Social intelligence in fishes

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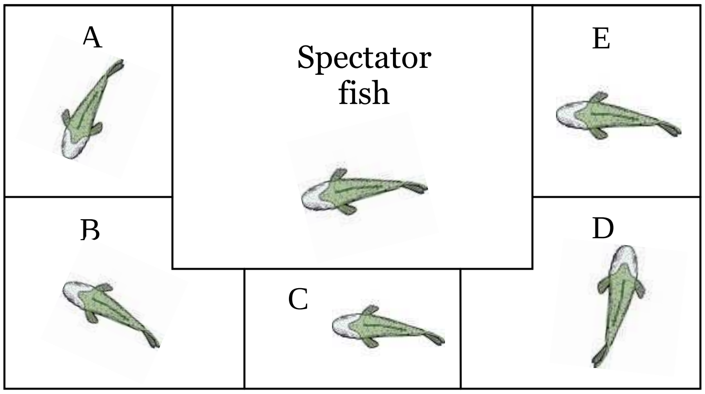
Following are examples of fishes being able to remember various things about other individuals such as their sex, competitive ability, or past behaviour. Then they seem to be aware of how the personal characteristics of these other fish may impact on their own lives, and they behave in a way that “makes sense” in light of what they seem to know.

In the preceding sentence I repeatedly used the word “seem”. I did so for good reasons. In my opinion it is impossible to know what goes on in the mind of a fish, and therefore we will probably never know for sure whether fishes “think” more or less like we do. No matter how smart some fishes may appear to be, it is always possible that their brain is wired in such a way that particular algorithms allow them to do clever things without necessarily giving them awareness of what they are doing. Personally, I do not find this ignorance of ours too disquieting. Generally I am content just to know what fishes can and cannot do.

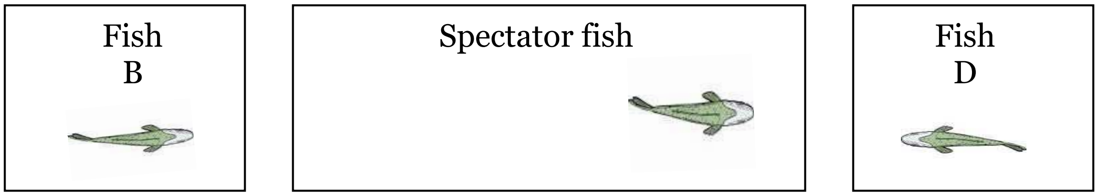
Hierarchy: if A > B, and B > C, then A > C

The title above illustrates what is known as “transitive inference”, the ability to use known relationships to deduce new ones. Mammals and birds are capable of such simple logical reasoning. However, it took until 2007 for the first example to be found in fishes. The study was conducted by Logan Grosenick, Tricia Clement, and Russell Fernald of Stanford University. It involved *Astatotilapia (Haplochromis) burtoni*, a cichlid from Lake Tanganyika that regularly fights over territories and resources (hey, it’s a cichlid!).

A male –let’s call him the “spectator”, though the technical literature prefers the term “eavesdropper”– was placed in a central aquarium surrounded by five other tanks in which five other similarly-sized males lived: we’ll designate those five other males as A, B, C, D, and E. Following is a view of this set-up from above.



In plain view of the spectator fish, male B was slipped into the tank of male A, who promptly thrashed him – the "prior residency effect", or home turf advantage, is a big factor in deciding who wins a fight in this cichlid. Following similar transfers of one fish into another's territory, the spectator male also saw B beating C, C beating D, and D beating E. Then the spectator male was transferred into a new aquarium sandwiched between two other tanks.



In one of those tanks was male B; in the other, male D. All three males could see one another. It was already known that in an experimental set-up like this (known as a choice test), *A. burtoni* prefers to spend more time next to the worse fighter. Now, note that both B and D had each won one fight and lost one fight. The only way the spectator fish could tell that D was subordinate to B was by remembering their respective relationships to C and making the appropriate inference. And indeed, the spectator spent more time next to male D. This procedure was repeated with eight different spectator fish, and sometimes with D > C and C > B to mix things up, and each time the spectator made the correct inference as to which between B and D was the subordinate individual.[1]

How smart does this make *A. burtoni*? Well, in humans, the capacity for simple inferences of this type appears around age four. Apes, rats, crows and possibly pigeons are also in the same league.

Putting two and two together

Here is an interesting experiment carried out by Karen Hollis and colleagues at Mount Holyoke College, in Massachusetts. Outside of the reproductive season, male threespot (=blue) gouramis *Trichogaster trichopterus* form dominance hierarchies. This hierarchy becomes evident at mealtime. When food is dropped in the water, dominants try to monopolize the food and they become aggressive towards subordinates. Subordinates, in turn, adopt a typical submissive posture (body angle at 15-60 º to the horizontal, all fins folded, blanching of colour). The subordinates simply hope to grab some of the drifting food that might escape the dominants' attention. In the experiment, dominants and subordinates who knew each other were separated and isolated. Each learned to associate a signal (a light being turned on) with the imminent arrival of food. They all expressed this learning by approaching the site where food was dropped and nipping at the water surface as soon as the light came on, even before the food actually arrived. Then pairs of fish were formed by reuniting a subordinate with a dominant. Under the watchful eyes of the experimenters, the light was turned on. In each pair the dominants went to the surface as usual. But the subordinates did not; instead most of them immediately adopted the submissive posture, even though food had not arrived yet. The subordinates knew that light signalled food, and they knew that food meant being beaten up by dominants if these were around, so they put two and two together. As soon as the light came on they anticipated being beaten up and right away they took measures to appease the dominants.[2]

Assessing the fighting ability of other fish by seeing them fight

Watching fights can allow a spectator fish not only to figure out the hierarchy of other fish around it, as in the case of *A. burtoni* above, but also to learn about the general fighting abilities of those individuals and use that information when the spectator subsequently interacts directly with them.

