

Social learning in fishes: a review

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Abstract

Animals acquire skills and knowledge from other animals, and fish are no exception. There is now strong experimental evidence that many species of fish exhibit social learning and traditional behaviours. Here, we review the literature pertaining to social learning in fish, focusing on (i) antipredator behaviour, (ii) migration and orientation, (iii) foraging, (iv) mate choice and (v) eavesdropping.

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Introduction

In making decisions, such as how to find food and mates or avoid predators, many animals utilise information that is produced by others. Such individuals are referred to as 'eavesdroppers' in the signal-receiver literature (McGregor 1993) and 'observers' in the

social-learning literature (Heyes and Galef 1996). Socially transmitted information may simply be a by-product of the 'demonstrating' individual's behaviour or a signal targeted towards a particular audience. Learning that involves the use of socially provided information is termed as 'social learning'. Social learning refers to any incidence in which

individuals acquire new behaviour or information about their environment via observation of, or interaction with, other animals or their products.

It is generally assumed that social learning is beneficial because naïve individuals can quickly and efficiently acquire locally adaptive behaviour from more knowledgeable individuals (Boyd and Richerson 1985), for instance, without having to incur the costs of exploration or the risks of learning about predators. Social learning is sometimes assumed to be more common in, of a more sophisticated form in, or even restricted to, 'intelligent' or 'large-brained' taxa. However, research over the last 50 years has demonstrated that social learning is common amongst fish, birds and mammals, and should now be regarded as a regular feature of vertebrate life (Lefebvre and Palameta 1988; Heyes and Galef 1996).

Many of the processes that underpin social learning lend themselves particularly well to shoals of fish, although they are by no means restricted to shoaling species. The terms used to describe different forms of social learning can be confusing; so, a brief description of some of the more commonly used terms is given in Table 1. In addition, a variety of other processes, some assuming more sophisticated psychological underpinnings, can also facilitate social learning in animals, described variously as imitation, goal emulation, copying, etc. (for reviews, see Whiten and Ham 1992; Heyes 1994). We do not know of any laboratory evidence that suggests that fish are capable of imitation, i.e., learning to produce particular bodily movements through observation. However, suggestive circumstantial evidence of imitation is provided by Mazeroll and Montgomery's (1995) report

that in the local migrations of Brown surgeonfish (*Acanthurus nigrofuscus*; Acanthuridae), followers not only take the route of leaders, but also reproduce their postural changes (e.g. dips and rolls). However, it is a feature of animal social learning that simple processes are sufficient both to allow individuals to acquire adaptive information and to mediate behavioural traditions in populations.

Over the last 20 years, the study of social learning has expanded greatly and is now a major topic of research in ethology, behavioural ecology and comparative psychology (Galef and Giraldeau 2001; Shettleworth 2001). Documented cases of social learning in fish are now commonplace, and our growing understanding of the underlying mechanisms is enabling further identification and clarification of such phenomena. Here, we review evidence that social learning plays a role in fish (i) antipredator behaviour; (ii) migration and orientation; (iii) foraging; and (iv) mate choice; and (v) that it is facilitated by eavesdropping.

Antipredator behaviour

It is well-known that the antipredator behaviour of many fish has a learned component, and countless species of fish improve their antipredator response with experience (Kieffer and Colgan 1992; Kelley and Magurran 2003). However, learning about predators is a risky business, and there is little room for mistakes or extensive training (Kelley and Magurran 2003). Given the large risks and limited opportunities for a social learning, it is easy to see the potential benefits of learning about predators from others. Not

Table 1 Processes of social learning

Term	Explanation
'Local enhancement' or 'stimulus enhancement'	The behaviour (or simply the presence) of one individual attracts the attention of another individual to a particular location or stimulus, about which the naïve individual subsequently learns something
'Social facilitation'	The behaviour of one individual induces an identical behaviour in another individual and the latter then learns something via the expression of this behaviour; for instance, it learns about the consequences of producing the behaviour in that context
'Guided learning' or 'exposure'	By following or being with a knowledgeable animal, an individual is exposed to similar features of the environment and comes to learn the same behaviour
'Observational conditioning'	The response of a demonstrator to a stimulus elicits a matching response on the part of an observer, that simultaneously perceives the original stimulus, and effectively learns that the response is an appropriate response to it
'Imitation'	Learning to produce particular bodily movements through observation of others

surprisingly, social learning of predator presence or identity appears widespread in fish (Suboski and Templeton 1989; Brown and Laland 2001).

