for each object and object part, while Table 4 defines the composition of these materials. A view of these materials is provided in Figure 5. For more details, refer to the file called poor-all in the supplementary materials contained in the zip file attached.

Object	Object Part	Name of Material
Tank	Front face	Material.003
	Back and side faces	Material.001
	Bottom	Material.002
Algae	Whole	Material.004
Rock	Whole	Material
Fish	Pupil	Pupil
	Eye Layer	Eyewhite
	Fins	Fins
	Fin "bones"	Bones
	Body	Body
Feeder	Whole	Feeder

Table 3: Objects and corresponding materials

	Diffuse			Specular			Transparency		Mirror	Texture	
Name	R	G	B	R	G	B	Type	Alpha	Reflectivity	Name	Type
Material.003	0.8	0.731	0.551	1	1	1	Z	0.08929	-	Texture.010	Noise
Material.001	0	0	0	0	0	0	-	-	-	Texture.002	Wood
Material.002	0.208	0.138	0.043	1	0.72	0.426	-	-	-	Texture.011	Noise
Material.004	0.027	0.073	0.008	0.001	0.017	0.0012	-	-	-	-	-
Material	0.253	0.253	0.253	0.272	0.272	0.272	-	-	-	Texture	Wood
Pupil	0	0	0	0	0	0	Z	0.912	0.484	-	-
Eyewhite	0.171	0.179	0.125	0.042	0.04	0.009	-	-	0.245	Texture.029	Voronoi
Fins	0.570	0.510	0.424	1	0.711	0.537	Z	0.283	-	Texture.027	Noise
Bones	0.319	0.284	0.204	0.203	0.180	0.1	-	-	-	Bones.003	Noise
Body	0.497	0.479	0.26	0.124	0.108	0.01	-	-	0.308	Texture.025	Noise
										Texture.026	Musgrave
Feeder	0.8	0.8	0.8	1	1	1	-	-	-	-	-

Table 4: Details of the materials

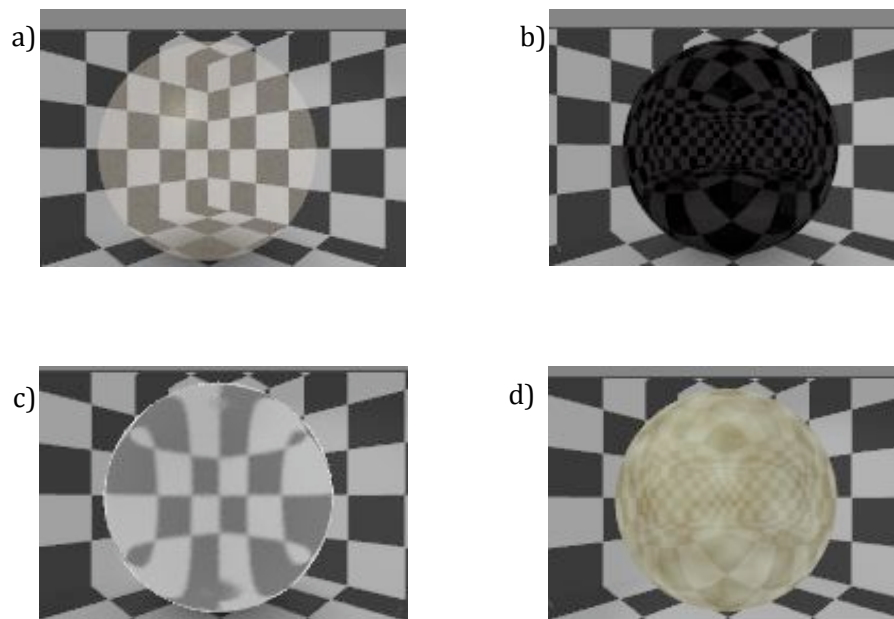


Figure 5: Preview of the different materials used in the animation for a) the fins, b) the pupil, c) the glass, d) eye membrane

Once the fish was complete with bones and textures, it was multiplied and then dissociated from its clones. Six different fish were created this way, and each was identified by a non rendered object of a different shape and named after it.

