How fishes try to avoid predators

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Fishes are delicious. At least herons, kingfishers, mergansers, and all marine birds seem to think so. Marine mammals seem to think so. Minks and bears seem to think so. The big fishes themselves concur. As a taxonomic group, fishes face one of the most diverse arrays of predators imaginable. Threat comes from below and from above, during the day and at night, and at almost all stages of life. Is it any wonder that most fishes – certainly all the small ones – are skittish creatures? When placed in a new environment, most wild fishes cower in nooks and crannies and don't dare raise a fin. They don't want to draw the attention of predators.

But of course, an animal cannot spend its whole life immobile. Fish may remain in constant fear of danger, but they also have other things to do, feeding and reproductive activities being the most obvious. The life of fishes is dictated by a triumvirate of imperatives: the need to reproduce, the need to eat, and the need to avoid being eaten. The problem is that these activities are not always compatible. Compromises must be achieved between courting a potential mate and looking out for enemies. Trade-offs must be accommodated between the necessity to search for food and the desire to avoid detection by a predator. This looks at the nature of these compromises, with predation risk as the underlying causal factor.

There has been extensive research on this topic. This reflects not only the importance of predation risk in the life of fishes, but also the relative ease of experimental manipulation. The basic protocol has been to compare the behaviour of a fish before and after the appearance of a predator. The comparison can also take place between a group of fish that sees a predator versus one that does not, or between natural populations that experience different levels of predation pressure.

In the lab, predators can be presented in a multitude of ways. A predatory fish species can be positioned in plain sight within the confines of an adjacent aquarium. A tame predatory bird can be tethered nearby. Resin models of a big bad fish can be cast and then dragged through the water. Wooden models of heron heads can be thrust fiercely through the surface. Cardboard silhouettes of kingfishers can be "flown" along a wire above the water. Fish can also be exposed to an inflow of water laced with the smell of a predator or the alarm substance of its prey.

The response of fishes to predation risk can be divided in four broad categories: (1) the fish can switch habitat, i.e. decamp to areas where there are fewer predators or better shelters; (2) they can stay in the same habitat but keep a low profile, reducing the frequency of conspicuous behaviours and the amount of time they spend exposed;

(3) they can remain exposed but increase the percentage of time spent vigilant, usually at the expense of the time and concentration necessary to do other things; and (4) they can shift their activity to other times of day when predators are not so abundant or not so successful.

Switching habitat

Predator-free ponds provide great opportunities for studying the effect of predation risk on habitat choice. All you need to do, with the permission of your local environmental government agency, is to introduce a predator to a site that encompasses various habitat types – open water and weeded areas, for example – and compare the spatial distribution of the prey before and after predator introduction. Alternatively, the pond can be fenced up into two halves, one with prey only and one with both prey and introduced predator. This has been done with bluegill sunfish and largemouth bass, minnows and pike, young crucian carp and Eurasian perch, and young Eurasian perch with their cannibalistic elders. In all cases, prey in the predator-free condition occupied both open waters and shallow weeded areas, whereas prey exposed to predators stayed in the shallow weeded areas most of the time. Confinement to the shallows usually led to slower growth rates, because food was not as plentiful there, and because there was more competition for it from the great concentration of refugees.[1]

In the above experiments, some prey could be seen to venture, sometimes even to set up shop, in the open waters where the predators operated most efficiently. Invariably these fearless individuals were large. Great size does confer some degree of immunity against predators. These large individuals were not constrained by the competitive bottleneck that affected their smaller brethren in the shallows. Therefore they grew more quickly and became even safer from danger, a case of the rich getting richer and the poor staying poor.

(The anti-predator benefits of large size are further illustrated by an intriguing observation. In the absence of predators, crucian carps develop slim bodies that are hydrodynamically efficient. But in the presence of predators, carps grow to become rounder and larger, a body shape that is not so economical for swimming, but more likely to deter predators because it is not so easy to swallow. It seems that the differential growth is induced by exposure to carp skin substances exuding from the faeces of the predator.) [2]