One of the first demonstrations of this ability came from the University of Göteberg in Sweden, where Jörgen Johnsson and Anders Akerman set up an aquarium in which two rainbow trout clashed under the watchful eye of a third individual hidden behind a one-way mirror. It soon became clear – at least to human eyes – that one of the clashing fish was dominant and the other was subordinate. Later, the spectator was placed in the presence of either the dominant fish it had already seen in action, or a dominant from another tank it knew nothing about. When paired with the familiar dominant, the former spectator reached a decision more quickly about how to proceed with the fight. Either it gave up earlier (eventually losing the fight) or it escalated the fight earlier (eventually winning). It was as if the former spectator had already made up its mind, based on the previous viewing, whether it was weaker or stronger than the dominant. In contrast, when paired with an unfamiliar contestant, former spectators fought more tentatively, and it took a longer time for a winner to finally emerge.[3]

In a similar vein, Siamese fighting fish *Betta splendens* and green swordtails *Xiphophorus hellerii* are more willing to engage the loser rather than the winner of a fight they have just witnessed, while they show no such discrimination between the winner and loser of a contest they have not witnessed.[4]

Remembering rivals

There is ample evidence that fish can recognize and remember individuals they have already fought with (a more direct interaction than simply watching, as in the section above). The typical experimental procedure here is to pit two fish against each other and let them fight it out. Then the loser is removed and the winner is left alone. A few days later, the winner is made to encounter either the fish it has defeated earlier or another individual it has never met before (to even things out, one has to make sure that this new individual has also been defeated by another fish a few days earlier). The usual outcome is that less aggression takes place between two protagonists who have already met as opposed to two who have never met before. This implies the two acquaintances recognize each other and remember how they stand relative to each other. Among the species for which this is true are sticklebacks, trout, swordtails, cichlids, and paradise fish.[5]

Similarly, territorial neighbours remember one another and put a brake on their bickering once their territories have become established. This phenomenon is called the “dear enemy effect”.[6] Now, if one territory owner is experimentally replaced by another fish, all neighbours become aggressive towards this newcomer, which shows that the previous lack of aggression was not based on fatigue but indeed on the recognition of a familiar neighbour.

By substituting dear enemies with strangers, researchers can determine how neighbours recognize one another. For many species, visual appearance is enough. For example, territorial sticklebacks display aggressively to a new neighbour even when the latter is in a separate aquarium a short distance away. Similarly, three-spot damselfish *Stegastes planifrons* on a reef direct more attacks at bottles that contain new fish as opposed to regular neighbours.[7] On the other hand, in catfish (yellow bullhead) it is the scent of a known dominant fish that is enough to trigger fearful reactions.[8] Neighbours can also be distinguished on the basis of their personal calls[9] and electric discharges.[10]

Remembering who was watching

Siamese fighting fish can be mindful of who is watching their battles. This was shown in the following experiment by Brodie Herb, Suzanne Biron, and Michael Kidd of the University of New Hampshire in Durham. Two males were allowed to display to one another through a glass partition while being watched by a female nearby. The males were aware of that female because they had interacted with her a few minutes earlier. The winning or losing status of each male was decided on the basis on the number of bites and the duration of gill cover openings (an aggressive display). Then, separately, each male was placed in a central compartment flanked by the female that had watched the fight at one end and a new female at the other end. The winner of the previous fight courted both females equally. The loser of the fight, on the other hand, spent more time next to the new female. It looked like the loser was aware that the spectator female had seen him lose and that she might have "formed a bad opinion" of him. (And indeed, other experiments by Claire Doutrelant in Peter McGregor's lab at the University of Copenhagen have revealed that spectator females pay more visits to a male they have seen winning a fight than to the loser. Non-spectator females treat both males equally.[11]) The losing male would stand a better chance with the ignorant female, and accordingly he devoted more time to her. The experiment was repeated many times with other males and females and the result remained the same.[12]

Recognition of cooperators and cheaters

The bluestreak cleaner wrasse *Labroides dimidiatus* performs a service for "client" fishes (belonging to other species) by removing and eating their ectoparasites. However, if given a choice, the wrasse would rather eat the more nutritious body mucus of their clients, something the clients definitely don't like (the clients visibly "jolt" and dart off when cleaners bite them). Now, clients must voluntarily submit to being cleaned. They can invite a bout of cleaning either by adopting a typical posture or simply by remaining motionless near a cleaning station (i.e., near the territory of a cleaner wrasse). Field observations by Redouan Bshary and colleagues indicate that (1) client fish almost always solicit a cleaner if they saw that the cleaner's interaction with its last client ended without conflict, (2) clients solicit less if they did not see the cleaner's last interaction, and (3) clients solicit least (or even flee) if the cleaner's previous interaction ended in conflict.[13] Choice tests in the laboratory have confirmed that client fish (in this case, the two-lined monocle bream *Scolopsis bilineatus*) spend more time next to a cleaner they have seen doing a good job as opposed to a cleaner they have seen doing nothing.[14] Thus, clients pay attention to the fairness of their potential cleaners.

And cleaners seem to know it. There is some evidence that cleaner wrasses try to maintain a good reputation by refraining from biting a client when many bystanders are watching (a so-called "audience effect"). When the bystanders are "choosy" species (those that readily abandon a cleaning station to seek other providers of the same service nearby), there is a reverse correlation between the number of bystanders present and the number of jolts observed during a cleaning session: the more bystanders, the less biting the cleaner does. This evidence is only partially convincing, however, as it is open to alternative interpretations (for example, maybe the cleaner feels less of a need to cheat, not because it wants to preserve its image, but because it sees it has a long queue of clients waiting and therefore a good supply of food coming).[15] More work is needed to demonstrate an audience effect in cleaner wrasses.

