Review

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Parasite avoidance behaviours in aquatic environments

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Parasites, including macroparasites, protists, fungi, bacteria and viruses, can impose a heavy burden upon host animals. However, hosts are not without defences. One aspect of host defence, behavioural avoidance, has been studied in the terrestrial realm for over 50 years, but was first reported from the aquatic environment approximately 20 years ago. Evidence has mounted on the importance of parasite avoidance behaviours and it is increasingly apparent that there are core similarities in the function and benefit of this defence mechanism between terrestrial and aquatic systems. However, there are also stark differences driven by the unique biotic and abiotic characteristics of terrestrial and aquatic (marine and freshwater) environments. Here, we review avoidance behaviours in a comparative framework and highlight the characteristics of each environment that drive differences in the suite of mechanisms and cues that animals use to avoid parasites. We then explore trade-offs, potential negative effects of avoidance behaviour and the influence of human activities on avoidance behaviours. We conclude that avoidance behaviours are understudied in aquatic environments but can have significant implications for disease ecology and epidemiology, especially considering the accelerating emergence and re-emergence of parasites.

This article is part of the Theo Murphy meeting issue 'Evolution of pathogen and parasite avoidance behaviours'.

1. Introduction

Pathogen and parasite avoidance behaviours (hereafter referred to as parasite avoidance behaviours) are traits aimed at reducing the exposure and infection risk for a host to a given parasite and may thereby increase host fitness. Avoidance behaviours complement other mechanisms of defence, including immunological resistance and tolerance [1,2], but are generally considered less energetically expensive than a true immune reaction [3]. In theory, behavioural avoidance should be favoured by selection if it ameliorates the negative impacts of parasites on host fitness [4], and should transcend the type of environment, terrestrial or aquatic, in which the host and parasite live. By contrast, specific costs associated with each of the three mechanisms [4–6] result in remarkable variation among the defence traits observed in wild and cultured fauna [7–9].

Quantitative evidence exists from terrestrial, marine and freshwater environments that organisms lower their likelihood of infection by using parasite avoidance behaviours [3]. Parasite avoidance can take many forms, including quarantine of new arrivals or shunning of infected individuals from social groups (reviewed in [10,11]), avoidance of food or habitat containing infectious agents (e.g. [12,13]), avoidance of infected mates (e.g. [14,15]) and avoidance of infected conspecifics (e.g. [16,17]; box 1 and figure 1), to name a few. The study of parasite avoidance behaviour has its roots in the study of terrestrial mammals [4,10], but its role in parasite epidemiology, ecology and evolution in aquatic (marine and freshwater) systems is increasingly apparent. As the number of reports of parasite avoidance behaviour in aquatic systems has grown, we are
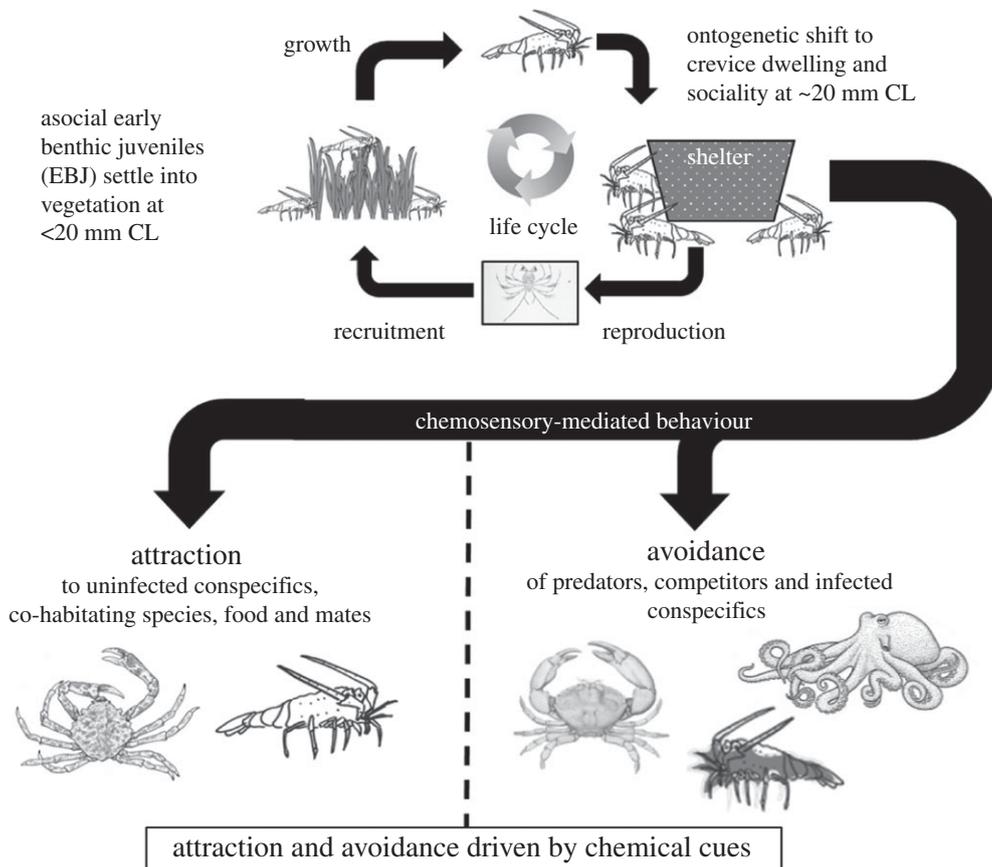
Figure 1. Life cycle of the Caribbean spiny lobster *Panulirus argus* and the role of chemosensory-mediated attraction and avoidance in its ecology. CL, carapace length. Juvenile *P. argus* are social but able to discern attractive chemical cues emanating from shelters containing healthy conspecifics and co-habiting crustaceans (spider crab *Damithrax spinosissimus*), from aversive chemical cues emanating from shelters containing competitors (stone crab *Menippe mercenaria*), predators (octopus *Octopus briarius*) and conspecifics infected with the lethal virus PaV1 (see box 1 for detailed case study). Spider crab (left) and octopus drawings used with permission from Helen Casey. All other drawings are public domain.

Box 1. Case study of the Caribbean spiny lobster.

The Caribbean spiny lobster *Panulirus argus* (figure 1) has a complex life history starting with a five- to seven-month pelagic larval period [18], which connects its Caribbean-wide population [19]. After the larval period, postlarval lobsters are attracted to chemical cues of red algae emanating from its preferred settlement habitat, shallow hard-bottom [18,20]. Early benthic juveniles (less than 20 mm CL) are asocial and spend several months hiding and foraging in complex vegetated habitat before going through an ontogenetic shift and emerging from the vegetation as social, crevice dwelling juveniles [21]. At this stage, they have developed acute chemosensory abilities which dominate their sensory ecology. They are attracted to chemical cues from healthy conspecifics [22] and the Caribbean king crab *Damithrax spinosissimus*, with which it often shares shelters [23]. Conversely, they avoid chemical cues from the predatory octopus *Octopus briarius* [24], their competitor the stone crab *Menippe mercenaria* [23], and conspecifics infected with the pathogenic virus PaV1 (Panulirus argus Virus 1) [25].

PaV1 was discovered in 2000 infecting juvenile lobsters in the Florida Keys [26], and has since been reported from throughout much of the Caribbean [27]. Prevalence of PaV1 has remained relatively stable in the Florida Keys, where it has been monitored since its discovery [28]. PaV1 is transmitted directly between juvenile lobsters via contact or ingestion of infected tissue [29]. Despite the efficacy of direct transmission in this social species, *P. argus* is able to detect and avoid shelters containing infected conspecifics before those individuals become infectious [17]. Even following a massive sponge die-off event, which dramatically reduced shelter availability and increased lobster aggregations, chemically mediated avoidance of infected conspecifics tempered transmission and reduced the likelihood of an epizootic [19]. However, in shelter-limited areas, avoidance of shelters containing infected conspecifics further decreases shelter availability, and in turn, increases the predation risk for both infected and healthy lobsters [25,30].

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now able to discern broad patterns in the form and function of avoidance behaviours, and compare these between terrestrial and aquatic systems.

