

Chapter 9

Impacts of Human Disturbance in Marine Mammals: Do Behavioral Changes Translate to Disease Consequences?



Melissa Collier, Janet Mann, Sania Ali, and Shweta Bansal

Abstract Humans have been altering wildlife habitats and wildlife behavior worldwide at an accelerated pace in recent decades. While it is well-understood how human-induced behavioral changes affect infectious disease risk in terrestrial wildlife, less is known in marine life. Here we examine this link in marine mammal populations by (1) conducting a systematic literature review to determine how human disturbances change marine mammal behavior in ways that can impact disease spread, and (2) using a mathematical modeling framework to examine how these behavioral changes might influence potential epidemics. Human disturbances can influence marine mammal behavior in ways that increase their exposure and susceptibility to pathogens, as well as their infectivity, or ability to effectively shed pathogens and infect conspecifics. When these changes to exposure, susceptibility, and infectivity are applied in four different marine mammal case studies (California sea lions, *Zalophus californianus*; Australian humpback dolphins, *Sousa sahulensis*; killer whales, *Orcinus orca*; Indo-Pacific bottlenose dolphins, *Tursiops aduncus*), epidemics are predicted to be larger and more likely to occur. Considering the rate at which human disturbance is increasing in the marine environment and the large number of marine mammal species and populations that are endangered or on the verge of extinction, we advocate for the careful consideration of the direct and indirect impact of human disturbance on marine mammal health.

Keywords Behavior · Contact networks · Epidemiological model · Human impacts · Marine mammal · Wildlife disease

M. Collier (✉) · J. Mann · S. Ali · S. Bansal
Department of Biology, Georgetown University, Washington, DC 20057, US
e-mail: mac532@georgetown.edu

© The Author(s), under exclusive license to Springer Nature Switzerland AG 2022
G. Notarbartolo di Sciara and B. Würsig (eds.), *Marine Mammals: the Evolving Human Factor*, Ethology and Behavioral Ecology of Marine Mammals,
https://doi.org/10.1007/978-3-030-98100-6_9

277

9.1 Introduction

Humans have been altering wildlife habitats worldwide at an accelerated pace in recent decades. According to a 2019 assessment by a 94 nation intergovernmental body, 75% of the terrestrial environment has been altered by human disturbance and approximately one million plant and animal species are at risk of extinction due to human threats (Diaz et al. 2019; Ceballos et al. 2020). Human disturbance also alters animal behavior—the adverse consequences of which have been well documented. For example, human activity decreases home range size in mammals (Shackelford et al. 2018), and exacerbates spatial and temporal avoidance of humans [e.g., caribous (Plante et al. 2018); cheetahs (Gaynor et al. 2018; Klaassen and Broekhuis 2018), coyotes and bobcats (Riley et al. 2003); leopards (Van Cleave et al. 2018)]. Importantly, these behavioral changes are known to impact pathogen transmission among terrestrial wildlife (Becker et al. 2015; Jones et al. 2018) but critical gaps remain, particularly for marine fauna. Approximately 66% of the marine environment is currently being altered by human-associated disturbances (Diaz et al. 2019) and marine wildlife disease has markedly increased over the past 40 years (Gulland and Hall 2007); recent reports suggest the true magnitude of marine disease is strongly underestimated (Simeone et al. 2015). Despite this, few studies have examined the link between human-induced behavioral changes in marine life and their potential consequences for infectious disease. Here, we examine this link by focusing on marine mammals given their visibility as flagship, sentinel, and umbrella species, concepts discussed below.

Marine mammals are ideal targets for studies of links between disturbance and disease. They are visible since they are large, surface to breathe, and pinnipeds breed and rest on land or ice. When marine mammals strand, they often garner considerable attention and concern from the public (Gulland and Hall 2007); consequently, the causes of strandings (e.g., fishery entanglements, disease) are well documented in some parts of the world (NOAA 2020). Because of their visibility and charisma, marine mammal tourism is a multi-billion dollar industry, producing more revenue than aquaculture and fisheries combined (Bearzi 2017). While mass mortalities of marine mammals are clearly of concern to the public, their status as top predators and sentinel marine species also attracts scientific scrutiny. Declines in top predator populations can alter population dynamics and abundance (Gulland and Hall 2007), cause extinction of endangered species, and alter the predator/prey ratios that can affect healthy ecosystems (Heithaus et al. 2008). Additionally, as sentinels for ocean health, protection of marine mammals necessarily extends to entire ecosystems thus making them umbrella species (Wells et al. 2004; Bossart 2006; Moore 2008). With extensive research on how human disturbance impacts marine mammal behavior, we can model how behavior change can affect pathogen transmission.

Human disturbance is a known cause of marine mammal mortality by way of fishing gear entanglement and bycatch, (Kraus 2017; Jannot et al. 2018), vessel strikes (Barcenas-De la Cruz et al. 2018), and loud sounds (Forney et al. 2017). But humans are also responsible for the increased risk of emerging infectious disease in

the oceans. For example, we have introduced pathogens into marine habitats via storm water runoff and human-made fresh water intrusions (Conrad et al. 2005; Miller et al. 2008; Reif et al. 2009; Schaefer et al. 2009), and immune function in many species has been greatly deteriorated from exposure to toxic chemicals and warming global temperatures (Harvell et al. 2002; Kakuschke and Prange 2007; Martin et al. 2010; Desforges et al. 2017). The frequency of marine mammal mass mortality events has increased substantially in the past several decades (Gulland and Hall 2007; Simeone et al. 2015; NOAA 2020). In the United States, there have been 70 recorded events of marine mammal mass mortalities since 1969 (NOAA 2020). While the causes of 47% of these mortalities are unknown, 12% have been identified as epizootics from infectious disease. Of these epizootics, 66% occurred after the year 2000; the two most recent epizootics are the 2013 cetacean morbillivirus outbreak on the United States Atlantic coast that resulted in more than 1650 common bottlenose dolphin (*Tursiops truncatus*) deaths, and the 2018 phocine distemper virus outbreak in the northeast United States that resulted in more than 3100 harbor (*Phoca vitulina*) and gray (*Halichoerus grypus*) seal deaths (NOAA 2020).

Humans may also be influencing the spread of pathogens within marine mammal species, which is vital to understanding population viability and vulnerability. Human disturbances can impact individual host competence, the ability of one host to transmit parasites effectively to another host (Martin et al. 2016). Host competence has both a behavioral component (e.g., host ability to transmit disease based on its social interactions), and an immunological component (e.g., host ability to both transmit and be infected by a pathogen based on their immune system's resistance and tolerance of parasites) (Barron et al. 2015).

Human disturbance influences both components of host competence in animal species (Martin et al. 2010; Jones et al. 2018). For example, increased ocean temperatures can suppress diverse immune responses in corals and sea crabs thus increasing their likelihood of infection (Martin et al. 2010). Similarly, when relocated by humans, captive primates increase their time spent in groups, thus increasing their exposure to potentially infected individuals (Dufour et al. 2011). Changes in host competence can impact disease spread through a population, which can be examined using wildlife contact networks. (Bansal et al. 2007; White et al. 2017a; Sah et al. 2018).

In contact networks individuals are represented by nodes that are connected by edges, which indicate contact capable of disease transmission between two individuals. When contact network structure is altered by human disturbances, there can be significant consequences on pathogen transmission (Carter et al. 2007; Dufour et al. 2011; Gaynor et al. 2018). For example, altering network connectivity to account for changes in wildlife population densities due to urbanization, translocation, or sickness behaviors (e.g., lethargy, decreased mating activity) influences pathogen transmission in terrestrial wildlife species (Jones et al. 2018).

Although humans clearly have direct impacts on marine mammals worldwide, the indirect effects of human disturbance on wildlife behavior and physiology, which in turn enhance infectious disease risk, are rarely considered. As such, we may be underestimating the true burden of anthropogenic pressure on wildlife species as a

whole. We examined the impacts of human disturbance in the marine environment on infectious disease risk in marine mammals. In particular, we (a) characterized how human activity alters the individual behavioral and immunological aspects of host competence of marine mammal species, and (b) considered the impact of altered host competence on disease transmission with an epizootological network modeling approach.

9.2 Impact of Human Disturbances on Marine Mammal Behavior

To examine ways in which human disturbance impacts host competence, we conducted a systematic literature review using the PRISMA framework (Liberati et al. 2009). A human disturbance was defined as any anthropogenic activity that acts directly on a marine mammal species, and was assigned to one of four categories: (1) coastal human activity (vessel traffic, construction, noise pollution, etc.), (2) human-associated feeding (provisioned animals, foraging using trawl nets, etc.), (3) marine debris, and (4) human-made pollution (polychlorinated biphenyls, polycyclic aromatic hydrocarbons, etc.) (Fig. 9.1). Indirect disturbances that resulted from intermediate species, such as prey depletion from over-fishing, were not considered. Climate change and extreme climate events were excluded as a disturbance category because they exacerbate disease transmission directly by increasing pathogen fitness (e.g., increasing pathogen development rates, relaxing overwintering restrictions on pathogen life cycles) (Harvell et al. 2002), making it difficult to parse out whether resulting disease consequences will be due to change in pathogen fitness or increased host competence.

We conducted an electronic database search for studies published since 1995 in Web of Science and Google Scholar using the terms “human”, “disturbance”, “marine mammal”, “behavior”, “response”, “pollution”, “boat,” and “fishery”, yielding a total of 757 studies. These were screened to exclude papers if: (1) the study subject was not a marine mammal or was in captivity; (2) there were no behavioral changes as a result of a direct human disturbance; (3) results did not demonstrate a potential impact to marine mammal health; (4) it was a review paper or not peer reviewed (gray literature and dissertations). In total, there were 126 studies that demonstrated human-induced impacts to individual marine mammal host competence (Figs. 9.2 and 9.3). The scientific quality or soundness of these studies was not evaluated but in aggregate they present a consistent picture. A complete summary of these studies can be found in the supplementary Table 1 (2020).