Cleaner wrasse sometimes work as male-female teams. Interestingly, when the female “cheats” and bites a client, the male, who is larger, chases her off, a type of punishment. It’s as if the male cares about the reputation of his cleaning station and punishes his partner if that partner’s actions tarnish their good name. Experiments in the laboratory (with preferred or less preferred foods which could be withdrawn when the preferred food was chosen – the equivalent of a client leaving after being cheated) showed that males punished misbehaving females (those who chose the preferred food, causing all food to be withdrawn), that females behaved better thereafter (they now chose the less preferred, but more permanent, food), and that this better behaviour allowed the male partners to feed more.[16]

Manipulating and deceiving others

We are still with the cleaner wrasse. Before cleaning a client, the wrasse often brushes its pelvic and pectoral fins against the dorsal fins and back of the client. Clients seem to like this caress because they often respond by drifting motionless, as if in a trance. Several researchers have proposed that this tactile stimulation by the cleaner wrasse is an attempt to manipulate the client, to encourage it to submit to a bout of cleaning. According to this view, the caress would be akin to a barber’s exhortation to passer-bys to stop and come in for a haircut. Consistent with this hypothesis are the observations that cleaners are more likely to give a caress when the clients are on the move rather than already motionless, and that swimming clients are more likely to stop if the cleaner starts by caressing them rather than going straight into an inspection of their body for parasites.[17]

Another possible function of the caress is to appease clients that are big and mean and could potentially attack the wrasse, particularly if the wrasse was bold enough to have bitten them in a previous interaction (to use jargon, the tactile stimulation would serve as a “preconflict management strategy”). In support of this interpretation, cleaners in the field are more likely to caress predatory rather than non-predatory clients, and are more likely to caress a client if the last interaction with this client ended badly (with a jolt by the client, indicating that the cleaner had bitten it).[18] Furthermore, laboratory work by Alexandra Grutter, of the University of Queensland in Brisbane, has shown that cleaner wrasses in the lab can tell the difference between a predator that is hungry (not fed for 10 days) versus one that is satiated (fed daily), and that it gives many more caresses to the hungry predators. This is all the more striking given that to Grutter’s eyes, the behaviour of the hungry and satiated predators seemed to be the same. Grutter concluded that the caress – which she called tactile dancing – enabled cleaner fish to avoid conflict with potentially dangerous clients.[19] Additional laboratory work showed that predators which received more tactile stimulation from cleaner fish attacked passer-bys less often, as if the caress had put them in an at-peace-with-the-world mood.[20]

Let’s leave the cleaner wrasse behind and have a look at a case of deception in another species. It concerns a remarkable behaviour reminescent of the “broken wing” display used by ground-nesting birds to lure predators away from their nest. (If you have already read this web site's page on parental care, you will recognize what follows). Perhaps the behaviour is mostly innate, but perhaps it also reflects a conscious attempt on the part of the fish to manipulate other fish.

Nest-raiding is an annoying habit of female three-spined sticklebacks. Shoals of females roam and sometimes fall upon the nest of a parental male, eating all the eggs inside and thoroughly devastating it. Males take a dim view of this and they have worked out a defensive ruse. When a parental male sees a menacing shoal of hungry-looking females coming his way, he often swims a short distance away from his nest and starts poking his snout into the ground. This is the same action a female would perform while raiding a nest. This display commonly fools the females into believing that a nest has been discovered. They rush to the site and start digging there too. Meanwhile, the male leaves this writhing mass of females and returns to his territory, hoping (consciously or not) that the cloud of sediments lifted by the "feeding" frenzy will conceal his own real nest.[21]

Another similar behaviour has been reported for the bowfin. Fry follow their male parent for a while after they hatch. Apparently, when a fry predator appears on the scene, the male sometimes moves away and thrashes about in the water as if injured, thus drawing the attraction of the predator onto himself and away from the fry.[22]

Here is another possible case of deception: if a male Atlantic molly *Poecilia mexicana* is given a choice between two females in an aquarium, it will quickly form an opinion of which female is more attractive (usually the bigger one) and he will spend more time next to her. But then, if a second male is unveiled from behind a transparent partition, the first male will move over to the female who was originally less preferred. Males are known to copy the mate choice of others in this species. So it may be that the first male is trying to draw the second male's attention to the female he (the first one) does not fancy so much, so that he will have less competition for his actual favorite.[23]

A complex of sailfin silverside species (genus Telmatherinidae) has recently come under scrutiny in the Malili Lakes of Sulawesi, Indonesia, for another possible case of deception. One species, *Telmatherina sarasinorum*, is an egg predator. It often follows courting pairs of the closely-related species *T. antoniae*. When those pairs lay eggs, *T. sarasinorum* darts in and picks at the eggs, eating them. On four different occasions in the field (out of 136 observation bouts in total), the following behaviour was witnessed: a male *T. sarasinorum* who was following a pair of courting *T. antoniae* eventually chased off the male *T. antoniae* and took his place, courting the heterospecific female. That female released eggs, at which point the male fell upon the eggs and ate them. This sneaky courtship behaviour on the male's part may simply be innate, but it is tempting to interpret it as a deliberate attempt at deception in order to get food.[24]

Recognition of competitors for food and for mates

Lee Dugatkin champions the view that the cognitive abilities of lowly fishes are more elaborate than we might think, and that fishes may use these abilities in strategic contexts. Here are two examples from Dugatkin's work where fishes recognize other individuals and choose to associate with those that provide less competition for food (bluegill sunfish) or less competition for mates (guppies).

