How do parasites affect fish behaviour?

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2008-2015

For most people in their right mind, parasites are disgusting little creatures. The mention of them evokes images of tiny crawlers entering the body of innocent victims by devious means, encrusting themselves within various organs (often with very unpleasant effects), living off their host's tissues, and then exiting the body, sometimes through scatological avenues, leaving behind hosts that are incapacitated, if not mere shells of their former selves (as is literally the case for some insects). The true facts are not always that gruesome (after all, parasites that have to spend a long time inside a host do not benefit if this host kicks the bucket, because then they die as well) but often enough parasitic reality is not pretty. Ask biology students about their parasitology course, and they will tell you that attending class is like visiting a little shop of horrors. I, for one, came out of my parasitology course with newly developed phobias (mercifully temporary) of such innocuous activities as eating meat and bathing in streams – they represent ways of transmission for some parasites.

But students will also tell you that parasites are fascinating because of the complexity of their life cycles and the intricate ways in which they complete these cycles. So fascinating, in fact, that many students eventually become parasitologists and devote their entire lives to studying the little critters. Most of these people work with parasites of livestock or humans, but a few with an equal taste for ethology and ichthyology pursue the more esoteric questions that occupy this page: how fishes avoid getting parasitized, and how fishes alter their behaviour once they get parasitized.[1]

How fishes avoid getting parasitized

This question has not been studied very much, and the few experiments I am aware of have all dealt with bloodsucking ectoparasites. These small invertebrates can be free-living, but when they perceive a passing shadow or some water disturbance, they jump. With luck, they land onto the fish that created the disturbance. They fixate themselves onto the skin or the gills and then they start their dirty work, sucking blood like miniature versions of lampreys. Because of this sit-and-wait strategy, ectoparasites resemble predators, and we would expect that any means of avoiding predators (shunning dangerous areas, shoaling more, moving less) should also work against these parasites. This, in essence, is what the studies have revealed.

Almost all of this work was carried out in the laboratory of Gerry FitzGerald, using populations of three-spined and blackspotted sticklebacks that were plagued by the crustacean ectoparasite *Argulus canadensis* (the Canadian fishlouse). Free-living parasites, along with infected and non-infected sticklebacks, could be captured in the field and brought back to the lab. A doctoral student, Robert Poulin, noted that when one half of his tanks was decorated with plastic plants while the other was left open, the fishlice preferred to stay near the bottom in the "vegetated" area. Sticklebacks also preferred to swim near the bottom in vegetated areas but only when parasites were absent. When free-living fishlice were present, the sticklebacks' choice of habitat changed: they spent more time near the surface and in open areas, presumably to avoid the more infested sectors of the tank.[2]

Poulin then investigated another strategy for avoiding these parasites: shoaling more. He released 30 sticklebacks in circular wading pools that might or might not contain free-living fishlice. He reported that, as compared to the absence of parasites, fish in the presence of lice spent more time shoaling and formed larger groups. The benefit from bigger shoals derived from a higher probability that the free-living parasites would be detected and eaten by shoalmates – fishlice cannot infect a fish from the inside and can therefore be consumed with impunity. Another benefit was a dilution of the risk of being targeted for an attack by any given parasite.[3] Poulin then switched to another system (and another lab) and made the following observation. Within experimental tanks, brook trout fry that ended up getting infected more quickly by ectoparasitic copepods were also those that moved more within their environment. This result suggested that reduced movement is another possible strategy for avoiding ectoparasites.[4]

Later, back in FitzGerald's lab, Lee Dugatkin wondered if sticklebacks would avoid the company of parasitized conspecifics, given that fishlice can jump from fish to fish. He divided a long aquarium into three sections with transparent partitions. He put 10 healthy fish on one side and 3 healthy fish together with 7 infected ones on the other. He then repeatedly put single fish in the middle and recorded which group they approached most often. By and large the sticklebacks spent more time close to the healthy school, probably because the infected fish on the other side displayed odd behaviours such as swimming erratically and rising to the surface.[5] (The avoidance, therefore, probably was not to external signs of parasitism per se, but to conspecifics that behaved abnormally. Nonetheless, the end result is that parasite transmission is reduced)

Even in the case of ectoparasites that cannot be transmitted directly from fish to fish, it may pay to avoid the company of parasitized shoalmates. This is because the abnormal behaviour or appearance of infected fish may draw the unwanted attention of predators that could then endanger the whole shoal. One workable system here is the association between the trematode worm *Crassiphilia bulboglossa* and its host, the banded killifish *Fundulus diaphanus*. This trematode encysts itself in the muscles of its host, and this cyst forms a black spot that can be seen externally through the skin. Jens Krause showed that, in choice tests, banded killifish preferred to associate themselves with completely unparasitized shoals rather than completely parasitized ones (surprisingly however, Krause's killies did not prefer unparasitized shoals over partially parasitized ones). The same experiment also revealed that, in this case, it is the black spot caused by the worm's presence that betrays infection to the eyes of shoalmates. When members of a shoal were injected subcutaneously with a speck of black ink, they still displayed the normal behaviour of healthy fish but were nevertheless shunned by their shoalmates in choice tests.[6]

