

Behavioral Defenses against Parasites and Pathogens

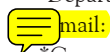
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INTRODUCTION

Parasites exert profound and pervasive costs on their hosts through mounting an immunity based defense, causing reduced growth and reproduction, and immunopathology (Sheldon and Verhulst, 1996; Zuk and Stoehr, 2003). Several chapters in this volume attest to the central importance of the host's immune system—and its effectiveness—in addressing these costs. Yet, natural selection should favor hosts that develop and maintain diverse anti-parasite behavioral strategies independent of host immunity and typical tissue reactions that either limit their exposure to parasites or that counter their negative effects (reviewed by Goater and Holmes, 1997).

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Hart (1994) was among the first to emphasise the importance of parasite-mediated selection for parasite avoidance behaviors, especially in the face of expensive immunity. Combes (2001) also emphasized avoidance behaviors in the context of 'exposure filters' that may limit infection rates. Such behaviors range in complexity from simple adjustments to host movement, posture and habitat choice, for example, to avoid biting arthropods, to sophisticated avoidance behaviors linked to fine-tuned parasite-detection strategies. Following intensive interest by both parasitologists and behavioral ecologists over the past decade, there is now a much better understanding of the extent of parasite avoidance behaviors across a broad range of both parasite and host taxa (recent reviews by Combes, 2001; Moore, 2002). However, most empirical tests regarding the effectiveness and extent of host avoidance behaviors involve the visible ectoparasites of ungulates, the avoidance by grazing mammals of fecal patches containing larvae of gastrointestinal nematodes, and the avoidance of parasitoids by insects. Much less attention has been devoted to studies aimed to evaluate parasite avoidance behaviors in aquatic systems, especially those involving fish (but see also Barber *et al.* 2000). The aim of this chapter is to review parasite avoidance behaviors in fish.

Hart (1994) and Moore (2002) stipulate two requirements that must be met before designating certain behaviors as 'avoidance'. First, parasites should be demonstrated to have a negative effect on host fitness, and second, anti-parasite behaviors should be demonstrated to decrease parasite intensity, or to ameliorate their negative effects. Implicit in these conditions is a third requirement: infective stages must be detectable. In Figure 5.1, we diagrammatically represent our view of potential host defense strategies that include host-avoidance behaviors. This framework provides the conceptual outline for our chapter. While very few studies support many of the links in Figure 5.1, there is abundant evidence from predator-prey interactions that fish can and do develop well-tuned behavioral responses to risk (Lima and Dill, 1990). Indeed, one underlying theme of our chapter is that the large number of studies on mechanisms of detection and avoidance of aquatic predators (and other aquatic stressors) provides a solid theoretical and empirical foundation for future studies involving parasite avoidance.

For our purposes, we define parasites to include typical ectoparasites of fish (copepods, brachyurans, and monogenean trematodes), helminthes (digenean trematodes, cestodes, acanthocephalans, and nematodes) and certain single-celled types (myxozoans and microsporidians). While our

