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Examining pathogen avoidance in predator-prey and scavenging systems

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That predators ‘cull the sick and the weak’ is an adage in ecological texts, but the mechanisms by which disease is curtailed within ecosystems has puzzled ecologists for many years. Advances in our understanding of host-pathogen interactions have revealed defense mechanisms implemented by hosts that minimize infectious diseases in wild populations. Defense mechanisms for hosts include adaptations that ameliorate fitness loss or preemptively limit pathogen exposure, and these mechanisms underlie fundamental questions about how scavenging or predation influence pathogen transmission. A key lens for our understanding of predator-prey and scavenging dynamics include behaviorally-mediated trade-offs weighed by consumers between nutritional gains and pathogen exposure risks. Consequently, the degree to which pathogens and associated diseases perpetuate through food webs can be partly attributed to behavioral responses of predators and scavengers, particularly their selection or avoidance of diseased prey and infected carcasses. Even so, examinations of avoidance or preference by predators and scavengers to diseased carrion are underrepresented. Here we identify areas for future research focused on behavioral immunity that could illuminate where, when, and how pathogen transmission reverberates through ecological communities. While directly attributing behavioral responses to pathogen exposure may be challenging, particularly for organisms with low susceptibility to spillover, identifying these responses through experimentation or observation help describe complex systems regarding infectious disease.

KEYWORDS

behavioral avoidance, disease, pathogen, predation, scavenging

1 Introduction

Because predation and scavenging often complete parasite life-cycles and promote pathogen transmission, scavenger-prey interactions lie at the heart of many topics in disease ecology. Consumption is often required for pathogen persistence, as a pathway from intermediate to definitive hosts where replication or reproduction occurs (Lafferty, 1999). Depending on the pathogen involved, its pathogenicity, virulence, and the predator-host response, these life-cycle stage impacts may range from minimal to detrimental within the definitive host. Consequently, many hosts have evolved behavioral, physiological, or genetic defense mechanisms to avoid infectious disease. Primary defense mechanisms for hosts include adaptations such as avoidance, resistance, and tolerance – all of which can ameliorate fitness loss or preemptively limit exposure to pathogens (Medzhitov et al., 2012; Curtis, 2014).

In response, pathogens can evolve traits that alter host behavior or impact host physiology or genetics to increase the likelihood of transmission. These responses are well described in many systems and provide foundational support for theories of parasite-host co-evolution (Figure 1). However, two of these mechanisms occur strictly within the host – tolerance and resistance. While resistance largely relies on host immune responses that reduce pathogen load, tolerance commonly reduces immune responses that cause tissue damage in an effort to promote host health, having little effect on the pathogen (McCarville and Ayres, 2018). While all mechanisms result in fitness consequences for the host, avoidance seems the only strategy that is behaviorally driven (i.e., behavioral immunity

[de Roode and Lefèvre, 2012]), requiring no internal physiological responses or adaptations within the host. Therefore, pathogen avoidance is a primary factor explicitly linked to the prevention, not just mitigation, of infectious disease.

While widely acknowledged that predators select infected prey and scavengers consume diseased carrion (Lafferty, 1992; Behringer et al., 2018; Vicente and VerCauteren, 2019), evidence of preference against diseased resources also exist to support theory on pathogen avoidance (e.g., Sarabian et al., 2023). Here, we discuss underlying mechanisms of behavioral pathogen avoidance and potential ramifications for disease transmission. Hypotheses concerning behavioral-driven foraging strategies are predicated upon trade-offs in nutritional gains, which incorporate evolutionary adaptations to pathogen susceptibility as well as awareness of pathogen exposure risk. Although these strategies drive fundamental questions about how active predation or scavenging influence pathogen transmission, examinations of avoidance by predators and scavengers to diseased carrion are underrepresented, and more data is needed through experimental or observational studies to disentangle behaviorally-driven trade-offs that influence disease dynamics in natural systems.

