Review

Ecological and Evolutionary Consequences of Parasite Avoidance

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Predators often cause prey to adopt defensive strategies that reduce predation risk. The ‘ecology of fear’ examines these trait changes and their consequences. Similarly, parasites can cause hosts to adopt defensive strategies that reduce infection risk. However, the ecological and evolutionary consequences of these behaviors (the ‘ecology of disgust’) are seldom considered. Here we identify direct and indirect effects of parasite avoidance on hosts and parasites, and examine differences between predators and parasites in terms of cost, detectability, and aggregation. We suggest that the nonconsumptive effects of parasites might overshadow their consumptive effects, as has been shown for predators. We emphasize the value of uniting predator–prey and parasite–host theory under a general consumer–resource framework.

Disgust Motivates Parasite Avoidance

Does the image below make you uncomfortable? If so, you’re not alone. In a psychological study, 16% of adults reported aversion to images showing clusters of circular objects, such as lotus seed heads (Figure 1) [1]. Termed ‘tryphophobia’ the fear, or disgust (see Glossary) (Box 1), of holes likely evolved as a disease-avoidance mechanism [2], as many pathogens that are transmissible by close contact (e.g., measles, smallpox, leprosy) cause clusters of pustules or lesions that are visually similar to holes. While tryphophobia has only recently garnered support in the scientific literature, parasite avoidance is older than human history [3]; animals ranging from aphids to ungulates employ a variety of strategies to avoid infection [4]. However, the ecological and evolutionary consequences of parasite avoidance are almost completely unexplored.

Figure 1. Lotus Seed Heads and Other Clusters of Circular Objects Such As Bubbles and Honeycombs Trigger Disgust or Revulsion in Many People. Termed ‘tryphophobia’, this might represent an overgeneralized disease-avoidance response. Photo credit: Vmenkov.

Highlights

Many predators cause prey to adopt defensive strategies that reduce predation risk. Similarly, costly, detectable, and aggregated parasites cause hosts to adopt defensive strategies that reduce infection risk.

Parasite-avoidance behavior has important ecological and evolutionary consequences for hosts, parasites, and the communities in which they live.

The cumulative effects of parasite avoidance might be as strong, if not stronger, than those associated with predator avoidance. Nevertheless, they have received far less attention from ecologists.

Although the potential for parasites to alter host behavior is well recognized, this is usually triggered through a parasite’s consumptive effects (i.e., infection). Here we emphasize the potential for parasites to alter host behavior through their nonconsumptive effects.

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In contrast to parasite avoidance, predator avoidance and its ecological and evolutionary consequences (collectively, the ‘ecology of fear’) [5] have received substantial attention. Predators prompt prey to adopt defensive strategies, with costs including reduced energy intake, increased investment in defensive structures, decreased reproductive success, emigration, and increased vulnerability to other predators. Indeed, the nonconsumptive effects (or ‘risk effects’) of predators are often stronger than their consumptive effects, and they can also trigger indirect effects that reverberate at the ecosystem level [6,7]. Over the last two decades, integration of nonconsumptive effects into predator–prey theory has revolutionized our understanding of predator–prey dynamics. However, despite clear similarities between predators and parasites [8], parasite avoidance has received far less attention, and the ‘ecology of disgust’ has not been proposed. Nevertheless, just as prey avoid costly, detectable, and aggregated predators, hosts should avoid parasites with similar characteristics. Furthermore, like predator avoidance, parasite avoidance should have far-reaching ecological and evolutionary consequences.