The use of socially transmitted information enables individuals to respond to threats without having to verify the presence of danger independently. Fish are particularly well equipped for rapid information transfer via sight and the lateral-line system. Such information may pass through a shoal much more quickly than the speed of an approaching predator or the diffusion of an alarm substance (Webb 1980; Potts 1984), resulting in what appears to be a synchronous response of shoal members. While such responses are not in themselves social learning (being merely manifestations of communication between shoal members), in the process, young and inexperienced individuals frequently learn to identify predators, acquire appropriate antipredator responses or refine these responses.

Members of fish shoals are able to make decisions about predators by observing changes in the behaviour of shoal mates. When fish return from a predator inspection visit, it appears that the behaviour of the rest of the shoal changes in response to the level of threat perceived by the inspectors as a manifestation in their behaviour (Pitcher *et al.* 1986). When fish are attacked or startled by the presence of a predator, they frequently display a fright response. It has long been known that the fright responses of many fish can be precipitated by a chemical alarm substance emitted by fish (von Frisch, cited in Pfeiffer 1974; see Brown 2003). However, von Frisch discovered that anosmic fish joined the fright reactions of conspecifics, and subsequent research has established that such fright responses can be visually transmitted. The fright response provides an obvious visual cue that a predator is in the vicinity. For example, European minnows (*Phoxinus phoxinus*; Cyprinidae) increased the frequency of flight responses after observing the flight response of conspecifics in a neighbouring tank that had been threatened by a predator (Magurran and Higham 1988). Not only is the speed of communication considerably increased over the diffusion of a chemical, but predator presence can be communicated to and by fish that have no direct experience with the predator. Social learning of fright responses has also been reported in mixed-species shoals, where the fright response of one species elicits a similar response in a second one (Krause 1993; Mathis *et al.* 1996).

Conceivably, the elevated antipredator responses of fish that have recently witnessed conspecifics and

heterospecifics behaving fearfully in the presence of a predator could be the result of a number of processes. Central to the story would seem to be the forming of an association between the fright reaction of conspecifics and the predator. Observers may learn the identity of a predator by avoiding anything that elicits fright responses in conspecifics. Evidence for this comes from the study of Suboski *et al.* (1990), who demonstrated that minnows could learn a fright response to olfactory cues from a novel predator, if these cues were presented at the same time as either the visual fright reactions or the alarm substance of the conspecifics. A similar mechanism can result in fish learning about risky habitats (Chivers and Smith 1995). The above are examples of observational conditioning. It would seem that many fish exhibit an unlearned fright response to the alarm substance (von Frisch, cited in Pfeiffer 1974), which would be sufficient for it to act as an unconditioned stimulus and would, through Pavlovian conditioning, explain the conditioned response to the predator when the alarm substance and predator are paired. It is less clear how the fright reactions of conspecifics should play this role. Perhaps, they too elicit an unlearned fear response, but more plausibly, they could have acquired higher-order conditioning properties through prior association with the alarm substance, or with other predators. In addition, observers may learn to flee, seek refuge, freeze or shoal tightly when others do so, or that these behaviour patterns are appropriate responses to the predator. Furthermore, observers may have their motivational or physiological state changed as a result of perception of fearful conspecifics in a manner that leaves them more likely to learn about all aspects of their environment. Clearly, a complete understanding of this apparently simple example of social learning awaits further analysis.

As yet, there is little direct evidence that fish learn antipredator responses to natural predators through social learning (for example, that they learn to respond differently to different threats, such as shoaling vs. hiding). Nevertheless, investigations into the avoidance responses of guppies to artificial predators (Sugita 1980; Brown and Laland 2002a) suggest that this is possible. Sugita (1980) found that guppies (*Poecilia reticulata*; Poeciliidae) learn to avoid an electric shock by following demonstrator fish into one of the two safe compartments in a shuttle box. Brown and Laland (2002a) exposed naïve fish to a model trawl apparatus, which simulates a predator. Half of the naïve fish were placed with demonstrators trained to

take one escape route and the others to demonstrators trained to take an alternative route. Both groups remained faithful to the demonstrated route and escaped more frequently than control groups, while the demonstrators were present. However, once the demonstrators were removed, although the experimental groups were still far more efficient at escaping than the control groups that had had no demonstrators, their fidelity to the demonstrated route degraded. These results suggest that the fish learnt an appropriate escape response by following the example set by demonstrators. While, in the absence of clear demonstration, functional aspects of traditional behaviour were maintained (i.e. to escape by swimming through a hole in the trawl), more arbitrary components were lost (i.e. utilisation of the previously demonstrated route when equally viable alternatives are available).