In the sunfish experiment, Dugatkin and his co-worker David Wilson, from the State University of New York at Binghamton, established a shoal of 6 bluegills. At regular intervals, the researchers took two fish from the shoal, and placed them together in a separate tank where 20 pieces of mealworm lay scattered on the floor. They noted how many pieces each fish took. They kept doing this until all possible pairwise associations had been tried within the shoal. Then, in a typical choice test, they arranged three aquaria end-to-end, and repeatedly placed one of the fish (the "test" fish) in the middle, and one "stimulus" shoalmate in each of the two end aquaria. The question was: would the middle fish consistently spend more time on the side of the shoalmate with whom it had had the most success in getting food?

By and large that is what happened. If a test fish had previously obtained, say, 12 pieces of food while foraging with stimulus fish A, but only 8 pieces while foraging with fish B, then in the subsequent preference test it spent more time next to A. However, if the preference test involved a regular shoalmate versus a stranger from another shoal, the test fish chose to spend more time next to the regular partner, irrespective of its former success at getting food with that partner. Dugatkin and Wilson concluded that bluegill sunfish can visually recognize individuals, that they prefer to be with recognized shoalmates over unrecognized strangers, and that in a choice of two recognized shoalmates, they strategically pair up with the one that is a poorer competitor for food.[25] Visual cues must be sufficient for this recognition to take place, as all fish were in separate aquaria during the preference tests.

With a different colleague, this time Craig Sargent from the University of Kentucky, Dugatkin wondered if male guppies would recognize and prefer to associate with other males that seem to be less attractive to females, making themselves "look good" by comparison. His experiments involved one female and three males (male A, male B, and a focal male) and three stages. In the first stage, adjacent aquaria were positioned in such a way that the focal male was close to a female and could see male A in the distance (the idea was that male A would then be perceived as a "loser"). In the second stage, the focal male was alone and could see a female next to male B in the distance (male B would be perceived as a "winner"). The third stage was a preference test similar to the one described above for the sunfish, involving the focal male having to choose between male A and male B. Out of 30 focal males so tested, 24 spent more time on the side of the loser male.[26] Females may very well assess the quality of prospective mates by comparing several of them sequentially, and it seems that males may deal with that by avoiding the company of perceived Don Juans.

Here is another example, this time from a research group at the University of Glasgow in Scotland. Neil Metcalfe and B.C. Thompson asked whether European minnows, like bluegill sunfish, could recognize and prefer to associate with shoalmates who are poor competitors for food. Metcalfe and Thompson started by figuring out the pecking order within a shoal of seven marked minnows. To do this, they dispensed 100 chironomid larvae, one by one at 15-second intervals, through a pipette in the middle of the aquarium, and counted the number of larvae caught by each individual. Then they captured one of the fish, and divided the rest into two groups, the three most efficient food-getters on one side and the three less greedy individuals on the other. These were the subshoals offered in a choice test to the captured minnow. The procedure was repeated many times with other shoals. After 28 trials, the results had become obvious: the great majority of the choosing fish were spending more time near the less greedy partners.[27]

Social learning: getting information from others about pathways, food, and predators

Fish can learn how to perform a behavior simply by watching other individuals in action. This is variously called observational learning, cultural transmission, or social learning. For example, fish could learn a particular route after following an experienced leader a few times. At the University of Cambridge, Kevin Laland and Kerry Williams trained guppies to swim through a hole marked in red while ignoring another one marked in green in order to get food on the other side of a partition. (Every time the fish tried to swim through the green hole, a trap door would abruptly slap shut in their face.) These experienced fish ("demonstrators") were then joined by a naive one (an "observer"), and for 5 days both the red and green hole yielded unfettered access to the food reward. The demonstrators stuck to their acquired habit of using the red hole, and the observer tended to follow them. At the end of the 5-day period, the demonstrators were removed and the behavior of the observer, now on its own, was observed. The observer consistently preferred the red hole, in tune with the socially learned pattern. Interestingly, newly-experienced observers could then be joined by other naive guppies and teach them in turn which door to use.[28]

A similar case has been documented for a coral reef species in the wild. At twilight, juvenile French grunts, *Haemulon flavolineatum,* follow traditional migration routes between their daytime resting sites and their nighttime foraging areas. These routes can be up to 1 km (0.6 mile) long. If groups of 10-20 individuals are marked and then transplanted to new populations, they follow the residents along what is for them – the transplants – a new migration route. If the residents are then removed 2 days later, the transplanted grunts continue to use the new route, as well as the resting and foraging sites at both ends. Two days was all it took for the transplanted fish to learn the locations of these sites from the other fish, as well as the fairly long migration route between them. In a control experiment, fish were transplanted to a site where the residents had already been removed, and they showed no particular directionality of movement at twilight, indicating that the migration route was not obvious and could only be learned socially.[29] This was the first – and still one of the few – demonstration of social learning in a free-living fish.[30]