Creating Movement

To create a moving object, each bone has to be assigned a position in the 3D space at defined time. These positions comprise location, rotation, and scale on the three axes and are referred to as keyframes. The keyframes are assigned to specific frames in the timeline, keeping in mind that the rendered animations are typically at 24 frames per second rate. Blender interpolates the appropriate transitions between the specified keyframes following a Bezier curve interpolation mode.

Following these procedures, six different paths were created through the tank for a length of 2:30. The parent-of-all empty object became really handy, as recording its location and rotation is enough to move the whole fish. The positions were assigned randomly and used all axes for movement. The empties were constrained using the Add Constraint function in Blender to stay in the tank. The exact function used was Limit Location, and limited movement in the way described in table 4.

Limit	Minimum	Maximum
X	-9.1	7.2
Y	-9.1	9.1
Z	-4.8	4.8

Table 4: Limit Location function details

Once the paths were done, the tails were registered with a bend each time the fish was changing direction. The creation of the tail bending involved moving the caudal control empty object, recording its location and rotation as a keyframe, thus moving the underlying Bezier curve and creating a nice bend in the spine.

The waving motion of the fins was then keyframed, each bone at a time. This sequence was repeated to cover the length of the motion pattern.

Each movement that involves a new subset of bones is saved as specific action strip. These action strips can then be modified using the Non-Linear Action (NLA) editor in blender. This editor allows the strips to be moved around to start at any particular time while keeping the relation between the keyframes, and also allows the length of the strip to be changed (speeding up the movement). These strips can also be repeated to give desired length.

Rendering the Animation

Rendering an animation is a two-step process. The first being the rendering of each frame into a single image, and the second, the rendering of these images in a video file. The images were rendered in a PNG format at a resolution of 100% at 24 frames per second. These images were then imported in the Video Sequence editor of Blender, and the sequence was repeated until the desired length was achieved. It was then rendered into a video, using a H.264 codec.

Testing the Animation

Once animations were ready, they had to be tested to ensure that they were of any relevance to the live fish.

Subjects

The subjects were ninespine sticklebacks (*Pungitius pungitius*) caught from Leicester, England in 2009. They were held in groups of 30 in a laboratory in 30L aquariums at a temperature of 10°C in a 12/12 light cycle. The experiments were conducted between November and December 2011. All fish were used only once for these experiments and only the ones that revisited the central patch were kept for analysis. In total, 63 fish were tried, and 60 were kept for analysis.

Setup

The basic setup consisted of a 30cm by 30cm glass tank, flanked on each side by CRT monitors, each plugged into an ACER computer. The monitors were of the same model and set on the same settings with a refresh rate of 60Hz. The observer was confined in a holding bay made of

transparent partitions and positioned in the centre of the tank. Everything was filmed with a Canon HG20 camera, set at a meter distance away on a tripod.

Tests

This round of experiments consisted of looking at the response of live fish to the animated ones. To examine this, fish were presented with different combinations of two animations (each side) varying in the composition of the shoal.

The test was divided in three consecutive stages: habituation, demonstration, and test phase. It started with a habituation phase of ten minutes, when the observers were constrained in a central transparent bay and presented with an empty tank image for ten minutes. Then the demonstration phase started, where the observer was watching a different animation on each side for ten minutes. After this phase, the observer was released while the animations continued and was free to shoal and associate for five minutes.

During the demonstration period, the fishes were presented with three conditions, composed of a combination of two different animations. In the first condition, fish were presented with an animation of three fish opposed to an empty tank scene. The second condition presented them with animations of two fish opposed to six fish. The third condition consisted of presenting observers with a shoal of three animated fish, compared to a shoal of three live fish. This shoal was placed in a separate tank of the same size, with the computer monitor displaying an empty tank scene placed at the rear. All animations were presented on alternating sides, to avoid any possible side bias.

During the test phase, the observer was released and its position was monitored every ten second for five minutes, according to outside markers delimiting the tank in three distinct zones: a central zone of twenty centimetres, with a right and a left side of each five centimetres. The side zones measured five cm, a bit less than two body sizes, and thus sensible for a shoaling

situation. They were considered in a zone when their body and pectoral fins had crossed marker.

We predicted that according to shoaling behaviour, fish would prefer the three fish shoal compared to the empty tank, the six fish shoal compared to the two fish shoal, and the live fish compared to the animated ones.