Migration and orientation

A number of studies have explored how, through social learning, fish may learn to orientate around their environment and, in the process, learn the route to food, resting or mating sites.

One of the most elegant demonstrations of social learning in a natural population of fish was carried out by Helfman and Schultz (1984). Helfman *et al.* (1982) had discovered that specific resting sites in coral reefs contained groups of French grunts (*Haemulon flavolineatum*; Haemulidae) that made daily migrations to the feeding grounds. These groups appeared to be joined occasionally by newly recruited juveniles, that had followed older individuals and subsequently learned the migration path. Helfman and Shultz (1984) tested this by transplanting individuals between resting locations, and then recorded their path towards foraging grounds. In the experimental condition, the transplanted juveniles were allowed to follow the residents for 2 days before the residents were removed. In a control condition, the resident populations were removed prior to transplanting. While the experimental fish learnt the same migration path as the resident adults, the control fish continued to use paths appropriate to their original resting site.

Bluehead wrasse (*Thalassoma bifasciatum*; Labridae) shows similar migratory traditions. These fish have mating locations that remain constant over many generations. Warner (1988, 1990) removed entire populations and replaced them with transplanted populations. Not only did the new fish estab-

lish new mating grounds, but these new locations remained constant over the subsequent generations. In the 12 years of studying 22 patches on the reef, not once was a new mating site established or lost, despite fluctuations in the wrasse population size. Combined with the observation that reef populations are not subjected to significant genetic differentiation (Warner 1988), this finding provides strong evidence of cultural variation.

In laboratory experiments, Laland and Williams (1997, 1998) found that naïve 'observer' guppies could learn a route to a foraging patch by following more knowledgeable 'demonstrators'. Observers were placed in the presence of demonstrators that had previously been trained to take one of the two routes to feed. Observers typically shoaled with the demonstrators and fed at the feeding site. When the demonstrators were removed, the observers continued to utilise the same route to feed, despite the availability of an alternative route. Traditions were established in small populations in which experienced fish were repeatedly replaced with naïve conspecifics, and yet, the route preferences remained. Laland and Williams (1997) found that as the number of demonstrators increased, the more likely it was that observers would remain faithful to the route. This is consistent with the hypothesis that animal social learning is commonly 'conformist', with the rate of transmission increasing with the number of individuals displaying the behaviour. The strength of social learning in the experiment of Laland and Williams (1998) was such that guppies would even maintain traditions for maladaptive circuitous routes for brief periods. This is the case even when the fish could see the foraging patch through a transparent partition and had been individually trained to take the shorter route (Bates and Chappell 2002). Similarly, Reeb (2000) has found that naïve golden shiners, *Notemigonus crysoleucas* (Cyprinidae), could be trained to make daily migrations to a food site by following trained demonstrator conspecifics.

The guided learning process suggested by the above findings probably underlie the traditions of coral reef fish, and perhaps, the migrations of walleye (*Stizostedion vitreum*; Percidae; Olson *et al.* 1978) and surgeon fish (Mazeroll and Montgomery 1995). It is still largely unknown if fish use social learning to aid in the navigation during large-scale migrations, such as those seen in salmoniids and eels (see Odling-Smee and Braithwaite 2003; Tsukamoto *et al.* 2003).