Not surprisingly, social fish will readily join other individuals they see in the act of eating.[31] Perhaps more surprisingly, they may also be able to read the mood of other fish who are expecting food but who have not received it yet. Consider the following experiment I conducted with Bruno Gallant. We set up two shoals of golden shiners *Notemigonus crysoleucas*, each shoal in its own aquarium. One shoal was always fed in the morning, the other in the afternoon. When fish are fed at the same hour every day, they begin, after a few days, to anticipate food arrival, becoming more active and more oriented towards the food source a few hours before mealtime. This is called food-anticipatory activity. In our case the golden shiners spent more time in the upper half of the aquarium, as the food was always delivered at the surface. We set up a third aquarium next to the other two, and placed a single fish there, one who was not used to being fed at any particular time of the day. That single fish could spend time next to the morning-fed shoal or next to the afternoon-fed one. If we did this in the morning, the choosing fish almost always ended up spending more time close to the morning-fed shoal (even though no food was delivered during that time). Conversely, if the test was carried out in the afternoon, the single shiner preferred the afternoon-fed shoal. The hungrier the test fish was (food-deprived for 48 hours rather than 24 or 1 hour), the more pronounced this preference was. It seems the single fish was able to determine which shoal expected food soon, just from watching its behaviour, and it strategically decided to stay close to that group, especially when it itself was strongly motivated to get food.[32]

Through cultural transmission, fishes could also learn where good food spots are. Nine-spined sticklebacks, when given a choice between two food patches they have watched for a while, prefer the patch over which more fish have been seen foraging, or over which fish were seen feeding more intensively.[33] Similarly, in a field experiment where Trinidadian guppies were given a choice between two distinctly marked feeders in their home rivers, the subjects chose the feeder where other guppies were already present, and in subsequent tests when both feeders were deserted, the subjects remembered the previously popular feeder and chose it. It seemed they had acquired a foraging patch preference just because they had previously joined other foragers there.[34]

Through social learning, fishes might learn not only where to get food, but also what to get and how to get it. Michel Anthouard from the Université Louis Pasteur in Strasbourg trained juvenile sea bass to push a lever in order to obtain food. Some fish became proficient at this task, others not. Anthouard then allowed groups of 4 naive individuals to watch either a pair of good demonstrators or a pair of poor ones from behind a glass partition. Every time the demonstrators pushed a lever, both the demonstrators and the observers got food. After a few days, he removed the lever from the demonstrators' tank and placed it with the observers, and noted how they dealt with the lever on their own. Those observers that had been exposed to the good demonstrators started to press the lever, and therefore obtained food, sooner and more often than the fish that had been stuck with dumb tutors.[35]

Now, admittedly such results may be hard to extrapolate to natural situations – there are no food levers in the wild – but conceivably some natural foraging patterns (leaf-turning, nosing around rocks, taking food at the surface) could be learned socially in some species. Working in the field in the Red Sea, Hans Fricke witnessed a special hunting technique in five individuals of the triggerfish *Balistapus undulatus*. These fish would bite off the spines of a sea urchin, grab the naked urchin in their mouth, bring it up to the surface, release it, and attack the vulnerable underparts while the urchin was slowly drifting down. In decades of field research, Fricke never saw this behaviour elsewhere – triggerfishes normally blow jets of water onto urchins to turn them upside down in order to get access to their underparts. It looks like the odd behaviour, limited to one area, was not innate but socially transmitted instead.[36]

Social learning of food may find some application in improving the survival of hatchery-reared salmon once they are released in the wild for restocking purposes. Studies have shown that prior to release, such fish – which have been fed on nothing but pellets all their life – can be taught to quickly accept novel, live prey items similar to those they will encounter in the wild, simply by watching an experienced salmon take such prey.[37] Mortality is very high in hatchery-reared salmon immediately after they are let loose in a stream, perhaps because they have trouble adjusting to new food in the wild. Social learning prior to release could give them the training they need to face a new world.

Fishes can also learn from others the identity of predatory species. Fathead minnows *Pimephales promelas*, for example, are one of those fishes that cannot recognize the predatory nature of a pike, be it by sight or by smell, unless it has had prior contact with a member of that species. Now, imagine that experienced minnows are placed together with naive individuals that have never encountered a pike, and all of these fish are exposed to a flow of water from a tank that holds a pike. What happens is this: the experienced minnows detect the pike smell and react with fear, dashing and seeking cover. Upon seeing them do so, the naive ones also react with fear. The interesting thing is that if the experienced minnows are now removed, and after a few days the pike smell is presented again to the previously-naive fish alone, they show a fright reaction on their own. They have learned that the pike odor signals danger, not because a pike attacked them – none did – but simply because they saw other fish show alarm to this odor. [38]

Such cultural transmission of predator recognition can even take place between species. For example, brook sticklebacks *Culaea inconstans* can learn the identity of a predator by watching the fright reaction of experienced fathead minnows.[39] The experiment works also when the smell of a habitat is used instead of the smell of a predator. Fish can learn to recognize the odor of dangerous sites when they are simultaneously exposed to it and to other fish that suddenly show a fright reaction.[40]

Here again, social learning could come to the help of hatchery-raised salmon meant to be released in the wild. The high mortality of salmon introduced in the wild could be caused not only by poor foraging, as mentioned above, but also by a lack of recognition of their natural predators. Fortunately, salmon can innately recognize that a predator is out and about when they smell the presence of a so-called "alarm substance" in the water. This is a special compound that is released in water when the skin of a prey fish is broken, such as when a predator catches the prey. Several experimenters have taken advantage of this system to teach hatchery salmon that the smell of some other fishes can be bad news. By being exposed to both a predator odour (a pike's, let's say, or an adult trout's) and the alarm substance of their own species, young hatchery salmon can learn to react defensively to the odour of the predator alone later on. There is some evidence that such pre-conditioned salmon survive better in the wild.[41]

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[1] Grosenick, L., Clement, T.S., and Fernald, R.D., 2007, Fish can infer social rank by observation alone, Nature 445, 429-432.

[2] Hollis, K.L., Langworth-Lam, K.S., Blouin, L.A., and Romano, M.C., 2004, Novel strategies of subordinate fish competing for food: learning when to fold, Animal Behaviour 68, 1155-1164.