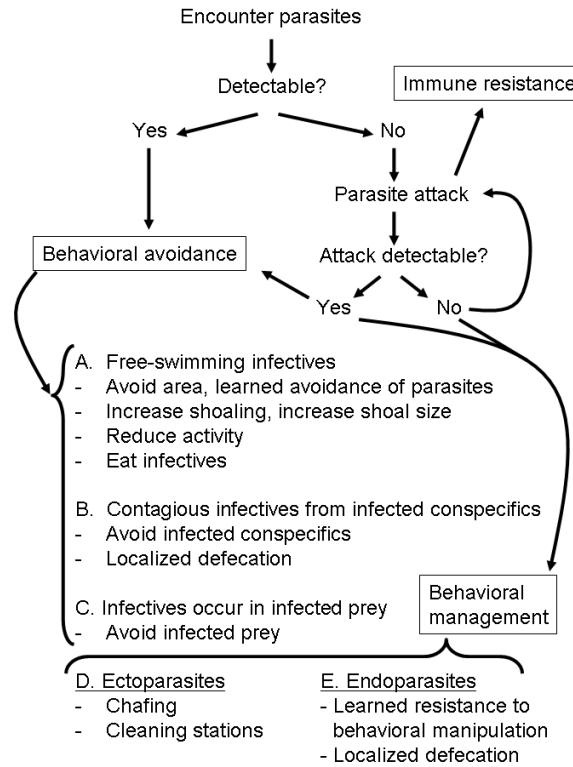


Fig. 5.1 The first step in parasite behavioral resistance is detection of the parasite. Parasite detection may occur either before the parasite contacts the host or after initial attack. Where behavioral avoidance fails, the immune system offers a second line of defense. When parasites are detected, behavioral avoidance of infection depends on the nature of the parasite threat. Generally, these fall into three broad categories: (A) avoidance of free-swimming swarms of the infective stage of the parasite avoidance, (B) avoidance of conspecifics infected with contagious parasites, or (C) avoidance of prey that are infected with early or intermediate forms of a parasite. Behavioral management of existing parasite load includes different strategies for ectoparasites (D) and endoparasites (E).

focus is on fish/parasite interactions, we also consider other aquatic host/parasite interactions where appropriate. We further place our discussion of behavioral avoidance into the context of the notoriously variable transmission strategies and life cycles of aquatic parasites. Generally, parasitic arthropods and nematodes actively seek their hosts, while parasitic viruses, bacteria, microsporidia, and fungi tend to rely on host contact. However, parasites defy tidy taxon-based categorization in the sense that many aquatic parasites such as aquatic trematodes (and some cestodes) possess a combination of active and passive stages within their

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complex life cycles (e.g., Haas, 1994). The larval stages have two obligate free-living stages (the miricidia and cercariae) that vary in the extent to which they rely on passive versus active contact with hosts. In this chapter, our focus is on avoidance behaviors of parasites that actively infect their host, primarily because these stages tend to be relatively large and perhaps more easily detectable, as also avoidable.

EVIDENCE FOR BEHAVIORAL AVOIDANCE IN FISHES

Behavioral Avoidance of Motile Infective Stages

Regardless of the active versus passive nature of parasite transmission strategies, high rates of encounter between hosts and parasites should lead to high rates of infection. One way for motile aquatic hosts to reduce exposure to motile infective stages is to reduce the overall activity. In a laboratory experiment, larval green frogs, *Rana clamitans*, and wood frogs, *Rana sylvatica*, reduced their activity by 25-33% when exposed to cercariae of the trematode *Echinostoma* sp. (Theimann and Wassersug, 2000). The authors concluded that reduced host activity in the presence of cercariae is an adaptive response to reduce their risk of exposure. Unfortunately, there are few comparable studies, and none involves fish hosts. Moreover, we do not know if similar host responses are present under natural conditions of exposure.

Experiments with ectoparasites provide indirect evidence that changes in host activity can affect the outcome of parasite/fish interactions. The time that brook trout (*Salvelinus fontinalis*) spent active in laboratory aquaria was positively associated with exposure to the copepod parasite *Salminicola edwardsii* (Poulin *et al.*, 1991). Thus, inactive fish acquired fewer parasites. When the fish were re-exposed to copepodids of *S. edwardsii*, fish with high infections from an initial exposure were found to be more active and further increased their rates of exposure. Thus, innately active individuals were infected with more parasites on each exposure. In this example, it is unknown whether fish could detect infective stages of *S. edwardsii* and thereby reduce their risk of exposure via reduction in swimming activity.

Many species of fish are known to shoal in response to risk imposed by a wide range of aquatic stressors (Krause and Ruxton, 2002). Although several studies have evaluated the shoaling behavior of infected fish (e.g., Ward *et al.*, 2005), only one research has evaluated shoaling as a direct

Who or what increased the fishes' rates of exposure.

response to parasite exposure. Poulin and Fitzgerald (1989) showed that three-spined stickleback (*Gasterosteus aculeatus*) and blackspot stickleback (*G. wheatlandi*) increased shoal attendance and increased the number of individuals per shoal (in large shoals of *G. aculeatus*) in response to the presence of the brachyuran *Argulus*. Increased group size and increased group cohesion is similar to the response of mammal herds to the threat of biting flies (Duncan and Vigne, 1979; Coté and Poulin, 1995; Moore, 2002). Although individual parasites achieved higher attack success in dense shoals than in small or sparse shoals, individual host fish reduced probability of parasite attack in large shoals—the greater the size of the shoal, the greater the benefit. Thus, in the case of this visually detectable parasite, risk of parasite infection evoked a shoaling response in hosts. It would be worthwhile to test for similar types of shoaling response in appropriate fish species that are exposed to trematode cercariae or penetrating myxozoan larvae.