Human-induced impacts were then considered through the lens of networks. Disturbances that affect the behavioral aspect of host competence impact host contact network structure by altering the number of interactions (edges) of affected individuals (Fig. 9.4a, b). Pathogens propagate through edges in contact networks and changes to these edges affect opportunities for pathogen exposure. Disturbances

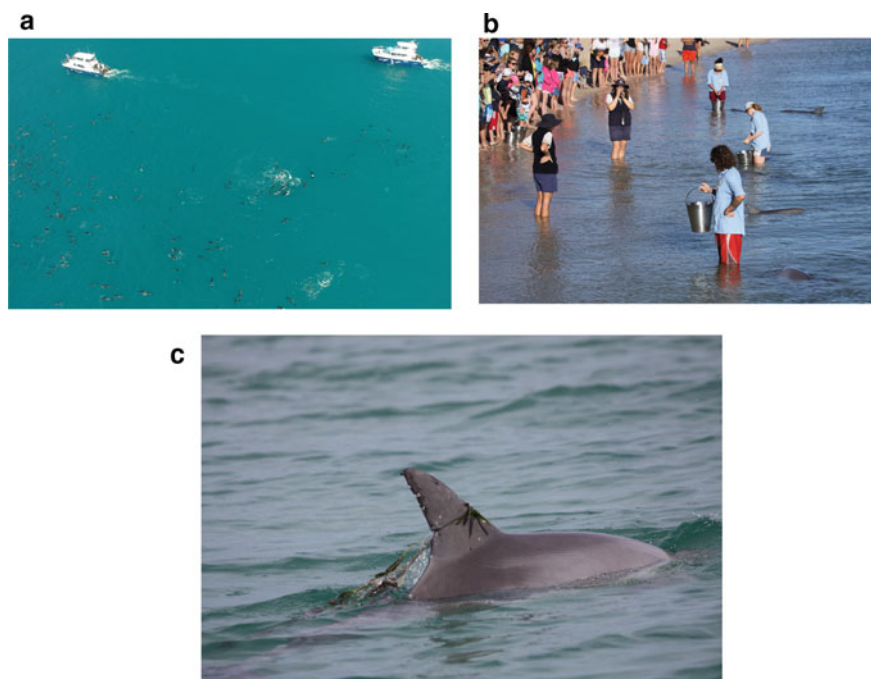


Fig. 9.1 Examples of three of the four human disturbance categories described in this chapter on odontocetes in New Zealand and Australia. **a** Two dolphin watching vessels slowly move along with a large (>500 animals) school of dusky dolphins, *Lagenorhynchus obscurus*, south of Kaikoura, New Zealand. In New Zealand, swim-with-dolphin activities are permitted, and the people aggregated at the stern of each vessel are about to receive permission to enter the water. The dolphins in this drone video snap-shot are traveling and socializing, with a particularly socially-active subgroup slightly right of center. Note that the boat operators are adhering to strict guidelines by not moving into the center of the school, traveling at slow speed, and in a manner to allow dolphins to approach the swimmers and vessels if they so wish (Photo from a video sequence by Lorenzo Fiori under research permit 55328-MAR issued by New Zealand department of conservation) **b** Dolphins (*Tursiops aduncus*) partake in human-associated feeding through a provisioning program at the Monkey Mia Dolphin Resort (Photo Credit: Ewa Krzyszczyk, Shark Bay Dolphin Research Project) **c** A dolphin (*T. aduncus*) is entangled in marine debris (Photo Credit: Madison Miketa, Shark Bay Dolphin Research Project)

that increase the immunological aspect of host competence impact a network by increasing the vulnerability of an individual (node) to pathogen spread (Fig. 9.4c, d). In other words, a pathogen will be more likely to transmit along edges connected to nodes with high immunological competence. Changes to competence brought on by human disturbances are summarized by the perspective of the network change below.

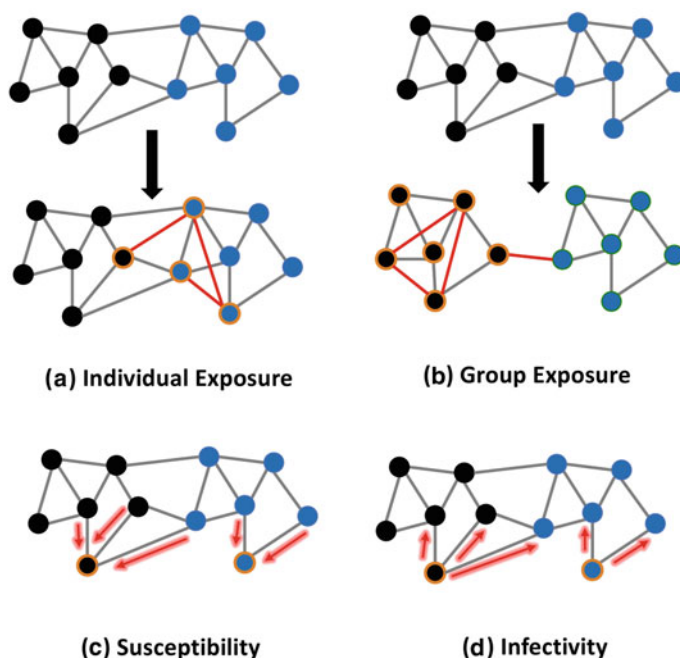


Fig. 9.4 A schematic representation of four changes to network structure. Nodes (circles) represent individuals, and edges (lines) represent interactions capable of disease transmission between individuals. The color of the node denotes group membership, and nodes outlined in orange represent human-affected individuals. **a** shows an increase to individual exposure, in which the degree (number of interactions) of human-affected individuals is increased (new red edges). **b** shows a change to group exposure, in which the modularity of the network is increased. Here, edges are increased within the group affected by human disturbance and decreased between the two groups. **c** shows increased susceptibility, where human-affected nodes will be more likely to be infected by their contacts, represented by the direction of the red arrows. **d** demonstrates increased infectivity of human-affected nodes, where these nodes will be more likely to infect their contacts upon infection

9.2.1 Behavioral Competence

Behavioral competence accounts for how social behavior affects transmissibility. Typically, any change in an individual's activity affects social contact behaviors and/or gregariousness, which can increase or decrease their exposure to pathogens (Barron et al. 2015). Specifically, disturbances influenced the *individual exposure* of hosts to transmission which can alter their degree (the number of unique associates to which an individual can transmit disease within their population) (Fig. 9.4a). Disturbances also influenced *group exposure* which affects network modularity (the tendency for a population to be tightly interacting within [sub]groups and sparsely interacting between groups) (Fig. 9.4b). Finally, disturbances influenced the *introduction of novel pathogens* by increasing contact with humans (zooanthroponosis or reverse zoonosis (Messenger et al. 2014)).

Individual Exposure. We found 18 studies on 11 marine mammal species that demonstrate increased risk of individual level exposure to pathogens within populations. For 15 of these studies, individual degree was increased as a result of coastal human activity which decreased the average distance between animals and increased their group sizes and aggregations.

Four studies showed increased degree between “human-associated feeders”, or animals that obtain food via anthropogenic pathways. Human-associated feeding has been seen in at least 25 different marine mammal species (Fertl 1997) such as California sea lions (*Zalophus californianus*), common bottlenose dolphins, and botos (*Inia geoffrensis*) removing fish from gillnets, rough-toothed dolphins (*Steno bredanensis*), and killer whales (*Orcinus orca*) stealing hooked fish, sperm whales (*Physeter macrocephalus*) depleting long-lines (Sigler et al. 2008), and bottlenose dolphins (*Tursiops* sp.) following trawl nets to forage for prey (Fertl 1997; Ansmann et al. 2012; Jaiteh et al. 2013) or begging from human vessels for food handouts (Bryant 1994; Read et al. 2003; Durden 2005; Fleishman et al. 2016; Hazelnorn et al. 2016). Human-associated feeders aggregated near human food sources, which increased their connections with other human-associated feeders, and their risk of exposure to pathogens. Similar results were seen in a separate review of 115 studies on terrestrial wildlife, where 95% of the studies demonstrated increased contact rates between human-provisioned hosts resulting in increased pathogen transmission risk (Murray et al. 2016).

Decreased individual exposure was seen in four studies on three cetacean species (*Tursiops* sp., *Lagenorhynchus acutus*) involving individuals entangled in marine debris. In each of these studies, entangled individuals decreased their individual degree (number of social interactions), while entangled. For example, a young adult bottlenose dolphin in Australia was uncharacteristically socially isolated when entangled in fishing gear, but resumed normal social contacts once freed from the line (Miketa et al. 2017). While encountering entangled individuals during behavioral research surveys is rare, similar results in group composition have been reported over time that show a decrease in contacts during periods of entanglement. While the risk of individual exposure to disease is reduced for entangled individuals, this may be outweighed by increases in immunological effects in such a setting.

Group Exposure. In 12 studies that examined group size and composition, 11 reported increases to group sizes and aggregations, a pattern which decreased the modularity of contact networks, thus increasing the probability of pathogen exposure for unique subgroups of individuals. However, one study found that human activity actually fractured groups and increased network modularity, thus decreasing the probability of group level exposure to pathogens (Arcangeli and Crosti 2009).

Increased modularity was documented in nine studies on two bottlenose dolphin species (*T. truncatus* and *T. aduncus*) engaged in human-associated feeding. Because not all individuals in a population participated in human-associated feeding, group level connectivity was affected. Typically, human-associated feeders displayed behaviors that are highly specialized for small communities (Ansmann et al. 2012; Jaiteh et al. 2013; Hazelnorn et al. 2016; Kovacs et al. 2017; Senigaglia et al. 2019). As a result, human-associated feeders were shown to have unique group sizes and

habitat preferences (Chilvers and Corkeron 2001), resulting in little interaction with “natural” foragers. This increased network modularity might decrease the risk of group exposure to pathogens.

There was both increased and decreased group level pathogen exposure risk that resulted from human disturbance. However, in all nine studies where exposure risk was decreased, there were also increases to either individual-level exposure (high contact with other conspecifics or with humans) or to pathogen susceptibility (discussed below). Therefore, while a particular human disturbance decreased behavioral competence by lowering group exposure risk, the same disturbance also negatively influenced pathogen spread in other ways.

Pathogen Introduction. Marine mammals that participated in certain methods of human-associated feeding increased their contact with humans in seven studies on two bottlenose dolphin species. This increased their potential exposure to novel pathogens, raising concern for zoonotic (wildlife to human) and reverse zoonotic (human to wildlife) disease transmission potential. Disease transmission from marine mammals to humans has been reported in managed care populations for many bacterial, viral, and fungal pathogens (Mazet et al. 2004; Waltzek et al. 2012). Few studies examine the potential for reverse zoonotic transmission in marine mammals. However, a recent study found evidence for human pathogens present in bottlenose dolphins that have high human contact due to a provisioning program in Shark Bay, Australia (Nelson et al. 2019), supporting the idea that the opportunity for pathogen transmission between certain provisioned and beggar animals and humans is much higher than with naturally foraging animals.