In this review, we discuss some of the fundamental differences and similarities between terrestrial and aquatic environments, including how the environment is likely to affect the development of parasite avoidance behaviours, the types of parasite avoidance cues used by animals and the mechanisms of parasite avoidance. Additionally, we highlight how the effectiveness of parasite avoidance in reference to the

environment can affect disease dynamics, and the consequence of indirect avoidance behaviours. Finally, we explore the effect of anthropogenic activities on parasite avoidance dynamics, especially within aquatic hosts, and how a greater understanding could advance our ability to understand disease epidemiology in wild, cultured and invasive species.

(a) Distinct properties of aquatic and terrestrial systems

Fundamental physical differences exist between terrestrial and aquatic environments. Parasites are abundant on terrestrial surfaces and in terrestrial soils, as well as aquatic surfaces and sediments, but unless they are associated with a mobile host/vector (or await a host to come into contact with them) parasites must move through the air or water to reach a host. Therefore, the distinct physical and chemical properties of air and water (fresh and salt) are responsible for many of the differences observed in parasite transport, parasite transmission, parasite longevity and viability, and the diffusion of parasite avoidance cues through these different fluids. For example, at a given temperature, the density and viscosity of seawater are approximately 800 and 50 times greater, respectively, than that of air. These properties facilitate the suspension of particles, and when combined with the movement of water via tides and currents, these particles can be transported long distances. Indeed, parasites, whether associated with a host or not, can be transported long distances in a relatively short period of time through the water (reviewed in [31]). This is not to suggest that long-distance dispersal of parasites in the terrestrial environment is not possible. Fungal spores from agricultural parasites present some of the most extreme examples, with some studies finding that spores can be transported thousands of kilometres by the wind [32]. However, parasites in the marine environment are estimated to spread at a rate two orders of magnitude faster than their terrestrial counterparts, with viruses of marine vertebrates topping out at greater than $12\,000\,\mathrm{km\,yr}^{-1}$ [31]. In addition to greater passive transport in the aquatic environment, many more infective stages of aquatic parasites are mobile relative to their terrestrial developmental stages or other solely terrestrial diseases. Several parasite taxa, including trematodes, acanthocephalans, monogeneans (all aquatic) and crustaceans (all aquatic), are much more common in aquatic environments [33], presumably because of the motile developmental stage(s) they possess.

Water is also a more hospitable and stable environment compared with air, because of its higher heat capacity, lower levels of damaging ultraviolet radiation and lack of desiccating effect. These factors likely contribute to parasite longevity outside their host. The efficient transport, motility and potential for increased longevity of aquatic parasites may explain the apparent rarity of vector-borne parasites in aquatic environments compared with terrestrial [34].

The aquatic environment, and in particular seawater, is rife with bacteria, viruses and other microbes important to marine food webs [35–37]. In this respect, it is perhaps not surprising that many of the parasites, ranging from parasitic microbes to higher order metazoans, are capable of remaining viable outside of a host for extended periods, and can be transported great distances. This situation is classically illustrated by an unknown parasitic infection that emerged in the Caribbean Sea, near Panama, in January 1983, and caused approximately 95% mortality of long-spined sea urchin (*Diadema antillarum*) populations on coral reefs around the Caribbean within just 13 months [38]. While this was an unequivocally rapid epizootic, the high connectivity of many aquatic metapopulations allows parasites to persist in host populations at low to moderate levels [19]. Interestingly, recent evidence from a terrestrial plant–fungal system even showed that more highly connected host populations experienced lower parasite re-infection rates than isolated populations, due to disease resistance imparted by higher gene flow between host populations [39]. Whether this holds true for aquatic host–parasite systems, which typically demonstrate greater connectivity than their terrestrial counterparts, is unknown and worthy of further research.

For the following sections of the paper, we first go through cues and mechanisms of parasite avoidance and discuss their specific characteristics in a comparative framework between aquatic and terrestrial systems. We then present possible trade-offs associated with parasite avoidance and how anthropogenic changes to aquatic ecosystems could shape these behaviours. We conclude with a synthesis and suggestions for future research on parasite avoidance behaviours that are lacking or deficient in aquatic and terrestrial systems.

2. Cues for parasite avoidance

A central prerequisite of parasite avoidance is that hosts have to be able to detect the risk of infection. Detection can happen before or after the actual encounter with a parasite (reviewed in [40]), following specific cues associated with parasite presence, contact or establishment, that subsequently trigger an avoidance mechanism(s) (see §3). In humans, 'disgust responses' are mechanisms for avoiding diseases and the behaviour can be triggered through visually revolting sores or lesions [41], repulsive body odours [42], slimy textures associated with microbial activity [43] or just a simple auditory cue of infection such as coughing, sneezing or wheezing. While it is interesting to consider whether other animals show a disgust response in the same respect that we do, there is also neurological evidence that humans are capable of detecting and responding to visual and olfactory cues of sickness prior to the production of overt cues for disgust [44]. Other animals can also use similar cues to detect and avoid infection. For instance, terrestrial animals have been shown to use visual cues, as in the warbling vireo, *Vireo gilvus*, which uses visual cues to detect and eject brood parasites (i.e. eggs) from the brown-headed cowbird *Molothrus ater* [45]. Others use chemosensory cues, such as the nematode *Caenorhabditis elegans*, which can detect secondary metabolites from the pathogenic bacteria *Pseudomonas aeruginosa* and avoid contaminated feeding areas [46]. The mouse *Mus musculus* also detects chemical cues, but uses those found in the urine to avoid conspecifics, or potential mates, infected with a variety of pathogens [15,47]. Other terrestrial animals use mechanosensory cues, such as the termite *Zootermopsis angusticollis*, which sends vibrational cues to warn unexposed conspecifics after it contacts the pathogenic fungus *Metarhizium anisopliae* [48]. Even auditory cues are occasionally reported for parasite detection, as seen in baywing *Agelaioides badius*, which rejects shiny cowbird *Molothrus bonariensis* brood parasites partly by distinguishing between the begging calls of host and parasite fledglings [49]. Avoidance can also be triggered by a combination of two or more sensory cues, such as visual combined with chemosensory cues or visual combined with

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chemosensory and tactile cues [50]. When used in combination, one cue can compensate for diminished effectiveness of another [51] or improve the responsiveness to a threat through an additive effect [52,53].

(a) Visual cues

Visual cues are highly effective at rapidly transmitting information, but in the aquatic environment the distance over which these cues can be transmitted is often significantly shorter than in the terrestrial environment; and can be further hindered by turbidity, water colour or depth [51,54]. This may explain why visual cues often operate in conjunction with chemosensory or mechanosensory methods, which can be combined to reduce infection risk in aquatic environments. One of the first reports of parasite avoidance behaviour in the aquatic environment was at least partially based on visual cues. Juvenile three-spine sticklebacks (*Gasterosteus aculeatus*) were shown to avoid shoals of conspecifics infected with the ectoparasite *Argulus canadensis*, in part, because the infected conspecifics behaved abnormally [16]. Another possibility is that hosts could observe larger parasites visually, although in the case of *Argulus* sp., parasites alone did not elicit the avoidance behaviour [16].

Parasites may also affect mate choice through visual cues, as is commonly reported for male secondary sexual characteristics (see §3d). Female guppies (*Poecilia reticulata*) select males with fewer parasites (nematode *Camallanus cotti* or monogenean *Gyrodactylus* sp.) because these males demonstrate a higher rate of mating display [55]. Not limited strictly to female choice, male pipefish *Sygnathus typhle* use the visual cue of the black spots induced by the trematode *Cryptocotyle* sp. to avoid mating with infected females. This is presumably because the parasite affects female fecundity, as it is not directly transmitted between fish [56]. In sum, visual cues for parasite avoidance operate in both terrestrial and aquatic systems, but are likely to be more efficient and common in the former.

(b) Chemical cues

While visual cues allow for rapid transmission of information, chemosensory cues can be transmitted over a greater distance reducing the risk of being in close proximity to the threat [57]. Unlike their terrestrial counterparts, aquatic organisms are continually bathed in an environment rich in chemical compounds. In this respect, it is not surprising that many aquatic organisms possess intricate chemosensory systems capable of deciphering this complex environment (reviewed in [58]).

