

Behavioral Immunity and Social Distancing in the Wild: The Same as in Humans?

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The COVID-19 pandemic imposed new norms on human interactions, perhaps best reflected in the widespread application of social distancing. But social distancing is not a human invention and has evolved independently in species as dissimilar as apes and lobsters. Epidemics are common in the wild, where their spread is enhanced by animal movement and sociality while curtailed by population fragmentation, host behavior, and the immune systems of hosts. In the present article, we explore the phenomenon of behavioral immunity in wild animals as compared with humans and its relevance to the control of disease in nature. We start by explaining the evolutionary benefits and risks of sociality, look at how pathogens have shaped animal evolution, and provide examples of pandemics in wild animal populations. Then we review the known occurrences of social distancing in wild animals, the cues used to enforce it, and its efficacy in controlling the spread of diseases in nature.

Keywords: social, disease, behavior, animal, COVID-19

Humans are currently beset by a pandemic caused by the severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2), subsequently named COVID-19, which has upended modern human society's economics, travel patterns, and social norms. COVID-19 is a member of the genetically diverse *Coronaviridae*, which infect humans, as well as a wide range of bird and mammalian hosts, including bats, from which the virus putatively jumped into the human population (Sohrabi et al. 2020). The World Health Organization and the US Centers for Disease Control and Prevention have recommended enhanced personal hygiene measures (e.g., frequent hand washing, the use of disinfectants), the use of personal protective equipment such as face masks, minimization of travel, widespread screening for infection, contact tracing, and the avoidance of close contact with other humans. The latter precaution—referred to as *social distancing*—is a term now common in the public lexicon and a behavior that has become a new social norm (Qazi et al. 2020, Wilder-Smith and Freeman 2020). Social distancing is a form of behavioral immunity, a more general phenomena first described in humans whereby individuals detect and avoid other individuals or environments in which the potential presence of disease-causing pathogens poses an increased risk of infection (Schaller 2006).

Humans are not the only animals that engage social distancing to thwart the spread of pathogens. A diverse assortment of wild species also practice social distancing (Hawley

and Buck 2020, Lopes 2020), a behavior that potentially plays a role in mitigating the challenges that emerging infectious diseases pose for humans and wildlife alike (Townsend et al. 2020). We begin our discussion of social distancing and its relevance to the control of disease in wild animals starting with the evolutionary trade-offs associated with social grouping, and the ways in which pathogens have shaped animal evolution. Despite host adaptations, pandemics are not uncommon in wild animal populations as demonstrated by a few examples that we describe. We go on to review known instances of social distancing by wildlife, summarize the cues typically employed by animals to gauge the risk of infection, and explore evidence as to whether social distancing is effective in ameliorating the spread of disease in nature.

Sociality: Evolutionary benefits and risks

Animals cluster and socialize for many reasons. Local patchiness in animal spatial distributions is often an indirect consequence of the capitalization of patchily distributed resources: food, water, shelter, or mating destinations. Aggregation has also evolved as an adaptation that congregates individuals for protection from predators, defense of communal resources, mating opportunities, cooperative care of young, and exchange of information (Broom et al. 2020). But whenever animals aggregate, there are potential costs of that association. Close proximity increases the

probability of competition, cuckoldry, infanticide, inbreeding, parasitism, and disease (Curley et al. 2015). The ability to identify and mitigate these risks allows animals to benefit from social interactions in spite of the drawbacks associated with aggregation (Curtis 2014) and the loss of interpersonal space (Prokopy and Roitburg 2001). Examples of such evolutionary trade-offs crisscross animal lineages and ecological purposes: from female elk (*Cervus elaphus*) that temporarily abandon the safety of the herd and prime foraging habitat in favor of self-isolation favoring the survival of their newborn (Brook 2010) to spiny lobsters that typically congregate by day in rocky dens to ward off predators but eschew scarce shelters if they are already occupied by diseased conspecifics (Behringer et al. 2006, Butler et al. 2015). Among social species, natural selection favors individuals who can balance the benefits and risks of sociality by recognizing and avoiding risky social situations (Loehle 1995).