9.2.2 Immunological Competence

Immunological competence accounted for the portion of host competence that examines how an individual’s immune system responds to pathogens (Barron et al. 2015). It should not be confused with the medical term “immunocompetence”, or the body’s ability to defend itself from pathogens (Owens and Wilson 1999). Instead it should be thought of from the point of view of the pathogen, where a host with higher immunological competence provides a more competent environment for the pathogen to reproduce and spread. Disturbances influenced immunological competence by increasing an individual’s *susceptibility*, or the probability that an individual will become infected with a pathogen upon exposure to it. Disturbances also influenced the immune system’s tolerance of pathogens, or their ability to reproduce to the minimum threshold number required for transmission (Downs et al. 2019). Therefore, disturbances potentially increased an individual’s outward *infectivity*, or ability to spread infection.

In the context of networks, increased susceptibility and infectivity of an individual is reflected by increased edge vulnerability, where pathogens are more likely to transmit on these more vulnerable edges. By increasing the susceptibility of a node, the individual becomes more vulnerable to transmission from any infected contacts

(Fig. 9.4c). By increasing the infectivity of a node, the individual becomes more likely to transmit to their contacts upon infection (Fig. 9.4d).

Susceptibility. Human disturbances impacted marine mammal behavior which can in turn contribute to energy loss. Energy loss has been linked to immunosuppression in vertebrate species (Demas 2004) by impeding “allostasis”, or the ability of an animal to maintain homeostasis during life-history events (e.g., migration, mating, reproduction) (McEwen and Stellar 1993), and contributing to disease risk (National Research Council 2005).

We found 79 studies on 29 marine mammal species where coastal human activity could contribute to energy loss in marine mammals. In 72 of these studies, marine mammals displayed short-term avoidance behaviors, where they increased the amount of time they spent traveling or diving away from the disturbance, and decreased the amount of time they spent resting, socializing, and foraging. In 11 of these studies, marine mammals reoriented or completely changed their swimming paths or patterns. Changes in movement or behavior in response to human presence and noise are known to elevate energy loss and consequently impact fitness (Williams and Ashe 2007). For example, minke whales (*Balaenoptera acutorostrata*) (Christiansen et al. 2013), killer whales (Williams et al. 2006), bottlenose dolphins (Symons et al. 2014), and beaked whales (*Ziphius cavirostris*) (Williams et al. 2017) subjected to increased boat traffic or noise, saw large decreases to their net energy gains or increased metabolic rates.

Some marine mammal populations also demonstrated long-term avoidance behaviors, such as abandoning their habitats. Eleven studies reported long-term avoidance behaviors. For example, the abundance of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Australia significantly decreased when the number of dolphin tour boats in their habitat increased, suggesting that the cost of tolerating their presence had exceeded any benefits of remaining in the area (Bejder et al. 2006). Although long-term avoidance will remove individuals from the disturbance, this type of shift can still negatively affect the animals and impact their energy budgets by forcing them from their preferred habitats and disturbing their cultural traditions. Cetaceans in particular have unique culture (shared behaviors acquired through social learning) which may inhibit the display of long-term avoidance behaviors, or make the resulting adaptations much more difficult (Rendell and Whitehead 2001; Whitehead et al. 2004). For example, increased tourist activity has significantly affected the southern resident population of killer whales in the British Columbia Canada/Washington State U.S. area (Bain 2002; Lusseau et al. 2009; Williams et al. 2009). While these animals could move to a different area (such as to the nearby Juan de Fuca Strait) to evade whale watching boats and heavy shipping traffic, their strong adherence to their current habitat and foraging grounds prevents them from doing so, and may make it difficult to adapt to foraging in a novel habitat (Osborne 1999; Bain et al. 2002; Cominelli et al. 2018). That population is now on the verge of extinction due to human impacts (Lacy et al. 2017).

Entanglements in fishing gear also changed the energy budgets of marine mammals, as noted in 4 studies on 3 cetacean species (*Tursiops* sp.; *Eubalaena glacialis*). Individuals showed significant decreases to foraging and diving behaviors

and increases in traveling while entangled in heavy and obstructive fishing gear (van der Hoop et al. 2014, 2016; Miketa et al. 2017).

Malnutrition might also increase marine mammal susceptibility to pathogens as it has been linked to immunosuppression and increased infection susceptibility in both humans and animal species (Schaible and Kaufmann 2007). The cellular immune system is depressed in malnourished individuals, which predisposes the host to increased morbidity and mortality as demonstrated in human systems (Mullen et al. 1979; Garre et al. 1987; Sullivan et al. 1990; Pelletier 2009) and more recently in animal systems (Moret and Schmid-Hempel 2000; Bradley and Altizer 2007; Obanda et al. 2011; Murray et al. 2016).

Human-associated feeding, such as food provisioning, contributed to malnutrition in marine mammals and decreased overall health in four studies in two bottlenose dolphin species. For example, human provisioning negatively affected both female reproductive success and calf survival at two sites in Western Australia (Mann 2000; Foroughirad and Mann 2013; Senigaglia et al. 2019). Additionally, observers in the United States witnessed wild beggar dolphins being fed beer, pretzels, liquor, candy bars, bread, bologna, and baited hooks from recreational boaters (Orams 2002), as well as spoiled bycatch or baitfish, which was deadly for bottlenose dolphins (Bryant 1994). Indeed, provisioned food was a source of immunosuppressive contaminants in 80% of studies on food-provisioned terrestrial wildlife (Murray et al. 2016).

Human-made pollution can also increase marine mammal susceptibility to disease (Martin et al. 2010). Marine mammals are consistently exposed to marine pollutants such as Polychlorinated biphenyls (PCBs), heavy metals, and polycyclic aromatic hydrocarbons (PAHs), resulting from mine drainage, offshore oil and gas exploration, industrial and domestic effluents, agricultural runoff, oil spills, and other human activity (Ansari et al. 2004; Lundin et al. 2018). These pollutants alter immune homeostasis resulting in immunosuppression and inflammation linked to hypersensitivity and autoimmune disease (Kakuschke and Prange 2007; Desforges et al. 2016). Immune impairment was seen in harbor seals exposed to cumulative environmental contaminants (de Swart et al. 1994, 1996), bottlenose dolphins compromised by the 2011 Deepwater Horizon oil spill in the Gulf of Mexico (Schwacke et al. 2014; Kellar et al. 2017), and in vitro studies of PCBs in California sea lion (Peñín et al. 2018), bottlenose dolphin (White et al. 2017b) and killer whale lymph node cells (Desforges et al. 2017). Pollutants were also linked to reproductive failure in harbor porpoises in the UK (Murphy et al. 2015). A total of 14 studies in 16 species documented pollutants at high levels in marine mammals, raising concern for the greater potential of disease spread among populations of marine mammals living in polluted waters.

Infectivity. Infectivity was defined as an infected individual's likelihood of passing along their infection to another individual upon interacting with them. Infectivity can increase in wildlife species with an increase in stress hormones. While it is well-known that the elevation of stress hormones is linked to immunosuppression in many taxa (and therefore increased susceptibility) (Apanius 1998), increased levels of stress hormones in an individual has also recently been associated with an increase in their suitability to pathogens (Vale et al. 2013; Becker et al. 2015; Gervasi et al. 2017). For example, one study on West Nile Virus (genus *Flavivirus*) in songbirds

showed that individuals with experimentally elevated stress hormones were significantly more viremic than control hosts, and only these individuals had viral loads at or above the infectious threshold (Gervasi et al. 2017).

Six studies on eight cetacean species reported increased stress in marine mammals associated with coastal human activity. For example, the complexity of dolphins' temporal dive patterns decreased upon an increase in vessel traffic (Cribb and Seuront 2016); the reduction of behavioral complexity is an indicator of stress in many species (Alados et al. 1996). Additionally, the stress levels of highly endangered North Atlantic right whales in the Bay of Fundy Canada were found to decrease following the events of September 11th, 2001 in which shipping traffic and noise were significantly lower than usual for several days (Rolland et al. 2012). Increases in stress can increase susceptibility and infectivity, meaning highly stressed individuals are more likely to both infect, and be infected by, their contacts.

9.3 The Effect of Human Disturbances on Disease Transmission Through a Population

Our literature review found that human disturbances in the marine environment increased individual host competence in marine mammal communities by altering their behavior and directly impacting their health. These individual changes also altered the contact network structure of a population by changing individual degree, group level modularity, and edge vulnerability. While highlighting the changes to individual host competence is a good first step, it is more beneficial for wildlife managers and researchers to understand how these impacts aggregate to influence population level transmission dynamics by examining the spread of disease on the resulting altered networks. In other words, how might the changes to network structure resulting from the individual host competence highlighted in our review translate to epidemic consequences on marine mammal populations as a whole?

To investigate links between contact networks and disease, we made predictions about infection spread using a susceptible-infected-recovered (SIR) model (Bailey 1957), focusing on four marine mammal case studies for which empirical data are available on contact networks in the published literature: 1007 California sea lions (Schakner 2017; Schakner et al. 2017), 50 Australian humpback dolphins (*Sousa sahulensis*) (Hunt et al. 2019), 43 killer whales (Guimarães et al. 2007), and 371 Indo-Pacific bottlenose dolphins (Leu et al. 2020)) (See supplementary Fig. 9.3). We modeled the changes to these empirical contact networks observed in our review to predict infection outcomes due to human disturbances.

Each case study contained contact network data for a small population. The nodes in the network represented individuals and edges represented social association through shared group membership or spatial proximity through shared space use; it was assumed that these contacts are sufficient for the transmission of infection

(Craft 2015; Leu et al. 2020). Edges were treated as binary as the impact of an interaction weight (e.g., contact duration, frequency of contact) on transmission is not known for most pathogens. Instead, edge weight-thresholding was used to remove edges with low interaction weight, (Croft et al. 2009; Farine and Whitehead 2015) to account for the stability of groups and individual interactions (See supplementary Fig. 9.2 and methods for a more detailed explanation).

On each network, infection spread was simulated using stochastic epidemiological simulations based on a chain binomial, susceptible-infected-recovered (SIR) model (Bailey 1957). The SIR model is a well-established method in mathematical epidemiology and proves to be a good model for fully immunizing infections. At each time step, susceptible nodes became infected with a probability proportional to a fixed transmission rate and the number of infectious individuals that have interactions within the network. Infected individuals were assumed to be infectious for 7.5 days on average, and lead to 1.1 new infections on average to reflect the characteristics of morbilliviruses in marine mammals, a pathogen known to cause mass epidemics in both pinniped and cetacean species (Swinton et al. 1998; Morris et al. 2015). See supplement for detailed methods. To minimize standard error, 500 disease simulations were performed on each network to determine the disease outcomes for each case study, with and without the modeled human disturbances.