How fishes alter their behaviour once parasitized

This brings us to the second question, that of altered behaviour in parasitized fish. The underlying theme here is that often fishes are not the only host in a parasite's life. An endoparasite's life cycle often starts with the first larval stage entering the body of an aquatic invertebrate such as a snail. From the snail a new larval form is transmitted to a fish, either through ingestion of the snail or directly through water. Once inside the fish, another larval stage of the parasite encysts itself. Then the fish gets eaten by another fish or by a bird, the final host, inside of which the adult parasite develops. The eggs of the adult parasite are then passed on in the predator's feces, hopefully over water in the case of a bird, and from there infection of a snail can start the cycle anew. So, once inside a fish, it is in the parasite's interest to somehow alter the behaviour or appearance of this fish in a way that increases its chance of being captured and eaten by the next host in the cycle. Most studies have looked for evidence of this so-called "manipulation hypothesis".

The most convincing results to date have come from a study by Kevin Lafferty and Kimo Morris, working with the Pacific (=California) killifish *Fundulus parvipinnis* and its two trematode parasites, *Euhaplorchis californiensis* and *Renicola buchanani*. The researchers put wild-caught killifish in a 150-liter tank, selected focus individuals, measured their behaviour, and caught them again in order to dissect them and count the number of parasites inside. They found correlations between the level of infection and the frequency of conspicuous behaviours such as flashing, contorting, shimmying, and coming to the surface. The heavier the infestation, the more common the odd behaviours were.

Lafferty and Morris then tested the idea that such behaviours could make the fish more susceptible to predation. First, they captured killies from two different populations, one known to be parasitized and the other never parasitized. Then they placed known numbers of these fish in outdoor pens accessible to various species of wild herons, gulls, and fish-eating ducks. After 20 days, only 4 out of 53 unparasitized fish had disappeared (that is only 8%), as compared to 51 out of 95 parasitized ones (54%). Disappearance was caused by predation and not by other factors such as disease or escape from the pens: the study included a control experiment with enclosures covered by netting that prevented bird attacks, and almost no fish from either population disappeared from these pens. Lafferty and Morris concluded that parasitized fish are more susceptible to avian predators, to the benefit of their parasites.[7]

How the parasites alter the fish's behaviour is unclear, but the fact that one of the trematode, *Euhaplorchis*, is found in the brain suggests that the production of some crucial neurotransmitters may be manipulated by the parasite. Indeed, a recent study has found differences in the expression of serotonin and dopamine in infected fish as compared to healthy ones.[8]

Other studies have explored parasite-host systems that reveal different mechanisms of host manipulation. For example, the common dace *Leuciscus leuciscus*, when heavily parasitized by the eyefluke *Diplostomum spathaceum*, has been found to spend more time in the top 10 cm of an aquarium, possibly because the eyesight of the fish is impaired by the parasite, causing a preference for the better-lit surface waters.[9] The ultimate hosts of this parasite, gulls, are known to be more successful at catching fish that are closer to the surface. The same parasite can also affect the eyesight of rainbow trout, reducing the fish's ability to match its colour with that of the environment, thus making them more visible to predators, and reducing also their reaction to moving objects – some of which might be predators.[10]

Another commonly studied system is that of sticklebacks and the cestode *Schistocephalus solidus*. These parasites live in the peritoneal cavity of sticklebacks in such great size and numbers that they sometimes cause a visible distension of the abdomen. The parasites divert for their own purposes much of the energy assimilated by the fish. Afflicted fish are therefore hungrier, and we know that hungrier fish are more willing to take risks in order to keep on foraging. Not surprisingly therefore, several studies have shown that parasitized sticklebacks, after being scared by the strike of a model heron bill, flee over shorter distances, remain motionless for shorter periods, and come back to a food patch sooner than healthy individuals.[11] They are also willing to risk looking for food at the bottom of tubes that are located fairly close to a big predatory cichlid (behind a clear partition), something that healthy fish will not do.[12] In a similar vein, parasitized nine-spined sticklebacks that perform aquatic surface respiration in hypoxic waters (see the page: Oxygen and fish behaviour) come back to the surface sooner than nonparasitized fish after being frightened by the passage of a model kingfisher over the aquarium.[13] Infected fish may have increased energetic demands, requiring more oxygen.

Hungrier fish are also known to form shoals that are smaller, less compact, and less cohesive, attributes that favour foraging but make the shoal more vulnerable to predation. In addition, hungry fish spend more time at the frontal periphery of the shoal where they can be the first to find food, even though they may also be the first to encounter predators. Do parasitized fish show the same tendencies? Many studies have revealed that they do. Sticklebacks with cestodes, European minnows with helminthes, fathead minnows with flukes, as well as killifish with trematodes, leave more room between themselves and their neighbours, and stay at the front or periphery of the shoal – or leave the shoal altogether – more often than their healthier counterparts.[14] In general, the method used in these studies was to set up a shoal, select a focus fish that was obviously parasitized (as betrayed by abdominal distension or by black spots on the body), measure its social behaviour, and compare it to that of a healthy individual within the same shoal.