Predation experiments can also be done in the lab. For his PhD thesis at Queen's University in Ontario, Vytenis Gotceitas built artificial weeded areas by attaching green polypropylene ropes to grids of wire mesh. Within wading pools, he installed patches of "weeds" in densities of 50, 100, 250, 500 or 1000 stems per square meter. He also introduced a great number of damselfly nymphs, a natural food supply for bluegill sunfish. He then released bluegills into the wading pool and observed their

behaviour before, during, and after the introduction of a piscivorous largemouth bass. Before the predator appeared, the bluegills stayed in open water or in low-density weed patches because this is where they had the most success finding and catching damselfly nymphs. When the predator was thrust upon the scene however, most bluegills moved to the high-density weed patches. That was a good choice, because Gotceitas could see that the largemouth bass was fairly successful at catching those few individuals that stayed in the low-density weed patches. Therefore, dense weeds were a good place for bluegills to seek refuge from predators. Let's remember though that dense weeds were also a poor place to forage. So, in the absence of predatory activity bluegills patrolled the sparse weeds to maximise their foraging success, but they moved to safer patches of dense weeds when a predator appeared, even if that meant poor foraging, a lab result that mirrored the field observations above.[3]

If habitat switches entail a trade-off between foraging and avoiding predation, then it should be possible to experimentally manipulate this balance and tip it either in favour of more foraging despite the risk of predation, or conversely more sheltering despite the risk of starvation. The simplest way to do this is to compare the behaviour of hungry and satiated fish. Both can be offered a choice between spending some time in a safe habitat devoid of food, or a risky one where there is food. This has been done in the lab for crucian carp facing pike, black gobies facing cod, pink salmon fry facing adult chinook, and juvenile coho salmon facing adult rainbow trout. In all cases, the hungry individuals spent more time in the risky area, close to the predator but with good access to food, than the better-fed fish.[4]

Those experiments hint at another way to affect the balance of foraging opportunity and predation risk. We can vary the quantity or the quality of food in the risky habitat. A choice can be offered between two patches, one that gives access to a little food and that is placed near an adjacent aquarium that contains no, or maybe only one, predator, versus another patch that offers more food but that is also next to an aquarium containing two predators. The question is: how much more food should the more dangerous patch contain in order to draw the wary prey there? Experiments of this kind have been done with juvenile creek chub facing predatory adults, young black surfperch at risk from kelp bass, European minnows exposed to a kingfisher, guppies facing cichlids, and upland bullies viewing a salmon.[5] The switch from safe to dangerous habitat took place when food was at least 3-4 times, and sometimes as much as 28 times, more abundant in the risky site, a substantial difference that may not always be present in natural situations. This could explain why, in the natural experiments described above, fish at risk from predation stayed in the shallow areas of ponds and lakes despite the lower food supply there. If fish have at least enough food to survive in the safe habitat, and the dangerous habitat is not that much better in terms of food availability, then prey may elect to stay in the safe habitat most of the time.[6]

Yet another way to tip the scale is to alter the availability of refuges in the various habitats. Prey may accept to venture in predator-rich areas if there is also structure

there to protect them. To demonstrate this, Douglas Fraser and Richard Cerri built compartmentalised channels within a spring-fed stream in the Hudson-Mohawk River watershed. Within each compartment they could manipulate the presence or absence of a predator (adult creek chub) and the structural complexity of the habitat (pieces of black pipe, wood, covers providing shade). The compartments were separated by wood dividers with slots big enough to let small minnows go in and out but too small to let the predators exit. Small minnows (young creek chubs and blacknose dace) were let loose in those channels, free to move from compartment to compartment. Their distribution could be determined at any time by dropping hinged gates which effectively made all fish prisoners of the compartments in which they happened to be at that moment. In this way, Fraser and Cerri observed that minnows tended to avoid compartments with predators but that this avoidance was less marked when structure was present in those compartments. Predator avoidance is a strong incentive at all times but the presence of structure can mitigate it somewhat.[7] Similar results have been obtained in the lab with other species.[8]

Of course, habitat shifts may not afford complete safety. Some predators have this nasty habit of adapting and venturing into the areas where their prey take refuge – predators have to make a living too, you know. For example, largemouth bass can switch from cruising in open waters to ambushing in vegetated areas.[9] Small prey fish may flee from harmful perch in open waters only to fall prey to a stalking pike in the weeds.[10] Minnows may think they are safe from large predatory fishes in the shallows, but then they are nabbed by a heron. As I said earlier, fishes are just too tasty. They are almost never completely safe. Nevertheless, the fact remains that habitat switches can at least help to decrease predation risk. Better a small risk of being caught by a pike in the weeds than guaranteed death from a bass in open waters.