[3] Johnsson, J.I., and Akerman, A., 1998, Watch and learn: preview of the fighting ability of opponents alters contest behaviour in rainbow trout, Animal Behaviour 56, 771-776.

[4] Oliveira, R.F., McGregor, P.K., and Latruffe, C., 1998, Know thine enemy: fighting fish gather information from observing conspecific interactions, Proceedings of the Royal Society of London B 265, 1045-1049; McGregor, P.K., Peake, T.M., and Lampe, H.M., 2001, Fighting fish *Betta splendens* extract relative information from apparent interactions: what happens when what you see is not what you get, Animal Behaviour 62, 1059-1065; Peake, T.M., Matos, R.J., and McGregor, P.K., 2006, Effects of manipulated aggressive "interactions" on bystanding male fighting fish, *Betta splendens*, Animal Behaviour 72, 1013-1020; Earley, R.L., and Dugatkin, L.A., 2002, Eavesdropping on visual cues in green swordtail (*Xiphophorus helleri*) fights: a case for networking, Proceedings of the Royal Society of London B 269, 943-952; Earley, R.L., Druen, M., and Dugatkin, L.A., 2005, Watching fights does not alter a bystander's response towards naïve conspecifics in male green swordtail fish, *Xiphophorus helleri*, Animal Behaviour 69, 1139-1145.

[5] Peeke, H.V.S., 1982, Stimulus and motivation specific habit and redirection of aggression in the three-spined stickleback, Journal of Comparative and Physiological Psychology 96, 816-822; Utne-Palm, A.C., and Hart, P.J.B., 2000, The effects of familiarity on competitive interactions between threespined sticklebacks, Oikos 91, 225-232; Johnsson, J.L., 1997, Individual recognition affects aggression and dominance relations in rainbow trout, *Oncorhynchus mykiss*, Ethology 103, 267-282; Höjesjö, J., Johnsson, J.,I., Petterson, E., and Järvi, T., 1998, The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*), Behavioral Ecology 9, 445-451; Morris, M.R., Gass, L., and Ryan, M.J., 1995, Assessment and individual recognition of opponents in the pigmy swordtails *Xiphophorus nigrensis* and *X. multilineatus*, Behavioral Ecology and Sociobiology 37, 303-310; Keeley, E.R., and Grant, J.W.A., 1993, Visual information, resource value, and sequential assessment in convict cichlid (*Cichlasoma nigrofasciatum*) contests, Behavioral Ecology 4, 345-349; Miklósi, Á., Haller, J., and Csányi, V., 1992, Different duration of memory for conspecific and heterospecific fish in the Paradise fish (*Macropodus opercularis* L.), Ethology 90, 29-36; Zayan, R.C., 1975, Défense du territoire et reconnaissance individuelle chez *Xiphophorus* (Pisces, Poecilidae), Behaviour 52, 266-310.

[6] For example: Leiser, J.K., and Itzkowitz, M., 1999, The benefits of dear enemy recognition in three-contender convict cichlid (*Cichlasoma nigrofasciatum*) contests, Behaviour 136, 983-1003.

---

[7] Waas, J.R., and Colgan, P.W., 1994, Male sticklebacks can distinguish between familiar rivals on the basis of visual cues alone, Animal Behaviour 47, 7-13; Thresher, R.E., 1979, The role of individual recognition in the territorial behaviour of the threespot damselfish, *Eupomacentrus planifrons*, Marine Behaviour and Physiology 6, 83-93.

[8] Todd, J.H., 1971, The chemical languages of fishes, Scientific American 224, 98-108.

[9] Myrberg, A.A., and Riggio, R.J., 1985, Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus partitus*), Animal Behaviour 33, 411-416.

[10] McGregor, P.K., and Westby, W.M., 1992, Discrimination of individually characteristic electric organ discharges by a weakly electric fish, Animal Behaviour 43, 977-986.

[11] Doutrelant, C., and McGregor, P.K., 2000, Eavesdropping and mate choice in female fighting fish, Behaviour 137, 1655-1669.

[12] Herb, B.M., Biron, S.A., and Kidd, M.R., 2003, Courtship by subordinate male Siamese fighting fish, *Betta splendens*: their response to eavesdropping and naïve females, Behaviour 140, 71-78. Fish can also be mindful of who is watching their courtship activities: Doutrelant, C., McGregor, P.K., and Oliveira, R.F., 2001, The effect of an audience on intrasexual communication in male Siamese fighting fish, *Betta splendens*, Behavioral Ecology 12, 283-286; Dzieweczynski, T.L., and Rowland, W.J., 2004, Behind closed doors: use of visual cover by courting male three-spined stickleback, *Gasterosteus aculeatus*, Animal Behaviour 68, 465-471.

[13] Bshary, R., and Schäffer, D., 2002, Choosy reef fish select cleaner fish that provide high-quality service, Animal Behaviour 63, 557-564; Bshary, R., 2002, Biting cleaner fish use altruism to deceive image-scoring client reef fish, Proceedings of the Royal Society of London B 269, 2087-2093.

[14] Bshary, R., and Grutter, A., 2006, Image scoring and cooperation in a cleaner fish mutualism, Nature 441, 975-978.

[15] Bshary, R., and D'Souza, A., 2005, Cooperation in communication networks : indirect reciprocity in interactions between cleaner fish and client reef fish, pp. 521-539 in (McGregor, P.K., ed.) Animal Communication Networks, Cambridge University Press, Cambridge. See also: Bshary, R., and Grutter, A., 2006, Image scoring and cooperation in a cleaner fish mutualism, Nature 441, 975-978; Soares, M.C., Bshary, R., and Côté, I.M., 2008, Does cleanerfish service quality depend on client value or choice options? Animal Behaviour 76, 123-130.