The power of pathogens

Among the most formidable costs of sociality is infection by pathogens, whose evolutionary power is reflected in the complex array of host adaptations and defenses present in the animal kingdom. Indeed, some theorize that the evolutionary effect of pathogens is so great that it contributed to the emergence of sexual reproduction, the argument being that the resultant increase in genetic and phenotypic diversity buffers populations from devastating epidemics (Hamilton 1980, Hamilton and Zuk 1982, Loehle 1997, Morran et al. 2011). The most obvious evolutionary adaptation by animals to infection is their immune system, the well-known suite of physiological mechanisms that provide relief from pathogens and parasites once acquired by hosts. But immune responses come at a cost: Some are direct (e.g., increase in metabolic rate, amino acid usage, or immunopathology; Lochmiller and Deerenberg 2000, Brace et al. 2015, Cressler et al. 2015), whereas others operate indirectly by posing trade-offs with important life processes (e.g., growth, reproductive success; Bonneaud et al. 2003, Genovart et al. 2010). Although hosts can sometimes mitigate the energetic or physiological costs of immune function by increasing resource intake (Ruiz et al. 2010), in natural environments, resources are often limited. If so, the repeated activation of the immune system to ward off infection can reduce host fecundity, metabolic rate, and food acquisition (Lee 2006, Bashir-Tanoli and Tinsley 2014). Hosts are generally better off if their immune system is engaged infrequently, which is why adaptations such as social distancing play an important role in reducing the probability of host exposure to pathogens. But when host adaptations fail to protect them from disease, the effects of pathogens on animal populations can be striking, such as during panzootics—the animal equivalent of human pandemics.

Panzootics in wild animal populations

Animals are plagued by pathogens to varying degrees. Some groups such as the Chiroptera (bats) tolerate a diversity of

pathogens, including those that can be zoonotic (i.e., transferred to humans; Wibbelt et al. 2010, Streicker and Gilbert 2020), whereas few pathogens are reported in other taxa (e.g., spiny lobsters, Palinuridae; Shields 2011). A number of factors, including phylogenetic history, environmental stress (e.g., temperature change, contamination), habitat degradation, and the introduction of a novel pathogen, can favor the rapid proliferation of a pathogen within animal populations, resulting in an epizootic (a nonhuman epidemic) or a panzootic if the geographic distribution of the event is large. There are many examples of epizootics and panzootics, but few are well known beyond the taxonomic borders of the scientists who study them.

For over 30 years, chytridiomycosis, caused by the pathogenic fungi *Batrachochytrium dendrobatidis* and *Batrachochytrium salamandrivorans*, has sent approximately 7% of all amphibian species into decline, catastrophic decline (more than 90% reduction in abundance), or likely extinction (Fisher and Barner 2020). White-nose syndrome, caused by another pathogenic fungus, *Pseudogymnoascus destructans*, has killed millions of bats in North America, resulting in the loss of 90% of some species (Langwig et al. 2016). Since its emergence in North America in 1999, West Nile virus has caused the decline of numerous bird species and has killed up to 45% of the American crow population (LaDeau et al. 2007). In Europe, rabbits (*Oryctolagus cuniculus*) are plagued by rabbit haemorrhagic disease, which is caused by a calicivirus that rapidly spread worldwide in a panzootic (Abrantes et al. 2012). The virus is so effective at reducing rabbit populations that it was purposely introduced for rabbit biocontrol in Australia and New Zealand, where rabbits are pests.

The rapid spread of pathogens now possible among humans because of more efficient and faster global travel is an obvious change in human–pathogen dynamics. The COVID-19 virus spread among humans across the globe in a matter of a few months (Boulos and Geraghty 2020), but that rate of spread is only slightly faster than that of some diseases in nature. For example, a herpes virus epidemic in pilchard fish spread along the Australian coast at a rate in excess of 1000 kilometers (km) per month, and morbillivirus infections spread among populations of seals and dolphins at more than 500 km per month (McCallum et al. 2003). Calicivirus in Australian rabbits and West Nile virus in birds in North America have rates of spread in excess of 100 km per month (McCallum et al. 2003). The rapid spread of terrestrial epidemics is often attributed to flying insect or migrating bird vectors (Altizer et al. 2011). But in the sea, where animal vectors of disease are largely absent, pathogens are efficiently spread by ocean currents or by migratory fish, sea turtles, and marine mammals (Kough et al. 2015). The near extirpation of the ecologically important long-spined sea urchin (*Diadema antillarum*) throughout the Caribbean in the early 1980s provides a perfect example. In January 1983, mass mortality of the previously abundant urchins was noted on coral reefs off the Caribbean coast of Panama,