Avoidance Strategies

Hosts avoid infectious agents (a collective term that includes parasitoids, pathogens, macroparasites, parasitic castrators, and trophically transmitted parasites) [9] through four general strategies [4]. First, hosts can avoid interacting with individuals with whom they are likely to share parasites, especially if they show signs of infection. For example, lobsters avoid sheltering with virus-infected conspecifics [10], primates avoid grooming group members infected by orofecally transmitted parasites [11], and male birds engage in elaborate cloacal displays to signal to choosy females that they are free from parasites [12]. Second, if hosts can detect infective stages, they can avoid them directly. For example, aphids drop from plants to escape questing parasitoid wasps [13], tadpoles increase their activity level to reduce the likelihood of penetration by trematode cercariae [14], and cattle enter ponds to evade warble flies [15]. Third, if infective stages are less detectable, hosts can use cues that are reliably associated with parasites to avoid becoming infected. For example, ungulates avoid foraging near feces [16], carnivores avoid eating carcasses of other carnivores [17], and ants avoid building nests near dead ants [18]. Fourth, animals can alter their niche to avoid parasites. For example, birds incorporate volatile-containing plant material into their nests to discourage parasites [19], slow lorises apply their own venom to their bodies to repel ectoparasites [20], and termites build partitions within their nests to separate corpses from the rest of the colony [21]. Not only do these avoidance strategies benefit the host, they can also benefit its offspring. For example, mosquitoes avoid ovipositing in water containing other larvae parasitized by a digenean, thereby reducing infection risk for their own larvae [22]. Together, these strategies constitute an animal’s first line of defense against parasites.

Direct Effects on Hosts

Although avoidance of natural enemies increases victim fitness, it also incurs significant costs. For instance, animals must weigh the risk of predation against the benefits associated with foraging, mating, offspring care, exploration, and other activities [23]. Similar trade-offs probably exist for animals living under the threat of parasitism. For example, oystercatchers, which serve as final hosts of trophically transmitted trematode parasites, are picky eaters. They select intermediate-sized cockles, avoiding the largest ones, which are heavily parasitized, as well as the smallest ones, which are energetically unprofitable [24]. Similarly, deer forego foraging opportunities where ticks are abundant, suggesting a trade-off between foraging and risk of parasitism [25]. Animals might also forfeit mating opportunities or choose otherwise inferior mates to reduce infection risk. For example, great tits delay laying their clutch when nest boxes

Glossary

Consumptive effect: a negative effect of one organism on another due to energy extraction.

Disgust: one of the six basic human emotions, typically experienced as revulsion accompanied by desire to avoid contact with the stimulus. Once considered a cultural construct, disgust is now considered to be an adaptive system for infection avoidance [4,8]. Although much less studied, animals also avoid infectious agents, and this behavior could be motivated by disgust.

Ecology of fear (and disgust): the melding of the optimal behaviors of a consumer and its resource, along with their population- and community-level consequences [30].

Landscape of fear (and disgust): the relative levels of perceived predation and infection risk experienced by a prey individual, represented as peaks and valleys on the landscape [61,62].

Macroparasite: (a.k.a., ‘typical parasite’); an infectious agent that does not multiply within its host and does not necessarily kill it [9]. For example, an adult trematode in a bird.

Nonconsumptive effect: a nonlethal effect of a consumer on its victim due to perceived risk of predation or infection.

Parasite: a natural enemy that feeds intimately on one host [9].

Parasitic castrator: an infectious agent that eliminates host fitness, typically without killing its host [9]. For example, a larval trematode in a small gonad.

Parasitoid: an infectious agent that requires the death of its host to complete development [9]. For example, a wasp that develops and pupates within a caterpillar.

Pathogen: (a.k.a., a macroparasite); an infectious agent that multiplies within its host and does not necessarily kill it [9]. For example, rinderpest, a viral pathogen of ungulates.

Trait-mediated indirect effect: an indirect interaction in which one species (the initiator) alters the phenotype (i.e., trait) of another species (the transmitter), thereby changing its per capita effects on a third species (the receiver) [83].
are infested by ectoparasites [26], and male grouse experimentally manipulated to appear parasitized are less successful at attracting mates than those that appear healthy [27]. This could affect reproductive skew and reduce effective population size [28,29]. Although parasite-avoidance behaviors carry significant costs, the net effect on host fitness must be positive, or else these behaviors would not be maintained.