9.3.1 *Modeling Human Disturbances*

We examined the impact of disease consequences when susceptibility, infectivity, and exposure was increased in four different scenarios:

1. Individual susceptibility to pathogens was increased, representing fitness costs of human avoidance, exposure to toxic chemicals, or malnutrition from human-associated feeding.
2. Individual susceptibility was increased in concert with infectivity, representing increased stress in marine mammals exposed to high human activity.
3. Individual exposure (degree) was increased, representing an increase in contacts for marine mammals exposed to high human activity or engaged in human-associated feeding.
4. Individual exposure was increased in concert with susceptibility and infectivity, representing individuals increasing their degree in response to high human activity, while also accounting for high stress levels.

Group exposure was not included as a scenario, since the impact of network modularity on disease consequences in contact networks has already been examined (Sah et al. 2017). Pathogen introduction was also not included as a scenario, as it is discussed in a separate analysis below.

To model each scenario, we considered a proportion of the population that may be exposed to human disturbances based on the typical group size for that species (Baird and Whitehead 2000; Parra et al. 2011; Harrison 2015; Sprogis 2018); 15% of

the individuals in each network (150 sea lions, 8 humpback dolphins, 7 killer whales and 55 bottlenose dolphins) were randomly selected to be affected by human disturbances. To determine by how much to increase susceptibility and infectivity in these human-affected individuals, we examined quantifiable changes in these characteristics due to pollution, stress, and malnutrition in the wildlife literature that varied between factors of 1.5 and 2 (Moret and Schmid-Hempel 2000; Hall et al. 2006; Gervasi et al. 2017). Based on our findings we increased both the susceptibility and infectivity of human-affected nodes by 1.6, an average of the changes found in the literature. To standardize increasing exposure of individuals for reliable comparison, we increased the total number of edges between human-affected nodes by a factor of 1.6. (see supplement for more detailed explanations of assumptions).

9.3.2 *Disease Outcomes Under Disturbance*

For each network we measured epidemic size at the population level. Epidemic size is defined as the proportion of individuals in each network that were infected, averaged over all 500 simulations. We also calculated epidemic size at the individual level, where we kept track of the proportion of human-affected and unaffected individuals that were infected over the 500 simulations. Finally, we carried out a tolerance analysis to understand how variation in our parameters and increased pathogen introduction would affect the results in all four scenarios. Results are only shown for the bottlenose dolphin and sea lion case studies; the humpback dolphin and killer whale networks showed similar results and are included in the tolerance analysis and are further discussed in the supplement.

Population Level Outcomes. In general, changes to host competence in all four scenarios had similar effects on the epidemic size for all marine mammal networks (Fig. 9.5). Increasing susceptibility alone did not increase epidemic sizes in any network, and increasing individual exposure alone only increased epidemic size in the sea lion and bottlenose dolphin networks. However, increasing susceptibility and infectivity together, as well as increasing all three, showed an increase in epidemic size for all networks, with the latter scenario by far the worst in all networks. This scenario also showed that the peak of the epidemic occurred earlier in all networks (Fig. 9.5).

Affected Individual Outcomes. A larger proportion of the human-affected group was infected in each of the simulations than in the unaffected group (Fig. 9.6). In the sea lion network, epidemic size of the human-affected group was higher in every scenario, (results that were also seen in the killer whale network). However, in the bottlenose dolphin network, this was only true in the third and fourth scenarios where individual exposure was included.

Tolerance Analysis. As human disturbances increase, how does wildlife tolerance impact disease dynamics? Tolerance is defined in one of two ways: (a) the minimum change required to behavioral or immunological competence for epidemic size to be significantly higher; and (b) the minimum proportion of the population that needs to

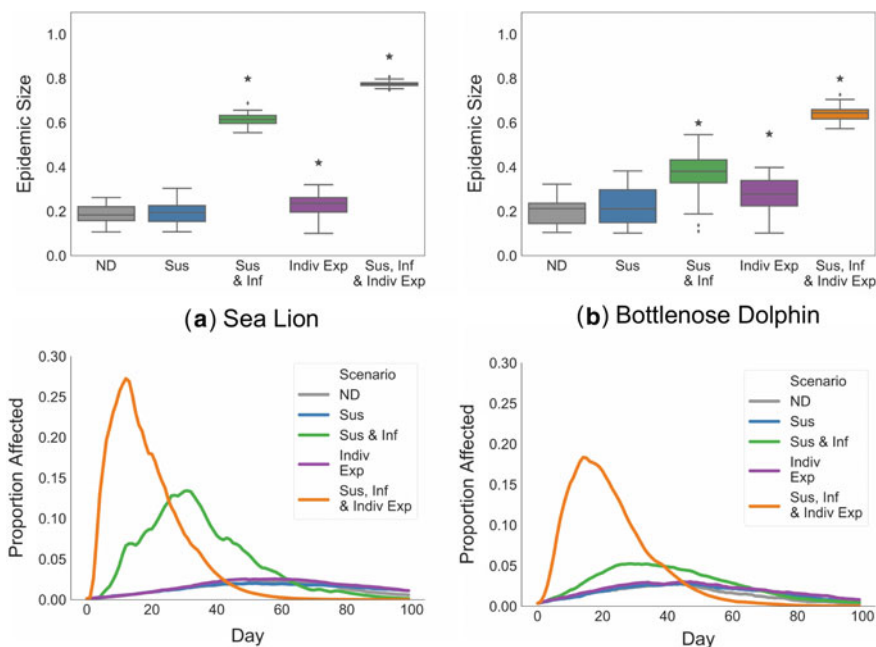


Fig. 9.5 For each network, we compare the epidemic consequences among a no disturbance (ND, gray) scenario and four human disturbance scenarios: increased susceptibility (“Sus”, blue), increased susceptibility and infectivity (“Sus & Inf”, green), increased individual exposures (“Indiv Exp”, purple), and increased susceptibility, infectivity and individual exposure (“Sus, Inf, & Indiv Exp”, orange). The top panels show the average epidemic sizes for each scenario in the **a** sea lion and **b** bottlenose dolphin populations. Stars indicate epidemic sizes that are higher than the baseline epidemic size in the no disturbance scenario. The bottom panels show the growth and decline of the epidemic through time, measured as the proportion of the population affected per day, for each scenario in the **a** sea lion and **b** bottlenose dolphin populations

be affected for epidemic size to be significantly higher. This tolerance is considered under all four scenarios discussed above: (1) increased susceptibility, (2) increased susceptibility and infectivity, (3) increased individual exposure, and (4) all three processes increased. Significant changes to epidemic size were measured via a one-way ANOVA, and pairwise t-tests with a Tukey HSD familywise error-rate correction to identify which specific scenarios have significant differences compared to the baseline, i.e., no human disturbance.

The results of these analyses are in Figs. 9.7a, b. In the first scenario (increased susceptibility), 15% of the individuals in each network needed to be between 1.7 and 4 times more susceptible to pathogens to see an increase in epidemic size. Alternatively, if the increase to susceptibility is maintained at 1.6, the number of individuals that would need to be disturbed in each network to see increased epidemic sizes ranged from 17% to more than 40%. This suggests that there must be major changes to

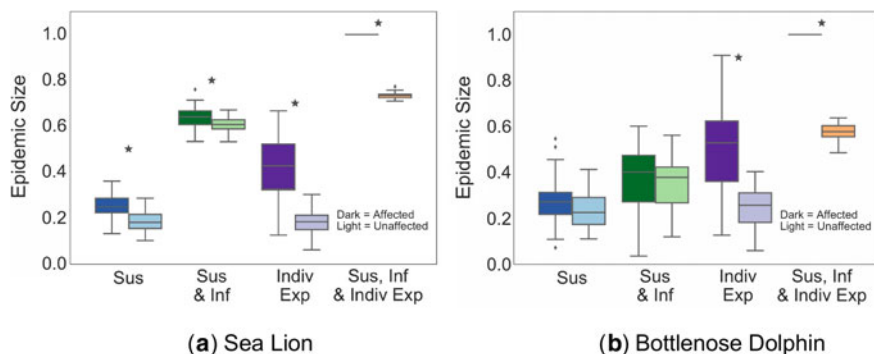


Fig. 9.6 We examined the difference in epidemic size among disturbed and undisturbed individuals. Within each the four scenarios (ND = no disturbance; Sus = increased susceptibility; Sus & Inf = increased susceptibility and infectivity; Indiv Exp = increased individual exposure; and Sus, Inf, & Indiv Exp = increased susceptibility, infectivity; and individual exposure) we compared the average epidemic size of the individuals affected by human disturbances (darker colors) to the average epidemic size of individuals that were not affected by disturbance (lighter colors) over 500 simulations for the **a** sea lion and **b** bottlenose dolphin networks. The results of the independent samples t-tests are denoted by asterisks which indicate a difference between the two epidemic sizes in each of the four scenarios

marine mammal susceptibility to influence epidemics, if this is the only change to their individual host competence.

In the second scenario, susceptibility and infectivity need only be increased by 1.7 or less on 15% of individuals in all four networks to increase epidemic size. In fact, in the sea lion network, these factors need only be increased by 1.1 to see a worse epidemic. When maintaining the increase at 1.6, only 5% of individuals in the bottlenose dolphin and sea lion network needed to be affected to increase epidemic size, and between 10 and 20% individuals in the humpback dolphin and killer whale network. This suggests that small increases in infectivity and susceptibility together will have a significant influence on epidemic outcomes across marine mammal species.