2 Pathogen avoidance and trade-off hypotheses – from microbes to mammals

Pathogen avoidance behaviors have been identified and studied in many systems, at multiple trophic levels, and across various taxa. At the microbial level, *C. elegans* nematodes apply learned behavior,

	Pathogen exposure	Host defense	Pathogen adaptation
Avoidance <i>behavioral</i>	Protozoal parasite (<i>Toxoplasma gondii</i>) infects feline species after consumption of infected rodents	Rodents avoid exposure to feline predators, limiting parasite transmission to felines necessary to complete parasite reproduction	Parasite interferes with amygdala in rodent brains, limiting innate fear of predation
Tolerance <i>physiological</i>	Iridovirus infects crickets (<i>Gryllus texensis</i>) during mating activity	Crickets present 'sickness behavior', a tolerance response to reduce negative impact on fitness	The virus is linked to suppression of phenoloxidase, an immune-related compound that likely promotes sickness behavior. Crickets increase mating behavior before death, ensuring further viral transmission
Resistance <i>genetic</i>	Simian immunodeficiency virus (SIV) infects primate host	Other host species use Apolipoprotein B Editing Complex (APOBEC3) viral inhibitors to resist viral infection	Viral infectivity factor (Vif) neutralizes APOBEC3 enzymes and allows for spillover to new species

FIGURE 1

The host-pathogen arms race describes ongoing adaptations of both parasites and hosts that drive co-evolution (Wang et al., 2021). Figure examples of pathogen adaptations to compensate for host responses to exposure have been identified across various host defense mechanisms including avoidance (Tong et al., 2021), tolerance (Adamo et al., 2014), and resistance (Nakano et al., 2020). Defenses can also manifest behaviorally, physiologically, or genetically; supporting co-evolution theory suggesting pathogens often find pathways to avoid, influence, or circumvent host defenses to promote their fitness and increase transmission.

using neuronal sensory mechanisms to identify and subsequently avoid harmful bacteria (Meisel and Kim, 2014). Fruit flies (*Drosophila nigrospiracula*) have been shown to use phototaxis, selectively moving along light–dark gradients to limit exposure to parasitic mites (*Macrocheles subbadius* [Horn et al., 2022]). Avian species are of particular interest, as they implement multiple strategies to minimize pathogen exposure, including hygiene and body maintenance (e.g., preening, sunning, dusting, bathing) as well as avoidance behaviors including pathogen consideration during nest site selection or even nest abandonment to actively avoid parasites (Bush and Clayton, 2018). Examples of pathogen avoidance range from insects (Eakin et al., 2014) to aquatic organisms (Behringer et al., 2006) to wild ungulates (Ezenwa, 2004) to primates (Sarabian and MacIntosh, 2015); indeed, behaviorally-mediated strategies to avoid infectious disease occur in nearly every relevant biotic system.

Specific to predator-prey and scavenging systems, avoidance is often described in the context of trade-offs (Fry, 1996), where risks of tropically-transmitted pathogen exposure are weighed against nutritional gains acquired through consumption (e.g., Oliva-Vidal et al., 2021). While it is generally accepted that the majority of infected prey are not avoided but rather selected by predators (Lafferty, 1992; Behringer et al., 2018), examples of reduced consumption of infected prey also exist (Figure 2). Two primary pathways mediate this process. The first is driven through pathogen influence on infected prey to avoid predation. An interesting example by Soghigian et al. (2017) described an obligate predator (*Toxohrynychites rutilus*) exposed to *Ascogregarina barretti*-infected and uninfected mosquito larvae (*Aedes triseriatus*) resulted in lower predation on infected larvae. The authors concluded that the

parasite influenced larval behavior to seek refuge from predation, likely because there was no benefit of trophic transmission from the definitive larval host to the dead-end predator species. In another example, tiger salamander (*Ambystoma tigrinum stebbinsi*) larvae exposed to *Ambystoma tigrinum* virus (ATV) incurred lower predation from dragonflies (*Anax junius*) than uninfected salamanders, but showed significantly higher activity in the absence of predators. Again, because this single-host pathogen relies on prey host survival for transmission, it was concluded that the virus increased anti-predator responses within its host (Parris et al., 2004).

The next more obvious mechanism of reduced consumption is through direct avoidance of infected prey by the predator itself. For instance, near-starvation was the primary state in which Stellar's eiders (*Polysticta stelleri*) would consume parasitized amphipods (Bustnes and Galaktionov, 2004); otherwise, they exhibited avoidance. Additionally, a meta-analysis conducted by Flick et al. (2016) concluded that predators preferred healthy over infected prey, and because fitness decreased in predators that consumed pathogen-infected prey, these items were considered a low-quality resource. While these examples are limited in comparison to predator selection for infected prey, avoidance or preference against infected prey is certainly more difficult to identify in wild populations, and therefore most occurrences are documented within controlled laboratory experiments (Sarabian et al., 2023). It has been suggested, however, that these processes are more widespread than current evidence suggests (Buck et al., 2018).