Analysis

Using a Bayesian approach, data was analysed with a logistic regression with a multinomial error structure and logit link function. We used Markov Chain Monte Carlo methods to fit the models in WINBUGS 1.4 and to generate credible intervals for each parameter. Parameter values were estimated using a sample of at least 3000 iterations, after a suitable burn-in period and thinning to remove autocorrelations. The model produced a range of likely values for true difference of time spent between both sides.

Results

Table 6 presented below shows sample size, value of the median, and 95% credible intervals for the modelled difference of time spent between both sides, as well as the MC errors. When the median and confidence intervals are positive it signifies that the difference was according to expectations.

	Sample size	Median	2.5%	97.5%	MC error
0 vs. 3	13	0.409	0.1468	0.669	0.001272
2 vs. 6	26	0.2475	0.04993	0.4346	7.913E-4
3 vs. 3	21	0.1373	-0.01203	0.2865	9.554E-4

Table 6: Modelled difference of time spent between sides

In the first condition, presenting an empty tank versus a shoal of three fish, the modelled data tells us confidently that they did prefer the three fish shoal. The second condition analysis also demonstrates a preference for the larger shoal. The third condition results point to a preference towards the live fish shoals, although very small and uncertain.

Discussion

The results clearly point out that the animation is being recognised by the fish; they are shoaling according to expectations, and the animation can thus be used for behavioural studies.

In the last condition, fish still showed a preference for the live demonstrators, suggesting that the animation is not on par with live fish. However, seeing that these were shoaling studies, the shoals were still presented when the association of the observer was recorded, allowing for attraction to interactions. These interactions are only possible with the real fish shoal. It is likely that the observer's preference for the live fish presentation is due to this difference in interaction. Moreover, given this possibility of responses from the demonstrating shoal, the small preference displayed (modelled median of 0.1375) serves to highlight that the fish contained in the animation are not supernormal. Supranormality of responses is always a concern in the use of animated stimuli but can here be ruled out by the responses of the fish (Künzler and Bakker, 1998).

Moreover, the textures applied to the overall scene were designed to represent the textures of each part to the experimenter's eyes. Although sticklebacks possess the same three RGB cones as humans, it is unknown how the fourth cone (UV vision) participates in the representation of the world. In this case, the fish seemed to accept and react to those textures and colours without too much suspicion.

Even if the fish displayed normal shoaling behaviour in response to the animations presented, the parameters contained in the animation have not been tested individually. In other words, the animations could contain certain parameters that are unnecessary, or that could elicit an unknown or inappropriate response from the observer. This means that the animation has to be used with care. It is important to avoid making suggestions about behaviour based on the response of a fish to the basic animation and to not make inferences on their perception system or to say what is required in order to appear like a fish. In this case, the only way to make credible propositions on behaviour is to vary or add one parameter, and use the basic animation

to compare responses from fish. The change in behaviour can thus be attributed to the change made in the animation.

Following these guidelines, the animation proved appropriate for use in behavioural studies, and elicited enough response from the observer to be considered as depicting another fish. The animation could thus be used for more complex studies, and hopefully could be used to transfer information to the observers by social learning, or in this case, technology learning.

Part II: Testing Public Information Cues

Introduction

Social learning is used as an alternative strategy to gain information on the quality of a resource when the information that could be gathered personally would be insufficient or impossible to gather. Within this, an error-free process based on collateral behavioural cues called public information can give individual information on quality by monitoring activities and performance of others.

Ninespine sticklebacks (*Pungitius pungitius*) are public information users, utilising shoal behaviour when interacting for a food source as an indication of the quality of the patch (Coolen et al., 2003). This process is thought to be highly beneficial for this species.

Public information comes directly from the observation of other individuals, thus there is something that differs in the behaviour of fishes feeding at different rates. While a few cues could be identified by analysing videos (Webster M., pers. comm.) they could hardly be isolated and studied separately. Hence we relied on a relatively new system, that could completely control the behaviours of the demonstrators. This follows the first part of the project, where the appropriate system and data file was created.

