Avoidance of parasites

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This is an update of David W. Thieltges, Robert Poulin, Kenneth Wilson, Avoidance of Parasites☆, Editor(s): Jae Chun Choe, Encyclopedia of Animal Behavior (Second Edition), Academic Press, 2019, Pages 688–695, ISBN 9780128132524, https://doi.org/10.1016/B978-0-12-809633-8.20828-5.

Abstract

Because parasites and pathogens are usually harmful, most animals have developed an array of precontact measures to avoid infection in the first place. These avoidance measures form a first line of defense against parasites; they range from camouflage to a variety of behavioral measures like movement or repelling behaviors, habitat choice and migration, selective foraging, and social interactions. In case avoidance fails, a second line of postcontact defenses, e.g., immune system, is called into action. Although costly, both avoidance and postcontact defenses result in selective benefits for the animal if parasite infection costs them even more in terms of fitness.

Keywords

Avoidance; Camouflage; Cost of defense; Foraging; Habitat selection; Migration; Repelling behavior

Glossary

Disgust An emotion hypothesized to have evolved to avoid disease risk.
Encounter–dilution effect Reduced parasite risk per individual in larger groups.
Final host (definitive host) The organism in which a parasite reaches maturity or reproduces.
Inducible defenses Avoidance behaviors triggered only in response to parasite cues.
Intermediate host An organism that harbors a non-reproductive stage of a parasite.
Selfish-herd effect Individual protection by positioning in the center of a group.
Virulence The degree of harm a parasite causes to its host.

Key points

- Avoidance is the first line of defense against parasites, often through behavior.
- Avoidance has costs, but it can be selected for if infection is worse.
- Strategies include visual and chemical camouflage, movement, and habitat choice.
- Feeding selectively based on visual or behavioral cues can help prevent parasite intake.
- Grouping behaviors can reduce parasite risk via encounter-dilution and selfish-herd effects.

Introduction

Infection by parasites (here, we include typical pathogens like protists, viruses, and bacteria) usually puts a high burden on animals. Infected hosts generally achieve lower fitness: they either show lower growth rates, reduced reproductive output, or even lower survival than uninfected members of their species. Therefore, animals are better off if they can avoid becoming infected with parasites in the first place. Not surprisingly, natural selection has favored many adaptations reducing the risk of infection (see Buck et al., 2018; Gibson and Amoroso, 2022 for examples). To reduce the contact rate with parasites, animals have evolved numerous precontact avoidance measures (Fig. 1). This first line of defense against parasites is mainly behavioral. If these precontact defenses fails, animals have a second chance to resist infections (Daversa et al., 2021). This second line of defense consists of postcontact defensive measures of a behavioral, physiological, or immunological nature (Fig. 1). Here, we focus our discussion on precontact behavioral avoidance measures. These involve a wide spectrum of adaptations serving to prevent infection, ranging from where to live or what to eat, all the way to whether or not to associate with other animals.

Avoidance is not free

It is often said that there is no such thing as a free lunch: everything has a hidden cost. Thus, we cannot expect that parasite avoidance is free. Whatever measures they use to prevent infections by parasites, animals must pay a cost in terms of reduced fitness (this also applies to postcontact defense measures). Behavioral actions initiated to avoid parasites may consume energy that will subsequently no longer be available for other purposes. For instance, green pea aphids defensively drop from their host plant in the presence of parasitoid wasps (Fill et al., 2012). The drop costs nothing, but climbing back up the host plant to return to feeding is costly enough to reduce aphid population growth. Alternatively, avoidance behaviors may take time away from other important activities such as searching for food or mates and can even divert energy away from development. For example, in the presence of parasitic mite cues, fewer *Drosophila* larvae were able to successfully pupate compared to larvae developing in the absence of any cues (Horn et al., 2023). The authors attribute this difference to reduced feeding and increased stress, both of which could negatively impact pupation. The cost of avoidance may be relatively small, but the examples above show that it is not insignificant. In theory, in the complete absence of parasites, these fitness costs result in a lower total fitness of resistant (ability to avoid) animals compared to susceptible ones (Fig. 2). However, in the presence of parasites, resistant animals achieve a higher total fitness compared to susceptible ones (Fig. 2). The investment in avoidance measures pays off for potential hosts when the costs of avoidance are