Aquatic and terrestrial organisms also fundamentally differ by the way in which they receive chemical cues. While terrestrial animals receive olfactory cues through the air and gustatory cues through water, there is no such distinction for aquatic animals—all chemical cues are mediated through water. Therefore, aquatic animals have evolved specific neuroanatomical pathways for distinguishing between these different types of cues, and these systems vary markedly between vertebrates (e.g. fish) and invertebrates (e.g. crustaceans) (reviewed in [58]). The chemicals which carry the information are typically small, unspecialized metabolic products [59,60], so aquatic animals must be able to detect minute differences in chemical composition amongst the vast mosaic of compounds. Their sensitive chemosensory systems are adapted to capitalize on the water solubility of these chemicals and the directional concentration gradients established

from their source. This forms an efficient mechanism for the transmission of information vital to many behaviours, including avoiding predators (reviewed in [61]), finding mates [62], finding appropriate habitat [18,63] and avoiding parasites.

Although chemoreception can be used effectively in either air or water, it is not without its disadvantages, regardless of the environment. In particular, turbulence in air or water can disrupt or limit chemoreception by diluting the chemosensory plume [64]. Research into this area has focused on foraging and predation in aquatic environments (e.g. [65,66]), but it has also been shown to affect parasite avoidance behaviours. While external chemoreception may have evolved as a mechanism of communication between unicellular organisms [67], the use of necromones (i.e. chemical compounds from dead animals or contagion) by terrestrial insects and aquatic crustaceans to avoid parasites suggests that this specific behaviour has ancient lineages and may have evolved in the sea over 420 Ma, prior to the divergence of Crustacea and Hexapoda [68]. This long history of chemosensory-driven behaviours among the Crustacea may explain why so much of their ecology is mediated by their chemical surroundings. The Caribbean spiny lobster *P. argus* provides an exceptionally good example (see box 1 and figure 1) of this. *Panulirus argus* uses chemosensory cues to detect and avoid shelters containing conspecifics infected with the virus PaV1, but in high-velocity flow environments this avoidance behaviour is diminished, presumably because the turbulence created by high flow interferes with chemoreception of infected individuals [25]. In addition to triggering *P. argus* to avoid infected conspecifics, chemosensory cues are used by this species to find healthy conspecifics and to avoid competitors and predators [17,23,25]. Chemosensory cues for parasite avoidance have remained important throughout the evolutionary history of vertebrates, including fish and amphibians. For example, Poulin *et al*. [69] found that rainbow trout infected with the trematode *Diplostomum* sp. release chemical alarm substances that increase the activity of unexposed conspecifics. While suggestive of a possible beneficial effect in parasite avoidance (see §3a), the exact role of alarm substances in parasite avoidance among fish is still largely unknown. Similarly, bullfrog tadpoles (*Rana catesbeiana*) have been shown to use chemical cues from conspecifics to avoid infection by the pathogenic yeast *Candida humicola* [70].

As we note above, chemosensory-driven parasite avoidance is not absent from the terrestrial environment, however, the very nature of the aquatic environment and the shear abundance of chemical compounds within it has necessitated a heightened evolution of chemoreception among aquatic taxa.

(c) Auditory and mechanosensory cues

Auditory and mechanosensory cues of parasite avoidance are probably much more common in terrestrial than aquatic systems. One reason for this may be that disease vectors, often detectable through sound (e.g. flying insects) and contact (e.g. biting insects), are more abundant in terrestrial systems [34]. In the aquatic realm, auditory cues associated with an infection risk seem unlikely and we are not aware of specific examples. However, mechanosensory cues in water have been proposed for trematode parasites that infect their hosts (e.g. many species of amphibians and fish) by piercing the skin and invading into host tissues [12]. In such cases, it is important to note that a response to a mechanosensory cue,

similar to a chemosensory cue, may depend on the number of infective stages present in the water. When parasite numbers are low, the response may be absent or require a cumulative exposure, which could result in some infection before avoidance is initiated. Fish hosts are also particularly well adapted for detecting very subtle movements, such as the detection of abnormal swimming behaviours, using mechanosensory cues detected via their lateral line, which could indicate a diseased individual. Mechanosensory cues could complement an avoidance behaviour primarily mediated by visual cues (see §2a) and are possibly more detectable in water due to its increased density relative to mechanosensory cues mediated by the movement of air in terrestrial systems.

3. Parasite avoidance mechanisms

Many of the mechanisms of parasite avoidance are principally similar across terrestrial and aquatic habitats (changes in activity, moving away from infection source, avoiding infected prey and mates, grouping), but differences also exist owing to the specific characteristics of water. Table 1 captures details of the comparison between marine, freshwater and a limited number of terrestrial taxa in behavioural avoidance mechanisms. Earlier reviews have covered some of these topics for fish [40,92] and other animals [3], although they did not provide a detailed comparative approach between terrestrial and aquatic systems. We also limit our review to avoidance and do not discuss mechanisms of parasite removal that take place after infection. Such post-infection mechanisms have been reviewed elsewhere (e.g. [40]).

Many avoidance mechanisms are sensitive to details of the parasite transmission process, infection burden, and the consequences (e.g. behavioural alterations) of infection. In some microparasitic infections, only a single contact may be needed for transmission (infection classified as 0 or 1), which could favour avoidance of sick conspecifics that transmit the infection. By contrast, effects of other parasites (usually macroparasites) often come about with increasing number of successful infections, i.e. in a density-dependent manner [93], when avoidance mechanisms (and the associated cues, see §2) may allow some infection to occur before the avoidance behaviour is activated. Further, infections may be transmitted between reproducing males and females, or vertically from parent to offspring, which can shape decisions of avoiding infected mates. These points apply equally to aquatic and terrestrial systems.

Implementing different avoidance mechanisms can also be influenced by how a parasite finds its host, and these processes can differ between aquatic and terrestrial systems. In aquatic environments, water currents can disperse passively transmitted propagules, such as bacteria, viruses and many larval macroparasites, more effectively than air. Infective stages that actively seek their hosts through motility (e.g. use of cilia or flagella) are also clearly more common in the aquatic realm. It is also worth noting that if an infection occurs, regardless of avoidance, it may shape avoidance of subsequent exposures. For example, species of gammarids [94], copepods [95] and fish [96] are known to become passive following a macroparasite infection, presumably because of the physiological consequence of infection. Overall, such conditions can result in mechanisms that decrease the likelihood of one infection, but increase the likelihood of another. Below, we provide some specific examples on the aspects described above, particularly from aquatic organisms.

(a) Changes in activity

An essential difference in parasite transmission strategies between aquatic and terrestrial environments is that motile infective stages are more common in water. This means that infective stages, particularly those of macroparasites, can actively seek their hosts [97]. Avoidance of such propagules can happen on a large scale by avoiding habitats of high infection risk (see §2b), or on a smaller scale through increases or decreases in host activity that target against parasite attachment and establishment. Evidence for the effects of host activity on infection probability in aquatic systems comes from amphibian tadpoles.

Responses in tadpole activity typically express as evasive movements or bursts of activity that aim to fend off parasites in close proximity, or prevent establishment once a parasite makes contact [82,98]. These are equivalent to responses in terrestrial animals against vectors of microparasite infections. Daly & Johnson [82] compared infection between active Pacific chorus frog (*Pseudacris regilla*) tadpoles to those immobilized using anaesthesia. They found that the anaesthetized tadpoles had up to 39% higher risk of becoming infected and harboured 2.8-times more parasite cysts. This suggests that microscale behavioural processes can determine infection in an environment rich in infective stages. Similar results have been reported for other amphibians [81,99,100]. Studies have also suggested that increased activity could take place without actual parasite contact, possibly through cues released by the parasite cercariae [99,101]. Overall, there is considerable variation in the behavioural responses to parasitism across different amphibian species [83,102,103], which suggests that it may be difficult to find general trends in activity responses to parasitism. Changes in host activity can also be tightly linked with other risks, such as from predators [83,99,100]. We discuss these trade-offs in more detail in §4.