Methods

Creating the Animations

The basic framework of the animation was taken from the previously tested document (see Part I), but with the modification of one parameter in order to recreate the cues seen to vary in videos of feeding shoals. Five different components of shoal behaviour were identified for investigation: 1) activity rate, 2) strike rate, 3) distance to feeder, 4) shoal cohesion, 5) position in the water column. These components were then recreated in the animations, creating one

seemingly rich, and one poor animation (these terms refer to the changes seen in feeding live demonstrators' videos). These modifications are further described below.

- 1) Activity rate: In the analysis of videos, fish feeding at a higher rate were seen to also move faster in the tank (move body length/minutes). When experimentally recreated, raising the water temperature was used to reproduce this increase. The test showed that the observers preferred the formerly more active side during the test phase. In Blender, activity rate was increased by augmenting the speed at which fish swam through the path in the tank. In the slow, or poor patch, fish went through the motion in 2:30 minutes, while in the rich or fast patch, they went through it in 1:30 minutes.
- 2) Strike rate: The striking pattern is very specific in the ninespine stickleback, where body angle changes and the fish bursts towards the food object, or the apparent food. In preliminary studies, it was also found that observers would prefer to associate with a patch that was formerly displaying more striking behaviours. In Blender, this was recreated by inserting a striking cycle (2 strikes per fish) at 1:30 and 9:00 in the representing the poor patch, and at 1:30, 3:00, 4:30, 6:00, 7:30, and 9:00 in the rich patch animation.
- 3) Distance to feeder: Since the fish in the demonstration phase were feeding from a white rectangular apparatus, they were overall closer to the feeder while in a high feeding patch. The preliminary studies with live demonstrators did not show any effects, and parallel studies failed to show any stimulus enhancement or stimulus recognition (Webster M., pers. comm.). In this case, distance to feeder was reduced in the poor patch animation by constraining the fish to swim in the half of the tank that was further away. In the rich patch animation, fishes were swimming only in the half of the tank in which the feeder was contained. These constraints were achieved using the built in Limit Location constraint, applied to the parent-of-all empty object. Movement was limited on the Y axis, from 0 to +/-9.1.

- 4) Shoal cohesion: In this case, shoal cohesion was taken as distance between individuals. This distance can be either in the water column axis (z) or on one of the plane axis (y), yielding two different conditions of tests for cohesion. In pre-test, this did not seem to have an impact on observer's patch quality assessment. To modify this component of shoal behaviour, fish were constrained using the same built in function, Limit Location. The first set of animation, cohesion on the z axis, had the fish freely swimming through the tank in the poor patch, and constrained on the z axis to -4.8 to -2 in the rich patch. The animations testing the cohesion between individuals on the y axis had the fish swimming through the whole tank in the poor condition, while constrained on the Y axis from -9.1 to 0.
- 5) Water column position: Sticklebacks are naturally substrate feeders. It would thus be expected that when in a rich environment, most of their time would be spent in the lower part of the water column. This did not seem to yield any response when isolated in live demonstrators. To investigate this, fish were restrained using the Limit Location function, to the higher third of the water column in the poor patch (Z from 2 to 4.8) and to the lower third in the rich patch (Z from -4.8 to -2).
- 6) Finally, to be sure anything was being transmitted at all, an all cues combined animation was created. In the poor patch animation, fish were random in the water column and in the tank plane, feeding at two deliveries per animation, and swimming at low speed through the tank (2:30). The rich patch animation showed a shoal reduced to the lower third and the half of the tank with the feeder, swimming fast through their motion (1:30) and striking every 90 seconds, for a total of six times in the length of the animation.

These components yielded seven different conditions, consisting of a poor and a rich animation. To be able to test these cues, a feeder like object was created from a box mesh object. This feeder was then assigned a white colour, similar to the apparatus used in the previous studies (Coolen et al., 2003; Coolen, 2005; van Bergen et al., 2004; Pike and Laland, 2010; Pike et al., 2010b; Duffy et al., 2009; Kendal et al., 2009).

Once these modifications to the files were done, the images were rendered in a PNG format, and then reinserted in the Video Sequence Editor. The strips of images were repeated until they were of the desired length.

Testing the Public Information Cues

The setup was kept the same then in the Part I of the experiments (see p. 26) with the same tanks, subjects, cameras, and monitors. In total, 179 fish were used, and 169 were included in the analysis. The fish were used only once, and only those who revisited the central patch during the test phase were kept for analysis.