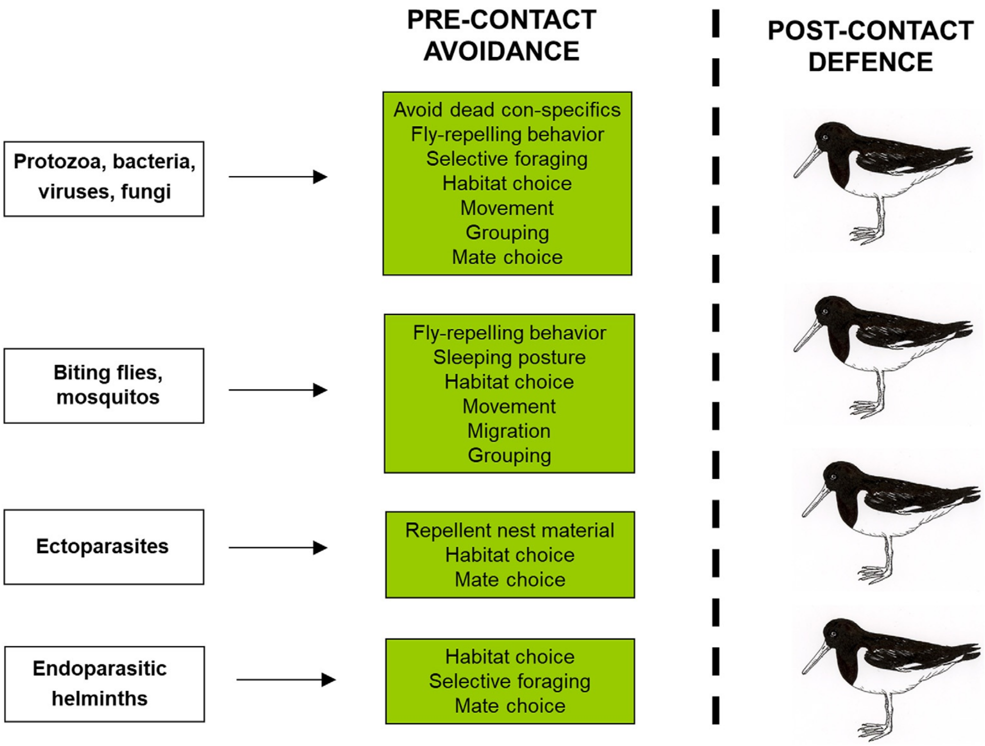

Fig. 1 Examples of precontact avoidance measures as a first line of defense against different types of parasites in birds. These are mainly behavioral measures to avoid contact with parasites in the first place. Once a host has come into contact with parasites, there is a second line of defense in the form of postcontact defensive measures that can be either behavioral, physiological, or immunological.

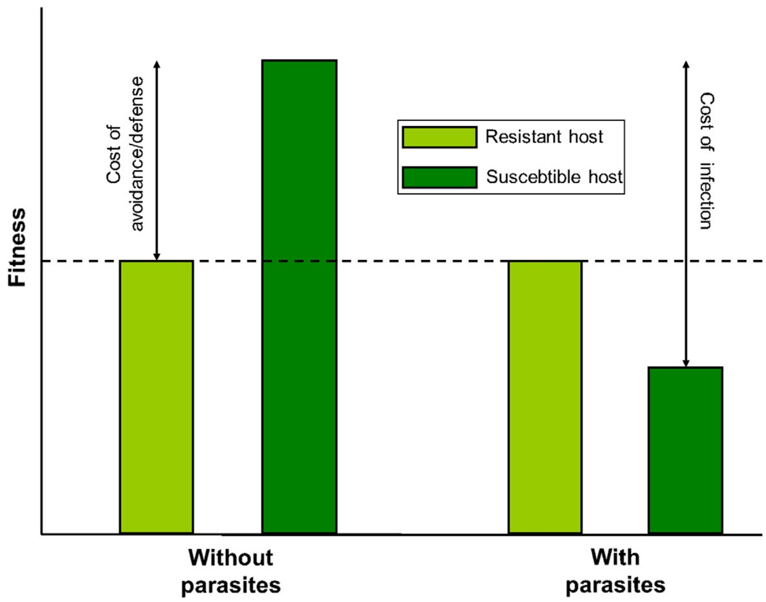

Fig. 2 Mechanisms of parasite and pathogen avoidance or defense are costly and thus reduce the fitness of resistant hosts compared to susceptible hosts in the absence of parasites. However, in the presence of parasites, the fitness of resistant hosts is higher than that of susceptible hosts with the latter suffering more from the costs of an infection. Precontact avoidance and postcontact defensive measures can only evolve if the cost of infection exceeds the cost of avoidance and defensive measures.

lower than the costs of infection. Only in this case will natural selection favor the evolution of avoidance mechanisms. In situations where the parasite is relatively benign, that is, it has hardly any effect on host fitness, and where avoiding it comes at some cost to the animal, we would not expect animals to have evolved avoidance behaviors.