Reducing conspicuous behaviours

Juvenile salmon usually hold station somewhere in a stream and occasionally dash upstream to intercept drifting prey. Larry Dill and Alex Fraser from Simon Fraser University wondered how this behaviour could be affected by predation risk. They compared the foraging behaviour of coho salmon that could feed under two different conditions, either undisturbed or after being distracted by the presentation of a photograph depicting an adult rainbow trout (a predator of young salmon). Their results were that, all other things being equal, the cohos that had seen the photograph were not willing to swim as far away as usual in order to catch drifting insects. Whereas unperturbed salmon were willing to swim 25 cm upstream in order to catch a big fly, disturbed salmon would only go 16 cm.[11] In Glasgow, Neil Metcalfe and his co-workers observed a similar reticence to venture out on the part of scared Atlantic salmon, adding that it took 2 h for the feeding behaviour to fully get back to normal after predator presentation.[12] The inference from both of these studies is that wary fish probably want to minimise the amount of time spent moving. Other studies in Dill's lab have shown that moving salmon are attacked by common mergansers (a

diving fish-eating duck) more often than stationary ones, and maybe the same would apply to predation by large trout.[13]

Here again it is possible to alter the trade-off between safety and foraging by playing with the hunger level of the salmon, or with the levels of predation risk. Dill and Fraser manipulated their cohos in this way. They observed that hungry salmon reduced their attack distance on drifting prey when scared by a predator, as expected, but not as much as better-fed individuals did. Because the cohos were hungry, they were willing to take a little bit more risk. Salmon which could see their own image in a mirror were also willing to take more risk by dashing a little further than lone individuals. Either they perceived the mirror image as a competitor for food and consequently they were more motivated to get the food, or they felt safer because they had a companion and reckoned there was less chance for them to be the specific target of an attack. Dill and Fraser also manipulated the balance in another way: they varied the frequency with which the predator image was presented. As expected, salmon which were exposed to the image of a predator more often (every 22 minutes) reduced their attack distance to a greater degree than salmon who saw the predator less frequently (only at 45-min intervals). The fish were able to estimate the higher level of risk and adjust their foraging behaviour accordingly.[14]

The need to avoid conspicuous behaviour in the presence of a predator can also have an impact on a fish's sex life, especially the males' courtship behaviour. Let's take the case of guppies. Males have two ways of mating with females. They can woo them with a sigmoid display, in which the body is arched and the fins are extended. Such a display is conspicuous, can take up to 5 seconds to perform, and must be done often before a female finally agrees to mate. The second strategy is sneakier. It is called gonopodial thrusting, a forceful insemination without the female's co-operation (a form of sexual coercion). Gonopodial thrusting is less conspicuous than sigmoid displays, but the chance of a successful insemination is also reduced because the female tries to resist it. The interesting point here is that when we compare the relative frequency of both strategies in the presence and in the absence of predators (cichlids or characids) at large in the same environment, the sneaky behaviour predominates when predators are present while the conspicuous display is more important in the predator's absence.[15] It seems that predator-wary fish abandon effective but conspicuous courtship displays and resort to less showy but safer alternatives if they can. Another option under predation threat is to shorten the duration of courtship before finally mating, as has been observed in pipefish, sand gobies, darters, razorfish, damselfish, and sticklebacks.[16]

Camouflage

There is one category of fishes for which reduced activity is an integral part of anti-predator strategy: cryptic species whose body colour matches the surroundings.[17] For camouflage to be effective against a static background, the fish must itself remain

motionless. There is evidence that freezing in cryptic species is a conscious effort to blend in and not simply an attempt to reduce conspicuous movements irrespective of the potential for camouflage. Tidepool sculpins, whose body markings mimic the appearance of sand, have been kept in aquaria with either a matching (sandy) or non-matching (white) bottom. When scared by the introduction of an alarm substance, the fish on matching sand reduced their movements to 65% of normal levels, as might be expected. However, the fish on a white substrate did not alter their activity. For them, immobility would have conferred no cryptic advantage, and consequently that tactic was not adopted.[18] Active search for a refuge was a better alternative in that case.