The phases of the experiments were also similar. It started with a habituation phase of ten minutes, where the screens were displaying an image of an empty tank with a feeder apparatus. After ten minutes, the screens displayed a black image for five seconds, mimicking the partitions used when manipulating real fish. The next ten minutes were devoted to the demonstration, and the animations were presented according to the seven conditions described above. The side the animations were presented on was also alternated, in order to overwrite any possible side bias. When the demonstration was finished, the screens went black for five seconds again, and the fish was released into the test phase with screens displaying the empty tank with feeder again. The position of the fish was recorded every ten seconds, for 90 seconds, starting after the subject first entered a goal zone. A fish was considered as being in a zone when it had crossed the line up to its pectoral fins.

As a control to verify that the added feeder was neutral to the fish, a simple test was done where fish contained in the observer bay were exposed to an empty tank opposed to an empty tank with feeder for a habituation phase of ten minutes, and thereafter released and free to swim in the tank. Their position was recorded every ten seconds for five minutes.

Analysis

The same methods were used to analyse these results (see page 27). This time, when median and confidence intervals were falling above zero, it meant that the fish were displaying a preference for the animation defined as rich.

Results

Table 6 contains the modelled results; medians, 95% intervals, and MC errors are given. The table also contains sample size.

	Sample size	Median	2.5%	97.5%	MC error
Feeder control	20	0.05008	-0.3124	0.4441	0.001989
Activity rate	31	-0.05247	-0.5067	0.4108	0.001661
Strike rate	18	0.4672	0.003676	0.8996	0.002805
Distance to feeder	19	-0.408	-0.7586	-0.03404	0.00135
Shoal cohesion (z)	19	-0.0976	-0.6365	0.1494	0.001883
Shoal cohesion (y)	23	-0.6212	-0.8552	-0.3362	0.001224
Water column	20	-0.3612	-0.8587	0.2303	0.003148
All cues	19	0.1382	-0.03669	0.4379	0.001124

Table 6: Modelled results of the difference in time spent between the “rich” and “poor” patch

- 1) Activity Rate shows a median close to zero and a 95% interval almost symmetrically distributed around zero, depicting no clear preference for any side when swimming speed was modified.
- 2) The strike rate modelled results show that the fish did prefer the side associated with a high strike rate.
- 3) The distance to feeder test demonstrated that the fish preferred the side where the demonstrators were swimming in the half of the tank that was far from the feeder.
- 4) The shoal cohesion tests showed an overall tendency to prefer shoals with more distance between individuals, with medians and confidence intervals below zero, so more time spent in the “poor” patch. This tendency was stronger when the distance between individual was reduced on the Y axis than on the Z axis. The modelling of results of a reduced distance between individuals on the Z axis suggests they would

prefer a less cohesive shoal; however evidence for this is uncertain and weak, and could actually go both directions.

- 5) The evidence for the water column position do not show any preference for either side.
- 6) The all-cues-combined test showed a small tendency to prefer the animation with was termed “rich” compared to the one that contained the poor feeding rate cues.

The feeder didn’t seem to change anything in the behaviour of the fish, with modelled difference of time spent centred on zero.

Discussion

The main intention of the experiment was to transfer social information to observer fish, in the context of a patch decision choice. When all the cues seen in a shoal of feeding live fish were combined together, the tested sticklebacks displayed a small preference for the side where the rich animation was formerly presented. The preference of the observers towards the rich animation does not seem to be as powerful as the one found in the previous public information experiments from Coolen et al. (2003). However, it does seem to imply that some information is being passed along, and different scenarios could explain this small impact.

When the cues were tested individually, the fish showed varying responses to them. They displayed a strong preference for a less cohesive shoal, fish that were more distant to the feeder, and a high strike rate.

