Abstract

1. Although infection often changes an animal's motivation or ability to forage, which should alter rates of contact with uninfected hosts, such links are likely complex and remain poorly understood. Here, we explore relationships among infection, foraging decisions, and contact rates and how these could vary with environmental factors to drive disease transmission.
2. Optimal foraging theory predicts that animals should gather the highest quality resources available from a patch, leaving only once the cost of continued foraging begins to outweigh the amount of energy gained. However, an animal's ability to locate and evaluate resource patches will vary with many factors, including disease, temperature, and habitat fragmentation. Although modeling suggests that such variation in foraging decisions can alter contact rates among infected and uninfected hosts, and thus transmission and evolution of infectious agents, empirical studies have only begun to test the direction and strength of such relationships.
3. We propose that sickness behaviors (e.g., lethargy and anorexia) will often alter foraging decisions in ways that reduce contact rates among infected and uninfected hosts, while parasite-driven behavioral changes will often do the opposite. Furthermore, we suggest that future studies empirically test how such associations vary with ambient temperature and habitat fragmentation, as human activity continues to alter these and other environmental pressures.
4. By revealing how environmental factors impact the links among infection, foraging, and disease transmission, we can improve our understanding and prediction of animal disease dynamics in the face of changing ecosystems.

Keywords

contact rate, disease, environmental factors, foraging, sickness behaviors

Introduction

The behavior of sick animals is key to disease transmission. For example, foraging during infection can influence disease transmission by altering the frequency of contact with other hosts, especially in group or social foragers, or at fomites (Bouwman and Hawley, 2010; Dolnik et al., 2010; Moyers et al., 2018; Shocket et al., 2018). While the magnitude of sickness behaviors like lethargy and anorexia can reduce overall foraging, and thus the potential for inter-individual contact (Lopes et al., 2016; Stockmaier et al., 2020), it remains unclear how subtler changes to foraging decisions will alter contact rates and transmission. For example, if infection alters a host's ability to locate resource patches or assess their quality, infected hosts may be less likely to contact healthy individuals than we would otherwise predict. Conversely, infection could alter a host's food preferences, causing infected hosts to forage more intensely at preferred patches and increasing the potential for contact with naïve individuals. Thus, although infection can alter overall foraging ability or time spent foraging, predictions of contact rates based on such metrics alone likely underestimate the impact of infection-induced foraging changes.

As a result of either host-driven sickness behaviors or parasite-manipulation, altered motivation to feed likely impacts an animal's ability to detect, assess, or manipulate food resources (Fig. 1). Such changes would impact critical aspects of foraging behavior, including the amount of time an animal spends searching for food (search time; Fig. 1B); the ability to assess the quality of resources in a patch; and the efficiency of resource intake once a patch is located, which will alter the time spent in a given patch and the amount of food remaining when departing (giving up density, GUD, Fig. 1B-C). Further, an infected animals' ability or motivation to move between resource patches likely changes with infection, which could impact the duration of any given visit to a resource. In such scenarios, we expect infected animals to exhibit foraging movements that differ from healthy animals, potentially visiting and remaining in suboptimal resource patches more often than their uninfected counterparts.

Revealing how infection alters such foraging decisions will improve our understanding of how the behavior of infected animals drives disease dynamics in the wild. Here we review several mechanisms by which infection can alter foraging decisions, highlight how those decisions should impact inter-host contact rates, and discuss how environmental conditions can modulate the links between foraging decisions and contact rates.

Mechanisms by which infection can affect foraging decisions

The mechanisms by which infection alters host behavior can be classified as host- or parasite-driven. Sickness behaviors, such as lethargy and anorexia, are generally considered host-driven and can aid in overcoming infection (Hart, 1988). Decreasing energy use through reduced movement (lethargy) can promote robust immune defense, whereas fasting (anorexia) can minimize the resources available to parasites (Adelman and Martin, 2009). However, sickness behaviors incur opportunity costs by reducing other fitness-enhancing behaviors, like reproduction, foraging, and predator vigilance. Therefore, the adaptive value of sickness behaviors likely depends on some balance: overexpression of lethargy to the point of prolonged immobility, for example, could completely deplete all stored resources, whereas underexpression of lethargy could limit energy available for immune responses, potentially prolonging infection. Moreover, such balances are context dependent. For example, maternal behavior of lactating mice injected with lipopolysaccharide (LPS) is differentially expressed in response to temperatures. At ambient temperatures of 22˚C, pup-retrieval is slower and nest-building activity decreased among LPS- compared to saline-injected mice. In contrast, a 6˚C, both pup-retrieval time and nest-building of LPS-injected mice are near control levels (Aubert et al., 1997). While we focus on the importance of context dependence with this example, it also illustrates the potential importance of environmental conditions in shaping relationships between sickness behaviors and foraging (see "Environmental conditions that could affect association between foraging and contact rate," below).