Trade-offs may be readily apparent when the predator or scavenger is aware of the risk, but even without direct knowledge, tendencies in differential prey selection or carrion partitioning by

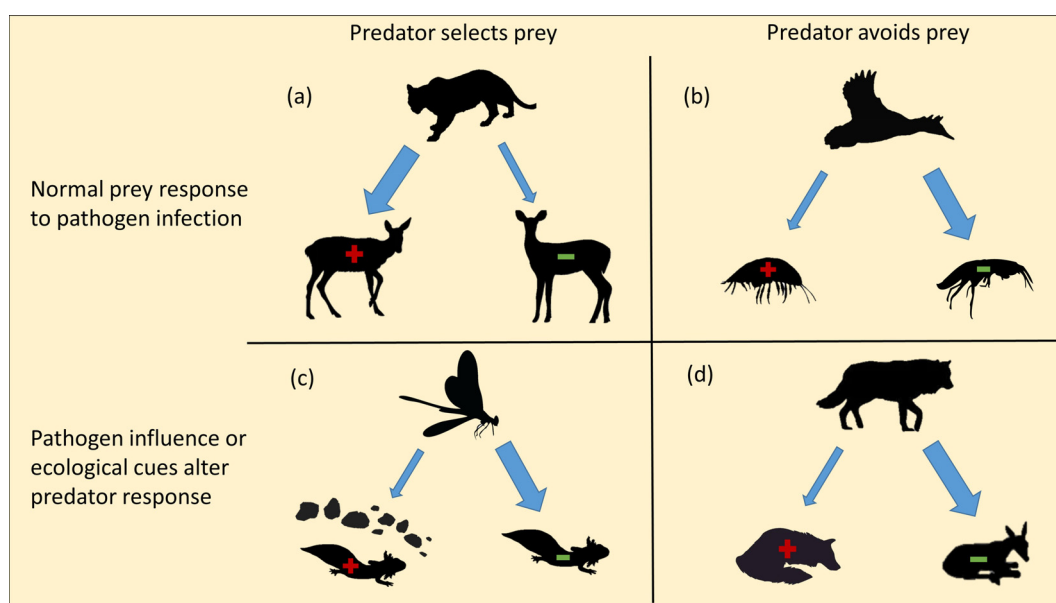


FIGURE 2

Differing scenarios with evidence of selection or avoidance of pathogens by predators or scavengers under various mechanisms that could influence outcomes. (A) Mountain lions select for CWD-infected deer (Krumm et al., 2010). (B) Stellar's eiders avoid infected amphipods (Bustnes and Galaktionov, 2004). (C) Viral pathogen influences salamander larvae to avoid predation by dragonflies (Parris et al., 2004). (D) Carnivore-carrion hypothesis shows scavengers select against carrion of similar species (Moleón et al., 2017). Green symbols indicate reduced disease, red symbols indicate high disease.

scavengers exists. For example, phylogenetic similarity has been linked to scavenging behavior, particularly in the carnivore-carrion avoidance hypothesis, where predators and scavengers avoid carnivore carrion and cannibalism (Moleón et al., 2017; Peers et al., 2021). Carrion partitioning has been further extended to community-level responses, where carnivore-carrion avoidance by vertebrate scavengers increased carrion insect diversity (Muñoz-Lozano et al., 2019). These behavioral shifts can cause a competitive release, increasing scavenger richness and potentially contributing to a 'dilution effect' where high consumer diversity correlates to reduced infection prevalence (Civitello et al., 2015; Khalil et al., 2016). Pfennig (2000) describe theory on the trade-off between pathogen exposure risk when consuming phylogenetically similar species and the nutritional gains acquired from predation, including an experimental approach that resulted in differing host fitness (quantified by growth rate) of *Scaphiopus couchii* tadpoles when fed infected conspecific versus allopecific prey. However, stochastic environmental conditions leading to poor resource availability (Oliva-Vidal et al., 2021), or relatively high carrion abundance (Cagnacci et al., 2003; Remonti et al., 2005), may override avoidance behaviors, making state-dependent factors such as hunger a confounding component in the general avoidance of conspecific prey or carrion. This is analogous to the starvation-predation hypothesis (Sinclair and Arcese, 1995), which suggests animals are more inclined to engage with risky circumstances as they experience sustained hunger.