Foraging

Given the interest among behavioural ecologists in prey choice (Stephens and Krebs 1986; see Warburton 2003), there has been surprisingly little attention given to how social learning might facilitate the acquisition of dietary preferences. However, social learning is implicated in patch choice, where the use of socially transmitted information is well established in fishes (Pitcher and House 1987; Ryer and Olla 1991). 'Forage area copying' (Barnard and Sibly 1981) appears to operate through a local enhancement process. Once discovered, the foraging behaviour of the finder of a patch acts as a cue to the rest of the shoal, which quickly joins it. Groups of fish find food faster than individuals because the probability of detecting a patch varies directly with group size, while the time spent on vigilance is inversely related to the group size (Morgan and Colgan 1987). In open water, goldfish (*Carassius auratus auratus*; Cyprinidae), bluntnose minnows (*Pimephales notatus*; Cyprinidae), Alaska pollack (*Theragra chalcogramma*; Gadidae), sticklebacks (*Gasterosteus aculeatus*; Gasterosteidae) and guppies forage more efficiently in social groups than alone (Pitcher *et al.* 1982; Pitcher and House 1987; Morgan 1988; Ryer and Olla 1992; Pehkuri *et al.* 1995; Day *et al.* 2001).

It is generally accepted that fish in large shoals find food sooner than those in small shoals, largely as a consequence of having more socially transmitted information available to them. However, Day *et al.* (2001) discovered that where the food patch is visually isolated from the shoal, smaller groups of fish discover it more quickly than larger groups. Day *et al.* interpreted this apparent contradiction as stemming from the fact that fish are generally reluctant to leave the safety of the shoal and forage on their own at a patch that is hidden. The larger the shoal, the stronger the apparent compulsion to remain. In small shoals, the protection conferred by the shoal is low, and individuals are more likely to break away and search for food. This reasoning is the logical inverse of the observation that fish will be more likely to join a large than a small shoal (Lachlan *et al.* 1998). Supporting this interpretation is Day *et al.*'s finding that individuals in large groups located food behind an otherwise identical transparent barrier faster than individuals in small groups.

Increased foraging efficiency in a social context is not only restricted to shoaling species. Juvenile Atlantic salmon (*Salmo salar*; Salmonidae) take up benthic foraging stations from which they dart to

the surface to intercept prey items and then return. Brown and Laland (2002b) set out to determine if the darting motion sends a message to other fish that food is available, and whether this cue could be utilised by the naïve fish to learn to forage on novel prey items. They found that 100% of the individuals that paired with pretrained demonstrators learned to accept the novel prey. Naïve fish paired with equally naïve individuals actually performed worse (50%) than the individuals learning in isolation (73%), a finding they interpreted as 'social inhibition'.

Social enhancement of foraging has also been reported in hatchery-reared juvenile chum salmon (*Oncorhynchus keta*; Salmonidae), Alaska pollack and rock bass (*Ambloplites rupestris*; Centrarchidae; Templeton 1987; Ryer and Olla 1991, 1992). Sundstrom and Johnsson (2001) also found an increase in foraging performance, when in visual contact with another feeding conspecific, in wild, but not in hatchery-reared, brown trout (*Salmo trutta*; Salmonidae), suggesting that the conditions under which hatchery fish are raised may diminish their ability to exploit social cues.

Finally, there is experimental evidence that fish can learn novel foraging behaviour through observation of conspecifics. Anthouard (1987) reports that juvenile European seabass (*Dicentrarchus labrax*; Moronidae) learned to press a lever to receive a food reward through observation of proficient trained demonstrators.

Mate choice

There is increasing evidence that social factors play a role in mate choice in a number of fishes (Westneat *et al.* 2000), including mollies (*Poecilia latipinna*; Poeciliidae; Schlupp *et al.* 1994; Schlupp and Ryan 1997; Witte and Ryan 1998, 2002), guppies (Dugatkin 1992; Dugatkin and Godin 1992, 1993; Briggs *et al.* 1996), gobies (*Pomatoschistus microps*; Gobiidae; Reynolds and Jones 1999) and the Japanese rice fish (*Oryzias latipes*; Adrianichthyidae; Grant and Green 1996). 'Mate choice copying' is said to have occurred when the probability of an individual selecting another as a sexual partner increases because other individuals (of the same sex) have selected the same partner (Gibson and Hoglund 1992). In the paradigm experiment (e.g. in guppies; Dugatkin 1992), two males are secured at the ends of an aquarium, one with a demonstrator female nearby. The observer, another female, placed centrally, watches the other female interact with one of the males. When, after the

demonstrator has been removed, the observer is allowed to choose between the two males, she consistently chooses the male that had the female nearby. In mollies, similar observations consistent with mate choice copying have been reported for males (Schlupp and Ryan 1997). Data also suggest that mate choice copying may occur in the wild (Witte and Ryan 2002).