When the fish were subjected to shoals that differ in their cohesion on the X axis, they showed a strong preference for the less cohesive shoal. There was also a small preference for shoals that were less cohesive on the Z axis; however this difference in time spent was weak. The animations were termed “poor” and “rich” following what was observed in the videos of live shoals feeding, where it was observed that the distance between individuals was shorter when feeding at a high rate. This reduced distance could be an artefact of the feeding apparatus used in the experiments. This apparatus was placed in a corner of the aquarium, and thus a high

feeding rate intrinsically meant that fish would spend more time in that same corner, reducing the overall distance between individuals. It is also interesting to note that sticklebacks are naturally substrate feeders, and thus there is no reason to believe that a rich patch would lead to an increase in cohesion (Tugendhat, 1960; Hynes, 1950). We can however infer from the strong preference of the observers towards the loosely connected shoal that this condition did result in a transfer of public information. Shoal cohesion was influenced by a variety of factors and thus can potentially inform individuals of characteristics of the environment other than solely patch quality. Indeed, cohesion is altered under predation threat in the walleye Pollock (*Theragra chalcogramma*) who reduces distance between individuals when the environment is characterised by chronic threat (Sogard, 1997). Reducing distance between individuals, along with increasing shoal size, are indeed considered to be the primary behavioural responses to alarming conditions (Hoare et al., 2004; Magurran and Pitcher, 1987). Therefore, in this situation, observer fish might be selecting the loose shoal based on cues that relate to the stress and predation levels of the environment rather than gaining information on the foraging quality.

The difference in activity rate did not seem to induce any preference in the observer fish. However, during preliminary tests, high activity rates lead to stronger association from the observers (Webster, M., pers. comm.). In these tests activity rate was increased by increasing water temperature in the tank containing the presented shoal. It could thus be that along with an increase in activity rate, other behaviours were triggered. In a salmon species, *Salmo salar*, juveniles adjust their daily activities depending on the temperature of the water (Fraser et al., 1993). This increase in water temperature was seen to be related to time spent in cover and feeding activities. It could thus be that increased water temperature does in fact alter other behaviours that were not represented in the animation. There is however much evidence pointing towards preferences for more active shoals in fish when making shoaling decisions, and suggesting that activity rate might be used as a proxy to estimate shoal size (Pritchard et al., 2001; Buckingham et al., 2007). It is therefore more likely that the animation did not convey the increase in activity rate in a realistic manner. The way activity was increased was by

accelerating the speed at which fish went through their defined pathway. This might be unrealistic as fish might also increase turning rate, or change the way they swim by increasing the amount of burst and stop motion when general activity rate increases.

An unexpected result arose in the strong preference for the animation where the fish were swimming further away from the feeder. There are many instances of demonstrated local enhancement in fish, but stimulus enhancement could never be validated (Webster and Hart, 2006; Brown and Laland, 2011). In other words, fish feeding from a specific stimulus, in this case the white feeder apparatus, did not display any lasting attraction to the feeder itself, but even less repulsion to the apparatus. Moreover, the control experiment testing the impact of the feeder on the fish clearly demonstrated that the fish did not seem to be bothered by the apparatus, preferring neither side. It would therefore seem that the only explanation of this result is something that has to do with the interaction of the shoal swimming closely to the feeder and the said apparatus. It could also be just a false positive result, and testing more individuals could highlight the validity of the results found here.

Striking rate is the only cue identified in a rich patch feeding shoal of live sticklebacks that is able to induce a preference strong enough to override the negative impacts found from the other conditions. The response to the particular striking motion seem very strong, with evidence pointing towards 46% more time spent close to the six deliveries animation side. The particular striking motion of the sticklebacks has been documented before, with clear stage of feeding bouts identified (Tugendhat, 1960). It is therefore conceivable that the recognition of this darting-like motion evolved because it is good indicator of prey density.

It seems that all these individual cues could be weighted by the observer fish and the decision to associate with patches could depend on a more generalised computation of the environment. Indeed, it seems that the fish would be assessing the trade-offs of associating with different patches based on cues received through public information. Even if the information gathered through shoal cohesion transmitted aversive information to the fish, when it was presented

with a high striking rate this aversion seems to be partly overridden, with fish slightly preferring the patch where high feeding activity was seen. At this stage, it is only speculative to say that these cues are in fact additive, but the difference of response to isolated cues compared to all the cues combined seems to suggest that the use of public information by ninespine sticklebacks is not only adaptive, but the decision they take based on received public information derives from integration of information on different aspects. This information would then be weighted and trade-offs assessed. It is however clear from these results that the public information signal used to assess foraging patch quality in the ninespine sticklebacks is most likely the striking rate, and that the amount for strike rate represented was enough to balance the aversion produced by increased shoal cohesion.

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