Beyond its effects on prey fitness, fear of predators can also regulate prey populations [30]. Indeed, a meta-analysis determined that nonconsumptive effects account for 63% of the net effect of predators on prey populations (via reduced fecundity, survival, density, or population growth rates) [7]. Although it is less studied, parasite avoidance might similarly affect host populations. For example, pea aphid populations declined by nearly 50% in the presence of a parasitoid wasp, because escape behavior (i.e., dropping from plants) reduced feeding opportunities [13]. In this study, the pea aphid was not a suitable host for the parasitoid, so population-level effects were attributed entirely to nonconsumptive effects. Hence, like predators, parasites probably limit victim populations through their nonconsumptive effects.

In addition to potential effects on host fitness and population dynamics, parasite avoidance probably also drives the evolution of behavior. For instance, migration might have evolved to help animals escape environmentally transmitted parasites such as many helminths and biting insects [31]. The infective stages of these parasites can accumulate where host density is high. Migration allows hosts to leave these parasites behind, returning to relatively uncontaminated habitats once infective stages have succumbed. For example, reindeer migrate from calving grounds where large numbers of larval warble flies are shed and will later emerge as adults. Warble fly intensity on reindeer in the summer range is negatively correlated with distance

**Box 1. Disgust**

The emotion disgust, which has recently received substantial attention in the psychology literature, is thought to have evolved as a disease-avoidance strategy [82,84,85]. Disgust could motivate avoidance of items or actions that are reliably associated with infection. For example, disgust motivates humans and many animals to avoid feces, and particularly those of conspecifics [86]. If feces were uninfected, then this avoidance behavior would be maladaptive, as it can limit energy intake [87] and reduce transfer of valuable information. Instead, the ubiquity of fecal avoidance in animals and across human cultures suggests that, throughout evolutionary history, feces have been contaminated with parasites, and avoidance behavior has reduced infection risk.

How might disgust differ from fear? These emotions seem to have opposing effects on sensory perception and attention [86]. Whereas fear generally stimulates sympathetic pathways, heightening information processing and physiological arousal, disgust tends to activate parasympathetic (and possibly also sympathetic [88]) pathways, reducing heart rate, blood pressure, and respiration. This leads to divergent responses; fear-inducing stimuli tend to grab our attention, whereas disgust-inducing stimuli tend to divert it (Figure 1). Thus, cognitive processes and behaviors are oriented in a manner congruent with each emotion’s evolutionary purpose: to protect the individual from the threat [88]. It must be noted, however, that the above studies measure responses in humans; ascribing emotions to animals is more difficult [90], and some have questioned whether animals even experience disgust [91]. Nevertheless, predator-avoidance behavior is generally assumed to be motivated by fear [7,92], whereas parasite-avoidance behavior could be motivated by fear or disgust, depending on the type of threat (but see Box 4). Detectable infective stages that actively search for hosts (e.g., parasitoids) might elicit fear in hosts, whereas cues associated with parasites (e.g., feces, carcasses) are usually assumed to elicit disgust.

While disgust might protect us from infection in the same way that fear protects us from predation, an overactive disgust response could be maladaptive. For example, tryophobia can be debilitating, as triggers are ubiquitous and frequently not associated with any real risk of parasitism [2]. Disgust might also play a role in psychopathologies such as obsessive-compulsive disorder, some eating disorders, certain forms of sexual dysfunction, and agoraphobia [93]. Indeed, in industrialized countries, our obsession with cleanliness might even explain increased incidence of autoimmune and allergic diseases [94].
migrated from the calving grounds, leading to the suggestion that postcalving migration is a behavioral adaptation to avoid these parasites [32].