Use of parasite-free refugia has also been shown to effectively reduce exposure. Karvonen *et al.* (2004) showed that rainbow trout avoided shelters when cercariae of *Diplostomum spathaceum* were released into it. The longer the trout waited to leave the shelter, the heavier was the rate of infection. In this case, the mechanism of parasite detection remains unknown. The trout were not parasite-naïve and, thus, learned recognition of chemical or other cues of the parasite is a possibility (see below). Alternatively, trout may have responded to tactile detection of penetrating cercariae without learning. The use of cercariae-conditioned water would help distinguish these alternatives. More studies of this type (Karvonen *et al.*, 2004) are needed to evaluate the degree to which behavioral responses are finely tuned, for example, to distinguish between cercariae that penetrate that particular host, from the many in a given habitat that do not.

Another form of behavioral avoidance can occur at the level of host habitat. One possibility is for hosts to avoid habitats in which direct evaluation of infection risk is possible. Evidence for this type of direct assessment is most common for the avoidance of biting insects and nematode larvae by grazing animals (reviewed in Moore, 2002). An empirical test of this idea involves sticklebacks (*Gasterosteus* spp.) exposed to the brachyuran, *Argulus canadensis* (Poulin and Fitzgerald, 1989). In parasite-free aquaria, sticklebacks were active near the bottom, adjacent to vegetation. In tanks containing free-swimming stages of *A. canadensis*, the fish swam along the surface away from vegetation. For this large,

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visually detectable parasite, shift in habitat use to avoid infection is probably an effective means of avoiding infection.

A second possibility is for hosts to avoid patches in which detection occurs via indirect indicators of infective stages. A crude way to evaluate this possibility is to determine whether variation in parasite avoidance behavior is associated with spatial or seasonal variation in the presence of infective stages. In north-temperate ecosystems, fishes are most at risk of cercariae infection during a narrow window of transmission in late summer and autumn (review by Chubb, 1979). Fathead minnows, *Pimephales promelas*, in lakes in northern Alberta, Canada are exposed to a maximum of approximately 30 cercariae of a brain-encysting trematode in their first fall (Sandland *et al.*, 2001) and up to approximately 500 in their second fall (C.P. Goater, unpubl. obs.). Similar examples of seasonally and spatially restrictive pulses of transmission are common in many different types of aquatic parasites (Chubb, 1979). Unfortunately, the extent to which variation in the expression of avoidance behaviors is associated with variation in crude indicators of transmission, such as site and season, has not been tested.

Evidence for more finely tuned assessment of infection status in aquatic systems is also rare, but enticing. Female grey tree frogs *Hyla versicolor* avoided ovipositing in experimental ponds in which they detected the presence of cercariae-releasing snails (Kiesecker and Skelly, 2000). Similarly, female mosquitoes avoided ovipositing in sites that contained infected snails (Lowenberger and Rau, 1994). In both cases, avoidance of infected snails would lead to reduction in exposure of the host's offspring to free-swimming cercariae released from snails. Kiesecker and Skelly (2000) showed that, in addition to detecting cercariae-releasing snails, female frogs could distinguish ponds with infected versus uninfected snails. These results indicate that behavioral avoidance of parasite infective stages can be finely tuned. Currently, the mechanisms underlying the detection of cercariae and/or the presence or absence of appropriate snails are unknown, but presumably it occurs via chemical cues.

There are several important components of parasite avoidance behavior that have not been studied in aquatic systems. One involves the avoidance of feces. Thus, for parasites with direct life cycles that spread to new hosts by infective stages contained in fecal matter, one might predict selection on hosts to: (1) avoid feces; and (2) to defecate in areas separate from foraging areas. Feces avoidance and localized defecation are well

documented in terrestrial vertebrates as a strategy to minimize exposure to infective stages of parasites (e.g., Hausfater and Meade, 1982). Fecal avoidance is especially important for species with limited home ranges or permanent stations where they reside much of the time. Certainly, nesting male fish would qualify as candidates for localized defecation but, to our knowledge, such data have never been collected. Sit-and-wait ambush predators face a similar problem in that they remain in place for long periods of time. Moreover, many prey species can detect conspecific chemical alarm cues released from ingested and digested prey contained in the feces of predators (Chivers and Mirza, 2001). Northern pike (*Esox lucius*), a sit-and-wait ambush predator, designates a specific area to defecate, and does so away from the area where it forages (Brown *et al.*, 1995). The authors argued that localized defecation could be explained by selection to avoid chemical labeling by their prey. An interesting alternative is that localized defecation could also limit the risk of infection with parasites originating from the host's own feces. Future studies may reveal similar attention to fecal management in other species of fish.