Note that in many cases avoidance mechanisms are inducible, that is, they are only triggered after parasites are detected, such that their cost is only incurred when necessary. This is generally the case with behavioral avoidance measures: the animal only starts to behave in a defensive mode when the presence of parasites is detected. Thus, the full cost of avoidance is not paid when there are no parasites around: This means that in Fig. 2, the magnitude of the cost of avoidance would be even lower compared to the cost of infection. Inducible behavioral defenses are also advantageous because by chance alone, many animals would never encounter parasites anyway. Doherty and Ruehle (2020) argue that the magnitude of these inducible responses in present-day animals could have evolved depending on the historical risk of infection, which integrates the probability of attack and the fitness effect of the parasite. In other words, even parasites that are rarely encountered can drive the evolution of strong avoidance behaviors if they are highly virulent—similar in magnitude to the avoidance responses triggered by more frequently encountered but less harmful parasites. Parasites are never distributed evenly among all individual hosts in an animal population, and thus it pays off to possess a defense mechanism that can only be turned on when needed. Behavioral avoidance can therefore be seen as an evolutionary cheap method of preventing infection, one that should be greatly favored by selection in most animals. Parasites may have even left permanent evolutionary footprints in the innate behavioral patterns of contemporary animal populations (Poulin et al., 2020). These “ghosts of parasitism past” could have shaped general habitat or dietary preferences into fixed traits in species whose ancestors were simply trying to avoid infection.

Ben Hart and others have stressed that two criteria have got to be met before any avoidance measure can be accepted to function as an effective defense against parasites (Hart, 1994). First, the parasites in question have got to exert detrimental effects on host fitness. This may result from as little as one infection event to numerous repeated infection events sufficient to lower fitness (Doherty and Ruehle, 2020). However, parasites typically do not exert dramatic effects on host fitness, such as causing gross pathology or mass mortality. In the majority of cases, the effects of parasites on their hosts are much more subtle. A healthy, well-fed, and non-stressed host may not suffer noticeably from moderate parasite burdens. However, this might change when the host experiences periods of starvation and other environmental or social stressors, or when the host must fight against conspecifics or has got to escape from predators. In such cases, parasites may act as additional stressors and cause a reduced fitness of infected hosts. Hence, seemingly benign parasites may nevertheless have an important effect on their hosts under certain circumstances. Second, the avoidance measure in question has got to be effective in preventing or reducing contact with parasites. Although this is a logical criterion, the effectiveness of a particular behavior is often not rigidly tested, and many reports of avoidance strategies are rather anecdotal. Most studies to date have focused on relatively small-scale, short-term avoidance behaviors (Love et al., 2024), limiting our understanding of the broader ecological and evolutionary implications of avoidance. However, circumstantial evidence generally supports the effectiveness of many avoidance behaviors, and there are also studies that quantitatively observed or experimentally tested the effectiveness of various avoidance measures. The ideal test of these two criteria would involve the experimental manipulation of parasite burdens to see whether animals make the expected adjustments in their investment in avoidance measures, or the experimental impairment of avoidance mechanisms to see whether impaired hosts acquire more parasites than unimpaired controls, or some other rigorous experimental demonstration. Most experimental studies have only one experimental group, allowing no variation in parasite burden or the strength of parasite cues. In the following section, various types of avoidance measures that animals have developed against parasites are discussed, though it is pointed out right now that rigorous demonstrations of their adaptive nature are often lacking.

Camouflage against infection

Perhaps the simplest way to avoid infection is to avoid being detected by parasites. Just as prey species use shape and color to camouflage themselves from predators, potential hosts might use a similar approach to avoid attacks by parasites. A particularly intriguing, though not properly tested, example of camouflage against parasites involves the conspicuous pattern of black and white stripes of zebras. Waage (1981) has suggested that this peculiar fur coloration pattern may be a means to avoid bites by tsetse flies. Biting arthropods are generally attracted by large uniform surfaces, a behavior that is thought to help flies find large animals that serve as hosts. The patchy color pattern of zebras is thought to camouflage their actual size by breaking up the regular outline and shape of the animals and may thus help to avoid fly bites. Caro et al. (2019) found that tabanid flies could not land properly on zebra color patterns, reducing their ability to probe for blood when zebras would actively swish their tails. This close-up disruption of fly landing patterns was also supported by observations of stable flies against various types of zebra pelts (Tombak et al., 2022).