Another example comes from a study of three darter species. The fantail, greenside and orangethroat darters wear dull colours outside of the breeding season and they freeze over mucky bottoms in response to predator signs. During the breeding season, the male fantail and greenside darters develop a conspicuous green body colour, but because they normally breed near matching green algae they keep on freezing when alarmed. In contrast, male orangethroat darters develop intense orange, blue, yellow and red breeding colours. Needless to say, they cannot find matching surroundings, and therefore it comes as no surprise that they abandon freezing as an anti-predator tactic and resort to fleeing instead.[19]

Increasing vigilance

If a fish is confident that it can escape from a predator as long as it has enough advance warning, then all it needs to do in a risky environment is to increase its time spent vigilant. For the fish ethologist, studying this topic poses a problem: how do you measure vigilance? How can you tell that a fish is vigilant? A fish cannot perk up its ears like a mammal. It cannot look up like a bird. We therefore have no choice but to resort to a more indirect sign. In most cases, what ends up being measured is foraging activity. This may seem completely unrelated, but the rationale is in fact sound enough: foraging requires concentration on the task at hand and is therefore incompatible with vigilance. Good vigilance demands a fish's undivided attention and it cannot be done while the fish is feeding.[20] The intensity of foraging can therefore be construed as an inverse index of vigilance. Ethologists therefore predict that fish should reduce their feeding rate when they perceive a risk of predation. Satisfyingly, this has indeed been observed in a variety of species, most notably salmon and sticklebacks.[21]

In one experiment conducted by Manfred Milinski, three-spined sticklebacks were placed in an aquarium in which stood a number of upright Plexiglas cylinders. At the bottom of each cylinder was a tasty Tubifex worm. However, the cylinder was of such a height that the fish lost sight of their surroundings while reaching for the worm at the bottom. In one treatment the sticklebacks were on their own, while in another treatment they could see the predatory cichlid *Oreochromis mariae* through a nearby transparent partition. The unthreatened sticklebacks fed enthusiastically in all

cylinders, but the wary fish reached for the worms less often and when they did, it was only in those cylinders furthest away from the cichlid. We can infer that they needed to remain vigilant.[22]

In Scotland, Neil Metcalfe and his co-workers placed juvenile salmon in an artificial stream channel and dropped food pellets a short distance in front of them. The current carried the pellets past the salmon, who could first orient towards the pellets and then "attack" them. Two pellet types were used, one which was too large to be swallowed and one which was just the right size. The salmon had been familiarised with both types and knew the difference between them. An experimental trial consisted of dropping a total of 6 pellets, 3 large and 3 small ones, one at a time at 10-minute intervals. One group of salmon was left undisturbed, but another group was shown the Fiberglas model of a predatory brown trout for 30 seconds before the trial began. Though brief, this presentation had an effect: during the hour-long trial that followed, the frightened salmon attacked the drifting pellets less often, and when they did they seemed not to discriminate very well, attacking the inedible large pellets as often as the edible small ones. The undisturbed controls attacked the edible pellets at a high rate and the inedible ones less often. These results suggest that fear of predation, and the consequent need for vigilance, rob juvenile salmon of the concentration needed to discriminate between food items.[23]

Concentration is also required of a fish that feeds on high-density swarms of *Daphnia*. This is because of the confusion effect, which we have already encountered in chapter 11; we had seen that predator confusion could benefit large shoals of prey fish, and it is not hard to imagine that it can also benefit large swarms of *Daphnia*. One experiment with guppies has confirmed that the concentration needed to overcome the confusion effect hinders vigilance and predator evasion. Guppies feeding on *Daphnia* at densities of 1, 5, 10, 15, or 20 per litre were subjected to surprise attacks by a live jewel cichlid. The outcome for the guppies depended on the density of the *Daphnia* on which they fed: the greater the density of *Daphnia*, the greater the probability of the foraging guppies being caught by the cichlid, from around 20% at the lowest density to 50% at the highest one. Overwhelmed by the whirlwind movements of all those little prey items in front of them, guppies did not see the predator coming and paid dearly for it.[24]

Consequently, we would expect wary fish to feed on low rather than high-density swarms, since this would require less concentration and allow better vigilance. Milinski has provided evidence that this is so. He filled test tubes with various numbers of *Daphnia* (0, 2, 20, or 40) and presented all tubes simultaneously to individual sticklebacks. Some of these sticklebacks had been previously frightened by the overhead flight of a model kingfisher, while others had been left alone. Milinski saw that most of the undisturbed fish at first attacked the tube that contained 40 *Daphnia*, probably because it represented a rich source of food and the fish, being unaware of any predator in the vicinity, were willing to invest the concentration necessary to try and isolate prey one at a time (eventually though, they switched to the less packed

tubes, maybe in frustration at their initial lack of success reaching the protected Daphnia within their tubes). In contrast, most of the frightened fish first bit the tube that housed only two *Daphnia*, and they maintained that choice. They wanted to keep an eye out for the return of the predator they had seen before and preferred prey that could be caught quickly, even if that meant settling for fewer of them.[25]