The role of host learning in parasite and/or habitat avoidance is also poorly understood. This is an important shortcoming. Predator-naïve fish do not recognize predators as dangerous until after they have had an opportunity to associate an olfactory (Chivers and Smith, 1994a), visual (Chivers and Smith, 1994b) or auditory (Wisenden *et al.*, 2007) stimulus with a predation event. Commonly, the releasing stimulus for this form of learning are chemical alarm cues released from injured epidermal tissue that occurs as a natural consequence of predatory attack. The same classes of chemical cues are reportedly released following exposure of juvenile rainbow trout to cercariae of *Diplostomum spathaceum*, even when the odor of the cercariae themselves invoked no response (Poulin *et al.*, 1999). Prey may learn to avoid predators directly by their odors or images. Additional cues for parasite avoidance can form with many other correlates of infection risk. For example, minnows can rapidly acquire recognition and avoidance of a specific habitat type associated with predation (Chivers and Smith, 1995). Alternatively, minnows can learn to associate novel odors with risk after watching a shoal mate exhibit alarm behavior to an odorant (Mathis *et al.*, 1996). Both conspecifics and heterospecifics can serve as models to impart acquired recognition of novel indicators of predation risk. The sophisticated learning mechanisms that arose to mediate risk of predation can be applied equally to risk of infection.

Likewise, it is conceivable that fish may learn to associate cercariae infection with certain species of snails (at least at certain times of the year) or with the types of habitats that contain infected snails. Fish might also learn to associate certain habitat types with the presence of highly pathogenic spores of microsporidians (e.g., *Glugea* in sticklebacks) or the habitats favored by the oligochaetes that serve as primary hosts of myxozoans.

Behavioral Avoidance of Infected Conspecifics

For parasites that are directly transmitted, selection should favor avoidance of hosts harboring infective stages. These would include some of the single-celled microparasites (e.g., the ciliate protozoan, *Ichthyophthirius* and other protist or fungal parasites) and certain macroparasites such as the monogenean trematodes. Consistent with this prediction, Milinski and Bakker (1990) showed that female sticklebacks avoided mating with males whose nuptial coloration had been dulled by the ectoparasitic ciliate *Ichthyophthirius*. In this case, choosy females accrued direct fitness benefits from reducing their risk of exposure to infective stages, and indirect fitness benefits by avoiding genes linked to parasite susceptibility. Outside of the mate choice context, bullfrog tadpoles (*Rana catesbeiana*) spent more time adjacent to uninfected tadpoles than tadpoles infected with the yeast *Candida humicola*, a pathogen that reduces host growth and survival (Kiesecker *et al.*, 1999). Further, tadpoles could express this preference based only upon chemical cues released from infected tadpoles, but could not do so when limited to visual cues alone. Kiesecker *et al.* (1999) elegantly demonstrated that spatial avoidance of infected conspecifics reduced an individual's risk of infection. Here again, the reliance of aquatic animals on semiochemicals for information management is remarkably similar to the mechanisms used for managing predator-prey interactions and reproductive decision making (Wisenden, 2003; Wisenden and Stacey, 2005).

Avoidance of conspecifics has also been evaluated in the context of shoaling behavior. Three-spined sticklebacks preferred to join shoals of conspecifics that were not infected with tumor-like growths caused by the microsporidian, *Glugea anomala*, perhaps to reduce the risk of direct transmission (Ward *et al.*, 2005). Likewise, sticklebacks preferred to shoal with uninfected conspecifics over those infected with *Argulus* (Dugatkin *et al.*, 1994). The simplest interpretation of these results is that individuals

reduced their risk of exposure by avoiding hosts with transmissible parasites. However, the explanation may be more complex in the light of results, indicating that killifish (*Fundulus diaphanus*) detect shoals of conspecifics infected with cysts of the trematode *Crassiphiala bulboglossa* (these are one of the causative agents of 'black spot' in fishes) and discriminate against them (Krause *et al.*, 1999). In this case, direct transmission from fish to fish is impossible. Perhaps individuals simply discriminate against 'sick' conspecifics, especially if they are detected at high density. Wedekind (1992) showed that female roach, *Rutilus rutilus*, could discriminate among males on the basis of the species of parasite with which they were infected. Thus, it is conceivable that individuals can assess the health status of conspecifics and assort themselves accordingly. Alternatively, hosts may avoid all parasites that infect epidermal sites of conspecifics to avoid potentially pathogenic secondary infections involving fungi (e.g., *Saprolegnia*) or bacteria. The adaptive significance of parasite-assortative shoaling needs further study.