Although cross-species transmission positively correlates with host phylogenetic relatedness, further examination is warranted to determine the degree at which parasites may be shared among hosts, particularly within predation interactions (Stephens et al., 2019). Extent, duration, or magnitude of exposure to various pathogens through predation or scavenging may correlate with spillover probability to non-target species. For example, the bioaccumulation of various pathogens transmitted through consumptive predation could have cumulative or additive effects that increase the likelihood of spillover infections (Malmberg et al., 2021). In addition, generalist predators are exposed to a broader spectrum of pathogens as they consume a wider variety of intermediate hosts (Scholz et al., 2020), allowing increased potential for parasite adaptations or co-infections that could increase novel spillover risk.

Some hosts directly identify the pathogen (typically a parasite or vector) they are intentionally trying to avoid (e.g., caribou avoidance of mosquito swarms [Johnson et al., 2021]), while others identify pathogens through various sensory mechanisms (e.g., discrimination against detectable fungi in ants [Pereria and Detrain, 2020]; bacteria detection and avoidance by *C. elegans* [Meisel and Kim, 2014]). Therefore, it is generally accepted that avoidance requires the host to recognize pathogen risk, typically through olfactory, gustatory, or visual cues (Medzhitov et al., 2012; Sarabian et al., 2018). Even tactile cues have been investigated as a sensory mechanism to identify pathogen presence (Oum et al., 2011). On the contrary, evolutionary responses to environmental or behavioral cues may not be directly associated with known pathogens. The 'ecology of disgust' (Buck et al., 2018; Sarabian et al., 2023), described in relation to the 'ecology of fear' (Clinchy et al., 2013), can both be generalized as the non-

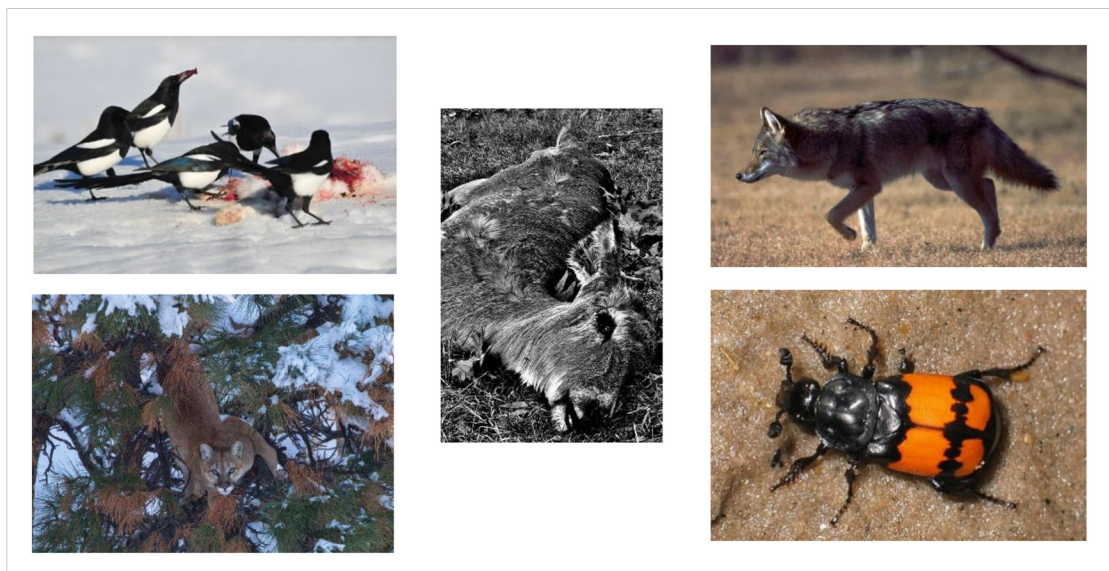
consumptive effects of risk avoidance in natural systems, as well as the trophic consequences thereof. Although the 'ecology of fear' is contextualized as avoidance of predation, while 'ecology of disgust' aligns with avoidance of disease, both are predicated upon environmental cues that trigger avoidance behavior, often times without direct evidence of risk. Furthermore, evidence suggests that disgust-mediated avoidance behavior is not only learned, but an innate process (Curtis, 2014). For instance, the carnivore-carrion avoidance hypothesis portrays no specific disease may be evident, although carnivores do generally carry more helminths than their ungulate prey (Stephens et al., 2019). Also, recent experimental evidence has shown large group sizes of carrion on the landscape impart environmental cues that suggest a disease-related die-off. These larger groups incurred lower scavenging rates than single carcasses, indicating behavioral avoidance by scavengers due to disease risk (Olson et al., 2022). These cues to ambiguous pathogen exposure extend well into human psychology (Curtis et al., 2004), even so far as to demonstrate that disease cues led women to avoid asymmetrical male faces thought to be linked to immunocompromised individuals (Ainsworth and Maner, 2019). Also, the tendency to generally avoid conspecifics is common across many species, and reductions in group sizes of social animals reduces exposure to pathogens (Curtis, 2014). Ultimately, although specific pathogens may be identified and behaviorally avoided after a learned experience (Meisel and Kim, 2014), general avoidance driven by ecological cues may result in these behaviors even when no detrimental pathogens exist; a sometimes costly consequence of avoidance.