Although not explicitly tested as parasite avoidance, other animals can behave in ways that suggest chemical camouflage. Several species anoint themselves with pungent-smelling substances obtained from plants, mud, peat, and other animals like small invertebrates (Messer et al., 2022). For example, capuchin monkeys anoint themselves with defensive compounds secreted by millipedes by vigorously rubbing them into their fur. This behavior was observed particularly during the rainy season, when biting insects are more prevalent (Valderrama et al., 2000), even though some of the compounds secreted by the millipede are toxic and carcinogenic. The authors argue that the millipede compounds not only mask capuchin odor molecules but repel the biting insects. Thus, it is easy to imagine that chemical camouflage is adaptive in other systems, like in aquatic animals avoiding detection or recognition by the larval stages of digenean trematodes. The free-swimming infective larvae (miracidiae or cercariae) of these parasites use chemical cues produced by their hosts to locate and identify animals such as snails or fish that they must penetrate and parasitize to survive and complete their life cycle. Trematode infection comes at a huge cost: parasitized snails are typically castrated permanently following infection, whereas other animals like fish that are infected by several trematode cercariae often incur greater risks of predation. Since trematodes use specific components of host mucus to find and recognize their hosts, one can speculate that natural selection would favor any host producing mucus with a different biochemical profile that would go unnoticed by the parasites. There may indeed be many more cases of camouflage, either visual or chemical, against parasite infection that have escaped the attention of biologists.

Moving away from parasites or repelling them

Another way to avoid contact with parasites is simply to move away from them. Cattle sometimes literally run away when approached by biting flies, a behavior referred to as gadding. The same behavior can be observed in other large grazing mammals like mule deer and elk that, by doing so, avoid not only blood-letting bites but also potential additional infections by pathogens transmitted by the flies. Fish can also avoid infections by moving away from infectious agents. Rainbow trout avoid eye fluke (trematode) infections by moving away from the infective cercarial stages of these debilitating parasites that use trout as secondary intermediate hosts in their life cycle (Karvonen et al., 2004). The parasite encysts in the eyes of the fish and heavy infections cause cataracts that impair the vision of infected fish. This in turn reduces the feeding ability and growth of the fish, as well as increasing their risk of predation. Avoiding infections with eye flukes by moving away from infective stages is thus of obvious advantage for trout.

Besides moving away from parasites, staying away from potentially infected individuals is another avoidance strategy. In particular, avoiding contact with dead conspecifics may be a successful strategy because their death may have been caused by parasites. Red foxes will delay scavenging on conspecific carcasses (Gonzálvez et al., 2021), which the authors interpreted as a means of avoiding meat-borne parasites. More generally, staying away from sick-looking individuals would also be of great benefit. Who among us would get close to or willingly embrace a friend with a runny nose and a persistent cough? Indeed, the recent COVID-19 pandemic brought to light noticeable shifts in our daily routines (masking, self-isolation, social distancing, etc.), all of which were intended to reduce the risk of infection, thereby curbing the transmission of the virus.

If moving away from parasites is not an option, potential hosts can still avoid contact with some of them by various body movements. For example, there are various fly-repelling behaviors that effectively reduce the number of fly attacks. In ungulates, ear twitching, head tossing, leg stamping, muzzle flicking, muscle twitching, and tail switching are common ways to avoid attacks by flies. These behaviors help to avoid or reduce the pain and loss of blood caused by biting flies, and also reduce the number of eggs deposited by parasitic warble or bot flies. They may also help against fly-borne pathogens. Small mammals and birds show similar avoidance measures like tail and ear flipping, face rubbing, foot stamping, bill snapping, head shaking, and wing flapping. These body movements protect them from loss of blood to mosquitoes and other flies as well as mosquito-borne pathogens like malaria. A less demanding way of avoiding parasites may simply involve changes in body posture. The sleeping posture of birds, for instance, in which a bird often sticks its head under its plumage and stands on just one leg, can be effective. This posture reduces exposure of the feather-free parts of the bird to mosquitoes. As mosquitoes transmit serious pathogens like avian malaria, this behavior protects potential hosts from infection. Native Hawaiian birds reportedly slept with their heads and legs exposed and not covered in their plumage before the arrival of mosquito-borne avian malaria with introduced birds. Today, the sleeping posture of Hawaiian native birds is like that of birds from other localities where avian malaria is common, indicating that this behavior might be an effective pathogen-avoidance measure that has been adopted by surviving native species.

Habitat choice, habitat modification, and migration

If parasites are associated with certain habitats, animals can avoid infections by choosing a different microhabitat within the area, modifying their habitat to make it less hospitable to parasites, or moving to another geographically distant habitat. As an example of microhabitat selection on a small scale, consider the oviposition behavior of female mosquitoes. It has been shown experimentally that female mosquitoes avoid water containing heavily parasitized mosquito larvae when they lay their eggs (Lowenberger and Rau, 1994). Although the trematode parasite infecting the larvae is not transmitted from larva to larva, infected larvae indicate the presence of the first intermediate snail host from which the cercariae that infect the larvae originate. Since trematode infection can be fatal to a mosquito larva, the decision to lay eggs in a particular site can have a devastating consequence for offspring, and the ability to use chemical cues to detect the presence of the parasite is very advantageous. By avoiding habitats with the snail present, female mosquitoes in search of a pool of water in which to lay their eggs can thus reduce the infection risk for their offspring. Backswimmers will disperse further in the presence of ectoparasitic mites or mite cues (Baines et al., 2020), supporting the idea that cue detection drives these avoidance behaviors. The right choice of habitat can protect offspring from parasites, but it may also be an important avoidance measure for adult animals. For example, when horse flies are abundant, hippopotamuses avoid foraging on land and remain submerged in water for longer periods.