[16] Raihani, N.J., Grutter, A.S., and Bshary, R., 2010, Punishers benefit from third-party punishment in fish, Science 327, 171.

[17] Bshary, R., and Würth, M., 2001, Cleaner fish *Labroides dimidiatus* manipulate client reef fish by providing tactile stimulation, Proceedings of the Royal Society of London B 268, 1495-1501.

[18] Idem.

[19] Grutter, A.S., 2004, Cleaner fish use tactile dancing behavior as a preconflict management strategy, Current Biology 14, 1080-1083.

[20] Cheney, K.L., Bshary, R., and Grutter, A.S., 2008, Cleaner fish cause predators to reduce aggression toward bystanders at cleaning stations, Behavioral Ecology 19, 1063-1067.

[21] Whoriskey, F.G., 1991, Stickleback distraction displays: sexual or foraging deception against egg cannibalism? Animal Behaviour 41, 989-995; Foster, S.A., 1988, Diversionary displays of paternal stickleback: Defenses against cannibalistic groups, Behavioral Ecology and Sociobiology 22, 335-340;

Ridgway, M.S., and McPhail, J.D., 1988, Raiding shoal size and a distraction display in male sticklebacks, Canadian Journal of Zoology 66, 201-205.

[22] Page 89 in: Morris, D., 1990, Animal watching: a field guide to animal behaviour, Jonathan Cape, London.

[23] Plath, M., Richter, S., Tiedemann, R., and Schlupp, I., 2008, Male fish deceive competitors about mating preferences, Current Biology 18, 1138-1141; Plath, M., Blum, D., Schlupp, I., and Tiedemann, R., 2008, Audience effect alters mating preferences in a livebearing fish, the Atlantic molly, *Poecilia mexicana*, Animal Behaviour 75, 21-29.

[24] Gray, S.M., McKinnon, J.S., Tantu, F.Y., and Dill, L.M., 2008, Sneaky egg-eating in *Telmatherina sarasinorum*, an endemic fish from Sulawesi, Journal of Fish Biology 73, 728-731.

[25] Dugatkin, L.A., and Wilson, D.S., 1992, The prerequisites for strategic behaviour in bluegill sunfish, *Lepomis macrochirus*, Animal Behaviour 44, 223-230. These results are controversial; see: Lamprecht, J., and Hofer, H., 1994, Cooperation among sunfish: do they have the cognitive abilities? Animal Behaviour 47, 1457-1458; Lombardi, C.M., and Hulbert, S.H., 1996, Sunfish cognition and pseudoreplication, Animal Behaviour 52, 419-422; a reply by Dugatkin and Wilson follows both articles.

[26] Dugatkin, L.A., and Sargent, R.C., 1994, Male-male association patterns and female proximity in the guppy, *Poecilia reticulata*, Behavioral Ecology and Sociobiology 35, 141-145.

[27] Metcalfe, N.B., and Thompson, B.C., 1995, Fish recognize and prefer to shoal with poor competitors, Proceedings of the Royal Society of London B 259, 207-210.

[28] Laland, K.N., and Williams, K., 1997, Shoaling generates social learning of foraging information in guppies, Animal Behaviour 53, 1161-1169. For follow-up studies, see: Laland, K., and Williams, K., 1998, Social transmission of maladaptive information in the guppy, Behavioral Ecology 9, 493-499; Reader, S.M., and Laland, K., 2000, Diffusion of foraging innovations in the guppy, Animal Behaviour 60, 175-180; Swaney, W., Kendal, J., Capon, H., Brown, C., and Laland, K.N., 2001, Familiarity facilitates social learning of foraging behaviour in the guppy, Animal Behaviour 62, 591-598; Bates, L., and Chappell, J., 2002, Inhibition of optimal behavior by social transmission in the guppy depends on shoaling, Behavioral Ecology 13, 827-831; Brown, C., and Laland, K., 2002, Social learning of a novel avoidance task in the guppy: conformity and social release, Animal Behaviour 64, 41-47. See also: Sugita, Y., 1980, Imitative choice behavior in guppies, Japanese Psychological Research 22, 7-12; Warren, J.L., Bryant, R.C., Petty, F., and Byrne, W.L., 1975, Group training in goldfish (*Carassius auratus*): the effects on acquisition and retention, Journal of Comparative and Physiological Psychology, 89, 933-938; Sumpter, D.J.T., Krause, J., James, R., Couzin, I.D., and Ward, A.J.W., 2008, Consensus decision making by fish, Current Biology 18, 1773-1777.

[29] Helfman, G.S., and Schultz, E.T., 1984, Social transmission of behavioural traditions in a coral reef fish, Animal Behaviour 32, 379-384.

[30] Maintenance of traditional mating sites could also be seen as an example of social transmission of knowledge in some free-living fishes; see: Warner, R.R., 1988, Traditionality of mating site preferences in a coral reef fish, Nature 335, 719-721.

[31] Keenleyside, M.H.A., 1955, Some aspcts of the schooling behaviour of fish, Behaviour 8, 183-248; Pitcher, T.J., Magurran, A.E., and Winfield, I.J., 1982, Fish in larger shoals find food faster, Behavioral Ecology and Sociobiology 10, 149-151; Pitcher, T.J., and House, A.C., 1987, Foraging rules or group feeders: area copying depends upon food density in shoaling goldfish, Ethology 76, 161-167; Ryer, C.H., and Olla, B.L., 1992, Social mechanisms facilitating exploitation of spatially variable ephemeral food patches in a pelagic marine fish, Animal Behaviour 44, 69-74; Baird, T.A., Ryer, C.H.,

---

and Olla, B.L., 1991, Social enhancement of foraging on an ephemeral food source in juvenile walleye pollock, *Theragra chalcogramma*, Environmental Biology of Fishes 31, 307-311; Krause, J., 1992, Ideal free distribution and the mechanism of patch profitability assessment in three-spined sticklebacks (*Gasterosteus aculeatus*), Behaviour 123, 27-37.