Research on host activity and parasitism outside of amphibian systems is scarce. In fish, fathead minnows (*Pimephales promelas*) showed lower activity when presented with chemical and visual cues of dead cercariae of *Ornithodiplostomum* sp. (Trematoda), but only after the fish had an earlier experience with the parasite [75]. While these results are suggestive of avoidance learning (see §3f), they also emphasize fine-tuned and variable outcomes of avoidance mechanisms across different systems. Clearly, fish can move over a wider range than tadpoles when increasing activity may result in further risk of infection or pose a trade-off with the risk of predation.

(b) Avoiding areas of infection risk

A mechanism tightly linked with changes in host activity is the avoidance of areas with high infection risk. As noted above, water facilitates the active and passive spread of infective stages in aquatic environments, which tends to homogenize the spatial structure of hot and cold spots of infection risk, relative to terrestrial systems. However, infection risk in water is, nevertheless, spatially and temporally structured because infections are aggregated in certain host individuals [104], infected intermediate hosts releasing the parasite propagules are aggregated [105,106], there is seasonality in parasite transmission at higher latitudes [12,107], and many infective stages have short lifespans [108]. Moreover,

Table 1. Aquatic and terrestrial examples of pathogen avoidance behaviour compiled in this review, with select additional examples. The table explores the host, parasite, transmission pathways, avoidance behaviour, avoidance cue and the effectiveness of this avoidance system for all examples presented. In many cases, some of the information on these behaviours is lacking, and this has been marked as 'unknown'.

host	parasite	transmission pathway	host avoidance behaviour	avoidance cue	effectiveness	reference
marine environment						
lobsters	*Panulirus argus*	PaV1 (virus)	horizontal	avoid social interaction with infected conspecifics, who give off a chemical signal that indicates that they are infected with the virus	chemosensory	highly effective at avoiding the contraction of disease, which is vectored through the water; this system is discussed in detail in box 1	[17]
amphipods	*Gammarus duebeni* (var. *celticus*)	*Nosema granulosis* (microsporidia)	vertical	reduced sperm allocation	unknown	reduced sperm allocation for infected females is a trade-off between avoiding siring infected young and procreation	[71]
	Pleistophora mulleri (microsporidia)	vertical/horizontal	avoidance of cannibalism, relative to infected conspecifics	unknown	effectiveness unknown	[72]
	Maritrema novaezealandensis (trematode)	multi-host	swim away from high densities of parasite cercariae	visual	susceptibility to infection, and effectivity of immunological response, can be dependent on prevalence of the parasite in a population, where avoidance behaviour is more common in populations with a high prevalence of the parasite	[73]
fish	*Paracalliope novizealandiae*	*Cryptocotyle* sp. (trematode)	multi-host	males avoid infected females	visual	females with black spots are avoided by males when seeking a mate; the black spots indicate trematode infection in females; the trematode is suspected to affect female fecundity	[56]
	Sygnathus typhle		multi-host				
freshwater environment						
fish	*Oncorhynchus mykiss*	*Diplostomum pseudospathaceum* (trematode)	multi-host	swim away from concentrations of trematode cercariae suspended in the water; increased grouping	tactile, visual	likely dependent on high densities of trematodes present in the water column to avoid interacting with the cloud of parasites	[12,74]
	Pimephales promelas	*Ornithodiplostomum* sp. (trematode)	multi-host	learning: lower activity to avoid infection	unknown	when presented with a cue from infective trematodes, the fish initially had little behavioural avoidance response; over time the fish lowered their activity when provided with the stimuli	[75]

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Table 1. (Continued.)

host	parasite	transmission pathway	host avoidance behaviour	avoidance cue	effectiveness	reference
	Ornithodiplostomum ptychocheilus and Posthodiplostomum minimum (trematodes)	multi-host	increased shoal movement away from parasites	visual	shoaling reduced the contact with high densities of parasite	[76]
Gasterosteus sp.	Argulus sp. (crustacean)	horizontal/free-living	habitat preference and shoaling; avoidance of conspecifics exhibiting abnormal behaviour	visual	fish select habitat based on the presence or absence of the lice; increased shoaling of parasitized fish, possibly to increase the chance of grooming; avoidance of conspecifics with abnormal behaviour	[16,77,78]
	Glugea anomala (microsporidia)	horizontal	decreased shoaling with infected conspecifics	visual	infected animals have visible lesions and infected tissues, which trigger conspecifics to avoid shoaling with infected animals	[79]
Galaxias sp.	trematode	multi-host	migratory behaviour results in reduced parasitism	unknown	possible side-effect of migration	[80]
Poecilia reticulate	Camallanus catti (nematode) or Gyrodactylus sp. (monogenean)	multi-host/horizontal	females select males with lower infection burden	visual	selection is based on male colour and display	[55]
amphibians Rana sp.	Echinostoma trivolvis (trematode)	multi-host	move away from large densities of cercariae	visual	effectivity of infection rate can increase within a temperature range, but this does not alter successful avoidance	[81]
Pseudacris regill	Ribeiroia and Echinostoma (trematodes)	multi-host	impaired behavioural response via anaesthesia	unknown	anaesthetized animals were unable to move and became 2.8× more likely to become infected by encysting trematodes; activity behaviour is stated to lower parasite encystment success	[82]
Anaxyrus boreas	Ribeiroia ondatrae (trematode)	multi-host	reduced host activity	visual	reduced activity is considered to lower the likelihood of the animal encountering a parasite, or high densities of parasites; additionally, there is a possibility that the reduction in activity was related to infection, not avoidance	[83]

(Continued.)

Table 1. (Continued.)

host	parasite	transmission pathway	host avoidance behaviour	avoidance cue	effectiveness	reference
terrestrial environment						
mammals	various mammals	*Amblyomma americanum* (tick/arachnid)	opportunistic	ectoparasitic, increased probability of subsequent secondary infection, causes irritation to host and reduces in increased host energy expenditure	visual avoidance	visual avoidance of areas with high food content due to the presence of parasites; this is an example of the parasite-as-predator avoidance theory	[84]
	Rangifer tarandus platyrhynchus	faecal patches containing infectious agents	horizontal/ opportunistic	avoidance of foraging areas with high amounts of faeces results in the avoidance of infection	visual, chemosensory	avoidance of areas with high amounts of faeces reduced the likelihood of contracting disease, but could result in a lack of quality grazing; this could have impacts on the nutritional related health of the deer	[85]
	Equus sp.	avoidance of biting flies	opportunistic pest	move to areas with low fly concentration and group to further dilute the impact of the pests	visual	avoidance dilutes the impact of the flies on the horses, resulting in loss of less blood and avoids contracting parasites from the biting flies	[86]
	Elephas maxiumus	avoidance of biting flies	opportunistic pest	use of a branch as a fly switch to prevent flies from landing and biting	movement reaction to batt away flies; touch-sensitive and visual assumed	the use of the branch tool to swat away flies means that the animal loses less blood and maintains fitness and avoids contracting parasites from the biting flies	[87]
	Mus musculus	various	various	use of urine cues to avoid mating and co-habiting with infected conspecifics	chemosensory	being able to detect infected conspecifics via their urine allows the mouse to avoid a range of diseases	[47]
birds	*Vireo gilvus*	parasitic birds	specialized	use of visual cues to eject the eggs of parasitic birds	visual	by being able to detect when parasitic birds have laid eggs in their nests, the warbling vireo avoids brooding eggs from the brown-headed cowbird *Molothrus ater*	[45]
	Agelaioides badius	parasitic birds	specialized	use of auditory cues to eject the eggs of parasitic birds	auditory	by being able to detect when parasitic birds hatch in their nests, the baywing avoids feeding chicks from the brown-headed cowbird *Molothrus ater*	[49]