In birds, the choice of nesting habitats can help to avoid parasites. Several field experiments, mostly using nest boxes in which parasites can be added or removed, have shown conclusively that birds are sensitive to the risk of infection when selecting a nest site. For example, great tits consistently choose parasite-free nests and avoid nests where ectoparasitic fleas are present. Similarly, cliff swallows can recognize old nests infected with ectoparasitic flies when they return to their nesting areas after migration, and then select only the cleanest nests. Sometimes the reuse of old nest sites will invariably result in high infection risk; in these situations, it pays to either modify these sites prior to reusing them or to create new ones. Many passerine birds do not bother to identify clean nests and prefer to build new, uninfected nests and thus avoid contact with ectoparasites by creating their own parasite-free habitat. An even more sophisticated way of ensuring a parasite-free habitat is the use of green plant material for nest construction that repels parasites due to secondary plant metabolites. This practice has been particularly well documented in European starlings (Clark and Mason, 1985). These birds regularly include green leaves among the twigs making up their nest. The leaves are not just a random sample of leaves from local trees; instead, they are selected only from one or two specific tree species in which the leaves exude chemicals that either repel or even kill arthropod ectoparasites such as lice or mites. House finches purposefully add cigarette butts to their nests to repel ectoparasites, a behavior that is seemingly driven by both current and past parasite loads (Suárez-Rodríguez and Garcia, 2017). These examples of habitat modification lead to a parasite-free space in which the birds can rear their offspring.

Habitat choice in relation to the presence of parasites can also occur on a larger scale in the form of animal migration (Poulin and de Angeli Dutra, 2021). For example, the seasonal migrations of reindeer may be, at least in part, related to a parasitic fly that lays eggs under their skin (Folstad et al., 1991). The larvae leave the skin after 3–4 months and drop to the ground to pupate. With the emerging adults the cycle starts again, and the number of pupae on the pasture determines the infection levels experienced by reindeer. In migratory herds, fewer parasitic fly larvae are found in the skin, which probably results from lower numbers of pupae dropped within their summer pastures by migratory herds compared to the higher numbers on pastures where animals have been present all year round. Migrating to habitats with a lower parasite and pathogen pressure is a strategy adopted also by caribous. During their summer grazing, they migrate to higher altitudes, where mosquitoes are less common compared to lower altitudes. Another particularly intriguing example of migration related to parasite and pathogen presence comes from Hawaiian birds. With the introduction of avian malaria, many native birds became extinct at the beginning of the last century. In contrast to the introduced birds, the native species were highly susceptible to the pathogen. While the invaders subsequently took over the lowland forest areas, some native birds survived by moving to higher mountainous zones, where avian malaria is absent. The birds now migrate downwards to lower areas during the day to feed while the mosquitoes are largely inactive. They then return to their high-altitude roosts in the evening before the mosquitoes become active again. Animals are therefore not at the mercy of parasites within their habitat: they can move, on small or large scales, to habitats that present lower risks.

Choosing what to eat

You are what you eat, or at least you harbor the parasites that you eat. In all cases where parasites are acquired during foraging and food consumption, potential hosts can avoid infections by feeding selectively on safe food items. For grazers, a very simple strategy is to avoid foraging on patches of grass contaminated with the feces of other grazers. The feces of animals often contain eggs and larvae of parasites, and other animals can become infected by feeding on contaminated pasture. Intestinal nematodes are often transmitted in this manner, and they can be particularly costly in terms of host fitness, i.e., reduced growth, when they reach high numbers in a host. To avoid becoming infected with these parasites or other pathogens, horses, cattle, sheep, and presumably other ungulates avoid grazing or browsing on forage in close proximity to recently dropped feces. It is probably the odor of feces that helps to avoid contaminated patches. Uninfected sheep avoid patches of vegetation with feces, but infected sheep will graze within these patches (Hutchings et al., 2001), suggesting that the avoidance behavior is mitigated by infection status. In this case, avoiding infection is no longer a concern if the sheep is already parasitized. Horses are reported to be even more restrictive in their feeding behavior, as they feed in certain areas and defecate in others.