In the third scenario, increasing the exposure of 15% of individuals in the network never increased epidemic size for the humpback dolphin and killer whale network due to the small size of these networks; once the maximum number of connections to add between affected individuals was added, then connectivity could no longer increase. Only when more individuals in these networks were disturbed (between 20 and 28% of the network) will increased individual exposure have an effect on epidemic size. However, in the larger bottlenose dolphin and sea lion networks, there was an increase to epidemic size when 15% of individuals in the networks were 1.3 and 1.8 times more connected to each other, respectively. This shows that increasing individual exposure of networks increases epidemic size, but only after a certain threshold of individuals are disturbed. This was likely due to our constraint of increasing exposure only between other human-affected individuals. Since contacts were only increased

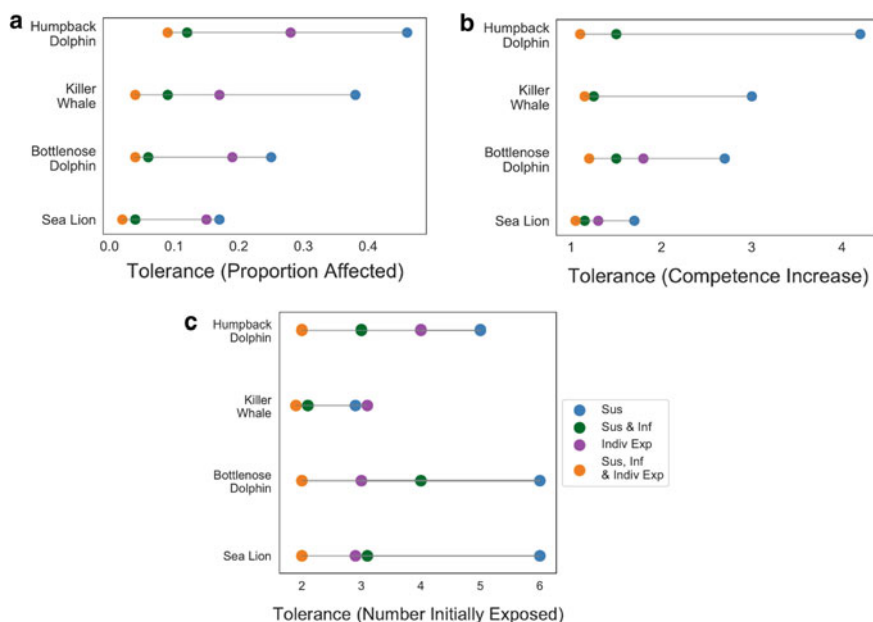


Fig. 9.7 We performed a tolerance analysis that examined the minimum increase in competence required to cause increases in epidemic size or probability for every scenario in each of the four marine mammal networks. Panel **a** shows the lowest increase in immunological competence (susceptibility and infectivity) and behavioral competence (individual exposure) that is needed in each of our scenarios to increase the average epidemic size when 15% of individuals in the network are affected by human disturbance. Panel **b** shows the smallest proportion of each network that would have to be affected by human disturbance to increase the average epidemic size when affected individuals have their behavioral or immunological competence increased by 1.6. Panel **c** shows the smallest number of affected individuals that must be initially exposed and infected with a pathogen to increase the probability of an epidemic to 50%, when competence is increased by 1.6 and 15% of individuals in the network are affected by human disturbance

between other affected individuals, epidemics are likely contained within the affected individuals.

In the final scenario, susceptibility, infectivity, and exposure need only be increased by 1.1 or 1.2 on 15% of individuals in each network to show an increase in epidemic size. Additionally, when parameters were maintained at an increase of 1.6, only a very small number of each population needed to be affected (between 2 and 10%) to see a worse epidemic. Predictably, these results showed that when all aspects of competence were increased in a small number of individuals, or by a small amount, epidemic outcomes will be worse than in a baseline scenario.

To consider the impact of pathogen introduction from human contact on disease consequences in marine mammal networks, we conducted a third tolerance analysis where tolerance was defined as the minimum number of human-affected individuals initially exposed to pathogens for the probability of an epidemic to be 50% or more. The probability of an epidemic was the proportion of simulations where epidemics

occurred. Figure 9.7c, summarizes the results of this analysis in each of the four disturbance scenarios. For all four networks, only 6 or fewer individuals needed to be initially exposed to pathogens for there to be a high epidemic probability.

9.4 Discussion

This chapter examines how human activity influences pathogen transmission potential in marine mammals. Human disturbances contribute to behavioral and immunological changes in marine mammals, which in turn increase individual susceptibility and infectivity, and alter exposure. Our scenarios predict worse epidemics across four different marine mammal contact networks, highlighting the concern that indirect effects of human disturbance on marine wildlife may exacerbate negative effects.

Increased susceptibility, infectivity and individual exposure on fewer individuals than half of a population is predicted to result in significantly larger epidemic sizes in four different marine mammal networks. In other words, disturbances need not affect an entire population for an epidemic to propagate. A small subset can have a substantial impact. Additionally, individuals affected by human disturbances typically drive epidemics, as increased susceptibility and individual exposure affect these individuals significantly more than undisturbed individuals. However, when human disturbances increase infectivity total epidemic sizes increase in affected and unaffected individuals, and only a small percentage of individuals need to be affected by disturbance to result in an increase in epidemic size. This highlights an additional importance of reducing human-induced stress on marine mammals.

The effects of increased [sub] group exposure on the disease consequences of wildlife populations has been demonstrated. Typically, networks with low modularity, (seen in marine mammal species exposed to high levels of human activity) have higher rates of group exposure, thus increasing the potential for an epidemic to spread across a population (Sah et al. 2017). In contrast, networks with high network modularity have low group exposure rates, and therefore result in lower disease burdens as they are able to “trap” infections within communities, which delays the spread of disease outbreaks (Sah et al. 2017). Human-associated feeding increases network modularity across marine mammal species, suggesting a potential decrease in disease consequences within a particular population, although this may be outweighed by other factors. For example, even though modularity is increased during human-associated feeding scenarios, their susceptibility may increase from declining health, and their exposure may increase from higher rates of human contact, or contact with other human-related feeders.

It took a small number of pathogen introductions (such as through increased human contact) for the probability of an epidemic to reach 50% or more. There has been little to no documentation of reverse zoonosis in marine mammals, although researchers are noticing surprisingly high rates in livestock and terrestrial species; there have been at least 56 documented human to animal disease transmissions among wildlife, livestock, and companion animals (Messenger et al. 2014). Findings

of reverse zoonosis in species, increased frequency of human contact with marine mammals, and small number of pathogen introductions required to increase epidemic probability, raise concern for the potential of increased epidemic probability from pathogens of human origins.

9.4.1 Study Limitations

Indirect anthropogenic effects such as prey depletion on behavior and health in marine species were not considered in this chapter. For example, southern resident killer whales of the northeastern Pacific's primary prey are the highly endangered Chinook salmon (*Oncorhynchus tshawytscha*). There is impact of the salmon fishery on declining killer whale health (Williams et al. 2011); high levels of pollutants and low lipid content in salmon also increase the amount of salmon southern killer whales must eat to maintain energetic demands, and expose them to higher levels of toxins (Cullon et al. 2009). Future research should focus on these indirect effects, to gather a more inclusive picture of the full impact of human disturbances on marine life and disease.

The effects of climate change on potential disease consequences in marine mammals were not considered here. Climate change has been linked to phenological shifts in marine mammals, and warming waters provide ideal habitats for many pathogen species (Harvell et al. 2002; Burek et al. 2008). Additional stressors of climate change include increased exposure to persistent organic pollutants (POPs) among marine mammals, direct loss of sea ice habitat, effects on body condition due to trophic shifts, and increased human habitation in the Arctic (Burek et al. 2008). Forecasts on the vulnerability of marine mammals to effects of climate change are available (Alter et al. 2010), but changes in disease dynamics are unknown. To establish clear links between climate change and disease spread, data from long-term studies are needed.

Methodological considerations regarding behavioral and disease consequences are vital. Social associations defined the edges of the contact networks used in this study, which do not always involve physical contact. Two of the most well-known marine mammal diseases, cetacean morbillivirus (of the genus *Morbillivirus*) and the fungus lobomycosis (*Lacazia loboi*), are believed to be transmitted by close breathing interactions and skin to skin contact, respectively (Reif et al. 2009; Van Bresseem et al. 2014). Therefore, the use of interaction types more specific to the route of transmission for common marine mammal pathogens are likely to produce more accurate epidemic size and probability results in a simulation. For example, one study (Leu et al. 2020) compares different modes of contact in a marine mammal with disease risk, and another study links infection with pox-like virus to associations with afflicted individuals in the year before becoming symptomatic (Powell et al. 2019). Data collection should be more specific to relevant disease transmitting interactions between animals to generate further information unique to particular pathogens of interest.

Edge weight, or the strength of interactions between individuals, was not included in this analysis. The impact of interaction strength on transmission is unknown for most systems, though it is reasonable to expect that risk of transmission may increase as individuals increase interaction frequency or duration (Silk et al. 2017). Data that provide insight into how transmission risk is impacted by increases in association strength are needed to reliably incorporate these measures into network analysis.

9.4.2 The Importance of Using Social Networks When Modeling Disease Spread

Contact networks provide a versatile and intuitive tool to examine how behavioral changes induced by environmental perturbations can shift disease dynamics (Jones et al. 2018). Contact networks allow for researchers to incorporate heterogeneity of individual contacts and potential changes to them. Examples of impacts of environmental perturbations on disease spread successfully modeled using contact networks include [as discussed in (Jones et al. 2018)]: simulations of potential pathogen spread through translocated tortoise (*Gopherus agassizii*) (Aiello et al. 2014) and guppy (*Poecilia reticulata*) (Wilson et al. 2015) populations, simulated pathogen spread in targeted removals of individuals among African buffalo (*Syncerus caffer*) populations when their networks have been impacted by drought (Cross et al. 2004), and simulated pathogen spread through a mouse (*Mus musculus domesticus*) network when infected individuals exhibit sickness behaviors (Lopes et al. 2016). Here, networks were perturbed to reflect behavioral and immunological changes caused by human disturbances in the marine environment, to model the effect of these perturbations on pathogen spread in different marine species.

Perturbations needed to increase epidemic sizes in each of the scenarios varied greatly among different networks (Fig. 9.7). These results demonstrate the importance of using social networks in wildlife disease analysis. Wildlife networks, especially marine mammal social networks, vary greatly by species. Many species such as killer whales and sperm whales live in stable, matrilineal groups (Rendell et al. 2019). Other species such as bottlenose dolphins live in highly dynamic fission–fusion societies in which number of contacts within a group is unstable and can vary greatly (Connor et al. 2000; Lusseau et al. 2006; Galezo et al. 2018). Some species such as gray whales (*Eschrichtius robustus*) and humpback whales (*Megaptera novaeangliae*) are generally solitary, but join large groups when breeding, hunting, or migrating (Rendell et al. 2019). Pinniped species such as California sea lions and elephant seals (*Mirounga sp.*) form massive social groups that haul out on land during the breeding season (Wolf et al. 2007). The sociality of a species affects a population's network structure and in turn, the disease consequences for that population (Sah et al. 2018). This chapter supported these findings and showed that making the same perturbation to different networks results in different disease outcomes.

9.4.3 The Effects of Covariation on Infection Transmission

There is positive covariation between behavioral and immunological competence that can increase infection transmission (Hawley et al. 2011). Increasing either behavioral competence (exposure) or immunological competence (susceptibility or infectivity) separately resulted in increases to epidemic sizes and probabilities. However, an increase in both aspects of competence at the same time (as in the increase susceptibility, infectivity, and exposure scenario) caused an extreme increase in epidemic size, resulting in positive covariation that further boosts the transmission of disease and potentially has detrimental effects on wildlife populations (Hawley et al. 2011). Possible scenarios for such positive covariation in marine mammals include increased exposure and increased immunological competence resulting from (1) elevated vessel traffic, combined with energy loss, and/or a polluted habitat; (2) shipping noise and density inducing stress; and (3) direct or indirect human contact (provisioning and human-associated feeding) that compromises marine mammal health.