The cues used to evaluate infection status in conspecifics are poorly known. In the case of *Glugea*-infected sticklebacks and black-spot infected killifish, detection is likely via visual cues. However, sticklebacks did not seem to avoid infective stages of *Argulus* when they were presented alone, even when chemical and visual stimuli from the parasite were made available to focal fish (Dugatkin *et al.*, 1994). In this case, the recognition and avoidance of the infected fish was cued either by altered behavior of infected hosts or perhaps by a chemical cue released by infected fish. It is also important to note that in each of the examples described above, fish were collected from the wild and thus presumably had opportunity to learn to recognize the parasite from previous experiences.

Behavioral Avoidance of Infected Prey

Many aquatic parasites have complex life cycles, with many involving the ingestion of resting stages. Thus, any discussion of avoidance of infective stages must also include avoidance of infected intermediate hosts. This feature has been covered in several reviews (Barber *et al.*, 2000; Moore, 2002). We will not duplicate that coverage here, other than to emphasize two points. First, despite the fact that some of the best empirical tests of this idea involve fish as hosts, no evidence for avoidance of infected intermediate hosts exists. Contrary to predictions, two empirical tests showed that fish prefer infected hosts to uninfected hosts. In one case,

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sticklebacks selected amphipods infected with larval stages of an acanthocephalan worm over uninfected ones (Bakker *et al.*, 1997), largely due to their ease of visual detection (the larvae are bright orange, and presumably easily detected through the exoskeleton). In the second case, three-spined sticklebacks strongly preferred to eat copepods infected with procercoids of the cestode *Schistocephalus solidus* over uninfected ones (Wedekind and Miliniski, 1996). Both cases involved parasites that have a negative effect on stickleback reproduction (e.g., Barber and Svensson, 2003). Therefore, they are precisely the types of systems where selection should be strong for avoidance, yet the outcome was prey attraction—not avoidance. Why should this be so? Lafferty (1992) explored this conundrum in a theoretical context, concluding that in such cases, the costs of infection must be balanced by the benefits of foraging on conspicuous (in the case of infected amphipods) or unhealthy prey that are easier to catch or to handle. When cost of infection to the final host is relatively small or delayed, a final host may potentially benefit from eating infected prey by using mature parasites in its gut to infect and compromise the antipredator competence of its prey (Lafferty, 1992). The costs and benefits of feeding on infected vs. uninfected prey is a ripe area for future study.

The second point we wish to emphasize is that learned avoidance of infected prey has not yet been evaluated. In the experiments described above and others reviewed by Moore (2002), discriminating hosts were exposed only once to infected prey. In the case of infected amphipods, the adult worms take approximately 30 days to reach maturity (longer at cooler temperatures). Thus, the pathogenic consequences of infection will almost certainly lag behind the point of ingestion. To what extent is it possible for fish to associate parasite-induced pathology to a prior ingestion event? We do not know the answer to this question, but we can predict that learned avoidance should be most likely to occur for parasites that are conspicuous within their intermediate hosts (e.g., *Plagiorhynchus* in *Gammarus*) and for parasites for which the lag between ingestion and pathology is shortest (e.g., packages of bivalve glochidia larvae within prey mimics).

Behavioral Management of Ectoparasites

Fish hosts have some options for behavioral management of parasite intensities after parasites have successfully contacted the host.

Ectoparasites may be dislodged and removed by chafing behavior, whereby a fish scrapes its body against a firm surface to remove a parasite (reviewed by Wyman and Walters-Wyman, 1985). Chafing is most likely to occur at the moment of parasite-host contact because dislodging a parasite is most likely to succeed if it is done before the parasite can firmly attach itself to the host fish. Chafing can be accompanied by body shakes, coughing motions or rapid starts (e.g., Thieman and Wassersug, 2000) or 'wiggling' (Baker and Smith, 1997) that serve to interrupt attachment of ectoparasites. Larval damselflies groom themselves in response to exposure to parasitic larval mites by rubbing a leg against an antenna, head, abdomen or another leg (Forbes and Baker, 1990). They also attempt to flee by rapid swimming.