It is not just herbivores feeding on contaminated pasture that are at risk: carnivorous animals can also become infected with parasites via infected prey. Many parasites use complex life cycles including intermediate hosts, and transmission to final hosts is often achieved by predation. In this case, a good avoidance measure for the predator serving as final host should be to avoid consuming infected prey. Infected prey can be identified either directly by, for instance, visual or olfactory clues, or by indirect estimates of the severity of infection using some kind of proxy. It must be pointed out here that prey serving as intermediate hosts for parasites often display aberrant behaviors or appearance, in what appears to be a manipulation of host phenotype by the parasite. The manipulated hosts are more visible, and often more susceptible to predation by the final host of the parasite. Why is it that if a parasitized prey is visually very distinct from a nonparasitized one, predators still choose the parasitized prey? Should natural selection not favor picky predators that discriminate against parasitized prey and thus avoid acquiring parasites? Well, no, according to a cost-benefit analysis of these situations based on optimal foraging principles. There are costs associated with prey capture, such as time and energy spent searching for and handling the prey. Presumably, the more visible parasitized prey is cheaper in that sense, being easier to see and capture. If the cost that comes with acquiring a parasite from this prey is very small, that is, smaller than the total cost of prey capture, then the predator benefits from selectively feeding on parasitized prey. Thus, in their coevolutionary arms race with hosts, many parasites avoid discrimination against their intermediate hosts by predatory definitive hosts by causing relatively little harm to the latter.

The situation can be more complex, of course, as illustrated by the following example (Norris, 1992): oystercatchers have been reported to reject their clam prey when it is infected with a particular trematode parasite, probably because they can notice the parasites from their bright coloration. In this case, the predator can see the parasite directly, but otherwise parasitized prey are not easier to detect and capture than nonparasitized ones, and so they should be avoided. In cases where the direct detection of parasites is not possible, oystercatchers follow a different strategy. Their favorite prey are cockles, abundant bivalves infected with small larval stages of trematodes that utilize the birds as final hosts. The infective stages are so small that visual inspection is not possible, and thus the oystercatchers employ an indirect avoidance strategy. In general, the energy intake to oystercatchers resulting from ingesting a single cockle is positively correlated with the cockle size, but with increasing size cockles also contain higher loads of the larval trematodes (Fig. 3). Although they would be more profitable in terms of energy intake, oystercatchers avoid large cockles and preferably prey upon smaller sizes. This is considered to be an avoidance mechanism against acquiring high parasite loads, suggesting that these higher loads are not worth the size of the meal. However, total avoidance is not possible in this case as all cockle size classes are infected with parasites to some degree.

There may also be food-related avoidance mechanisms in humans. For example, disgust as a human emotion might have evolved to protect us from the risk of disease by preventing us from ingesting potentially infectious food items (Curtis et al., 2004). It might also work with nonfood acquired parasites, as disgust responses in test persons are also common to other objects in the environment that represent potential threats in terms of infection, like images of wounds, sick people, and ectoparasites. Another way humans avoid contact with infective agents might be use of spices in cooking. When the frequency of spice use in meat-based recipes was compared among 36 countries and correlated with the local temperature regimes, an interesting pattern emerged. As mean annual temperatures (being a proxy for the relative spoilage rates of unrefrigerated foods) increased, the proportion of recipes containing spices as well as the number of spices per recipe and the total number of spices used increased (Billing and Sherman, 1998). As spices often contain antimicrobial secondary metabolites (with garlic, onion, oregano, thyme, cinnamon, tarragon, cumin, cloves, lemon grass, bay leave, capsicum, and rosemary being effective against $>75\%$ of bacteria tested), the use of spice might be an effective prophylaxis against pathogen contact. Cannibalism taboos might serve a similar function and prevent contact with parasites. Such aversion to cannibalism can also be found in various animals and might be a very general avoidance measure against parasites. However, even in cannibalistic amphipods, healthy adults will avoid eating juveniles infected with microsporidians; infected adults discriminate less between infected and uninfected juveniles (Bunke et al., 2015).

Joining others to form groups

Group-living is often thought as mostly an adaptation against predation: think of a school of fish or a herd of wildebeests. Forming groups can also help to avoid parasites (Mooring and Hart, 1992). In fish, schooling can protect individual hosts from free-swimming, blood-sucking crustacean parasites (Behringer et al., 2018). In experimental situations, sticklebacks exposed to the highly mobile crustacean ectoparasite *Argulus canadensis* formed larger schools than control fish kept in identical conditions but without parasites. In addition, the attack success of the ectoparasite decreased as the size of the school it attacked increased. Similarly, in birds and mammals, individual hosts experience reduced fly bites with increasing group size (dilution) as long as the