9.4.4 Considering Marine Mammal Cycles

When considering disease transmission through social systems, these consequences might be further impacted by natural marine mammal cycles. Marine mammal circadian (cycles within a 24-h period) and circannual (cycles within a one-year period) rhythms can work in concert with human cycles to impact the spread of disease in a population. Biological rhythms play an important role in factors such as immunity, parasite activity, and disease incidence (Martinez-Bakker and Helm 2015). For example, infections occurring during a socially busy time of day may lead to new infections generated at the same time on following days, suggesting a synchronization of host and pathogen circadian rhythms (Colman et al. 2018). If the aligning of circadian rhythms maximizes transmission periods to the most social times of the day, any type of human disturbance that might increase number of social contacts or decrease host immunity during these highly social times, could increase transmission risk. Marine mammal and human circannual rhythms might also affect disease transmission; transmission risk could be much higher during the warm and typically breeding season when tourism and boating activity is high, and contact rates are also high. Seasonal changes in immunity (such as decreased immunity during migration and breeding seasons) could also align with human rhythms to either increase or decrease infection risk (Martinez-Bakker and Helm 2015). Future work in this area can identify circadian and circannual rhythms unique to the wildlife species of interest that co-align with human rhythms and help us examine how such synchronization might affect infectious disease risk.

9.5 Conclusions

As human activity increasingly encroaches on wildlife emphasis on potential disease outcomes is vitally important, especially for endangered and threatened species. This research can inform management strategies aimed at mitigating future epidemics, which is especially important for species that may already be at high risk of infection. In marine populations, special focus on reducing runoff and marine debris, or establishing wildlife sanctuaries areas free from motorboat traffic, could lessen impacts of human activities on disease transmission among marine mammal populations. We suggest that scientists, conservation biologists, and wildlife managers take into consideration effects of human activities on disease transmission when assessing potential anthropogenic impacts of increasing activity in a particular habitat.

References

- Aiello CM, Nussear KE, Walde AD, Esque TC, Emblidge PG, Sah P, Bansal S, Hudson PJ (2014) Disease dynamics during wildlife translocations: disruptions to the host population and potential consequences for transmission in desert tortoise contact networks. *Anim Conserv* 17:27–39
- Alados CL, Escos JM, Emlen JM (1996) Fractal structure of sequential behaviour patterns: an indicator of stress. *Anim Behav* 51:437–443
- Alter SE, Simmonds MP, Brandon JR (2010) Forecasting the consequences of climate-driven shifts in human behavior on cetaceans. *Mar Policy* 34:943–954
- Ansari TM, Marr IL, Tariq N (2004) Heavy metals in marine pollution perspective—a mini review. *J Appl Sci* 4:1–20
- Ansmann IC, Parra GJ, Chilvers B, Lanyon JM (2012) Dolphins restructure social system after reduction of commercial fisheries. *Anim Behav* 84:575–581
- Apanius V (1998) Stress and immune defense. In: Moller AP, Milinski M, Slater PJ (eds) *Advances in the study of behavior: stress and behavior*, vol 27. Academic Press, pp 133–153
- Arcangeli A, Crosti R (2009) The short-term impact of dolphin-watching on the behaviour of bottlenose dolphins (*Tursiops truncatus*) in western Australia. *J Mar Animlas Their Ecol* 2:3–9
- Bailey NTJ (1957) *The mathematical theory of epidemics*. Charles Griffin & Co, London
- Bain DE, Trites AW, Williams R (2002) A model linking energetic effects of whale watching to killer whale (*Orcinus orca*) population dynamics. University of Washington, Friday Harbor, WA, Friday Harbor Laboratories
- Bain DE (2002) A model linking energetic effects of whale watching to killer whale (*Orcinus orca*) population dynamics. Friday Harbor, WA
- Baird RW, Whitehead H (2000) Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Can J Zool* 78:2096–2105
- Bansal S, Grenfell BT, Meyers LA (2007) When individual behaviour matters: homogeneous and network models in epidemiology. *J R Soc Interface* 4:879–891
- Barenas-De la Cruz D, DeRango E, Johnson SP, Simeone CA (2018) Evidence of anthropogenic trauma in marine mammals stranded along the central California coast, 2003–2015. *Mar Mammal Sci* 34:330–346
- Barron DG, Gervasi SS, Pruitt JN, Martin LB (2015) Behavioral competence: how host behaviors can interact to influence parasite transmission risk. *Curr Opin Behav Sci* 6:35–40
- Bearzi M (2017) Impacts of marine mammal tourism. In: Blumstein D, Geffroy B, Samia DSM, Bessa E (eds) *Ecotourism's promise and peril: a biological evaluation*. Springer, pp 73–96

- Becker DJ, Streicker DG, Altizer S (2015) Linking anthropogenic resources to wildlife-pathogen dynamics: a review and meta-analysis. *Ecol Lett* 18:483–495
- Bejder L, Samuels A, Whitehead H, Gales N, Mann J, Connor R, Heithaus M, Watson-Capps J, Flaherty C, Krützen M (2006) Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conserv Biol* 20:1791–1798
- Bossart GD (2006) Marine Mammals as sentinel species for ocean and human health. *Oceanography* 19:134–137
- Bradley CA, Altizer S (2007) Urbanization and the ecology of wildlife diseases. *Trends Ecol Evol* 22:95–102
- Bryant L (1994) Report to congress on results of feeding wild Dolphins L 1989–1994 by National Marine Fisheries Service
- Burek KA, Gulland FMD, O'Hara TM (2008) Effects of climate change on arctic marine mammal health. *Ecol Appl* 18:S126–S134
- Carter SP, Delahay RJ, Smith GC, Macdonald DW, Riordan P, Etherington TR, Pimley ER, Walker NJ, Cheeseman CL (2007) Culling-induced social perturbation in Eurasian badgers *Meles meles* and the management of TB in cattle: an analysis of a critical problem in applied ecology. *Proc R Soc B Biol Sci* 274:2769–2777
- Ceballos G, Ehrlich PR, Raven PH (2020) Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proc Natl Acad Sci USA* 117:13596–13602
- Chilvers BL, Corkeron PJ (2001) Trawling and bottlenose dolphins' social structure. *Proc R Soc B Biol Sci* 268:1901–1905
- Christiansen F, Rasmussen MH, Lusseau D (2013) Inferring activity budgets in wild animals to estimate the consequences of disturbances. *Behav Ecol* 24:1415–1425
- Collier MA, Ali S, Mann J, Bansal S (2020) Impacts of human disturbance in marine mammals: do behavioral changes translate to disease consequences? Full methods and analysis. *EcoEvoRxiv*. <https://doi.org/10.32942/osf.io/9pr8g>
- Colman E, Spies K, Bansal S (2018) The reachability of contagion in temporal contact networks: how disease latency can exploit the rhythm of human behavior. *BMC Infect Dis* 18:219
- Cominelli S, Devillers R, Yurk H, MacGillivray A, McWhinnie L, Canessa R (2018) Noise exposure from commercial shipping for the southern resident killer whale population. *Mar Pollut Bull* 136:177–200
- Connor RC, Wells R, Mann J, Read A (2000) Social relationships in a fission-fusion society. In: Mann J, Connor R, Tyack P, Whitehead H (eds) *Cetacean societies: field studies of dolphins and whales*. The University of Chicago Press, Chicago, pp 91–126
- Conrad PA, Miller MA, Kreuder C, James ER, Mazet J, Dabritz H, Jessup DA, Gulland F, Grigg ME (2005) Transmission of *Toxoplasma*: clues from the study of sea otters as sentinels of *Toxoplasma gondii* flow into the marine environment. *Int J Parasitol* 35:1155–1168
- Craft ME (2015) Infectious disease transmission and contact networks in wildlife and livestock. *Philos Trans R Soc Lond B Biol Sci* 370:20140107
- Cribb N, Seuront L (2016) Changes in the behavioural complexity of bottlenose dolphins along a gradient of anthropogenically-impacted environments in South Australian coastal waters: implications for conservation and management strategies. *J Exp Mar Bio Ecol* 482:118–127
- Croft DP, Krause J, Darden SK, Ramnarine IW, Faria JJ, James R (2009) Behavioural trait assortment in a social network: patterns and implications. *Behav Ecol Sociobiol* 63:1495–1503
- Cross AC, Lloyd-Smith PC, Bowers JO, Hay JA, Hofmeyr CT, Getz MM (2004) Integrating association data and disease dynamics in a social ungulate: Bovine tuberculosis in African buffalo in the Kruger National Park. *Ann Zool Fennici* 41:879–892
- Cullon DL, Yunker MB, Alleyne C, Dangerfield NJ, O'Neill S, Whittar MJ, Ross PS (2009) Persistent organic pollutants in chinook salmon (*Oncorhynchus tshawytscha*): implications for resident killer whales of British Columbia and adjacent waters. *Environ Toxicol Chem* 28:148
- de Swart RL, Ross PS, Vedder LJ, Timmerman HH, Heisterkamp S, Loveren HV, Vos JG, Reijnders PJH, Osterhaus ADM (1994) Impairment of immune function in harbor seals (*Phoca vitulina*) feeding on fish from polluted waters. *Ambio* 23:155–159