3 Pathogen persistence and environmental reservoirs

Within predator-prey disease dynamics, specific pathogens are likely disproportionately impacted by disease avoidance. The ability for pathogens to persist outside a live host influence this process, such as the variable persistence of viruses – largely impacted by dynamic abiotic conditions (Labadie et al., 2020). Infectious bacterial pathogens also vary in persistence, from moderate persistence of *Brucella abortus* bacteria that result in bovine brucellosis (21 – 81 days [Aune et al., 2011]), to highly persistent anthrax spores (*Bacillus anthracis*) which can remain infectious for decades (Carlson et al., 2018). However, assemblages of prion pathogens may be considered some of the most resilient infectious agents identified to date. For example, chronic wasting disease (CWD) represents one unique form of many transmissible spongiform encephalopathy diseases that result from the transmission of misfolded infectious proteins, or prions (Escobar et al., 2020). These prions have fatal neurodegenerative effects on infected individuals, with CWD specifically adapted to multiple wild cervid species (Haley and Hoover, 2015). Because of the complexities involved in CWD transmission in wild populations, including predation and scavenging of diseased prey and multiple modes of transmission for prions, this disease provides a unique system for consideration of pathogen avoidance, which we discuss in further detail.

BOX 1 Consequences of Scavenging: Increased or decreased pathogen transmission?

The contention over carrion-mediated transmission of CWD lies in whether the consumption of infected tissues reduces prion load and new host accessibility, or if the spatial distribution and movement ecology of consumers exacerbates the spread of prions in the environment (1). Predators and scavengers alike may resist infection of high concentrations of CWD prions in similar fashion as identifiable genetic adaptations in other species that provide resistance to a variety of harmful pathogens (e.g., vultures [Chung et al., 2015]), or through natural spillover barriers that exist among different carnivore species (Otero et al., 2015; Wolfe et al., 2022). Concerning the spread and transmission of CWD, eliminating or sequestering prions through digestion has been found, with studies showing both ephemeral persistence and significant reductions in prion inoculum after being passed through carnivore digestive systems (Nichols et al., 2015; Buane et al., 2021). However, even if these reductions occur, passage of viable prions through the digestive track of predators and scavengers persist nonetheless, and have been identified in multiple species (Fischer et al., 2013; Nichols et al., 2015; Buane et al., 2021). Ultimately, while evidence suggests that scavenging likely limits disease spread in most scenarios, even if scavengers become infected (Le Sage et al., 2019; Vicente and VerCauteren, 2019), others contend scavengers can play an active role in perpetuating disease (Carucci et al., 2022).



I. Various consumers encounter CWD-infected carcasses in natural systems. Species range across taxa and likely vary in their ability to promote or impede prion transmission.

Selective predation influences disease dynamics and system complexity, with outcomes dependent upon factors such as the degree of selection, predation intensity, and overall ecosystem productivity (Hall et al., 2005; Brandell et al., 2022). In fact, CWD models incorporating highly selective predation versus random removal of host species predicted rapid declines in disease prevalence and even elimination of the pathogens in closed population models (Wild et al., 2011). Specifically, some evidence suggests that apex predators such as mountain lions (*Puma concolor*) show selection for CWD-infected mule deer (*Odocoileus hemionus* [Krumm et al., 2010]) that may limit prevalence of the disease in wild populations (Fisher et al., 2022). At this time, CWD in cervids has no identifiable negative fitness consequences for consumers of ungulates that harbor the prion pathogens (e.g., Jennelle et al., 2009), and optimal foraging suggests shifts away from diseased resources should only be observed if there is a high fitness cost of becoming infected (Lozano, 1991). However, the disease itself manifests obvious physiological symptoms and conditions that indicate disease (Mysterud and Edmunds, 2019), potentially activating avoidance in some consumer species via ‘ecology of disgust’ theory. Interestingly, anecdotal evidence from our observations within endemic CWD regions suggest scavengers often avoid carcasses of ungulates which succumb to clinical infection, resulting in carcasses persisting on the landscape longer

than mortalities not associated with the disease. In addition, observations during ungulate necropsies suggest olfactory and visual cues indicative of CWD infection emanate from CWD-infected carcasses during inspection. Because it is generally accepted that animal sense and perception is more acute and attuned than of humans (Scanes, 2018), it is unlikely these cues would go unnoticed by scavengers.