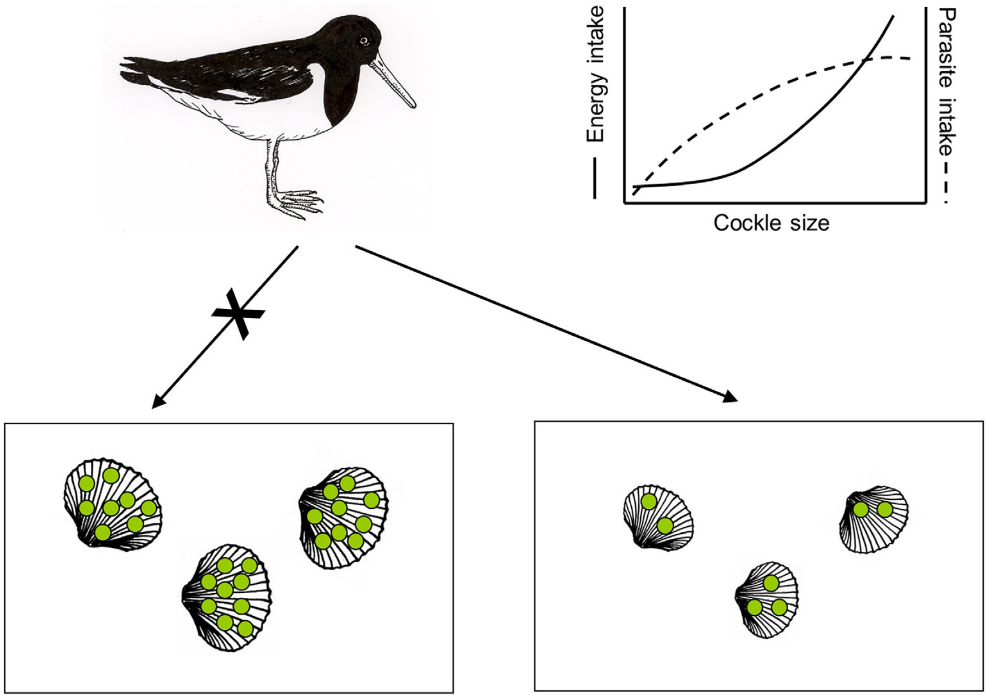

Fig. 3 Selective prey selection can help to avoid acquiring parasites. Oystercatchers take smaller cockle prey individuals with suboptimal energy gains. Smaller cockles harbor fewer infective stages of trematode parasites (green dots), which utilize the birds as final hosts, compared to larger cockles. By preferring smaller cockles, the birds thus reduce their parasite intake and avoid acquiring high loads of parasites. Total avoidance of parasites is not possible in this case because all cockle sizes are infected to some extent. Schematic graph based on Norris K (1992) A trade-off between energy intake and exposure to parasites in oystercatchers feeding on a bivalve mollusc. *Proceedings of the Royal Society of London Series B* 266: 1703–1709.

larger group does not attract more flies per capita due to its higher visibility (encounter). This has been coined the encounter–-dilution effect. A good example of this phenomenon is seen in heifers, which usually graze in a normally dispersed manner on the pasture. However, when heifers are attacked by horse flies, they form grazing lines and continue grazing by moving along parallel to each other with the dominant animals well protected in the center. If the horse fly attacks become more severe, the heifers will stop grazing and form bunches. With this behavior, the heifers reduce the number of bites per individual and thus protect themselves from annoying bites and also from transmission of arthropod-borne pathogens. However, this dilution effect resulting from grouping only works against attacks of biting flies that satiate after biting one or two hosts. Otherwise, grouping might actually increase the risk of becoming bitten. Besides cattle, caribou, reindeer, horses, and primates are known to form larger groups when biting fly intensity is high, and some studies have shown that denser grouping reduces the number of bites per host. Grouping is also an effective avoidance measure against parasites in birds. Black grouse in Finland are often harassed by black flies during summer (Rätti et al., 2006). By grouping together, grouse reduce their individual risk of getting bitten by these flies. As black flies transmit the two most common blood parasites of grouse, this behavior is an effective avoidance measure and a convincing example for the encounter–dilution effect in birds (Fig. 4).

To protect themselves even more, individual hosts can position themselves in the center of a large group and thus further reduce the risk of contact with parasites. This is called the selfish-herd effect; it can help individual hosts to avoid fly bites and potential subsequent infections with pathogens if they manage to position themselves in the center of a group where exposure is lower than at the periphery (Fig. 4). While there are only a few tentative examples from birds, this avoidance strategy has been well documented in mammals. In reindeer calves parasitized by warble flies, individual parasite load not only decreases in larger groups because of the encounter-dilution effect, but also decreases with body mass of individual calves. In reindeer, body mass is itself positively correlated with fitness and social status, and heavier individuals are thus better able to occupy the best central positions within the herd that provide protection from fly bites via the selfish-herd effect.