While it may seem intuitive that chafing behavior should reduce infection, explicit evidence of such is difficult to find in the literature. Larval damselflies groom themselves in response to contact with the parasitic mite *Arrenurus* and successfully dislodge the parasite (Baker and Smith, 1997). Wyman and Walters-Wyman (1985) experimentally induced significant increases in chafing behavior in two species of fish by carefully loosening a scale or inserting a small particle of charcoal under a scale. Fish naturally infected with an external fungal infection also showed heightened levels of chafing.

If chafing and shaking are analogous to autogrooming by terrestrial vertebrates, cleaning stations by coral reef fishes are analogous to allogrooming, or perhaps 'anting' behavior of birds (Clark *et al.*, 1990). Client fishes visit cleaning stations (the territory of an individual of a cleaner species, often a member of the wrasse family) to be rid of their ectoparasites. Unlike other types of behavioral resistance to parasite attack, there is an impressive amount of literature documenting the benefits and interrelationships between the individual cleaner fish and their client fishes (Rhode, 1993; Losey *et al.*, 1999). Cleaners occasionally 'cheat' by nipping healthy mucus and scales from clients rather than searching diligently for ectoparasites and dead and infected tissue (Bshary and Grutter, 2002). However, because the majority of non-predatory reef fishes continue to actively visit cleaning stations, the benefits from doing so must outweigh the risk of encountering a cheating cleaner. Indeed evidence clearly shows a net benefit of cleaner fish in reducing parasite load of client fish (Grutter, 1999). The cleaner wrasse *Labroides dimidiatus* consumes 1200 ectoparasitic gnathiid isopods per day from the client species *Hemigymnus melapterus*. Individuals of *H. melapterus* that visit a

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cleaner show a 4.5-fold reduction in the number of isopods compared to individuals that were prevented from visiting a cleaner. This benefit occurred within a 12-h time span, strongly suggesting that behavioral management of parasite load occurs daily through visits to a cleaner station.

Behavioral Management of Endoparasites

The opportunities for management of endoparasites in fishes and other aquatic animals are probably limited in scope. Behavioral thermoregulation is one possibility, but has only rarely been assessed in fish. In a laboratory test, sunfish (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) injected with *Aeromonas hydrophila* showed a 2.6° C increase in mean preferred temperatures compared to unexposed controls (Reynolds *et al.*, 1975). Follow-up experiments involving goldfish (*Carassius auratus*) as hosts indicated that short-term 'behavioral fever' decreased host mortality relative to controls, presumably through temperature-induced enhancement of the immune response (Covert and Reynolds, 1977). Evaluation of behavioral fever in fish exposed to other types of parasites would be a useful addition.

Although some terrestrial vertebrates have been documented to consume the leaves of specific plants to reduce infection by endoparasites (reviewed by Lozano, 1998), there are no comparable examples in fish. Perhaps herbivory pressure that selected for noxious secondary plant compounds in terrestrial plants does not occur to the same degree in aquatic plants, thus pharmacological opportunities may be more limited for aquatic animals. A more likely behavior to arise in fishes is the consumption of roughage to dislodge intestinal parasites from the gastrointestinal tract as is known to occur in some primates (Wrangham, 1995; Huffman *et al.*, 1996).

CONSTRAINTS ON THE EVOLUTION AND EXPRESSION OF ANTI-PARASITE BEHAVIOR

In this chapter, we have emphasized the shortage of supportive evidence for parasite avoidance behaviors in fish. The lack of devoted attention to this topic must certainly be a contributing factor. Yet it is also possible that selection for avoidance behaviors is opposed by various constraints and trade-offs that may make them too costly or unlikely to evolve.