Parasite avoidance also appears to shape host sociality, including group size and territoriality. Epidemiological theory predicts and empirical evidence demonstrates that, for parasites transmitted by close contact, parasite prevalence and intensity increase with group size [33,34]. This suggests that parasite-avoidance behaviors should reduce group size and increase territoriality. However, group size only explains a small amount of variance in parasite transmission [35], and animals might employ other strategies to reduce infection risk in large groups. For instance, recent studies suggest that modularity (subgrouping) within social groups reduces parasite richness and prevalence [36,37]. Group members can also cooperate to reduce disease transmission, a behavior referred to as ‘social immunity’, best studied in social insects [38]. Additionally, for mobile parasites that do not require close proximity for transmission, conspecifics might dilute risk [39], so that parasite-avoidance behaviors act to increase group size [40,41] (Box 2). Thus, parasite avoidance probably shapes sociality.

Parasite avoidance might also shape the evolution of individual and population-level differences in personality [42,43]. Individual variation in behavior can lead to differential parasite exposure, potentially contributing to heterogeneity in parasite burden. Exploratory, social, or promiscuous
individuals might be at higher risk of infection than sedentary, solitary, or monogamous individuals. For example, trematode infracommunities in pumpkinseed sunfish differ along a shy–bold continuum [44]. Risk could also vary with parasite transmission mode. For instance, across 127 primate species, socially contagious diseases were positively associated with rates of social learning, and environmentally transmitted diseases were positively associated with rates of exploration [45]. In principle then, local parasite communities could select for particular personality trait combinations, and population-level differences in personality traits might be partially explained by local differences in infection risk [42,46]. It has even been suggested that parasite avoidance could play a role in the evolution of culture in animal and human societies [45–47] (Box 3).

In addition to affecting behavioral traits, parasite avoidance might also shape physical traits. Evolutionary biologists have long puzzled over the maintenance of extravagant secondary sexual characteristics, such as large tails and bright plumage, that are preferred by the choosier sex but seem to confer a fitness disadvantage to the bearer. One hypothesis states that such ornaments indicate current disease status, potentially allowing the choosier sex to avoid mating with sick individuals [48]. This would provide dual benefits to the choosy individual; they avoid exposing themselves to pathogens that could impair their own fitness, and potentially also obtain heritable disease resistance for their offspring [49]. Furthermore, because infection can impair a host’s ability to perform parental care, choosiness could confer an additional benefit in some species [49]. In fact, parasite avoidance might explain the evolution of certain mating systems. Because it limits sexual encounters, monogamy decreases the risk of sexually transmitted diseases (STDs), and should be the optimal mating strategy (at least from the female perspective) for long-lived, widely dispersing animals (e.g., many birds and some mammals) when STDs are prevalent ([29,50] but see [51]).

**Direct Effects on Parasites**

Aside from its consequences for hosts, parasite avoidance probably also has profound consequences for parasites. According to the ‘ecology of fear’, fierce predators and vigilant prey create an equilibrium: fearful prey are difficult to catch and this reduces predator carrying capacity [30]. Parasite avoidance should similarly reduce parasite populations and dampen epidemics. For example, avoidance of baculovirus-infected cadavers reduces gypsy moth
infection rates by 4–7% [52], which could impact parasite populations. Although parasites have yet to be integrated into the original ecology of fear models, the effects of pathogen avoidance by humans have been explored through behavioral change and agent-based models [52,53]. These models are difficult to parameterize, but animals (and insects in particular) might offer opportunities to combine modelling and empirical approaches to measure how parasite avoidance affects parasite (and host) population dynamics.