Foraging behaviors, such as search time, giving up density (GUD), and patch quality assessment are linked to—and often negatively affected by—sickness behaviors (Makin et al., 2020; Schwanz et al., 2012). This being said, a lethargic animal might respond differently than an anorexic animal. When looking for food, we can predict that lethargic animals will have greater search times because they are moving slowly. Meanwhile, anorexic individuals might show similar search times to healthy individuals, as their movement is relatively unaffected, but their motivation to find food may reduce their total number of searches. Lethargy and anorexia are both likely to decrease GUD: finding food patches when lethargic is time-intensive (Fig. 1B, D), and motivation to eat is decreased with anorexia (Fig. 1C, D). Regardless, the animal probably stays at a given resource patch longer than it would when healthy. In addition, the impact of patch quality on such foraging decisions is likely less pronounced when animals are expressing sickness behaviors. Because sick animals show a reduced drive to both eat and move, low-quality patches are more likely to satisfy these internal motivations for sick as opposed to healthy animals.

Unlike host-driven behavioral changes during infection, parasite-driven behavioral changes should be, by definition, linked to the parasite increasing its own fitness, specifically transmission to new hosts (Moore, 2002). For instance, rabies virus alters neuronal expression of [^{3}H]5-hydroxytryptamine, an important metabolic intermediate in the biosynthesis of serotonin (Bouzamondo et al., 1993; Ceccaldi et al., 1993). By altering the serotonin pathway, rabies changes mammalian hosts' behavior, increasing aggression and hydrophobia (Mallewa et al., 2007; Warrell et al., 1976), which enhance the pathogen's probability of transmission via saliva. In bees, parasite-driven changes in foraging behavior result from chemical changes in floral preference (see Koch et al., 2017), such that floral preference can vary with parasite characteristics. For example, Schmid-Hempel and Schmid-Hempel (1990) found that 62.8% of healthy European honeybees (*Bombus pascuorum*) foraged at *Prunella grandiflora* while 37.2% foraged at *Betonica officinalis* based on availability of the two plants. In contrast, honeybees parasitized by fly larvae (*Sicus ferrugineus* and *Physocephala rufipes*) foraged at *P. grandiflora* 28% and *B. officinalis* 72% of the time, thus suggesting a switch in floral preference with infection. In this same host-parasite system, honeybee foraging behavior was further altered alongside parasite stage; honeybees parasitized by third instar larvae, but not first or second instar, were less likely to collect pollen than non-parasitized bees (Schmid-Hempel and Schmid-Hempel, 1991). Such changes in foraging behavior will likely lead to different habitat/resource usage by infected versus uninfected animals, which will have important consequences for contact rates and disease transmission.

As with sickness behaviors, parasite-driven changes in behavior can negatively affect search time, GUD, and patch quality assessment (Allan et al., 2010; Fritzsche and Allan, 2012). For example, the fungal pathogen, *Batrachochytrium dendrobatidis,* can delay growth and development rates in Fowler's toads (*Anaxyrus fowleri*) likely due to a parasite-driven shortening of search times and reduction in overall foraging efficiency (Fig. 1C–D; Venesky et al., 2009). Predicting the effect of parasite-driven responses on foraging behaviors is complex, as parasite-driven behaviors are likely to vary among specific parasite and host pairs. Some parasites cause their hosts to pursue unconventional resources, essentially overriding traditional foraging theory: search time, GUD, and patch quality become contingent on parasite-driven fitness criteria, rather than host fitness. For example, juvenile hair worms (genus *Chordodes*) that infect several insect species induce hosts to forage for a single resource: water, the essential medium for hairworm reproduction (Schmidt-Rhaesa, 2002; Thomas et al., 2002, 2003). As with host-driven mechanisms, such parasite-driven behavioral changes can induce profound alterations to foraging behavior, with the potential to impact contact rate.