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Table 1. (*Continued.*)

host	parasite	transmission pathway	host avoidance behaviour	avoidance cue	effectiveness	reference
insects						
social insect species	general entomopathogens	horizontal/ opportunistic	allogrooming	unknown	allogrooming prevents parasite burden from reaching mortality-inducing levels	[88]
Formicoidea	general entomopathogens	horizontal/ opportunistic	corpse removal from the nest	unknown	removal of decaying conspecifics decreases the growth and spread of entomopathogenic disease	[89]
Zootermopsis angusticollis	entomopathogenic fungus	horizontal	vibrations from infected conspecifics trigger responses from unexposed conspecifics	warning behaviour from infected conspecifics	infected conspecifics vibrate to alert uninfected co-habitants of their infection status; this results in their removal and avoidance of disease	
isopods						
Armadillidium vulgare	*Wolbachia* sp. (bacterium)	vertical	reduced sperm investment from male to infected females	unknown	effective in avoiding females with decreased fertility due to infection	[90]
nematodes						
Caenorhabditis elegans	*Bacillus megaterium* (bacterium)	potential opportunist	avoid consumption of the bacteria	unknown	effective at avoiding this species as low food quality; potential pathogen	[91]
	Bacillus thuringiensis (bacterium)	opportunistic	immunological and stress response result in a behavioural response to physically evade the pathogen	chemosensory	immunological and stress response, alongside behavioural response, seem to be co-evolved and effective at avoiding this bacterial species by moving away from high densities of bacteria	
	Microbacterium nematophilum (bacterium)	opportunistic	defensive tail-swelling response in the host, and aversive behaviour	chemosensory	movement away from a lawn of bacteria reduces likelihood of infection	
	Photorhabdus luminescens (bacterium)	opportunistic	physical escape and reduced ingestion of pathogenic bacteria	chemosensory	capable of distinguishing between infective strains and avirulent strains to consume as food	
	Serratia marcescens (bacterium)	opportunistic	movement away from the bacterium	chemosensory	avoidance is dependent on the expression of cyclic lipodepsipentapeptide serrawettin W2 (secreted surfactant) by the bacteria and the correct functioning of the AWB neurons of *C. elegans*	
	Pseudomonas aeruginosa (bacterium)	opportunistic	learning of avoidance to virulent and avirulent strains	chemosensory	this behaviour is adaptable, and allows the animal to learn whether to avoid or tolerate the presence of bacteria	

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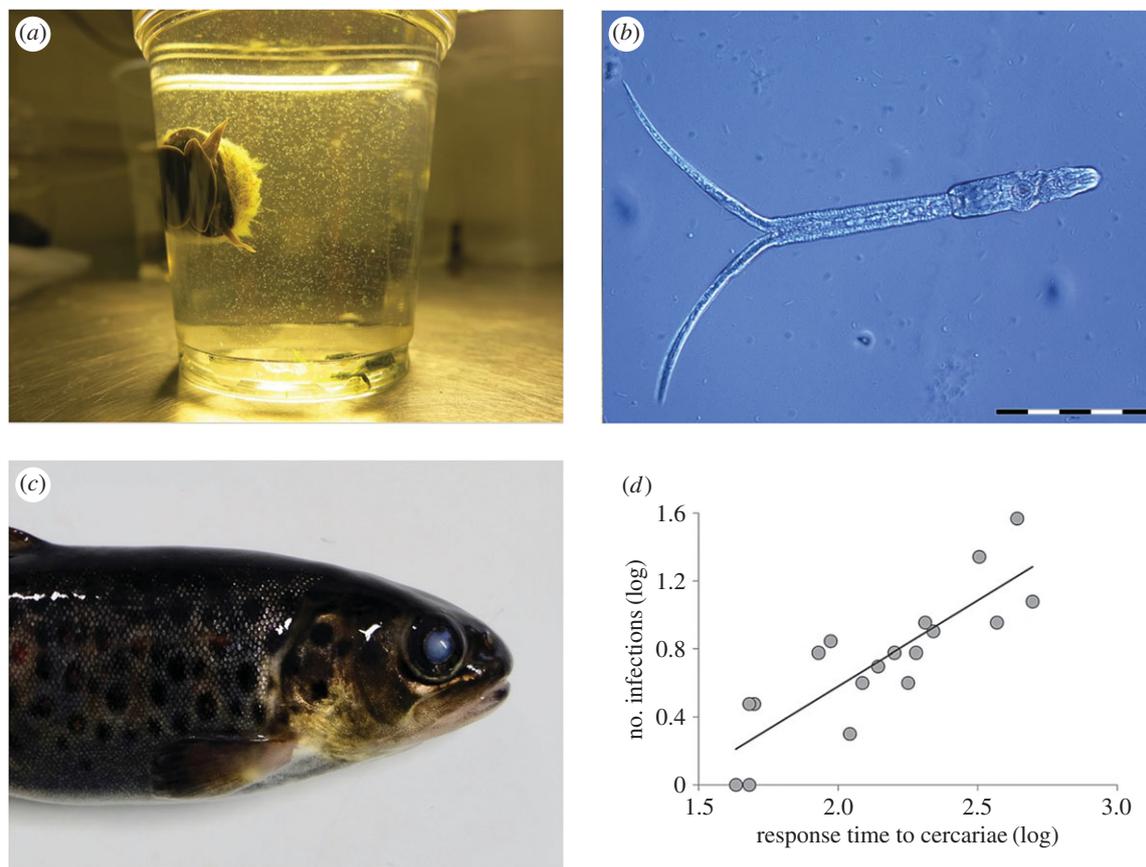rstb.royalsocietypublishing.org   Phil. Trans. R. Soc. B 373: 20170202

Figure 2. Parasite avoidance by fish in the *Diplostomum* system. Trematodes of the genus *Diplostomum* are ubiquitous parasites of freshwater fishes, with species like *D. pseudospathaceum* infecting the eye lenses of fish. (*a*) An infected first intermediate snail (*Lymnaea stagnalis*) host of the parasite can release tens of thousands of cercaria larvae per day (dense swarm of cercariae can be observed visually in water); (*b*) a cercaria (photos by Anssi Karvonen and Anna Faltýnková, respectively). (*c*) In the eye lens, parasites develop to metacercariae, which in high numbers can cause opacity of the lens, reduction in vision and severe fitness consequences for the fish (photo by Ines Klemme). Fish can recognize the presence of cercariae in water and avoid them by swimming away. (*d*) The response time to cercarial presence is correlated with the number of infections in the eye lenses (reproduced from Karvonen *et al.* [12], © 2004 Cambridge University Press).

parasite infective stages can actively seek host microhabitats [97], and their release can coincide with the diurnal rhythm [109] or seasonal activity of the host [12]. This makes it possible for animals to detect and avoid certain habitats, areas within habitats, temporal factors, or avoid hosts that are of higher infection risk than others (reviews e.g. in [40,110]).

Spatial avoidance through detection of infective stages in water has been studied in detail in many species of fish. For example, Poulin & Fitzgerald [77] showed that sticklebacks preferred vegetated benthic habitats when crustacean fish lice (*Argulus* sp.) were absent, but moved to the surface when the parasites were added. In that system, the infective stages were clearly visible to the fish. Similarly, rainbow trout move away from shelter to open water when exposed to cercariae of *Diplostomum* sp. (figure 2), possibly following mechanosensory or chemical cues [12]. These examples illustrate that aquatic hosts can identify spatial aggregations of parasites and avoid them. A particular feature of aquatic systems compared to terrestrial systems is that water currents and active dispersal can create a gradient of infective propagules from an infected host or other source releasing them. This can have significant implications for aquatic epidemiology, parasite detection and decisions in the spatial avoidance of parasites. Unfortunately, it is poorly understood whether hosts can specifically respond to the concentration of infective stages, or whether cues associated with these stages are what guide the magnitude and direction of evasive movements. More data are clearly needed both from aquatic and terrestrial systems. Overall, many more empirical tests of spatial avoidance in different types of aquatic systems, including temporal changes in infection pressure, are needed.

At a larger scale, migrations can be important in terms of disease epidemiology and the spatial avoidance of parasites [111,112]. While the principles of how migration mediates avoidance are similar between aquatic and terrestrial systems, much of the evidence comes from the latter [112]. One of the best-known examples of the effect of animal migration on parasite infection is from reindeer, *Rangifer tarandus*, where populations that migrate outside their calving areas have lower infestation of parasitic flies compared with non-migrating populations. This has been suggested as a defensive strategy against infection [113,114]. Similar processes have been described for the monarch butterfly *Danaus plexippus*, which benefits from the migratory culling of individuals infected with the protozoan parasite *Ophryocystis elektroscirrha* (individuals weakened by infections are lost during migration and decrease infection pressure on survivors [115]), and for several terrestrial animals (reviewed in [111]).