Finally, just as parasite avoidance shapes host evolution, it could also shape parasite evolution. Avoidance behavior should select for undetectable infective stages and asymptomatic infections (except when transmission depends on detection). For example, many STDs are undetectable, both by infected hosts and potential partners [54]. For parasites that are detected indirectly via cues (e.g., feces, carcasses), avoidance behavior should select for infective stages (e.g., eggs, larvae, cysts) that can outlast or disperse away from these cues. For instance, larval lungworms (Dictyocaulus viviparus) disperse from feces aboard the projectile sporangia of the fecal fungus, Rhiobolus spp. [55]. Other fecally transmitted parasites (e.g., ascard nematodes, coccidians, cyclorrhhydidean tapeworms) have infective stages that can persist for months or even years in the environment, allowing them to outlast avoidance cues. Hence, as part of a perennial arms race, hosts have evolved strategies for avoiding parasites, and parasites have evolved strategies for overcoming these avoidance behaviors.

Indirect Effects
Beyond their direct effects on prey and hosts, natural enemies can also indirectly affect species with which victims interact. Predators cause density-mediated indirect interactions (DMIIs) if they kill their prey, or trait-mediated indirect interactions (TMIs) if they scare their prey. Although evidence is limited, a few examples suggest that infectious agents can also cause
TMIEs if they scare (or disgust) their hosts (Figure 2) [56]. For example, in the presence of parasitoid flies, Azteca ants less effectively control their prey, including the coffee berry borer and the fall armyworm, both important pests of coffee [57,58]. Nonconsumptive effects can also reverberate upward through food webs, affecting other consumers of hosts. For example, tadpoles increase their activity level to escape trematode cercariae, rendering them more susceptible to larval odonate predators [59]. Finally, nonconsumptive effects can propagate sideways through food webs, affecting competitors of hosts, or other species that interact with hosts nontrophically. For example, in the presence of parasitoid flies, invasive fire ants adopt a defensive posture, which reduces food acquisition, thereby favoring their competitor, a native ant [60]. Thus, through their nonconsumptive effects, parasites can trigger trait-mediated indirect effects on species with which hosts interact. For predators, we now recognize that the ecosystem-level consequences of nonconsumptive effects often exceed those of consumptive effects [7]. The same might hold for parasites, but no such comparison has been made.

The Landscape of Disgust
Laundre [61] proposed that prey perceive predation risk on a three-dimensional ‘landscape of fear’, in which the height and distribution of peaks is determined by the cost, detectability, and aggregation of predators. Similarly, hosts might experience infection risk on a three-dimensional ‘landscape of disgust’, which could be superimposed on the landscape of fear [62]. However, predators and parasites probably differ in cost, detectability, and aggregation.

Because avoidance behavior is associated with significant costs, victims should only avoid consumers that reduce their fitness. Avoidance of infected conspecifics is more common than avoidance of infected heterospecifics [4], presumably because parasites carried by conspecifics pose a higher risk. Although predators are immediately lethal to their victims, the lethality

Figure 2. Potential Direct and Indirect Effects of Parasite Avoidance in an Aquatic Ecosystem. Tadpoles increase activity levels to avoid trematode parasites (A). As a result, fewer larval parasites find hosts (B), resulting in lower infection intensity (C). Avoiding infection reduces time spent feeding, causing tadpoles to grow more slowly and metamorphose later. This also results in more resources for competitors such as zooplankton (D), mollusks, and herbivorous arthropods. Finally, increased activity renders tadpoles more susceptible to predators such as larval dragonflies (E).
of infectious agents varies. Some infectious agents (e.g., parasitoids, parasitic castrators) completely eliminate victim fitness, while others (e.g., macroparasites) cause negligible or dose-dependent pathology [9]. Therefore, animals are probably less likely to avoid nonlethal parasites than predators, and might be willing to accept a higher risk of parasitism than predation, especially if they could simultaneously reduce their risk of predation. For example, although tadpoles avoid both predators and parasites, if forced to choose, they prefer to forage under the threat of parasitism [53]. Furthermore, the costs of avoiding parasites might outweigh the benefits, particularly if the host is hungry [16], risky food is valuable [64], or infected prey are easier to capture [65]. For example, birds preferentially consume trematode-infected killfish, even though this results in parasite transmission, presumably because the caloric subsidy outweighs the cost of infection [66]. Parasite-avoidance behavior can also vary based on past experience and current parasite burden. For example, sheep accept fecally contaminated food less readily if they are already infected [16]. Some animals even learn from past exposure to parasites [67], perhaps in the same way they learn to avoid toxic substances [68]. Finally, if hosts can compensate for fitness losses associated with infection (as might be possible for parasites with long prepatent periods) [69], this could weaken avoidance behavior. Hence, behavioral flexibility could make parasite avoidance more difficult to detect than predator avoidance. Furthermore, because parasitism is usually less costly than predation (at least at the individual level), nonconsumptive effects of parasites could be weaker than those of predators.