[32] Reebs, S.G., and Gallant, B.Y., 1997, Food-anticipatory activity as a cue for local enhancement in golden shiners (Pisces: Cyprinidae, *Notemigonus crysoleucas*), Ethology 103, 1060-1069.

[33] Coolen, I., van Bergen, Y., Day, R.L., and Laland, K.N., 2003, Species difference in adaptive use of public information in sticklebacks, Proceedings of the Royal Society of London B 270, 2413-2419; van Bergen, Y., Coolen, I., and Laland, K., 2004, Nine-spined sticklebacks exploit the most reliable source when public and private information conflict, Proceedings of the Royal Society of London B 271, 957-962; Coolen, I., Ward, A.J.W., Hart, P.J.B., and Laland, K.N., 2005, Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues, Behavioral Ecology 16, 865-870; Kendal, J.R., Rendell, L., Pike, T.W., and Laland, K.N., 2009, Nine-spined sticklebacks deploy a hill-climbing social learning strategy, Behavioral Ecology 20, 238-244; Pike, T.W., Kendal, J.R., Rendell. L.E., and Laland, K.N., 2010, Learning by proportional observation in a species of fish, Behavioral Ecology 21, 570-575. However, a close relative of nine-spined sticklebacks, the three-spined stickleback, does not seem to be influenced by the memory of where other fish have foraged: Coolen, I., van Bergen, Y., Day, R.L., and Laland, K.N., 2003, Species difference in adaptive use of public information in sticklebacks, Proceedings of the Royal Society of London B 270, 2413-2419; Webster, M.M., and Hart, P.J.B., 2006, Subhabitat selection by foraging threespine stickleback (Gasterosteus aculeatus): previous experience and social conformity, Behavioral Ecology and Sociobiology 60, 77-86.

[34] Reader, S.M., Kendal, J.R., and Laland, K.N., 2003, Social learning of foraging sites and escape routes in wild Trinidadian guppies, Animal Behaviour 66, 729-739.

[35] Anthouard, M., 1987, A study of social transmission in juvenile *Dicentrarchus labrax* (Pisces: Serranidae), in an operant conditioning situation, Behaviour 103, 266-275.

[36] Bshary, R., Wickler, W., and Fricke, H., 2002, Fish cognition: a primate's eye view, Animal Cognition 5, 1-13.

[37] Brown, C., and Laland, K., 2001, Social learning and life skills training for hatchery reared fish, Journal of Fish Biology 59, 471-493; Brown, C., and Laland, K., 2002, Social enhancement and social inhibition of foraging behaviour in hatchery-reared Atlantic salmon, Journal of Fish Biology 61, 987-998; Brown, C., Markula, A., and Laland, K., 2003, Social learning of prey location in hatchery-reared Atlantic salmon, Journal of Fish Biology 63, 738-745. See also: Magnhagen, C., and Staffan, F., 2003, Social learning in young-of-the-year perch encountering a novel food type, Journal of Fish Biology 63, 824-829.

[38] Mathis, A., Chivers, D.P., and Smith, R.J.F., 1996, Cultural transmission of predator recognition in fishes: intraspecific and interspecific learning, Animal Behaviour 51, 185-201. See also: Suboski, M.D., Bain, S., Carty, A.E., McQuoid, L.M., Seelen, M.I., and Seifert, M., 1990, Alarm reaction in acquisition and social transmission of simulated-predator recognition by Zebra Danio fish (*Brachydanio rerio*), Journal of Comparative Psychology 104, 101-112; Kelley, J.L., Evans, J.P., Ramnarine, I.W., and Magurran, A.E., 2003, Back to school: can antipredator behaviour in guppies be enhanced through social learning? Animal Behaviour, 65, 655-662; Vilhunen, S., Hirvonen, H., and Laakkonen, M.V.-M., 2005, Less is more: social learning of predator recognition requires a low demonstrator to observer ratio in Arctic charr (*Salvelinus alpinus*), Behavioral Ecology and Sociobiology 57, 275-282.

---

[39] Mathis, A., Chivers, D.P.,. and Smith, J.F., 1996, Cultural transmission of predator recognition in fishes: intraspecific and interspecific learning, Animal Behaviour 51, 185-201. See also: Krause, J., 1993, Transmission of fright reaction between different species of fish, Behaviour 127, 37-48.

[40] Chivers, D.P., and Smith, R.J.F., 1995, Chemical recognition of risky habitats is culturally transmitted among fathead minnows, *Pimephales promelas* (Osteichthyes, Cyprinidae), Ethology 99, 286-296.

[41] Brown, G.E., and Smith, R.J.F., 1998, Acquired predator recognition in juvenile rainbow trout (*Oncorhynchus mykiss*): conditioning hatchery-reared fish to recognize chemical cues of a predator, Canadian Journal of Fisheries and Aquatic Sciences 55, 611-617. Also: Berejikian, B.A., Smith, R.J.F., Tezak, E.P., Schroder, S.L. and Knudsen, C.M., 1999, Chemical alarm signals and complex hatchery rearing habitats affect antipredator behavior and survival of chinook salmon (*Oncorhynchus tshawytscha*) juveniles, Canadian Journal of Aquatic Sciences 56, 830-838.