One of the few examples in aquatic systems comes from migratory and non-migratory species of fish from the genus *Galaxias* [80], inhabiting freshwater streams (all adults and offspring of the resident species) and pelagic marine habitats (offspring of the migratory species). By comparing infection levels of trematode parasites in different host populations, Poulin *et al.* [80] found that offspring of the migratory species had lower infection levels compared with resident ones.

Although it could not be concluded whether this is an adaptation to avoid parasitism, or a side-effect of the migratory behaviour, these results suggest that migrations can alter parasitism. Similar effects could take place in migrations of anadromous salmonid fishes through processes of migratory 'escape' from parasites (loss of parasite infective stages from the environment during host absence [11]) or migratory culling. However, to our knowledge, there are no detailed comparative analyses of parasite infections in resident versus migratory salmonids that would support or refute such hypotheses. Overall, it is important to note that in addition to decreased infection, migrations in many cases result in increased parasitism, depending on the mode of transmission and specificity of the parasite [111]. This may be synonymous between aquatic and terrestrial systems.

(c) Avoidance of infected prey

Several parasite taxa are transmitted trophically between predators and prey. Often these trophically-transmitted parasites also change the phenotype (appearance, behaviour, etc.) of their intermediate host to enhance transmission to a predatory next host [110]. Thus, by identifying and discriminating such changes or other signs associated with infection in the prey, predators could theoretically avoid becoming infected. Overall, examples of parasite-induced changes in host phenotype are abundant in both aquatic and terrestrial systems, and the topic of avoiding infected prey is covered in earlier reviews [92,110]. Thus, we do not go into this topic in great depth here, but state that current evidence largely suggests that rather than avoiding infected prey, hosts prefer eating prey whose behaviour has been altered by infections [116]. In cases where discrimination of infected prey has been reported, parasites are typically not trophically-transmitted and can actually induce anti-predatory phenotypic changes that protect the host from predation (e.g. [117,118]). Wisenden *et al.* [40] summarized underlying reasons for the general lack of avoidance of infected prey, some of which are related to energy budgets and cost-benefit ratios of consuming infected prey (see also [119]). However, data are lacking to compare between aquatic and terrestrial systems.

Avoiding cannibalism can clearly reduce the chance of intraspecific transmission of parasites in aquatic or terrestrial animals. Cannibalistic behaviour presumably occurs due to starvation, to maintain a social hierarchy, or to reduce competition for sex, space or food, while also gaining a nutritional benefit [72,120,121]. Cannibalistic behaviour has been reported in over 3000 species and has been noted to be influenced by parasitism. While cannibalism may indeed be a route of parasite transmission, there is little evidence from terrestrial or aquatic animals that it is a widespread and significant source of infection (reviewed in [122]). Bolker *et al.* [123] further addressed this issue in a theoretical framework using tiger salamander *Ambystoma tigrinum* larvae and the lethal ranavirus, ATV (Ambystoma tigrinum virus), as a model system. Larval salamanders can develop into one of two predatory morphs, specializing on invertebrates, or invertebrates and conspecifics, based on their abundance. They tested the hypothesis that infection risk explains the evolutionary lack of widespread cannibalism. They concluded that because disease transmission and cannibalism are both often density-dependent and interfere with one another (i.e. high disease prevalence reduces population size and, therefore, the likelihood of cannibalism,

and vice versa), this reduces the evolutionary pressure that infection risk might otherwise have on reducing cannibalism. While cannibalism would logically seem problematic for the transmission and spread of parasites among populations of terrestrial or aquatic organisms, empirical and modelling evidence suggests this is not the case.

(d) Avoidance of infected conspecifics and mates

Risk of contagious infections and 'bad' decision-making in social contexts may also result in another form of avoidance behaviour, the avoidance of infected conspecifics and mates. The prerequisite for such a behaviour is that infected individuals can be identified, which can take place through a number of cues (see §2). In the aquatic environment, these are predominantly chemical, but include visual cues that may be more likely to predominate in the terrestrial realm. One example comes from the Caribbean spiny lobster *P. argus* that can identify and discriminate conspecifics infected with the lethal virus PaV1 using chemical cues [17,25] (box 1 and figure 1). In fishes, sticklebacks prefer shoals of conspecifics not infected with the microsporidian, *Glugea anomala*, which causes clear visible swelling of skin cells [79]. Further examples have been described in bullfrog tadpoles [70] and other species of fish (reviewed in [40]). All of the examples above come from directly transmitted pathogens, where avoidance of infected conspecifics is reasonable because of the direct infection risk. However, hosts could also identify signals of infection associated with non-contagious infections [124]. An example includes macroparasites with complex life cycles that can also cause visible symptoms in their hosts, such as epidermal spots [124], opaque eyes [93] (figure 2), and changes in body shape [125]. While these infections cannot be passed directly between hosts, hosts can differentiate between infections in relation to their risk and this provides an interesting field of research both in aquatic and terrestrial environments about 'unnecessary avoidance'.

Hamilton and Zuk [14] were the first to put forth the handicap theory that mate selection, particularly selection by female birds for males with exaggerated secondary sexual characteristics (e.g. colour, song, display behaviour), could be driven by parasites. They showed an association between male secondary sexual characteristics and parasite load, whereby heavily parasitized males had less attractive characteristics, indicative of a weak immune system, and were avoided in favour of males with more overt characteristics. This same relationship was later demonstrated in the aquatic environment using male guppies, where display rate was associated with parasite load and female selection (e.g. [55]), and in three-spine sticklebacks where male colour intensity indicated parasite load to females [126]. Lopez [127] also demonstrated that in addition to genes for immunocompetence, an acquired resistance could affect male display and female mate choice.

Avoidance responses in mating systems may also vary based on the transmission mode of the parasite or the presence of sexual competitors. In the amphipod *Gammarus duebeni*, males may choose to mate with conspecifics infected with a vertically transmissible microsporidian, or choose to avoid them [71]. The transmission pathway of this parasite poses little threat to the male but would result in the production of infected young. Despite this, males may still choose to mate with infected females, but can limit their reproductive effort by providing a lower quantity of sperm, thus reducing the
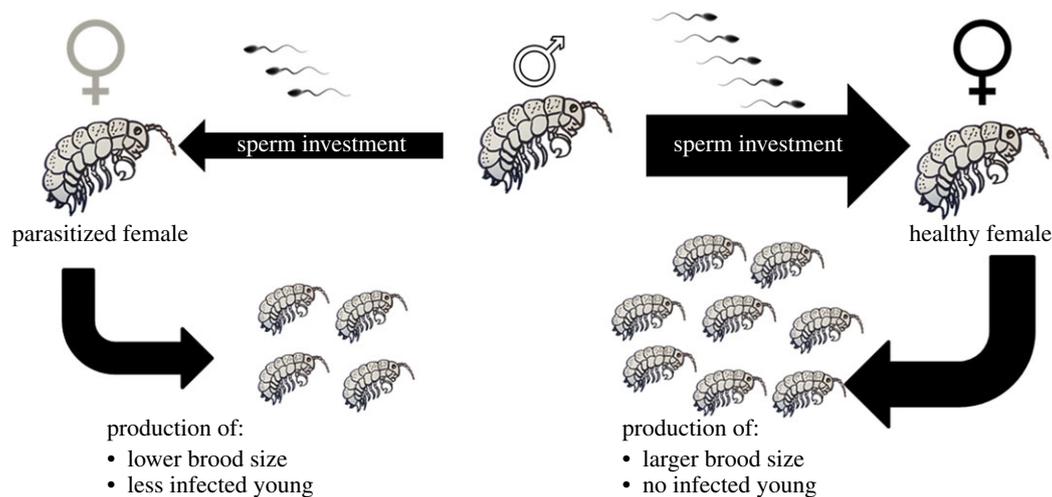
Figure 3. Diagrammatic representation of sperm investment in the amphipod *Gammarus duebeni*. Parasitized females receive a lower sperm investment from males, relative to those females who are uninfected. Hypothetically, this will lead to an increased chance of uninfected offspring within the population via larger uninfected brood sizes and increased health status, as identified by Dunn *et al.* [71].

number of infected offspring [71] (figure 3). A secondary factor, which may drive males to breed with infected females, is competition from conspecifics. This may regulate and balance the parasite avoidance behaviour, allowing for reproduction but limiting parasite transmission [128]. Parallel studies in terrestrial systems have found that European woodlice (*Armadillidium vulgare*) females infected with *Wolbachia* sp. bacteria receive less sperm than uninfected females [90].