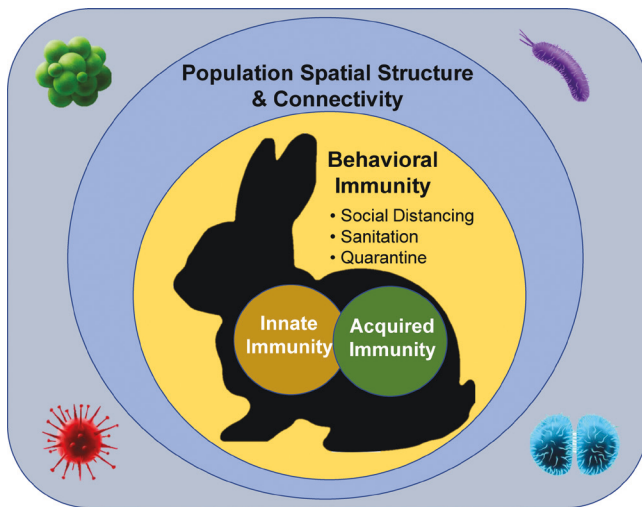


Figure 1. Graphical depiction of the multiple lines of defense that hosts (e.g., rabbit silhouette) employ against pathogens (seen at four corners). The first involves population-level processes such as spatial structure (e.g., fragmentation) and population connectivity (e.g., reduced movement, migration). Social distancing by individual hosts confers an additional line of defense referred to as behavioral immunity, which also includes sanitation and quarantine behaviors. Finally, are the host's own physiological responses to infection, conferred by innate immunity, acquired immunity, or both.

and by January 1984, the mass-mortality event had swept throughout the Caribbean, killing upward of 95% of the urchins (Lessios et al. 1984). It is also not uncommon for epizootics to emerge, spread uncontrollably over large areas, and then disappear before the causative agent can be identified. Such is the case for the long-spined sea urchin panzootic, whose putative pathogen remains a mystery.

Pandemics are less common in modern human populations, owing to our more formidable surveillance and response mechanisms (Thompson and Brooks-Pollock 2019). Unlike wild animals, humans also employ therapeutics to blunt the impact of pathogens. Among the most effective are vaccines, which curtail recurring outbreaks through induced herd immunity before infections reach epidemic or pandemic levels. Many of the human viral diseases with which we are most familiar (e.g., smallpox, measles, polio, influenza) caused repeated pandemics throughout history until surveillance and immunization tempered or eliminated those outbreaks, as is hoped for with the recent approval of vaccines for COVID-19. But immunization is not practical for most wildlife populations, and the ecological conditions that spark outbreaks are considerably less certain than those for humans (Lloyd-Smith et al. 2005).

To counteract the transmission of infectious agents, humans and animals share the same general repertoire of natural defenses, including population subdivision and limitations on connectivity, sanitation measures, individual social

distancing, and host-specific innate and acquired immunity (figure 1). Humans have added therapeutics, such as vaccination to this catalogue of natural defense mechanisms, although some ants and bees consume plants and fungi that appear to have therapeutic properties (Spivak et al. 2019).

The prevention of disease in wild animal populations

Population subdivision. At the largest scale, the spatial distribution (i.e., degree of fragmentation) of a population and the level of host connectivity among fragmented subpopulations influences the spread of disease. Fragmented populations, combined with the limited movement (i.e., connectivity) of individuals among subpopulations, offer a spatial bulwark against the spread of disease (McCallum and Dobson 2002, Brooks et al. 2008). However, such conditions also promote greater pathogen virulence (Cote and Poulin 1995, Thrall and Burdon 2003, Ezenwa 2004). Therefore, the spatial fragmentation of populations poses an evolutionary trade-off with respect to defense against disease, which is compounded by other well-known trade-offs associated with genetic bottlenecks, resource depletion, and susceptibility to environmental stochasticity (Schnell et al. 2013).

Innate and adaptive immunity. From simple protozoans to humans, all organisms have an innate immune system, whose function is to recognize and eliminate invasive elements determined to be non-self (Buchmann 2014). Although invertebrates are only equipped with innate immunity systems, vertebrate animals have evolved an adaptive or acquired immune component to augment their innate system. The core function of a host's adaptive immune system is to recognize and diminish infection by pathogens via a complex array of physiological responses. These immune system adaptations are derived from the host's prior exposure to the same species or strain of pathogen. The exposure can be through prior infection, passive transfer from the mother, or vaccination. What is underappreciated is that invertebrate and vertebrate animals also engage in various behaviors that offer them behavioral immunity and that operate to reduce the probability of host infection and therefore preclude activation of their metabolically costly innate and adaptive immune systems.