In addition to differences in costliness, predators and parasites should also differ in detectability. Predators are typically larger than their prey [9], and can often be seen, heard, or smelled [30]. In contrast, most parasites are smaller than their hosts, and often orders of magnitude so [9]. When hosts can detect infective stages directly (e.g., by sight, as in parasitoids, or by skin sensations, as in ectoparasites; Box 4) [4], they usually exhibit strong avoidance behaviors [57,58]. However, parasite avoidance can occur even when infective stages are too small to detect directly. Just as prey can use cues from predated conspecifics to avoid predation [70], hosts can use (often subtle) cues from infected conspecifics or contaminated environments to avoid infection [4] (Box 1). However, indirect cues could be more reliable indicators of infection than predation risk, as predators are typically more mobile than parasite infective stages.

Finally, in addition to differences in costliness and detectability, natural enemies might also differ in distribution. Predators and parasites have comparable biomass in ecosystems [71], but that biomass is distributed differently on the landscape. In a given area, questing predators are generally rarer than questing infective stages, but each predator is bigger and (in most cases) represents a greater threat. Therefore, the scale at which prey avoid predators might differ from the scale at which hosts avoid parasites. For example, gypsy moth cadavers must be less than 1 mm away from the potential host to induce avoidance behavior [52]. Furthermore, because predators are generally more mobile than parasites, the predator-induced landscape of fear might be more dynamic than the parasite-induced landscape of disgust. Finally, due to body size differences [9], hosts can modify the distribution of parasites more readily than prey can modify the distribution of predators, allowing for avoidance through niche modification [4]. Despite these differences, however, both predator and parasite avoidance should be most pronounced when risk is aggregated and associated with predictable habitats or cues. For example, infective stages of the raccoon roundworm, Baylisascaris procyonis, are concentrated in raccoon latrines, which are avoided by disease-susceptible species [72]. Thus, in addition to being costly and detectable, parasites should be more often avoided when they display some degree of aggregation.
**Importance of Parasite Avoidance**

Parasite avoidance by humans can have far-reaching and often unexpected consequences. For instance, to avoid mosquito-borne illnesses such as malaria, humans have drained swamps, released non-native predators, and applied insecticides, with profound impacts on global biodiversity [73]. However, avoidance of high-risk areas such as wetlands and tropical forests has protected these habitats from development throughout human history. For example, early efforts to construct a canal linking the Atlantic and Pacific oceans (now the Panama Canal) were abandoned because thousands of workers died of malaria [74]. The direct and cascading effects of human parasite avoidance are well documented, and similar behaviors in other animals might have parallel, although perhaps more subtle, consequences.

The effects of parasite avoidance might be as strong, if not stronger, than those associated with predator avoidance. Because parasites are more ubiquitous than predators, cumulative exposure and lifetime fitness costs are often substantial and potentially higher than the average fitness costs of predation across a population. Furthermore, stress induced by predators is generally assumed to be acute and transitory (but see [75]), whereas parasites might induce chronic stress, which could be more costly. Finally, top predators and extremely large species are often immune to predation, at least as adults [76], whereas all organisms are susceptible to parasites. Given that top predators and large taxa often play keystone roles in ecosystems, parasite-avoidance behaviors could have strong cascading effects [62]. Moreover, since top predators and large taxa are less likely to need to balance predation and infection risk, they might be particularly responsive to parasite risk. Together, these factors suggest that the direct and indirect effects of parasite avoidance could be as important as those associated with predator avoidance.