Consequences of changes to foraging behavior on contact rates and transmission

Changes to a host's foraging behavior during infection can directly alter intra and interspecific contact rates, with important implications for the spread and potential management of communicable diseases. Compared to healthy individuals, we might predict that sick animals will forage at different locations or consume different foods. For example, wild Taiwan field mice (*Apodemus semotus*) are often infected with gut helminths that are transmitted fecal-orally. A field experiment found that naturally infected mice spent similar amounts of time in feces-contaminated and uncontaminated foraging patches, whereas mice whose infections were reduced with an anthelminthic drug spent less time in feces-contaminated food patches (Hou et al., 2016). Such patterns suggest that altered foraging decisions among infected individuals could reduce contact rates with uninfected conspecifics. Such alterations, however, may be further complicated by interactions with the behavior of healthy hosts. For example, among male house finches, infection with *Mycoplasma gallisepticum* often reduces aggression, which can lead other, healthy males to prefer feeding near infected conspecifics (Bouwman and Hawley, 2010), potentially increasing intraspecific contact rates. This issue could be compounded under conditions of high feeder density, which can increase transmission of conjunctivitis—especially if aggressive interactions can remain low (Moyers et al., 2018).

Altered foraging behavior can also be critical for trophic transmission, or transmission from an intermediate host, generally a prey item, to a definitive host, typically a predator (Lafferty, 1992). Parasites that rely on trophic transmission often change the behavior of their intermediate host to increase the likelihood of predation. For example, when infected with the parasitic worm, *Pomphorhynchus laevis, Gammarus pulex*, a small algae-feeding crustacean, alters its circadian foraging patterns, drifting in search of food at night when it is more vulnerable to predation by European bullhead (*Cottus gobio*), the parasite's definitive host (Lagrue et al., 2007).

Another potential consequence of changes to foraging behavior on contact rates and transmission involves a foraging-mediated "hydra effect" (Penczykowski et al., 2022). Such an effect would occur when sickness-induced foraging depression leads to an increase in resource production and density, thereby increasing the number of organisms that patch can support before degradation. As healthy individuals move to this productive patch, more become infected, continuing this cycle. Using modeling and field data, Penczykowski et al. (2022) documented a foraging-mediated hydra effect in a zooplankton-algal system in which a fungal pathogen virulently depresses host foraging rate. More generally, pathogen-induced sickness behaviors—such as lethargy and anorexia—could reduce foraging rate, thereby increasing the amount of an available food resource in each patch or across a landscape.

Environmental conditions that could affect association between foraging and contact rate

While foraging decisions and their effects on inter- and intraspecific contact rates are likely to be important for pathogen transmission, the nature of such associations will be shaped, at least in part, by environmental conditions. Although myriad environmental factors could impact these relationships, for brevity, we focus on two examples that are critical in the face of anthropogenic climate change and land-use change. Specifically, temperature and resource distribution are changing rapidly in numerous ecosystems, with the potential to alter the links directly and indirectly between foraging decisions and infectious disease dynamics.

Temperature is critical when considering foraging behaviors in general. Increased energetic demands brought about by low temperatures can lead to increased time spent foraging (Persson, 1986; Reiskind and Janairo, 2015). In contrast, increasing ambient temperatures can increase foraging success and resource availability (Avery and Krebs, 1984; Bergman, 1987; Stevens et al., 2002). Ambient temperatures can even change the endogenous rhythms of foraging behaviors: regardless of photoperiod or season, juvenile salmonids are diurnal foragers at temperatures above 10˚C, but become nocturnal foragers when temperatures drop below 10˚C (Fraser et al., 1993). Temperature can also have profound effects on parasite persistence, as many parasites have lower fitness and decreased transmission probability at temperatures near their thermal maxima when compared to their thermal minima (Dijk and Morgan, 2008; Paull et al., 2012; Sánchez et al., 2021). While temperature is clearly important for foraging behavior and parasite persistence, how temperature effects the interaction between these variables and contact rates remains unclear.

To our knowledge, only one study has simultaneously investigated the effect of temperature on disease transmission and foraging behavior, implying an effect on contact rate. Using a freshwater zooplankton-fungus system, Shocket et al. (2018) determined that hosts (*Daphnia dentifera*) increased their foraging rate at warmer temperatures, thereby increasing their contact rates and facilitating larger epidemics. Although warmer temperatures often reduce parasite fitness (see above), in this scenario the resulting increase in foraging rate outweighed these negative effects. This suggests that rising temperature due to climate change could prove important in shaping linkages between foraging behavior and pathogen transmission.