Sanitation. Like humans, social animals practice sanitation. Those behaviors include disinfection through grooming (e.g., many animal taxa; Sachs 1988, Konrad et al. 2012, Zhukovskaya et al. 2013), selection of habitats with fewer infectious agents (e.g., avoidance of habitats with high concentrations of feces; reindeer, kangaroo, fishes; Folstad et al. 1991, Garnick et al. 2010, Poulin et al. 2012, Zhukovskaya et al. 2013, Bui et al. 2016), and rejection of potentially infective food sources (*Caenorhabditis elegans*, oysters; Meisel and Kim 2014, Ben-Horin et al. 2018), among other behavioral sanitation strategies (Hart and Hart 2018).

Not surprisingly, species with the most advanced social structures—eusocial animals—have evolved the most

sophisticated sanitation behaviors (Cremer et al. 2007, Hart 2011). Eusocial animals have evolved a sophisticated social organization in which a single female or caste produces the offspring, and other castes of nonreproductive individuals cooperatively care for the young and the maintenance of the nest or colony. Those maintenance activities include behaviors that reduce the spread of disease through colony hygienics. For example, some ants use poisons to disinfect their colonies and prevent epizootics (Tragust et al. 2013), and others (e.g., European fire ants, *Myrmica rubra*) remove potentially infectious ant corpses from the colony (Diez et al. 2012). Similarly, honeybees (*Apis mellifera*) detect diseased or dead larvae, prepupae, and pupae while still in their brood chambers and remove them from the hive to reduce the likelihood of disease in the colony (Mastermann et al. 2001). Still other species of ants and bees practice altruistic suicide, in which infected individuals abandon their colonies as a sanitation measure to prevent the transmission of pathogens (Henize and Walter 2010, Rueppell et al. 2010). The converse of such altruistic behaviors is practiced by other species when uninfected members of the population drive away or avoid infected conspecifics (Daly and Johnson 2011), not unlike quarantine strategies used by humans. This has been observed in honeybees that act as guards at the entrance to their nest and deny entry to diseased bees, warding off parasite colonization of the hive (Drum and Rothenbuhler 1985). Such antisocial behaviors serve to isolate and reduce household-scale interactions through social distancing and are distinct from behaviors associated with colony sanitation.

Social distancing. The extensive press coverage of the COVID-19 pandemic has informed the public about the effectiveness of reducing close contact among humans to reduce the transmission of pathogenic viruses. The importance of local interactions in the transmission of communicable diseases among hosts has long been established in the scientific literature (Thrall and Burdon 2002, Brooks et al. 2008), as is the effectiveness of host segregation in reducing the spread of pathogens (Grenfell et al. 1995, Riley 2007). Mankind is now engaged in a massive application of social isolation designed to confer on humans behavioral immunity to the COVID-19 virus.

Social distancing can only be effective if it exceeds the spatial scale over which pathogen transmission is likely. The present worldwide metric with respect to COVID-19 is the familiar recommendation that humans maintain a separation of at least 2 meters (approximately 6 feet). However, recent research on this indicates that gaseous clouds from human exhalations may travel even further (Setti et al. 2020). Measurements of the distance over which infectious pathogens can be spread among hosts are largely unreported for wild animals. Among marine or aquatic species for which pathogen transmission is typically waterborne, it is the viability of the pathogen in the watery medium along with water current velocity that dictate the spread of infective agents (Kough et al. 2015). Our own laboratory

experiments with the Caribbean spiny lobster (Butler et al. 2008) suggest that waterborne transmission of the PaV1 virus among lobsters is on the order of 2 meters—a social distancing metric that is coincidentally similar to that designed to protect humans from infection during the current COVID-19 crisis.

From primates to arthropods, the rather eclectic mix of species known to engage in social distancing (figure 2) suggests that the phenomenon has evolved independently many times across animal taxa and its occurrence may perhaps be under reported. It is important to distinguish active social distancing from the behavioral byproducts of infection wherein sick individuals move less and therefore have fewer social encounters. True social distancing involves specific behaviors that have evolved in response to transmissible pathogens and parasites so as to increase spatial distances among conspecifics and therefore reduce the spread of disease. Chimpanzees (*Pan troglodytes*), our closest primate relative, are hypothesized to benefit from avoidance of individuals outside of their social group (Freeland 1976), and they ostracize individuals infected with communicable diseases such as polio (Goodall 1986). Mandrills, a more distantly related Old World monkey, select safe social partners and avoid interactions with members of their group that they perceive to have orofecally transmitted parasites (Poirotte et al. 2017). Social distancing also effects reproductive interactions, as is seen among female house mice (*Mus musculus domesticus*) who avoid mating with parasitized males that could infect them (Kavaliers and Colwell 1995). However, the degree to which social distancing is expressed may vary depending on social relationships, such as kinship. Recent research with vampire bats (*Desmodus rotundus*) whose immune systems were experimentally challenged by lipopolysaccharide injections revealed that mother–offspring social interactions were less affected by illness than interactions with other conspecifics (Stockmaier et al. 2020).