The first constraint is that infective stages of many fish parasites may not be detectable. Although chemical detection thresholds have been evaluated for fish in the context of mate selection and predator avoidance (Wisenden and Stacey, 2005), no such data exist for parasite infective stages. Thus, it may be no coincidence that the best examples of avoidance behavior come from fish exposed to large and visible ectoparasites. Although it is not possible to generalise on the relative costs of ecto- versus endoparasites of fishes, many of the parasitic brachyuran, copepod, and isopod arthropods, and also the monogenean trematodes, certainly have strong negative effects on fish growth and reproduction (review by Rhode, 1993; Barber *et al.*, 2000). Indeed, for many aquatic parasites, selection is likely to favor cryptic infective stages that restrict detection by visual, chemical, or tactile cues. Further, some species of aquatic trematodes have infective stages that are shaped and colored to encourage attraction, not avoidance, by potential fish hosts (e.g., Dronen, 1973; Beuret and Pearson, 1994). We should not expect parasite avoidance behaviors in those systems where strong counter-selection of this sort is common.

Avoidance behaviors may also be costly, both energetically and in the form of trade-offs with conflicting demands. Direct energetic costs associated with grooming are well documented in mammalian and avian host-parasite interactions (Hart, 1994), but have not been evaluated in aquatic systems. A second energetic cost is reductions in foraging opportunities. Predator-induced reductions in fish activity have strong negative effects on the foraging behavior of individuals. Similar costs are likely to exist for anti-parasite behaviors. Thus, avoidance behaviors that alter host activity (Poulin and FitzGerald, 1989; Thiemann and Wassersug, 2000; Karvonen *et al.*, 2004) should also be expected to reduce foraging opportunities. This hypothesis is untested.

A third potential constraint is that anti-parasite behaviors may conflict with anti-predator behaviors. Thus, alteration in habitat choice to open, non-vegetated regions of a pond by sticklebacks to avoid an ectoparasite may come at a cost of increased predation (Poulin and FitzGerald, 1989). However, there are very few tests of potential trade-offs between parasite and predator avoidance strategies. In a laboratory test, exposure to predator kairomones and cercariae of *Echinostoma* sp. reduced the swimming activity of *Rana clamitans* tadpoles by 48% and 30%, respectively (Thiemann and Wassersug, 2000). Predator-induced reduction in host swimming activity led to a 16% increase in the numbers

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of encysted *Echinostoma* sp. found in the kidneys. The authors speculate that the presence of fish predators masks the typical bursts of activity (Taylor *et al.*, 2004) that tadpoles elicit when they detect penetrating cercariae. Thus, a reduction of activity is beneficial in the presence of cercariae only, but it promotes attack when predator cues are present. Likewise, *Daphnia magna* avoid surface water during the day to avoid visually hunting predators. However, increased time at the bottom exposes *Daphnia* to the spores of *Pasteuria ramos*, a bacterial endoparasite (Decaestecker *et al.*, 2002). We need more studies that assess parasite avoidance behaviors in the context of predation and other aquatic stressors. Larval damselflies also suffered increased predation when they engaged in anti-mite behaviors (Baker and Smith, 1997).

Lastly, it is also conceivable that changes in host activity and other avoidance behaviors to one parasite may come at a cost of increased exposure to others. Thus, inactivity induced by motile cercariae may lead to increased exposure to parasites that require direct contact with substrate. Thus, selection may not exist for specific anti-parasite behaviors directed to one species, but for a low-level, generalized response to parasite risk.

CONCLUSION

We conclude that the requirements for parasite avoidance behaviors (Hart, 1997) are met in fish/parasite interactions. Fish are exposed to an enormous diversity of types and numbers of parasites, possibly on a daily or even hourly basis. This diversity is probably paralleled by a diversity of behavioral responses involving detection and then avoidance of infective stages. The evidence for avoidance behaviors is strongest for pathogenic ectoparasites that tend to have large, visible infective stages. For other parasites, the evidence is enticing that fish possess sophisticated detection capabilities that lead to avoidance behaviors that reduce infection risk. However, for this latter group, the evidence is scant, being restricted to only a handful of empirical studies. Thus, for the five anti-parasite behaviors that we have identified in this chapter, there are only one or two solid examples of each that involve fish as hosts. Not surprisingly, our understanding of parasite avoidance strategies lags far behind that for predator avoidance strategies. Can hosts associate risk of infection with seasonal or microhabitat cues and then engage avoidance behaviors to minimise that risk? What role does past exposure experience and learning play in the development and expression of subsequent avoidance

behaviors? Do the risk avoidance behaviors that fish employ in their aquatic habitats include parasites at all, and if so, are they traded off with behaviors associated with features such as predation and foraging? In answering these and other questions, we should recognise that chemical ecology is at the forefront of ecological interactions in aquatic environments. We predict that parasite-host interactions will prove to be no exception.

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