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**Box 4. Avoidance of Parasites That Have Already Contacted Hosts**

Unlike predator–prey interactions, parasite–host interactions are durable [105], persisting, in some cases, for the entire lifetime of the host. Therefore, hosts can avoid parasites even after they have begun to feed, which is not possible in predator–prey interactions. This creates a gray area between consumptive and nonconsumptive costs. Avoidance of parasites that have already contacted their host likely varies from typical avoidance in at least three ways: (i) its timing, (ii) its completeness, and (iii) its emotional triggers.

For parasites that have already contacted their host, an animal can incur nonconsumptive costs before, after, or even while incurring consumptive costs. For instance, many animals engage in (potentially costly) therapeutic self-medication behaviors to treat existing infections [106]. Although the parasite is exerting consumptive costs on the host, self-medication reduces future costs associated with infection. A similarly complex timeline occurs for grooming and preening behaviors, which are energetically costly, but effective against many ectoparasites [19]. Such behaviors are typically triggered by skin sensations [107], which only occur after parasites have contacted hosts. Through grooming and preening, hosts can avoid becoming infected by parasites that have not yet begun to feed, and can also avoid further costs from parasites that have already begun to feed. Further confusing the differentiation of consumptive and nonconsumptive effects, many ectoparasites (e.g., ticks) vector bacterial and viral pathogens, so their removal can result in the complete avoidance of other infections.

Avoidance of parasites that have already contacted their hosts also differs from typical avoidance in the completeness of the avoidance behavior. While predator-avoidance behavior is either successful or not in deterring a predation event, costs associated with infection can be dose dependent. Therefore, avoidance of established parasites could simply reduce the consumptive costs of infection (i.e., by reducing the intensity of the infection) without removing the infection entirely.

Finally, a different suite of emotions could motivate avoidance of parasites that have already contacted their host. Fear seems unlikely, as escape would not protect against these parasites. Disgust also seems unlikely, because its behavioral features (e.g., nausea, appetite suppression) are ineffective against many established parasites, and because animals frequently consume groomed ectoparasites, a behavior inconsistent with disgust. Kuper and Fessler [107] recently proposed an ectoparasite defense system which involves cutaneous sensory and itch-generating mechanisms, suggesting that avoidance might be motivated by an emotion akin to irritation.
Most animals experience both predation and infection risk, and avoiding one consumer type could increase exposure to the other. For example, tadpoles increase their activity level to avoid trematode cercariae, but decrease their activity level to avoid predators. An individual faced with both threats must choose between these behaviors [63], allowing one consumer to potentially facilitate the other [59]. Predators and parasites might also exert opposing selection pressures on sociality. Aggregating with conspecifics usually decreases predation risk (via safety in numbers, group defense, and other mechanisms), but generally increases infection risk (but see Box 2). Similarly, communication (both intentional and eavesdropped, and within and across species) often reduces predation risk (via alarm calls, facilitation of group defense, and detection of predators), but generally requires close contact with another individual, thereby increasing infection risk. Although trade-offs between predation and infection risk have received more attention, predators and parasites can also exert synergistic pressures on victims. For example, marsupials avoid dingo feces, and although the response is usually attributed to predator avoidance [77], it likely decreases both predation and infection risk, as the predator and the prey share parasites. Thus, predator-avoidance and parasite-avoidance strategies might align or conflict with one another.