Species that congregate in large aggregations to reduce predation risk or improve foraging success (e.g., flocks of birds, herds of ungulates, schools of fish) are at a particularly high risk of infection by pathogens and parasites, so many have evolved behaviors to reduce that risk. For example, house finches (*Carpodacus mexicanus*) avoid other finches that are experimentally sickened (Zylberberg et al. 2013), a dramatic change for this highly social, flocking species. Laboratory studies of juvenile three-spined stickleback fish (*Gasterosteus aculeatus*) confirm that individual fish avoid schools of conspecifics if the school contains individuals infected with ectoparasites (Dugatkin et al. 1994). Healthy bullfrog tadpoles (*Rana catesbeiana*) avoid other tadpoles infected by a fungus (*Candida humicola*) that reduces tadpole growth and can lead to death (Kiesecker et al. 1999). Similarly, chorus frog tadpoles (*Pseudacris regilla*) exposed to the free-swimming infectious stages (cercariae) of trematodes, exhibited bursts of activity (e.g., fast swimming, twisting) not seen in unexposed tadpoles (Daly and Johnson 2011). Moreover, experimentally anesthetized tadpoles that














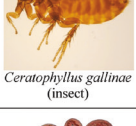

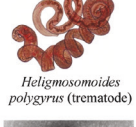
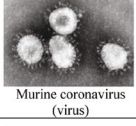





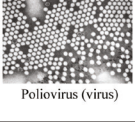
	Host	Pathogen/Parasite	Social Behavior
Invertebrates	 Spiny Lobster (<i>Panulirus argus</i>)	 Panulirus argus virus 1 (virus)	<ul style="list-style-type: none"> • Social Distancing (Behringer et al. 2006)
	 Ants (several species, e.g., <i>Lasius niger</i> and <i>Myrmica rubra</i>)	 <i>Metarhizium</i> sp. (Fungus)	<ul style="list-style-type: none"> • Social Distancing (Stroeymeyt et al. 2018) • Sanitation (Diez et al. 2012)
	 Honey Bee (<i>Apis mellifera</i>)	 <i>Varroa</i> spp. (mites)	<ul style="list-style-type: none"> • Sanitation (Currie & Tahmasbi 2008) • Quarantining (Boecking & Drescher 1992)
Fish	 Guppy (<i>Poecilia reticulata</i>)	 <i>Gyrodactylus turnbulli</i> (Monogenean)	<ul style="list-style-type: none"> • Social Distancing (Stephenson et al. 2018)
	 Stickleback (<i>Gasterosteus aculeatus</i>)	 <i>Argulus canadensis</i> (crustacean)	<ul style="list-style-type: none"> • Social Distancing (Dugatkin et al. 1994)
Amphibians	 Bull frog tadpole (<i>Rana catesbeiana</i>)	 <i>Candida humicola</i> (Fungi)	<ul style="list-style-type: none"> • Social Distancing (Kiesecker et al. 1999)
Birds	 Many Species	 <i>Ceratophyllus gallinae</i> (insect)	<ul style="list-style-type: none"> • Sanitation (Bush & Clayton 2018)
Mammals	 House Mouse (<i>Mus musculus domesticus</i>)	 <i>Heligmosomoides polygyrus</i> (trematode)  Murine coronavirus (virus)	<ul style="list-style-type: none"> • Social Distancing (Kavaliers & Colwell 1995) (Boillat et al. 2015)
	 Marsupials	 Intestinal parasites (within feces)	<ul style="list-style-type: none"> • Sanitation (Sharp et al. 2015)
	 Mandrill (<i>Mandrillus sphinx</i>)	 <i>Balantidium coli</i> and others (protozoans)	<ul style="list-style-type: none"> • Social Distancing & Sanitation (Poirotte et al. 2017)
	 Chimpanzee (<i>Pan troglodytes</i>)	 Poliovirus (virus)	<ul style="list-style-type: none"> • Social Distancing (Goodall 1986) • Sanitation (Nashida 1988)

Figure 2. Summary of host taxa, their pathogens, and types of social behaviors used by the host to reduce infection by the pathogen.

could not engage in bursts of activity were 20%–40% more likely to become infected and, when infected, harbored three times as many parasitic cysts. Guppies (*Poecilia reticulata*) infected by an ectoparasite (*Gyrodactylus turnbulli*) are shunned by other guppies in the school (Stephenson et al. 2018). Social distancing is also common in social arthropods such as hymenoptera (ants, bees, wasps) and spiny lobsters (Rosengaus et al. 1999, Behringer et al. 2006, de Roode and Lefevre 2012, Anderson and Behringer 2013, Bulmer et al. 2019).