(e) Grouping and sociality

Animals can also group in response to parasitism, which can act as a mechanism of avoidance if it dilutes or reduces the risk of infection on an individual host. Again, much of the evidence comes from terrestrial systems, such as ungulates infected with biting insect parasites [110,129]. Grouping and shoaling of aquatic organisms, such as fish, have more often been considered in association with predation (reviewed in [92]), while avoidance of parasitic infections has received less attention.

One of the first studies on grouping in response to parasitism was conducted using stickleback fish and their brachyuran ectoparasite *Argulus canadensis* [78]. In that study, Poulin & Fitzgerald [78] observed that parasitized fish formed larger shoals, and had a higher tendency to join shoals. More recently, Stumbo *et al.* [76] showed similar results in fathead minnows (*P. promelas*) exposed to cercariae from two harmful trematodes. The fish residing in the centre of more cohesive shoals had lower infection levels compared with non-shoaling conspecifics or those on the perifery of the shoal. Further, Mikheev *et al.* [74] investigated how individual rainbow trout, *Oncorhynchus mykiss*, avoided areas of infection risk from the trematode *Diplostomum pseudospathaceum* compared with fish groups in experimental tanks consisting of compartments with and without parasites. They found that both individual fish and groups of fish avoided the infection, but also that groups were more effective in their avoidance [74]. This suggests that individuals in a group may benefit from reactions of others to avoid both infection and predation, which results in lower overall levels of infection and consumption in tandem.

Despite the benefits of group living, in terms of predator and parasite avoidance, it can also come with a cost in the form of

higher within-group parasite transmission. This is true for many contagious diseases that can transmit effectively between hosts in close proximity. In other words, while grouping can clearly decrease infection risk for an individual to indirectly transmitted parasites through a dilution effect, it can also increase the risk of directly transmitted infections. Heavily parasitized hosts in a group may show impaired decision-making capability because of the infection. Such behaviours could result in misguided collective movements among less-infected conspecifics, and in turn, possibly lower food acquisition rates, and raise the risk of infection or predation. These topics have been discussed in detail in previous reviews (e.g. [92]).

(f) Avoidance learning

The ability of hosts to avoid infection is not necessarily intrinsic, and it is possible that hosts could also learn to avoid conditions with higher infection risk with experience from parasites they have encountered earlier. However, there is little direct evidence of avoidance learning in the aquatic environment. Most of the evidence so far comes from terrestrial insects and mammals learning to avoid flavours or odours previously associated with food-transmitted infections [130,131], or initiating a faster avoidance response after a previous infection, or by observing conspecifics becoming infected [132,133]. In aquatic systems, evidence for learning of risks comes almost entirely from predator-prey interactions (reviewed in [134]). For example, fish such as the minnow *P. promelas* can learn to identify habitats of high predation risk [135] or odours that are associated with alarm behaviour in conspecifics ([136], reviewed in [40]).

Principally, similar processes could be operating in parasite avoidance. For example, fathead minnows *P. promelas* tend to avoid trematode parasites *Ornithodiplostomum* sp., but activation of this behaviour requires an initial contact with the parasite, suggesting plasticity in the behaviour [75]. A recent study on sea trout (*Salmo trutta trutta*) has also shown that the fish can learn to identify visual signals of their environment that are associated with infections [137]. In that study, fish were given a choice between two compartments, one with cercariae of the trematode *D. pseudospathaceum* and the other without cercariae, marked with different colours. After the first four repeated trials, fish made a significantly higher

proportion of accurate choices between the compartments, i.e. entering the parasite-free compartment more often. Interestingly, the avoidance disappeared in the following trials as the fish presumably became immunologically competent to the parasite [137]. These results suggest that hosts can identify specific characteristics of their environment associated with parasitism, but also that the tendency to avoid parasites can be strongly linked with other components of defence, such as immunological resistance and tolerance (see also [138,139]).

Outside the context of avoidance learning in individuals, variation in parasite exposure between host populations can result in different avoidance adaptations. For example, in the amphipod *Paracalliope novizealandiae*, individuals from a population not commonly infected with the trematode *Maritrema novaezealandensis* had less pronounced avoidance behaviour and were more susceptible to infection compared with an infected population [73]. Indeed, as avoidance behaviours can be costly in terms of energy expenditure and trade-offs with other life-history functions, selection should reduce avoidance behaviours when they are no longer needed [140], increasing fitness in the parasite-free environment, but decreasing it in the presence of parasites [91]. For example, comparative studies suggest that levels of parasitism and predation experienced by host species in the wild can influence their parasite avoidance decisions [141]. Overall, such selection pressures for avoidance should show similarities across aquatic and terrestrial habitats, but comparisons are currently hampered by the lack of empirical examples particularly from the aquatic realm.

4. Trade-offs and negative consequences of parasite avoidance behaviours

(a) Immunological trade-offs

In general, hosts can rely on different forms of defence against infections. Traditionally, most research has emphasized the immune system, which for invertebrates consists of an innate branch that works through mechanisms such as RNA interference [142], cellular melanization responses [143] and the production of anti-microbial peptides [144]. Aquatic vertebrates, like mammals, fish, reptiles and birds also have an adaptive immune system capable of 'learning' to defend against parasites by producing an array of immunoglobulins [145], among other adaptions, that link behaviour and immunocompetence [138,139]. However, innate and acquired immune systems are energetically costly, which could make the evolution of parasite avoidance behaviours selectively advantageous. This could also result in trade-offs between defensive components, but empirical data are scarce. Conversely, excessive use of avoidance behaviours could also affect host condition through energy expenditure on low-risk scenarios. This could limit the benefits of other life-history traits (see §4b) as well as the upkeep of beneficial microbes within the 'microbiome' [146], and the efficiency of immune-related responses [147].

(b) Ecological trade-offs

Despite the presence of parasites, organisms must continue to forage, find mates, evade predators, and so on, in order to survive and reproduce. This often brings them into contact with parasites and creates a trade-off between these different life-history functions. One of the ecological conflicts that has received recent attention concerns the interactions between parasite and predator avoidance. It is possible that changes in host behaviour in response to parasites, such as increases in activity (§3a) or shifts in habitat (§3b), could make them more susceptible to predation or vice versa. In aquatic systems, several studies have illustrated such conflicts in amphibian tadpoles. For example, Koprivnikar & Penelva [101] reported stronger behavioural responses of *Lithobates pipiens* tadpoles to predation than parasitism. Similar results have been reported, for example, in *P. regilla* and *Anaxyrus boreas* [83]. Further, Raffel *et al.* [148] discussed the concept of 'parasites-as-predators' in this context, exploring the link between multiple predators and multiple parasites and how avoidance of one may result in the interaction with another. Although aquatic examples of the 'parasites-as-predators' concept are scarce, it has been considered in terrestrial examples, particular with mammal hosts of the lone star tick (*Amblyomma americanum*) [84]. The study by Fritzsche & Allan [84] found that 'food abandonment' was significantly associated with avoidance of parasitism, just as one would expect from the presence of a predator. Overall, these examples clearly illustrate the need for comprehensive studies of avoidance of different natural enemies.