Given the potential ecological and evolutionary effects of parasite avoidance, why has it received so much less attention than predator avoidance? One explanation is that because parasites are generally less costly than predators (at least at the individual level), host-avoidance behaviors are more likely to depend on context, thereby reducing their detectability by researchers. Furthermore, due to their size, parasites are far less obvious than predators. Consequently, parasites are often detected indirectly via cues (Box 1), making it difficult to attribute avoidance to parasites. Finally, in recent decades, parasitologists have emphasized the fascinating ways in which parasites modify host behavior through their consumptive effects (i.e., infection) [78], perhaps overshadowing the potential for parasites to alter host behavior through their nonconsumptive effects. Together, these factors might have led ecologists to fail to recognize parasite-avoidance behaviors, or to underestimate their strength and importance. Nevertheless, behavioral avoidance is a critical defense that protects animals (and possibly plants; Box 5) from their parasites [4]. It is entirely possible that the costs associated with these nonconsumptive effects could be greater than those associated with consumptive effects, as has been shown for predators. Thus, recognition of the importance of nonconsumptive effects could revolutionize the field of parasite-host ecology, as it has for predator–prey ecology.

**Box 5. Do Plants Avoid Parasites?**

Animals often use cues from predated or infected individuals to avoid becoming the consumer’s next victim [70], and growing evidence suggests that plants might do something similar. Infected plants, or those under attack from herbivores (many of which qualify as parasites [9]), often produce volatile organic compounds. Neighboring plants can ‘eavesdrop’ on these chemical signals and ready their own defenses [108]. Termed ‘priming’, this imparts resistance, reducing damage to the receiver plant and improving its fitness. Though most evidence of this phenomenon involves responses to herbivorous arthropods, plants can also develop associational resistance to bacterial and fungal pathogens [109,110]. Hence, like animals, plants might use cues from infected individuals to avoid infection.

Parasite avoidance also plays a critical role in shaping plant evolution and ecosystem structure. The Janzen-Connell hypothesis, proposed in the 1970s and extensively tested in recent decades, posits that specialist natural enemies (including pathogens) render the area near a parent tree inhospitable for its seedlings [111]. This prevents any one species from dominating the forest, contributing to the maintenance of biodiversity. Furthermore, this hypothesis suggests that plants avoid pathogens by evolving dispersal mechanisms that increase the distance between seeds and parent plants. Indeed, seeds of many tropical trees are dispersed away from parent plants by large vertebrates with which they coevolved [112]. Seed dispersal is recognized to shape species composition and maintain diversity [113], and can also drive downstream effects on ecosystem processes such as carbon storage [114].
Concluding Remarks and Future Directions

As part of the sixth mass extinction, predators and parasites are vanishing from ecosystems at a disproportionately high rate [79,80]. As these consumers disappear, so too will avoidance behaviors [30]. However, loss of one consumer could strengthen the relative importance of others in eliciting avoidance behavior, which might be especially important if avoidance behaviors differ directionally or in the spatial distribution of risk. Moreover, loss of one consumer could cause victim populations to irrupt, thereby creating opportunities for other consumers to fill the open niche [81]. Hence the interaction between predator and parasite avoidance is likely to change in the future, with profound effects on victim behavior and distribution.

With a few notable exceptions, most evidence for behavioral avoidance of parasites comes from a limited set of systems: ants/aphids and their parasitoids [13], social insects and their pathogens [21], tadpoles and their trematodes [63], and ungulates/primates and their helminths [16]. We suggest that parasite avoidance is probably far more widespread than is currently appreciated, and we recommend identifying it and investigating its management implications (Box 6) in other systems. Furthermore, only a small number of studies have demonstrated that through their nonconsumptive effects, infectious agents can trigger trait-mediated indirect effects on species with which hosts interact, and no study has tested the strength of these effects relative to other types of indirect effects [56]. Such studies altered our understanding of the role of predators in ecosystems and they could do the same for parasites (see Outstanding Questions). Though the field is in its infancy, it is clear that hosts frequently avoid parasites, and that this behavior can have far-reaching ecological and evolutionary consequences.

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