For the past two decades, we have investigated social distancing among Caribbean spiny lobster (*Panulirus argus*) and its consequences for transmission of a novel virus (PaV1), the first member of the new Mininucleoviridae family (Subramaniam et al. 2020). Unlike the solitary clawed lobsters (Homaridae) that occur in the North Atlantic and with which North Americans and Europeans are most familiar, the more geographically widespread spiny lobsters (Palinuridae) are social. Nocturnal foragers, they rest and aggregate for protection by day in rocky dens in groups of a few to hundreds of individuals (Zimmer-Faust and Spanier 1987). Seasonal migrations of spiny lobsters also occur en masse, strung out on the seafloor in dramatic single-file lines or queues (Herrnkind and Cummings 1964, Kanciruk and Herrnkind 1978). Juvenile Caribbean spiny lobsters are particularly susceptible to the PaV1 virus, which is transmitted short distances in the water among lobsters and is lethal in more than 90% of infections (Butler et al. 2008). However, healthy lobsters detect and avoid PaV1-infected lobsters, refusing to share shelters with their diseased conspecifics (Behringer et al. 2006), a behavior that is regulated by chemical cues (Anderson and Behringer 2013).

Social distancing cues

Although a number of species of wild animals engage in social distancing, they all require a means by which uninfected individuals can detect infectious conspecifics; that is, they must respond to a cue that is a reliable predictor of the risk of infection. Human social distancing and the cues we use to detect infected people differ fundamentally from the practice in wild animals. Moreover, infected hosts can sometimes be asymptomatic, providing no visual, auditory, or olfactory cues indicating infection. It is this lack of obvious cues that makes recognition of COVID-19 infections so problematic. Absent diagnostic testing, humans rely on visual cues such as a feverish appearance (Curtis et al. 2004) or auditory cues such as a cough, a sneeze, or language to avoid presumably infectious individuals (Angle et al. 2016, Townsend et al. 2020), but the accuracy of those cues for determining a disease state is often low (Michalak et al. 2020).

Humans also produce unique body odors when our immune systems are activated (Olsson et al. 2014), a change in odor that our canine companions can detect (Angle et al. 2016). But we humans are poorly equipped to recognize the subtle changes in odor associated with infection, because our olfactory senses have diminished through evolutionary