That method is not as elegant as the one used by Lafferty and Morris. As described above, these two researchers identified some fish by external marks unrelated to parasitism, measured their behaviour, and dissected them later to learn of their parasite load. This is an example of what we call a "blind" experiment because the observers did not know in advance what category (heavily parasitized, slightly parasitized, unparasitized) the focal fish would belong to. Therefore, they could not be biased while scoring the fish's behaviour. Observer bias – an unconscious tendency to measure ambiguous behaviour in a way that will make the results fit the expectation – is a constant danger in ethological studies. Researchers must compensate (but not overcompensate!) by trying to stay conscious of this danger or by using blind protocols.

Parasitism and mate choice

It may sometimes fit the ethologist's purpose not to know in advance the level of parasitism in fish, but the same cannot be said of the fish themselves. Females looking for a mate, for example, probably want to know if the prospective father of their young will have the stamina to care for the eggs and fry (in the case of parental species), and stamina is generally curtailed by parasitism. Females would also prefer males that could pass on to their offspring whatever heritable trait they may possess for resistance to parasites. Females would therefore be looking for a body feature that could reveal the male's infection level.[15] By choosing to mate with males that have such features, with a preference for those males that show marks of health, females could create a selection pressure for the existence of sexual ornaments that reliably divulge the male's level of parasitism. This hypothesis was first published in 1982 by William Hamilton and Marlene Zuk,[16] originally in the context of bright colors in birds, but tested a few times with fishes since then.

The most striking of these tests was carried out by Manfred Milinski and Theo Bakker at the University of Bern. They started by placing two male three-spined sticklebacks next to a tank containing a female that was ready to spawn, and noting how much time the female spent near each male. They found that she usually spent more time close to the male with the brightest red color on his belly. That this preference was based on color and not on some other correlated characteristic (such as courting intensity, for example) was elegantly demonstrated by offering the same choice of two males under green light, which rendered the red color uniformly black, and finding that the female then chose at random. Milinski and Bakker next offered a choice between males that had never been parasitized versus males that had been recently infected by a ciliate, *Ichthyophthirius multifiliis*, a parasite that impairs body condition and reduces the intensity of body colors. By the time of the tests, the external white spots caused by the ciliates had dropped off the fish, but the red coloration of the formerly parasitized males was still duller than that of their unparasitized conspecifics. As expected, the female sticklebacks spurned the dull males under normal lighting, but not under green lighting. Conclusion: when it is visible, the red coloration of breeding male sticklebacks is perceived by females as a badge of health, including resistance to parasites.[17]

Similar results and conclusion have been obtained with guppies. When infected by external parasites, male guppies lose brightness in their orange spots, and they also court less assiduously. Because of this, females shun them as prospective mates.[18] Avoidance of this kind can work both ways, and in some species the tables are turned on the females. In pipefishes for example, if females show external signs of parasitism such as black spots – either natural ones or artificial ones that have been created by injecting ink underneath the skin – males spend less time next to them.[19]

Other effects of parasites

Parasite infection can be correlated with behaviours that do not seem to give rise to increased predation risk. Some of these effects suggest a debilitating effect of parasites, but others are harder to interpret. For example: Salmon harbouring helminth parasites seem to orient less well during their seaward migration.[20] Infected minnows are less well synchronized with their shoalmates.[21] Upland bully *Gobiomorphus breviceps* and guppy females infected with various parasites have problems discriminating between males of different quality and size.[22] Parental male three-spot damselfish, *Stegastes planifrons*, experience more egg loss when they are parasitized, though it is unclear if this is due to a lesser ability to protect the nest from predators or from parasite-induced hunger which leads to egg cannibalism by the father.[23]

Sticklebacks blighted with *Schistocephalus* (them again!) generally prefer to eat smaller prey.[24] Perhaps the infected sticklebacks cannot compete with other fish for the larger food items, or maybe the overabundant internal parasites constrict the stickleback's stomach so much so that only small prey can be consumed. On the other hand, though sticklebacks parasitized with *Schistocephalus* consume smaller prey items, when they have an ample food supply and no competition they seem to eat a lot of those small preys, as they end up growing *faster* than non-parasitized fish, even when the weight of the parasites is subtracted.[25] It is unclear whether this is a response of the host fish to try and better marshal defenses against the parasite, or a manipulation of the host's physiology by the parasite to make it more visible to predators. Faster growth leads to bigger body size, and bigger fish are more visible to predators.

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Fisheries 10: 131-165; Barber, I., and Wright, H.A., 2006, Effects of parasites on fish behaviour: interactions with host physiology, pp. 110-149 in: Fish Physiology Volume 24, Behaviour and Physiology of Fish, (K.A. Sloman, R.W. Wilson, and S. Balshine, eds.), Elsevier Academic Press, San Diego.

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