In addition to effects of temperature, habitat fragmentation, and its inverse, connectivity can help shape foraging behaviors and disease dynamics. Habitat fragmentation and connectivity have complex interactions with host foraging behaviors. For example, in southern Mexico, howler monkeys (*Alouatta palliata mexicana*) in a large (>600 ha) preserved forest forage over a wide area for *Ficus* spp. seeds, likely reducing contact rates. In a small, disturbed (i.e., fragmented) area, howler monkeys are restricted to clumps of trees where they must repeatedly forage, resulting in localized foraging and likely increasing contact rates (Serio-Silva and Rico-Gray, 2002). Similarly, female lesser horseshoe bats (*Rhinolophus hipposideros*) in a highly fragmented landscape exhibit spatially clustered foraging activity, albeit over a greater absolute area than the howlers discussed above (Reiter et al., 2013).

The influence of habitat fragmentation on disease dynamics is similarly complex and can vary by spatiotemporal scale. This complexity is exemplified by Lyme disease transmission from ticks to other hosts. At a regional scale, Lyme disease risk is highest in areas of 'intermediate fragmentation' (Diuk-Wasser et al. 2021; Jackson et al., 2006), but at a local scale, Lyme disease risk increases with increasing patch size (i.e., decreasing fragmentation; Diuk-Wasser et al., 2021; Moon et al., 2019). These patterns can be related to the density, distribution, and thus probability of contacting, competent hosts, specifically white-tailed deer, which are positively associated with tick density in suburban environments (Brownstein et al., 2005; Stafford et al., 2003). It will be important to monitor these links in the future, as the pace of urbanization continues to accelerate.

Urbanization is a growing ecological problem that can compound the effects of fragmentation and temperature by altering animal behaviors, disease risk, and health either directly or indirectly, and at multiple scales (i.e., individual–population; Pinter-Wollman et al., 2018). For example, some bat species respond positively to urbanization, with human-made water serving to attract the insectivores and buildings serving as roosting locations. For other species, however, these urban environments might be "ecological traps", environments that are detrimental to reproduction and survival, yet preferred by organisms (Russo and Ancillotto, 2015). With features that attract animals despite limited or low-quality resources, such environments can increase population densities, augmenting contact rates and the potential to spread pathogens. Such environments could even facilitate foraging-mediated hydra effects (see above). Further, urbanization exposes animals to novel stressors, such as light and sound pollution, pesticides, and urban predators, all of which can alter microbiota and increase susceptibility to infection (Fuirst et al., 2018; Russo and Ancillotto, 2015). Lastly, because urban areas generally have higher temperatures than their rural counterparts ("urban heat islands", Kim, 1992) and temperature is an important factor in shaping foraging decisions, such environments could exacerbate the links among temperature, foraging behaviors, and contact rates.

Finally, recent theoretical models have examined the effects of resource density or spatial heterogeneity on disease prevalence (Hall et al., 2007) and links among sickness-induced lethargy, host contact rates, and pathogen spread (Franz et al., 2018). Notably, in landscapes with limited, patchily distributed water resources, Franz and colleagues (2018) found that sickness behaviors can actually increase host-host contact rates and promote disease spread. In this scenario, infected hosts exhibit decreased foraging behaviors and rarely leave a given water source, enhancing contact rates with healthy hosts who must also visit water. This model highlights the potential for interactions between host foraging motivation and landscape features (highly fragmented resources) to shape contact rates. Moreover, this framework can predict the evolution of pathogen virulence, which increased in the above water-limited example (Franz et al., 2018).

Conclusions and Future Directions

Infection can dramatically influence foraging behaviors and contact rates, thereby altering dynamics of parasite transmission. For brevity, we focused here on the effects of sickness behaviors and parasite-driven host responses on search time, patch quality assessment, and GUD/departure times, but such linkages are by no means constrained to these foraging behavior metrics. Infection could alter additional traits related to foraging, including food preference, ability to locate patches, and perceived distance to nearest patch. We also noted how temperature, habitat fragmentation/connectivity, and urbanization can affect the associations between foraging behavior and contact rate. These environmental conditions, however, are only a small subset of factors that may shape the links between foraging and infectious disease dynamics.