Cues for Social Distancing in the Animal Kingdom

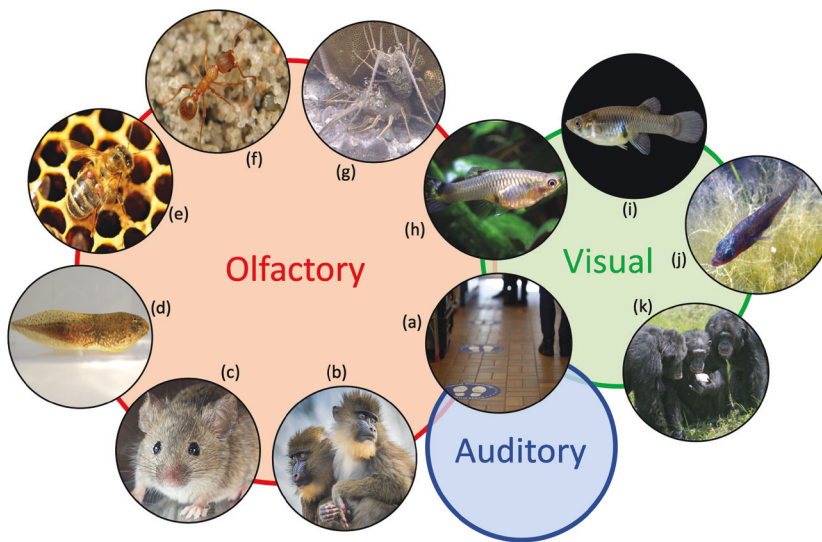


Figure 3. Animals from a wide range of taxa use olfactory and visual cues to detect and distance themselves from infected members of their population, whereas only humans and ants have been documented to use auditory cues. (a) Human (*Homo sapiens*; photograph: GoToVan, Flickr), (b) mandrill (*Mandrillus sphinx*; photograph: Zweer de Bruin), (c) house mouse (*Mus musculus*; photograph: David Illig, Flickr), (d) bullfrog tadpole (*Lithobates catesbeianus*; photograph: Dave Huth, Flickr), (e) honeybees (*Apis mellifera* with parasitic mite *Varroa destructor*; photograph: AbsoluteFolly, Flickr), (f) European fire ant (*Myrmica rubra*; photograph: Ryszard, Flickr), (g) Caribbean spiny lobster (*Panulirus argus*; photograph: Donald C. Behringer), (h) guppy (*Poecilia reticulata*; photograph: Holger Krisp), (i) mosquitofish (*Gambusia affinis*; photograph: Robert Hrabik, Missouri Department of Conservation), (j) three-spined stickleback (*Gasterosteus aculeatus*; photograph: S. Rae, Flickr), (k) chimpanzee (*Pan troglodytes*; photograph: Matthew Hoelscher, Flickr).

time. This loss in olfactory acuity represents an evolutionary trade-off in favor of the development of enhanced brain function and greater reliance on vision and verbal communication. Indeed, half of the genes that code for olfactory receptors in humans are now nonoperational, a loss in olfactory function that is among the most rapid of any animal lineage examined—four times faster than any other primate (Gilad et al. 2003). However, human reliance on vision has resulted in our keen ability to identify individuals by appearance rather than by smell, which has changed the means by which humans detect illness in conspecifics. Indeed, humans are socially perceptive enough to identify potentially infected conspecifics through their physical appearance or behaviors (e.g., coughing or sneezing, bedraggled appearance, lethargy) and tend to avoid contact with them (Schaller and Park 2011). Taken to the extreme, human xenophobic behavior and disgust toward out-groups is theorized to have evolved as cultural traits that reduce the transmission of pathogens (Navarrete and Fessler 2006, Curtis et al. 2011).

In contrast, olfaction appears to be the most important mechanism used by wild animals to detect illness in conspecifics, and some animals then use that information for social distancing (figure 3). Chemical cues emitted from bullfrog tadpoles (*Rana catesbeiana*) infected by a potentially deadly fungus (*Candida humicola*) elicit an avoidance response by healthy tadpoles (Kiesecker et al. 1999). Healthy spiny lobsters use odors to detect infected conspecifics that they ostracize. The common guppy (*Poecilia reticulata*) is unusual in that it uses both visual and olfactory cues to avoid conspecifics infected by an ectoparasite (*Gyrodactylus turnbulli*; Stephenson et al. 2018). Auditory detection of infectious individuals appears to be uncommon in nature. A rare example occurs in termites that produce vibrational signals when they encounter spores of pathogenic fungi (Rosengaus et al. 1999, Bulmer et al. 2019) and, in response, their termite nestmates flee from the signal, which is hypothesized to reduce disease within the termite nest. But is there evidence that social distancing actually reduces the spread of disease in nature?

Effectiveness of social distancing in wild animals

For a behavior to evolve as a defense against pathogens, it must reduce or eliminate infections that negatively alter host fitness (Hart 1990). But the effectiveness of host behavior in mitigating pathogen infection remains largely unquantified relative to immunological defenses, with a few exceptions (Hart 1990, Ezenwa 2004, Raberge et al. 2009). Stephenson and colleagues (2018) demonstrated in a laboratory transmission experiment that when guppies avoided infected conspecifics, the speed of ectoparasite transmission and the number of parasites transmitted declined. In another laboratory study, investigators controlled the exposure of ant (*Lasius niger*) colonies to a fungal pathogen (*Metarhizium brunneum*), measured the subsequent transmission of the pathogen, and quantified changes in ant social patterns using a network model (Stoeymeyt et al. 2018). They found that pathogen exposure induced behavioral changes in exposed ants that altered the colony's social contact network and helped contain the outbreak of disease. Lopes and colleagues (2016) used a hybrid experimental or modeling approach to assess the effect of social behavior on disease transmission in mice. They first simulated a disease outbreak in wild house mice by simulating infections in tagged mice, then monitored their social

interactions. They found that pathogen exposure induced behavioral changes in exposed mice that altered the colony's social contact network and helped contain the outbreak of disease. Lopes and colleagues (2016) used a hybrid experimental or modeling approach to assess the effect of social behavior on disease transmission in mice. They first simulated a disease outbreak in wild house mice by simulating infections in tagged mice, then monitored their social