One interpretation of these findings is that the observing female utilises the presence of the female near a male as an indication of his quality, and biases her male choice accordingly (Dugatkin and Godin 1992). However, there are a number of other interpretations (some detailed below), and researchers have struggled to replicate some prominent findings (Brooks 1996, 1999; Lafleur *et al.* 1997). Furthermore, in experiments where no mating takes place, it is not clear whether the observer's choice bears any relation to mating. Indeed, there is contradicting evidence for some species that suggests that they do not copy the choice of others, but rather, females avoid locations where they observe courtship occurring (feral guppies; Brooks 1999).

Mate choice copying is by no means the only way that socially influenced mate choice may occur. For example, in a number of species, females prefer males with a greater number of eggs present in their nest (sticklebacks, Goldsmith *et al.* 1993; bullhead (*Cottus gobio*; Cottidae) Bisazza and Marconato (1988); darter (*Etheostoma flabellare*; Percidae), Knapp and Sergeant (1989); fathead minnows (*Pimephales promelas*; Cyprinidae), Unger and Sergeant (1988); blennys (*Aidablennius sphinx*; Blenniidae), Kraak and Weissing (1996); sand gobies (*Pomatoschistus minutus*; Gobiidae), Forsgren *et al.* 1996 and others). Although the observing female may not have witnessed the laying of these eggs, conceivably their presence is a cue suggestive of mating success, or prior female choice. Once again, there are other explanations. In the case of the sand goby, females seem to use egg number as an estimate of a male's ability to defend their nests rather than prior female choice (Lindstrom and Kangas 1996). In sticklebacks, males steal eggs from neighbouring nests in an attempt to bolster their attractiveness (Largiader *et al.* 2001). Indeed, Patriquin-Meldrum and Godin (1998) argue that sticklebacks do not copy the mate choice of others. Further, there may be an alternative reason for females selecting nests with large numbers of eggs already present, which have nothing to do with mate choice *per se*; for instance, predator risk dilution (Jamieson 1995). While these other processes can

generate mating patterns similar to mate choice copying, they do not necessarily constitute social learning. The varying degrees to which different species rely on mate choice copying clearly remains open for additional investigation (for further discussion, see Lafleur *et al.* 1997; Westneat *et al.* 2000).

Eavesdropping

Male Siamese fighting fish, *Betta splendens* (Belontiidae), monitor aggressive interactions between neighbouring conspecifics and use the information on relative fighting ability in subsequent aggressive interactions with the males they have observed (Oliveira *et al.* 1998). Similar observations have been made in rainbow trout, *Oncorhynchus mykiss* (Salmonidae) (Johnsson and Akerman 1999). This exploitation of communicated signals in a network has become known as 'eavesdropping' (McGregor 1993). Oliveira *et al.*'s findings suggest that the level of aggression that eavesdroppers observe in interactions between a pair of demonstrators strongly affects their subsequent agonistic interactions. Male Siamese fighting fish also alter their threat displays depending on the audience as females also eavesdrop on male–male displays. In the presence of female observers, males reduce the number of aggressive components (e.g. bites) in their display and tailor it more towards a sexual display (Doutrelant *et al.* 2001). Despite the obvious correspondence in subject matter, unfortunately, eavesdropping has been largely ignored within the social learning literature.

Concluding remarks

In summary, there is now unequivocal evidence from laboratory and field studies that a variety of different species of fish are capable of social learning, including learning how to find food, which food to eat, to recognise predators and assessing mate and rival quality. When viewed in the context of the burgeoning literature on fish cognition (Bshary *et al.* 2002), it is quite apparent that the abilities and complexity of social behaviour of this group have previously been seriously underestimated.

We end by noting that the widespread use of social learning by fish may have important implications for conservation and fisheries reintroductions (Suboski and Templeton 1989; Brown and Laland 2001; Brown and Day 2002). Typically, over 95% of all fish released from hatcheries die from predation or starvation in the first few weeks following release (Brown and

Laland 2001), which is an enormous waste of resources. It is conceivable that hatchery-reared fish could be trained *en masse* to recognise predators and prey using social learning protocols. The evidence presented above suggests that it may be possible to cut postrelease mortality figures dramatically by allowing hatchery fish to learn from more experienced or wild conspecifics.

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