- de Swart RL, Ross PS, Vos JG, Osterhaus AD (1996) Impaired immunity in harbour seals (*Phoca vitulina*) exposed to bioaccumulated environmental contaminants: review of a long-term feeding study. *Environ Health Perspect* 104:823–828
- Demas GE (2004) The energetics of immunity: a neuroendocrine link between energy balance and immune function. *Horm Behav* 45:173–180
- Desforges JPW, Sonne C, Levin M, Siebert U, De Guise S, Dietz R (2016) Immunotoxic effects of environmental pollutants in marine mammals. *Environ Int* 86:126–139
- Desforges JP, Levin M, Jasperse L, De Guise S, Eulaers I, Letcher RJ, Acquarone M, Nordøy E, Folkow LP, Jensen TH, Grøndahl C, Bertelsen MF, St Leger J, Almunia J, Sonne C, Dietz R (2017) Effects of polar bear and killer whale derived contaminant cocktails on marine mammal immunity. *Environ Sci Technol* 51:11431–11439
- Diaz S, Settele J, Brondizio E, Ngo HT, Guèze M, Agard Trinidad J, Arneith A, Balvanera P, Brauman K, Watson R, Baste I, Larigauderie A, Leadley P, Pascual U, Baptiste B, Demissew S, Dziba L, Erpul G, Fazel A, Fischer M, María Hernández A, Karki M, Mathur V, Pataridze T, Sousa Pinto I, Stenseke M, Török K, Vilá B, da Cunha M, Mace G, Mooney H (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services
- Downs CJ, Schoenle LA, Han BA, Harrison JF, Martin LB (2019) Scaling of host competence. *Trends Parasitol* 35:182–192
- Dufour V, Sueur C, Whiten A, Buchanan-Smith HM (2011) The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. *Am J Primatol* 73:802–811
- Durden WN (2005) The harmful effects of inadvertently conditioning a wild bottlenose dolphin (*Tursiops truncatus*) to interact with fishing vessels in the Indian river Lagoon, Florida, USA. *Aquat Mamm* 31:413–419
- Farine DR, Whitehead H (2015) Constructing, conducting and interpreting animal social network analysis. *J Anim Ecol* 84:1144–1163
- Fertl D (1997) Cetacean interactions with trawls: a preliminary review. *J Northwest Atl Fish Sci* 22:219–248
- Fleishman E, Costa DP, Harwood J, Kraus S, Moretti D, New LF, Schick RS, Schwarz LK, Simmons SE, Thomas L, Wells RS (2016) Monitoring population-level responses of marine mammals to human activities. *Mar Mammal Sci* 32:1004–1021
- Forney KA, Southall BL, Slooten E, Dawson S, Read AJ, Baird RW, Brownell RL (2017) Nowhere to go: noise impact assessments for marine mammal populations with high site fidelity. *Endanger Species Res* 32:391–413
- Foroughirad V, Mann J (2013) Long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins. *Biol Conserv* 160:242–249
- Galezo AA, Krzyszczyk E, Mann J (2018) Sexual segregation in Indo-Pacific bottlenose dolphins is driven by female avoidance of males. *Behav Ecol* 29:377–386
- Garre MA, Boles JM, Youinou PY (1987) Current concepts in immune derangement due to undernutrition. *J Parenter Enter Nutr* 11:309–313
- Gaynor KM, Hohnowski CE, Carter NH, Brashares JS (2018) The influence of human disturbance on wildlife nocturnality. *Science* (80-) 360:1232–1235
- Gervasi SS, Burgan SC, Hofmeister E, Unnasch TR, Martin LB (2017) Stress hormones predict a host superspreader phenotype in the west Nile virus system. *Proc R Soc B Biol Sci* 284:20171090
- Guimarães PR, de Menezes MA, Baird RW, Lusseau D, Guimarães P, dos Reis SF (2007) Vulnerability of a killer whale social network to disease outbreaks. *Phys Rev E—Stat Nonlinear, Soft Matter Phys* 76:042901
- Gulland FMD, Hall AJ (2007) Is marine mammal health deteriorating? Trends in the global reporting of marine mammal disease. *EcoHealth* 4:135–150
- Hall AJ, Hugunin K, Deaville R, Law RJ, Allchin CR, Jepson PD (2006) The risk of infection from polychlorinated biphenyl exposure in the harbor porpoise (*Phocoena phocoena*): a case-control approach. *Environ Health Perspect* 114:704–711

- Harrison J (2015) Sea lion numbers are increasing, and so is predation on salmon and steelhead in the Columbia river. In: Northwest power conservation council sea lion numbers are increasing, and so is predation on salmon and steelhead in the Columbia river. Accessed 19 Aug 2020
- Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS, Samuel MD (2002) Climate warming and disease risks for terrestrial and marine biota. *Science* (80-) 296:2158–2162
- Hawley D, Etienne RS, Ezenwa VO, Jolles AE (2011) Does animal behavior underlie covariation between hosts' exposure to infectious agents and susceptibility to infection? Implications for disease dynamics. *Integr Comp Biol* 51:528–539
- Hazelkorn RA, Schulte BA, Cox TM (2016) Persistent effects of begging on common bottlenose dolphin (*Tursiops truncatus*) behavior in an estuarine population. *Aquat Mamm* 42:531–541
- Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. *Trends Ecol Evol* 23:202–210
- Hunt T, Parra GJ, Allen S, Bejder L (2019) Data from: assortative interactions revealed in a fission-fusion society of Australian humpback dolphins. Dryad Digit Repos
- Jaiteh VF, Allen SJ, Meeuwig JJ, Loneragan NR (2013) Subsurface behavior of bottlenose dolphins (*Tursiops truncatus*) interacting with fish trawl nets in northwestern Australia: implications for bycatch mitigation. *Mar Mammal Sci* 29:1–16
- Jannot J, Somers K, Tuttle V, McVeigh J, Carretta J, Helker V (2018) Observed and estimated marine mammal bycatch. *Nat Oceanic Atmos Adm*
- Jones KL, Thompson RCA, Godfrey SS (2018) Social networks: a tool for assessing the impact of perturbations on wildlife behaviour and implications for pathogen transmission. *Behaviour* 155:689–730
- Kakuschke A, Prange A (2007) The influence of metal pollution on the immune system: a potential stressor for marine mammals in the North Sea. *Int J Comp Psychol* 20:179–193
- Kellar NM, Speakman TR, Smith CR, Lane SM, Balmer BC, Trego ML, Catelani KN, Robbins MN, Allen CD, Wells RS, Zolman ES, Rowles TK, Schwacke LH (2017) Low reproductive success rates of common bottlenose dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico following the Deepwater Horizon disaster (2010–2015). *Endanger Species Res* 33:143–158
- Klaassen B, Broekhuis F (2018) Living on the edge: multiscale habitat selection by cheetahs in a human wildlife landscape. *Ecol Evol* 8:7611–7623
- Kovacs CJ, Perrtree RM, Cox TM (2017) Social differentiation in common bottlenose dolphins (*Tursiops truncatus*) that engage in human-related foraging behaviors. *PLoS One* 12:e0170151
- Lacy RC, Williams R, Ashe E, Balcomb KC, Brent LJN, Clark CW, Croft DP, Giles DA, MacDuffee M, Paquet PC (2017) Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. *Sci Rep* 7:1–12
- Leu ST, Sah P, Krzyszczyk E, Jacoby A-M, Mann J, Bansal S (2020) Sex, synchrony, and skin contact: integrating multiple behaviors to assess pathogen transmission risk. *Behav Ecol* 31:651–660
- Liberati A, Altman DG, Tetzlaff J, Mulrow C, Gøtzsche PC, Ioannidis JPA, Clarke M, Devereaux PJ, Kleijnen J, Moher D (2009) The PRISMA statement for reporting systematic reviews and meta-analyses of studies that evaluate health care interventions: explanation and elaboration. *J Clin Epidemiol* 62:e1–e34
- Lopes PC, Block P, König B (2016) Infection-induced behavioural changes reduce connectivity and the potential for disease spread in wild mice contact networks. *Sci Rep* 6:1–10
- Lundin JI, Ylitalo GM, Giles DA, Seely EA, Anulacion BF, Boyd DT, Hempelmann JA, Parsons KM, Booth RK, Wasser SK (2018) Pre-oil spill baseline profiling for contaminants in Southern resident killer whale fecal samples indicates possible exposure to vessel exhaust. *Mar Pollut Bull* 136:448–453
- Lusseau D, Wilson B, Hammond PS, Grellier K, Durban JW, Parsons KM, Barton TR, Thompson PM (2006) Quantifying the influence of sociality on population structure in bottlenose dolphins. *J Anim Ecol* 75:14–24
- Lusseau D, Bain DE, Williams R, Smith JC (2009) Vessel traffic disrupts the foraging behavior of southern resident killer whales *Orcinus orca*. *Endanger Species Res* 6:211–221

- Mann J (2000) Unraveling the dynamics of social life: long-term studies and observational methods. In: Mann J, Connor R, Tyack P, Whitehead H (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, pp 45–64
- Martin LB, Hopkins WA, Mydlarz LD, Rohr JR (2010) The effects of anthropogenic global changes on immune functions and disease resistance. *Ann NY Acad Sci* 1195:129–145
- Martin LB, Burgan SC, Adelman JS, Gervasi SS (2016) Host competence: an organismal trait to integrate immunology and epidemiology. *Integr Comp Biol* 56:1225–1237
- Martinez-Bakker M, Helm B (2015) The influence of biological rhythms on host-parasite interactions. *Trends Ecol Evol* 30:314–326
- Mazet JAK, Hunt TD, Ziccardi MH (2004) Assessment of the risk of zoonotic disease transmission to marine mammal worker and the public: survey of occupational risks. Davis, CA
- McEwen BS, Stellar E (1993) Stress and the individual mechanisms leading to disease. *Arch Intern Med* 153:2093–2101
- Messenger AM, Barnes AN, Gray GC (2014) Reverse zoonotic disease transmission (Zooanthroponosis): a systematic review of seldom-documented human biological threats to animals. *PLoS One* 9:e89055
- Miketa M, Krzyszczyk E, Mann J (2017) Behavioral responses to fishing line entanglement of a juvenile bottlenose dolphin in Shark Bay, Australia. *Matters* 3:e201711000011
- Miller MA, Miller WA, Conrad PA, James ER, Melli AC, Leutenegger CM, Dabritz HA, Packham AE, Paradies D, Harris M, Ames J, Jessup DA, Worcester K, Grigg ME (2008) Type X *Toxoplasma gondii* in a wild mussel and terrestrial carnivores from coastal California: new linkages between terrestrial mammals, runoff and toxoplasmosis of sea otters. *Int J Parasitol* 38:1319–1328
- Moore S (2008) Marine mammals as ecosystem sentinels. *J Mammology* 89:534–540
- Moret Y, Schmid-Hempel P (2000) Survival for immunity: the price of immune system activation for bumblebee workers. *Science* (80-) 290:1166–1168
- Morris SE, Zeller JL, Fauquier DA, Rowles TK, Rosel PE, Gulland F, Grenfell BT (2015) Partially observed epidemics in wildlife hosts: modelling an outbreak of dolphin morbillivirus in the northwestern Atlantic, June 2013–2014. *J R Soc Interface* 12
- Mullen JL, Gertner MH, Buzby GP, Goodhart GL, Rosato EF (1979) Implications of malnutrition in the surgical patient. *Arch Surg* 114:121–125
- Murphy S, Barber J, Learmonth JA, Read FL, Deaville R, Perkins MW, Brownlow A, Davison N, Penrose R, Pierce GJ, Law RJ, Jepson PD (2015) Reproductive failure in UK harbour porpoises *Phocoena phocoena*: legacy of pollutant exposure? *PLoS One* 10:e0131085
- Murray MH, Becker DJ, Hall RJ, Hernandez SM (2016) Wildlife health and supplemental feeding: a review and management recommendations. *Biol Conserv* 204:163–174
- National Research Council (2005) Marine mammal populations and ocean noise: determining when noise causes biologically significant effects. Washington, DC
- Nelson TM, Wallen MM, Bunce M, Oskam CL, Lima N, Clayton L, Mann J (2019) Detecting respiratory bacterial communities of wild dolphins: implications for animal health. *Mar Ecol Prog Ser* 622:203–217
- NOAA (2020) Active and closed unusual mortality events. In: NOAA Fish. <https://www.fisheries.noaa.gov/national/marine-life-distress/active-and-closed-unusual-mortality-events>. Accessed 19 Aug 2020
- Obanda V, Iwaki T, Mutinda NM, Gakuya F (2011) Gastrointestinal parasites and associated pathological lesions in starving free-ranging African elephants. *South African J Wildl Res* 41:167–172
- Orams MB (2002) Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tour Manag* 23:281–293
- Osborne RW (1999) A historical ecology of Salish sea resident killer whales (*Orcinus orca*): with implications for management. University of Victoria, Victoria, British Columbia
- Owens IPF, Wilson K (1999) Immunocompetence: a neglected life history trait or conspicuous red herring? *Trends Ecol Evol* 14:170–172