Parasite avoidance behaviours may also include other types of ecological trade-offs. In dolphins, for example, the practice of inquisitive, sexual or dominance behaviour has been observed among males in response to deceased conspecifics, despite the likelihood of parasites (particularly bacterial diseases) being contractible from the cadaver [149,150]. In addition to the examples noted in §3d, some amphipods also exhibit cannibalistic behaviour in times of hardship, or when other food is not available, despite the risk of contracting infection [72]. In these examples, stricter parasite avoidance would likely result in lower infection rates, but could also lead to reduced fitness through lower foraging and reproduction. Similar trade-offs also occur in terrestrial environments. For example, trade-offs in nutrient intake were highlighted in a recent study where small mammals and birds, susceptible to the raccoon roundworm parasite *Baylisascaris procyonis*, were shown to avoid contaminated raccoon latrines that otherwise provide nutritious seed forage to animals not susceptible to the parasite [151].

Organisms should balance between parasite avoidance, parasite risk behaviours and susceptibility to infection, depending on the specific characteristics of each particular environment. Hosts are also often exposed to, and infected by, more than one parasite species. Such co-infections are common in natural and artificial environments [152]. The overall defence of a host against parasitic infections may, therefore, represent a balance between the risk of infection from multiple parasites. While interactions between parasite and predator avoidance behaviours in aquatic systems have been studied (see examples on tadpoles above), evidence of trade-offs in avoidance against different parasite taxa is virtually absent both in aquatic and terrestrial ecosystems.

5. Impacts of human activities and environmental change on parasite avoidance in aquatic environments

(a) Increase in environmental temperature

Many key aspects of parasite biology, aquatic and terrestrial, are strongly controlled by temperature. Therefore, ongoing

climate change is generally predicted to increase parasite transmission and reproduction [153,154]. For example, experimental data predicts that an increase of 10°C in temperature can increase release of infective stages of trematode parasites (cercariae) up to 200-fold [155]. Similarly, long-term time-series data on pathogenic fish diseases suggests an increase in disease occurrence with temperature [156]. Increasing temperature can also shape parasite avoidance behaviours. If detection and behavioural avoidance responses are connected to the level of infection risk [85], they should rise concomitantly with the emergence, re-emergence or proliferation of parasites. Longer term responses could include changes in allocation to different defence components (avoidance, immunity and tolerance) and in trade-offs between avoidance, foraging and predator avoidance (see §4b). Such ecological and evolutionary consequences of increasing parasite exposure form an open and interesting field for future research.

(b) Eutrophication

Similar to water temperature, eutrophication in aquatic systems [157,158] is predicted to increase infections among aquatic organisms [153], with potential effects also on avoidance behaviours. Eutrophication could also directly influence some of the avoidance cues perceived by hosts. For example, eutrophication increases water turbidity, which could impair visual cues from parasite infective stages. However, such questions await empirical tests. Eutrophication may also change host and parasite distributions through habitat loss. For example, in Gull Lake (Michigan, USA), anoxic conditions following eutrophication shifted mayflies to shallow waters where they became exposed to *Crepidostomum* trematodes transmitted from shallow-living sphaerid clams. When the lake later recovered, the process was reversed [159,160]. Similarly, eutrophication and resulting anoxic conditions have led to hybridization of deep- and shallow-living species of whitefish in Swiss pre-alpine lakes [161], which has likely exposed the deep-living species to new parasitic taxa in the shallows [162]. Thus, in both examples, human activity has forced hosts out of a potential parasite refuge into contact with new infectious agents, creating a novel selection landscape for parasite avoidance strategies.

(c) Aquaculture

Intensive aquaculture favours persistence of diverse parasite infections, including bacteria, viruses, protozoans and monogenean, trematode and crustacean macroparasites [163–165] that benefit from conditions of high transmission among abundant and dense numbers of susceptible hosts. Again, in comparison to terrestrial systems, water can effectively mediate infections coming from the wild, making it challenging to prevent them from entering aquaculture facilities. This, along with parasite replication, can result in rampant density-dependent exposure within the facilities. Aquaculture conditions also limit or prevent opportunities for spatial parasite avoidance, which may not only increase infections, but also prevent learning of cues associated with infections in the wild [137]. The latter can be particularly important for the survival of fish intended for fishery stock enhancement or recovery [166]. Unfortunately, research on parasite avoidance and its significance in aquaculture systems is lacking.

(d) Invasive species

Anthropogenic activity can result in movement of invasive and non-native species (INNS) that can carry a multitude of parasites to novel invasion sites. In some cases, this has resulted in the infection of native species [167,168]. Susceptible native species are unlikely to have evolved avoidance behaviours capable of responding to the non-native parasites, resulting in increased infection risk relative to an INNS that co-evolved an avoidance behaviour to the parasite [169]. Consequences of susceptibility to non-native parasites include reduced competitive ability with the native host, decreased reproductive success or even extirpation from the invasion range of the parasite [170]. Alternatively, INNS which lose their parasites when introduced to a novel invasion site can reduce their resistance or avoidance of infection risk as such traits lose their benefit in the absence of their co-evolved parasites [171]. Presently, a number of aquatic invasive species, many carriers of parasites, are being moved around the globe. Their introduction into novel habitats will undoubtedly have an effect on native fauna. However, lack of data on the effects of introduced parasites on native host behaviours make it difficult to draw general conclusions.

6. Conclusion and future directions

Research on parasite avoidance behaviours began in terrestrial systems decades before aquatic systems. However, accumulation of empirical evidence in recent years now suggests that parasite avoidance plays an important role in the defence of many aquatic organisms, ranging from small crustaceans to vertebrates such as fish and mammals. These behaviours operate through a complex of cues and avoidance mechanisms that complement the overall defence repertoire of an organism and, depending on the specific details of each host–parasite system, can provide effective and energetically efficient protection against infection. The distinct properties of parasite transmission in aquatic versus terrestrial systems generate marked differences in avoidance behaviours found in these environments, while many of the principal mechanisms remain similar. For example, the presence of suspended parasites in the water column could theoretically bring an organism into increased contact with disease-causing agents, but no comparative studies exist to assess whether parasite avoidance behaviour is more common in aquatic relative to terrestrial species.

While the knowledge of parasite avoidance behaviours in aquatic systems has increased over recent decades, some aspects are still in their infancy. For example, we know a great deal about the large-scale spatial distribution of infections among sessile taxa, such as corals and oysters, but very little about how avoidance of infected conspecifics or infected habitat drives the spatial distribution of mobile species, such as fish or crustaceans, at the population or ecosystem scale. We also need more research into the predicted outcomes for host–parasite interactions from ongoing climate change as this could dramatically alter our understanding of how hosts defend themselves against infections. Predictive models and the few available long-term datasets (e.g. [153,154,156]) suggest that parasitic infections are likely to increase with rising temperatures. Theoretically, this should impose selection towards measures that decrease host exposure to infections, but the exact outcomes are difficult to predict given the versatility of different host–parasite interactions and environmental

variation. More research and long-term data gathering are needed to tackle questions of parasite avoidance, particularly in different taxa and at different levels of infection risk, to gain empirical support for these predictions.

Changes in infection pressure and avoidance also connect closely with the function of the other components of the defence system, the immune system that eliminates infections, and tolerance that is built up to mitigate deleterious effects of infection without killing the parasite (e.g. [1,2]). The relationships between these components and their underlying mechanisms are fundamental to understanding host–parasite evolution, and can carry significant medical and economic implications. While recent studies in animal systems have begun to explore relationships between resistance and tolerance, in particular (e.g. [8,9]), the role of avoidance in complementing or offsetting these functions is still poorly understood. Further, the effects of factors such as host infection history on parasite avoidance strategies and changes in avoidance through experience and learning are virtually unexplored areas for research. Comprehensive studies on defence scenarios with hosts under different parasite pressures and with different infection experience, incorporating the role of all three defence components—immunological resistance, tolerance and behaviour—are needed.

To summarize, while the evidence for behavioural defences against parasite infections is accumulating, we still need to identify more instances of parasite avoidance behaviours in aquatic environments. They are apt to be much more common than we realize, particularly in the complex marine environment, but it will require creative, interdisciplinary approaches to discover them. Building our understanding of parasite avoidance behaviours across taxa and across the terrestrial–aquatic divide will encourage the development of unifying theories and holistic views of their role in the host–parasite evolutionary arms race.

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