Overall, the effect of foraging behaviors on disease transmission is multifactorial: no single factor will drive contact rates and precise relationships will differ among host-parasite systems. Still, theoretical work has shown that links among foraging decisions, contact rates, and landscape features can predict not only the transmission of parasites, but also the evolution of their virulence (Franz et al. 2018). However, little empirical work exists to refine the parameterization of such models or test their predictions. We therefore recommend that future empirical studies focus on not only how foraging decisions change with infection, but also how such changes shape intra- and inter-specific contact rates. Such studies would be especially valuable when incorporating heterogeneous environmental conditions and/or testing differences between host-driven (sickness behaviors) and parasite-driven alterations to foraging. Because human-driven climate change and land-use change continue to shape environmental factors that can affect the links among foraging behavior, contact rates, and infectious disease dynamics, such studies have never been more relevant.

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Figures

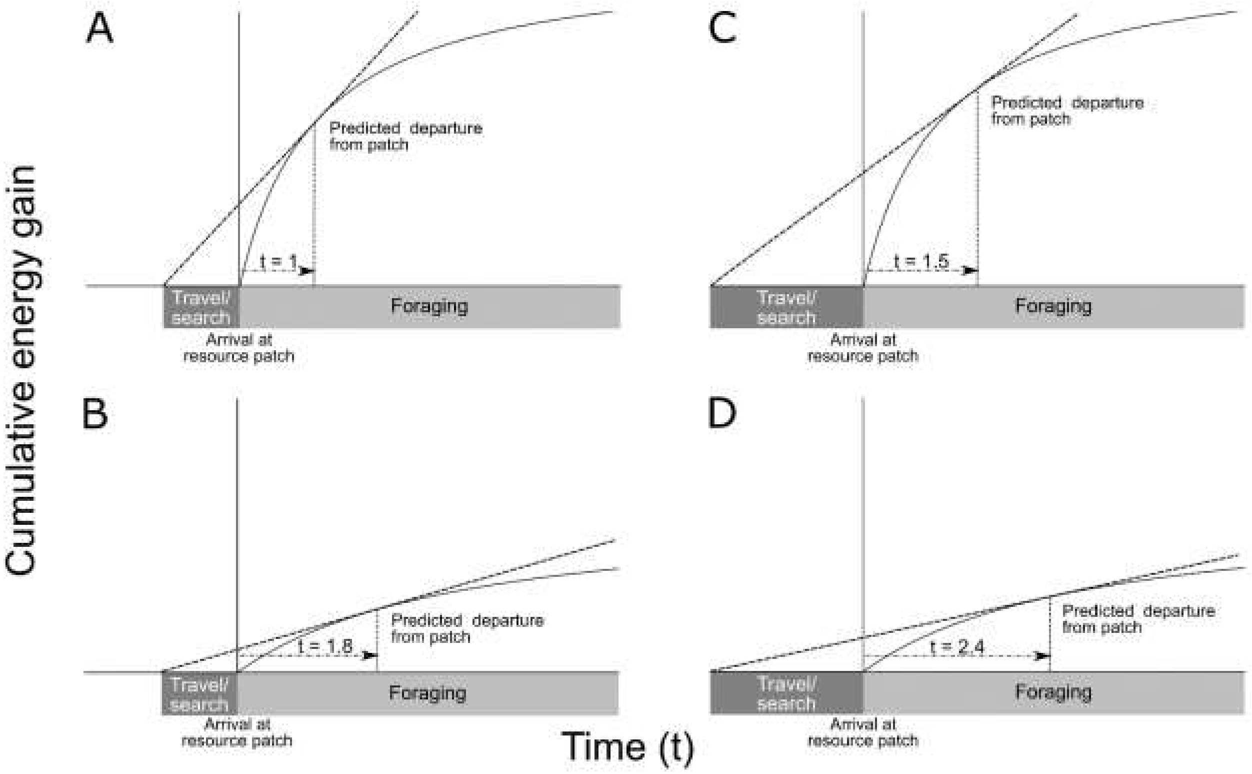

Figure 1. Generally, uninfected animals (A) should forage more efficiently (i.e., gather more resources per unit time) than infected conspecifics expressing sickness behaviors that increase travel and/or search time only (B), decrease foraging efficiency only (C), or increase travel and/or search time and decrease foraging efficiency (D). The intersection between the dashed line and solid curve indicates the point of diminishing returns, and thus the optimal time of departure from a given patch (shown by the horizontal arrow). In such cases, infected animals are predicted to spend more time in a given resource patch than uninfected animals. Depending on landscape characteristics and resource quality, this could increase or decrease contact rates between infected and uninfected hosts (see main text).