- Parra GJ, Corkeron PJ, Arnold P (2011) Grouping and fission fusion dynamics in Australian snubfin and Indo-Pacific humpback dolphins. *Anim Behav* 82:1423–1433
- Pelletier DL (2009) The potentiating effects of malnutrition on child mortality: epidemiologic evidence and policy implications. *Nutr Rev* 52:409–415
- Peñín I, Levin M, Acevedo-Whitehouse K, Jasperse L, Gebhard E, Gulland FMD, De Guise S (2018) Effects of polychlorinated biphenyls (PCB) on California sea lion (*Zalophus californianus*) lymphocyte functions upon in vitro exposure. *Environ Res* 167:708–717
- Plante S, Dussault C, Richard JH, Côté SD (2018) Human disturbance effects and cumulative habitat loss in endangered migratory caribou. *Biol Conserv* 224:129–143
- Powell SN, Wallen MM, Miketa ML, Krzyszczyk E, Foroughirad V, Bansal S, Mann J (2019) Sociality and tattoo skin disease among bottlenose dolphins in Shark Bay, Australia. *Behav Ecol* 31:459–466
- Read AJ, Waples DM, Urian KW, Swanner D (2003) Fine-scale behaviour of bottlenose dolphins around gillnets. *Proc R Soc London Ser B Biol Sci* 270:S90–S92
- Reif JS, Peden-Adams MM, Romano TA, Rice CD, Fair PA, Bossart GD (2009) Immune dysfunction in Atlantic bottlenose dolphins (*Tursiops truncatus*) with lobomycosis. *Med Mycol* 47:125–135
- Rendell L, Cantor M, Gero S, Whitehead H, Mann J (2019) Causes and consequences of female centrality in cetacean societies. *Philos Trans R Soc B Biol Sci* 374:20180066
- Rendell L, Whitehead H (2001) Culture in whales and dolphins. *Behav Brain Sci* 24:309–324
- Riley SPD, Sauvajot RM, Fuller TK, York EC, Kamradt DA, Bromley C, Wayne RK (2003) Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conserv Biol* 17:566–576
- Rolland RM, Parks SE, Hunt KE, Castellote M, Corkeron PJ, Nowacek DP, Wasser SK, Kraus SD (2012) Evidence that ship noise increases stress in right whales. *Proc R Soc B Biol Sci* 279:2363–2368
- Sah P, Leu ST, Cross PC, Hudson PJ, Bansal S (2017) Unraveling the disease consequences and mechanisms of modular structure in animal social networks. *Proc Natl Acad Sci* 114:4165–4170
- Sah P, Mann J, Bansal S (2018) Disease implications of animal social network structure: a synthesis across social systems. *J Anim Ecol* 87:546–558
- Schaefer AM, Reif JS, Goldstein JD, Ryan CN, Fair PA, Bossart GD (2009) Serological evidence of exposure to selected viral, bacterial, and protozoal pathogens in free-ranging Atlantic bottlenose dolphins (*Tursiops truncatus*) from the Indian river Lagoon, Florida, and Charleston, South Carolina. *Aquat Mamm* 35:163–170
- Schaible UE, Kaufmann SHE (2007) Malnutrition and infection: complex mechanisms and global impacts. *PLoS Med* 4:e115
- Schakner ZA, Petelle MB, Tennis MJ, Van der Leeuw BK, Stansell RT, Blumstein DT (2017) Social associations between California sea lions influence the use of a novel foraging ground. *R Soc Open Sci* 4:160820
- Schakner ZA (2017) Data from: social associations between California sea lions influence the use of a novel foraging ground. Dryad Digit Repos. <https://doi.org/10.5061/dryad.7d80n>
- Schwacke LH, Smith CR, Townsend FI, Wells RS, Hart LB, Balmer BC, Collier TK, De Guise S, Fry MM, Guillette LJ, Lamb SV, Lane SM, McFee WE, Place NJ, Tumlin MC, Ylitalo GM, Zolman ES, Rowles TK (2014) Health of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana, following the deepwater Horizon oil spill. *Environ Sci Technol* 48:93–103
- Senigaglia V, Christiansen F, Sprogis KR, Symons J, Bejder L (2019) Food-provisioning negatively affects calf survival and female reproductive success in bottlenose dolphins. *Sci Rep* 9:8981
- Shackelford N, Standish RJ, Ripple W, Starzomski BM (2018) Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. *Conserv Biol* 32:672–684
- Sigler MF, Lunsford CR, Straley JM, Liddle JB (2008) Sperm whale depredation of sablefish longline gear in the northeast Pacific Ocean. *Mar Mammal Sci* 24:16–27

- Silk MJ, Croft DP, Delahay RJ, Hodgson DJ, Boots M, Weber N, McDonald RA (2017) Using social network measures in wildlife disease ecology, epidemiology, and management. *Bioscience* 67:245–257
- Simeone CA, Gulland FMD, Norris T, Rowles TK (2015) A systematic review of changes in marine mammal health in North America, 1972–2012: the need for a novel integrated approach. *PLoS One* 10:e0142105
- Sprogis K (2018) The short-term impact of dolphin-watching on the behavior of bottlenose dolphins (*Tursiops truncatus*) in Western Australia. *Glob Chang Biol* 24:1203–1210
- Sullivan DH, Patch GA, Walls RC, Lipschitz DA (1990) Impact of nutrition status on morbidity and mortality in a select population of geriatric rehabilitation patients. *Am J Clin Nutr* 51:749–758
- Swinton J, Harwood J, Grenfell BT, Gilligan CA (1998) Persistence thresholds for phocine distemper virus infection in harbour seal *Phoca vitulina* metapopulations. *J Anim Ecol* 67:54–68
- Symons J, Pirotta E, Lusseau D (2014) Sex differences in risk perception in deep-diving bottlenose dolphins leads to decreased foraging efficiency when exposed to human disturbance. *J Appl Ecol* 51:1584–1592
- Vale PF, Choisy M, Little TJ (2013) Host nutrition alters the variance in parasite transmission potential. *Biol Lett* 9:20121145
- Van Bresse MF, Duignan PJ, Banyard A, Barbieri M, Colegrove KM, de Guise S, di Guardo G, Dobson A, Domingo M, Fauquier D, Fernandez A, Goldstein T, Grenfell B, Groch KR, Gulland F, Jensen BA, Jepson PD, Hall A, Kuiken T, Mazzariol S, Morris SE, Nielsen O, Raga JA, Rowles TK, Saliki J, Sierra E, Stephens N, Stone B, Tomo I, Wang J, Waltzek T, Wellehan JFX (2014) Cetacean morbillivirus: current knowledge and future directions. *Viruses* 6:5145–5181
- Van Cleave EK, Bidner LR, Ford AT, Caillaud D, Wilmers CC, Isbell LA (2018) Diel patterns of movement activity and habitat use by leopards (*Panthera pardus pardus*) living in a human-dominated landscape in central Kenya. *Biol Conserv* 226:224–237
- van der Hoop J, Moore M, Fahlman A, Bocconcelli A, George C, Jackson K, Miller C, Morin D, Pitchford T, Rowles T, Smith J, Zoodsma B (2014) Behavioral impacts of disentanglement of a right whale under sedation and the energetic cost of entanglement. *Mar Mammal Sci* 30:282–307
- van der Hoop JM, Corkeron PJ, Kenney J, Landry S, Morin D, Smith J, Moore MJ (2016) Drag from fishing gear entangling North Atlantic right whales. *Mar Mammal Sci* 32:619–642
- Waltzek TB, Cortés-Hinojosa G, Wellehan JFX, Gray GC (2012) Marine mammal zoonoses: a review of disease manifestations. *Zoonoses Public Health* 59:521–535
- Wells RS, Rhinehart HL, Hansen LJ, Sweeney JC, Townsend FI, Stone R, Casper DR, Scott MD, Hohn AA, Rowles TK (2004) Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. *EcoHealth* 1:246–254
- White ND, Godard-Coding C, Webb SJ, Bossart GD, Fair PA (2017b) Immunotoxic effects of in vitro exposure of dolphin lymphocytes to Louisiana sweet crude oil and Corexit™. *J Appl Toxicol* 37:676–682
- White LA, Forester JD, Craft ME (2017a) Using contact networks to explore mechanisms of parasite transmission in wildlife. *Biol Rev* 92:389–409
- Whitehead H, Rendell L, Osborne RW, Würsig B (2004) Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biol Conserv* 120:427–437
- Williams R, Ashe E (2007) Killer whale evasive tactics vary with boat number. *J Zool* 272:390–397
- Williams R, Lusseau D, Hammond PS (2006) Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biol Conserv* 133:301–311
- Williams R, Bain DE, Smith JC, Lusseau D (2009) Effects of vessel on behaviour patterns of individual southern resident killer whales *Orcinus orca*. *Endanger Species Res* 6:199–209
- Williams TM, Kendall TL, Richter BP, Ribeiro-French CR, John JS, Odell KL, Losch BA, Feuerbach DA, Stamper MA (2017) Swimming and diving energetics in dolphins: a stroke-by-stroke analysis for predicting the cost of flight responses in wild odontocetes. *J Exp Biol* 220:1135–1145
- Williams R, Krkošek M, Ashe E, Branch TA, Clark S, Hammond PS, Hoyt E, Noren DP, Rosen D, Winship A (2011) Competing conservation objectives for predators and prey: estimating killer whale prey requirements for chinook salmon. *PLoS One* 6:e26738

- Wilson ADM, Krause S, Ramnarine IW, Borner KK, Clément RJG, Kurvers RHJM, Krause J (2015) Social networks in changing environments. *Behav Ecol Sociobiol* 69:1617–1629
- Wolf JBW, Mawdsley D, Trillmich F, James R (2007) Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Anim Behav* 74:1293–1302