Why is this important? Although CWD infection occurs by direct transmission through live animal interactions, environmental transmission also provides a pathway of infection to new hosts (Escobar et al., 2020). Because CWD prions are environmentally maintained within soil, various fomites, and even taken up by plants (Escobar et al., 2020), the impact of local infectious zones (LIZ) in the environment created by the death of infected organisms can have major consequences to efforts aimed at reducing pathogen spread (Lozano, 1991). While many disease models (e.g., SIR¹ [Bjørnstad et al., 2020]) depend on estimates of host ‘infectious periods’, they cannot easily account for LIZ impacts, and the interminable persistence of environmental prions compound the risk of exposure through LIZs both spatially and temporally

1 Compartmental model of Susceptible, Infectious, and/or Recovered cohorts to describe spread of disease.

(Blackburn et al., 2019). Accordingly, evidence suggests CWD disease dynamics may heavily shift toward these environmental reservoirs, exacerbating disease spread and rendering current management efforts less effective in mitigating CWD (Almberg et al., 2011).

Because vertebrate scavengers are positively associated with the speed at which carcasses decompose (Wenting et al., 2022), preferences associated with scavenging behavior can impact the persistence of prions within the environment associated with diseased carrion. It should be noted, however, that scenario-dependent feeding behaviors, movement characteristics, or digestive processes of consumers can influence pathogen transmission trajectories (Duffy et al., 2019); although the net impacts of these processes are largely unexplored in natural systems (Box 1). Even if unrelated to pathogen avoidance, various scavenging strategies including responses to carcass size (Moleón et al., 2015), carcass type (Olson et al., 2016), or alternative prey availability (Peers et al., 2020) likely influence environmental pathogen persistence in carrion. Resultantly, the hardy nature of prions render viable pathogen transmission to new host species that can extend years (Haley and Hoover, 2015). Therefore, consumptive processes that may dilute, sequester, or eliminate pathogens can impede the spread of disease, but disentangling these dynamics requires increasing our understanding of scavenging patterns (Carrasco-Garcia et al., 2018).

4 Conclusions

Advances in infectious disease research continuously unveil systems and processes which bolster our understanding of the host-pathogen interface. While much research has focused on how pathogens interact within hosts post-inoculation, less focus has been placed on investigating behavioral mechanisms of pathogen engagement or avoidance. For infectious diseases like CWD, obvious best-case scenarios include a combination of high selectivity of infected prey by predators, and near-absolute consumption of diseased carrion. These mechanisms, in tandem, minimize horizontal transmission from live infectious animals and limit the development of environmental LIZs created through infected prey mortalities. While research has been applied to show these two mechanisms exist, we have asked comparatively few questions concerning the situations where they do not. Within predator-prey or scavenging systems, is avoidance of infected organisms more common than we suspect in natural systems, or is it simply more difficult to detect and therefore less apparent outside of controlled laboratory experiments? The combination of ecological theory supporting behavioral pathogen avoidance, and limited yet compelling evidence of its existence in natural systems warrants consideration of these processes. As increasing evidence mounts to support behaviorally-mediated avoidance (Sarabian et al., 2023), questions also remain as to what degree predators and scavengers require cognizance of the risk posed by specific pathogens in order to influence their feeding behavior, or

alternatively if innate responses to ambiguous disease cues largely impact disease-nutrition trade-offs? Particularly for scavenging, if carrion are not directly avoided by scavengers because of disease cues, but instead due to cues associated with poor carrion condition confounded by disease status, preferences against these low-quality resources would still play a key role in infectious disease dynamics. Finally, if both theory of selection for diseased prey by predators and theory of avoidance of diseased carrion by scavengers hold, thinking critically about these seemingly opposing forces on the status, transmission, and sustainability of infectious diseases in wild populations will be essential to mitigate or manage their spread. Therefore, identifying and understanding behavioral immunity in natural systems among predator and scavenger species, even with low likelihood of spillover risk, will enhance our understanding of how species' may behaviorally promote or prevent infectious disease.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

JC: Conceptualization, Writing – original draft, Writing – review & editing. JM: Conceptualization, Writing – review & editing. JH: Conceptualization, Supervision, Writing – review & editing.

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