Although the above examples all deal with foraging as the antithesis of vigilance, there is no reason to believe that other behaviours besides foraging could not be measured with the same intent. Reproductive activities such as mate choice, nest-building, fighting with territorial neighbours, and caring for eggs also require a certain amount of concentration and can therefore be implicated in a trade-off with vigilance. Already some researchers have reported that female guppies stop paying attention to courting males, or show less discrimination between them, when they perceive a predation risk.[26] There is scope for more research involving such vigilance-incompatible behaviours.

Altering the timing of activity

With the help of a few students, undergraduate student Lyne Boudreau and I once placed minnow traps in a stream to see if lake chub would be caught mostly during the day or at night. I expected the answer to be during the day because chub kept in aquaria are almost exclusively diurnal. To my surprise the chub ended up being caught only at dawn and dusk. This was with unbaited minnow traps. When we baited the traps with dry dog food pellets, the chub were caught at dawn and dusk as before, and also during the day, as previously expected. We interpreted these findings as follows: the chub were among the largest minnows in the stream and under the full light of day they were particularly visible to kingfishers and mergansers, two fish-eating birds that had been spotted in the vicinity. Accordingly, the chub restricted their activity to dawn and dusk, a time when low light levels impaired the hunting behaviour of the birds. Only when the balance between predation risk and foraging success was tipped in favour of foraging, by adding nutritious bait to the traps, did the chub accept to venture out during the day.[27]

This example suggests that fish may shift the peak of their activities to those daily times when predators are less active or less successful. It is no strong proof however. Maybe the chubs were crepuscular because their preferred prey happened to be crepuscular as well. A convincing experiment would require all avian predators to be removed from the vicinity of the stream, in the hope that the chub's activity would then shift back to being fully diurnal. To do so would be impossible, for practical as well as ethical reasons. The situation might be more tractable in the lab, as predators could be presented at the same time every day, day after day, in the hope of teaching the fish to reduce activity at that time and to compensate by becoming more active at other times.

I am aware of only one experimental study that has convincingly linked predation regime and a prey's shift in diel timing of activity. Douglas Fraser, James Gilliam, and collaborators conducted a field study in Trinidad, in which they looked at guppy behaviour in predator-free and predator-present pools. The predator was another fish, *Hoplias malabaricus*. The scientists found that guppies were strictly diurnal in the presence of the predator, but were active day and night when free from predation. Night foraging was as profitable as day foraging, and therefore the guppies grew much better in the predator-free condition. So this was a case where predation seemed to limit the activity phase of a fish who could otherwise be active all the time.[28]

This page delved into the effect of predation risk on fish behaviour. I insist on the word "risk". In all cases covered here, the fish were wary but they were not under direct attack from an enemy. When an attack does happen, the behavioural response of prey fish is fairly straightforward: they flee or try to hide. How long they remain hidden or "frozen" depends on how scared they feel, and how eager they are to resume feeding or courting. Shoals under attack can also "explode", with all fish swimming in all directions (a reaction called flash expansion), or they can show a "fountain effect", splitting up in two, each halves passing by the predator's sides before rejoining behind it. Other fishes rely on anatomical and physiological defences rather than behaviour. They grow bony plates and spines on their body, or they synthesise toxins which are stored in skin or flesh. Some develop body markings that mimic the appearance of foul-tasting species, hoping to fool experienced predators into leaving them alone. Others sport false eyespots on their tail, and this may deflect predator attack away from the sensitive head area, or confuse the predators when the prey suddenly starts swimming "backwards".[29]

It is tough being a fish. Everybody wants to make a meal out of you. It must make for a stressful existence. Yet, fishes endure. Some of them even thrive (with the notable exception, these days, of those species that are commercially-exploited by people, a smart predator with whom it is hard to cope). Fish survival in the face of so many predators bears witness to the care fishes take in minimising predation risk.

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sooner than the nose-down foragers. Predators may be aware of this relationship, because when they were given a choice between two groups of guppies on the other side of one-way mirrors (so that the guppies could not react), the predators preferred to attack nose-down foragers over head-up foragers, and any group of foragers over non-foragers; see: Krause, J., and Godin, J.-G.J., 1996, Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey, Behavioral Ecology 7, 264-271.

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