The evolutionary ecology of avoidance

Avoidance is only the first line of defense, and natural selection has favored other safeguards in case avoidance fails. This second line of defense ranges from mechanical and physiological barriers (digestive enzymes and acids, scales, hairs, mucus, etc.), behavioral defenses like grooming and preening, all the way to immunological defenses. We seem to know much more about the function and costs of these postcontact defensive measures, especially immune responses, than we do about avoidance behaviors (Sheldon and

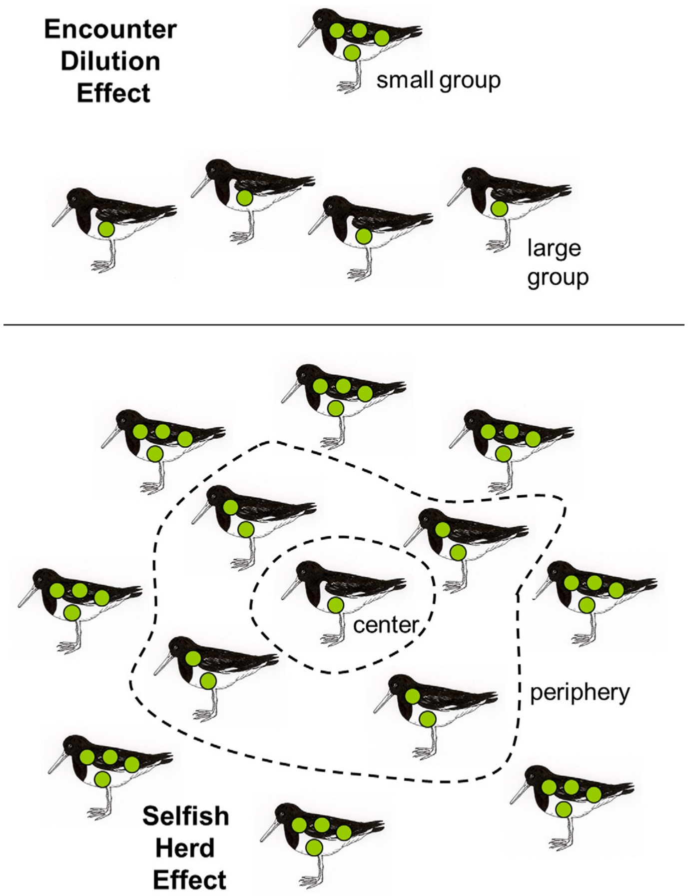

Fig. 4 Forming groups can help to avoid parasites. In birds and mammals, individual hosts suffer from reduced fly bites (green dots) per capita with increasing group size (dilution), as long as the larger group does not attract more flies due to a higher visibility (encounter). Positioning themselves at the center of a large group can also help individual hosts to avoid fly bites and potential subsequent infections via the selfish-herd effect.

Verhulst, 1996). New model systems have been studied within the past 5 to 10 years, yet we are still far from understanding the real magnitude that parasite avoidance may have at ecological and evolutionary timescales. Some studies suggest that much of what an animal does is aimed at avoiding parasites, and yet several important questions about the evolution and ecology of parasite avoidance remain unanswered. Most of these questions could be tackled using either an experimental or a comparative approach (Gibson and Amoroso, 2022): What is the actual fitness cost of avoidance behaviors? How have avoidance behaviors evolved, and were they originally serving a different purpose before being co-opted for defense against parasites? Is the diversity of avoidance behaviors shown by an animal, or the time and energy invested in their expression, roughly proportional to the number of different parasite species, their virulence, or their local abundance, that this animal faces? What are the genetic and mechanistic bases of avoidance? Is there an evolutionary trade-off between precontact and postcontact defense mechanisms? What population- and ecosystem-level impacts are shaped by parasite avoidance? Many more questions come to mind, but the main one concerns the effectiveness of avoidance behaviors. Clearly, parasites are doing well: some estimates suggest that more than half of living species are parasitic and that all the remaining free-living animals have parasites. Within any vertebrate population, it is almost impossible to find a single individual that does not harbor at least some parasites. It is easy to argue that many individuals escape predation and hence that antipredation behaviors must work. But no one escapes parasitism. Still, it may be that antiparasitic defenses are very efficient and that the average number of parasites per host would be several times higher without these defenses.

Conclusion

Parasite avoidance represents a vital, yet often overlooked, component of animal defense strategies. Through a diverse array of behaviors—from camouflage and movement to selective feeding and social grouping—animals actively reduce their risk of infection before it occurs. While these avoidance measures come with costs, they are generally outweighed by the fitness consequences of parasitism. Understanding the ecological and evolutionary significance of these behaviors not only highlights their adaptive value but also underscores the pervasive role parasites play in shaping animal biology and behavior.

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