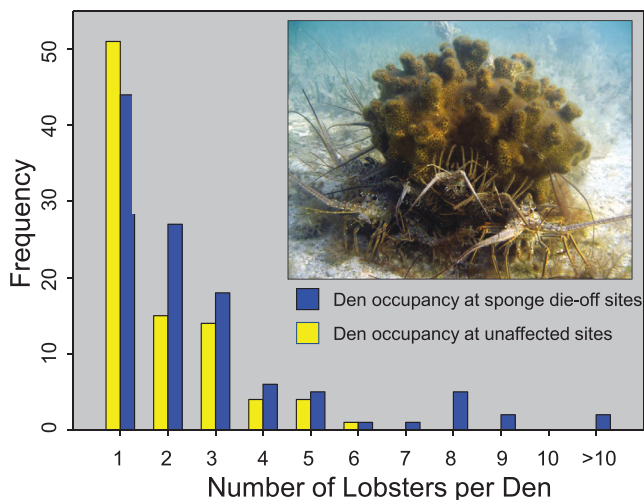


Figure 4. Following the mass die-off of large sponges that served as the primary shelter for juvenile spiny lobsters in the Florida Keys, lobsters were forced into unnaturally high aggregations under the remaining shelters such as this coral head. Data collected at 13 unaffected control sites (the yellow bars) and 12 sites that experienced sponge die-offs and therefore the loss of habitat (the blue bars) demonstrate the increase in the frequency of dens occupied by larger groups of lobsters at the sponge die-off sites. Such dense aggregations of hosts would normally portend higher rates of pathogen transmission and disease prevalence, but social distancing by lobsters that avoided shelters occupied by conspecifics infected with the PaV1 virus prevented an epizootic (Photograph: Mark Butler).

interactions. They observed reduced social connectivity of immune-challenged mice compared with others, which subsequent modeling demonstrated to be theoretically effective in reducing the spread of disease. Despite the ingenuity and compelling insights these studies offer into the potential effectiveness of social distancing in slowing the spread of disease, they all relied either on laboratory studies of wild animals or modeling to gauge behavioral effectiveness.

Tests of whether social distancing is effective in reducing the spread of disease in nature are few. The reasons for this are simple. First, there are relatively few documented cases of social distancing in wild animals. Second, it is nearly impossible to conduct a controlled experiment testing the effectiveness of social distancing among wild animals in a natural setting. So our research team took advantage of a natural experiment to test the practice and outcome of social distancing among Caribbean spiny lobsters in their natural habitat (Butler et al. 2015). In 2007, a mass die-off of sponges in the Florida Keys (Florida, United States) resulted in the loss of the primary shelter used by juvenile lobsters over a region of approximately 2500 square kilometers. Lobsters responded to this loss of shelter by hyperaggregating in the few remaining shelters such as coral heads (figure 4), which increased their potential exposure to the contagious PaV1

virus. Despite this large-scale spatial reorganization of the lobster population, viral prevalence in lobsters remained unchanged after the sponge die-off and for years thereafter. Field experiments demonstrated why the disease did not spread uncontrollably in the population as might be expected: Uninfected lobsters exhibited social distancing and vacated shelters if occupied by PaV1-infected lobsters despite the scarcity of alternative shelters and the higher risk of predation incurred when searching for a new shelter (Behringer and Butler 2010, Butler et al. 2015). These empirical results were confirmed in simulations from a spatially explicit, individual-based epidemiological model (Dolan et al. 2014). Combined, the results of these field experiments and simulation modeling provide compelling evidence that social distancing can prevent epizootics in a wild animal system, which is mirrored in the current human experience with COVID-19. The varying degrees of social distancing edicts imposed by different countries, states, and localities in response to the COVID-19 pandemic and the corresponding inverse relationship with levels of viral transmission provide a similarly convincing argument for the effectiveness of social distancing in humans.

Conclusions

Pathogens have immense power to drive population dynamics, alter community stability, and manipulate the behavior of animals. The COVID-19 pandemic underscores that power in human society but also highlights the effectiveness of behaviors such as social distancing in ameliorating the spread of disease. But social distancing as a mechanism of behavioral immunity is not a unique human construct. A number of species spanning the animal kingdom have independently evolved behaviors to thwart pathogens, augmenting their innate and acquired immune systems. Animals that are evolutionarily distant from humans—such as ants, bees, and lobsters—use social distancing effectively and efficiently, perhaps in part because of their keen ability to detect subtle cues of infection in others. The examples of social distancing in wild animals in the present article, although they are compelling, are likely a small fraction of those that actually exist in nature and reflect the limited investigations conducted thus far on this phenomenon in the wild. What lessons might we learn about the human experience with pandemics from an expanded view of diseases, their spread, and their prevention in nature?

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