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Anthropogenic noise pollution and wildlife diseases

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Abstract

There is a global rise of anthropogenic noise and a growing awareness of its negative effects on wildlife, but to date the consequences for wildlife diseases have received little attention. In this paper, we discuss how anthropogenic noise can affect the occurrence and severity of infectious wildlife diseases. We argue that there is potential for noise impacts at three main stages of pathogen transmission and disease development: 1) pre-infection exposure probability, 2) infection upon exposure, and 3) severity of post-infection consequences. We identify potential repercussions of noise pollution effects for wildlife populations and call for intensifying research efforts. We provide an overview of knowledge gaps and outline avenues for future studies into noise impacts on wildlife diseases.

Noise pollution can affect wildlife diseases through impacts on parasites and hosts

Like humans, many animals can perceive sound, although their spectral range of sensitivity can strongly differ from ours [1–3] (**Box 1**). Industrial activities, motorised traffic, and a variety of other modern technologies produce an array of human-made sounds (i.e. **anthropogenic noise**, see **Glossary**). These cause environmental pollution and can threaten biodiversity. Indeed, cumulative evidence indicates that **noise pollution** can impact animals by altering individual behaviour and physiology (e.g. site occupancy, territorial and reproductive behaviour, and stress metabolism) and species interactions (e.g. through feeding efficiency or hiding tendency) that can ultimately affect population dynamics and community composition [4,5]. Accordingly, noise pollution is causing an 'acoustic climate change', likely to alter ecosystem functioning [6,7] and, as such, is gaining increased attention among resource managers and policy makers [8–11].

Among the biological repercussions of anthropogenic noise pollution are potential effects on wildlife diseases [12], but those are largely neglected to date. Other environmental stressors, such as chemical pollutants, eutrophication, ocean acidification, and temperature changes are well known to have far-reaching impacts on **parasites**, **hosts** and **diseases** [13–16]. It is very likely that noise pollution also has repercussions for wildlife diseases as it can act on three main stages of parasite transmission and disease development: 1) pre-infection exposure probability, host and parasites could react to noise pollution in a way that alters host exposure patterns to parasites; 2) infection upon exposure, noise pollution may affect host susceptibility and parasite **infectivity**; and 3) severity of post-infection consequences, noise pollution could impact host stress levels and immunocompetence as well as the **virulence** and production of **infective stages** of parasites (**Figure 1**).

In this paper, we outline the potential for noise pollution to affect wildlife diseases based on an ecological framework of **parasite-host interactions** which includes micro- as well as macro-parasites (and we use ‘parasite’ rather than ‘**pathogen**’ to reflect this ecological perspective). We cover both terrestrial and aquatic systems and consider any type of noise pollution. We start by exploring how noise pollution could affect host exposure patterns to parasites (section 1). Then, we explore the potential impacts of noise pollution on the probability of infection upon exposure, addressing both host susceptibility and parasite infectivity (section 2), before discussing the resulting post-infection fitness consequences for hosts and parasites (section 3). Our overview identifies potentially major repercussions of noise pollution effects for wildlife health and we call for intensifying research efforts by highlighting various knowledge gaps and outlining relevant and urgent avenues for future studies into noise pollution impacts on wildlife diseases.

Noise impacts on parasite exposure patterns

The first stage at which noise pollution can affect parasite-host interactions is through an impact on exposure patterns. Natural selection favours host behaviours that minimises exposure to parasites, while parasite behaviour tends to increase host exposure [17]. The co-evolution of parasite and host traits has taken place in a world with fluctuating sound levels related to natural sources from abiotic (e.g. waves, storms, thunder, earthquakes) and biotic origins (animals producing sounds while communicating, foraging, or moving), leading to a minimal overlap of biotic with abiotic sounds [18]. However, during these evolutionary processes, neither parasites, nor hosts have experienced the impact of anthropogenic noise, which has been on the rise over the last decades [7]. Accordingly, noise pollution was shown to interfere with the detection of natural sounds through masking and distraction, and to lead to manifold changes in the behaviour of exposed organisms [7,19]. Many of the documented noise pollution effects have the potential to influence parasite exposure patterns and thus to alter transmission and disease dynamics.

Low host densities can inhibit parasite transmission by reducing exposure to parasites [20]. The first response of many motile animals in an area with noise pollution is to flee, resulting in temporal or spatial shifts in site occupancy [21,22]. This can lead to changes in species distributions and local densities [23,24], and noise pollution could thus lead to reduced parasite exposure of hosts in noise-affected areas. For instance, noise can push animals out of otherwise preferred areas into marginal habitats. This leads to areas with (temporarily) higher population densities, which could facilitate parasite transmission. Several examples of such noise-induced density changes in habitat occupancy in both terrestrial [25,26] and aquatic species [27,28] have been observed, but to date it has not been investigated whether this affects parasite exposure of individuals [29].

Noise pollution can also affect intraspecific communication and alter the relative proximity among hosts and thereby affect exposure probability. Intraspecific interactions based on acoustic signals such as territorial and mating behaviours have been shown to be modified under noisy conditions in a range of species (e.g. [30,31]). Reduced encounter rates between males and females in noisy environments could limit the propagation of sexually-transmitted parasites. Conversely, noise can change group dynamics [32]. For instance, individuals could spend more time in close proximity to facilitate communication, increasing the chances of parasite transmission. At the same time, noisy conditions might make it harder to distinguish between high- and low-quality mates through masking impact on vocally driven mate choice (e.g. [31,33]). This could allow low-quality mates with high parasite burdens to mate, producing low quality offspring. Moreover, they would spread their genes and parasites through the population [34]. Masking of interspecific communication between hosts, could also prevent parasites from eavesdropping to locate hosts. Empirical evidence is still scant, but less or no calling in response to noise reduced parasitoid attraction to crickets [35]. Noise masking cricket mating calls is detrimental to communication among conspecifics, but will have beneficial effects through reduced attraction of parasitoids to the crickets [36]. Noisy urban conditions have also been shown to clear an area from blood-sucking midges – and consequently vector-borne diseases they transmit – that would otherwise have used auditory cues to tune on their calling frog hosts [37]. Disruption of host seeking could be especially beneficial to birds with begging calls. These calls could be used by parasites to find nestlings [38]. By avoiding early infection young birds could have higher survival rates and increased overall health.

Noise impact on intraspecific interactions can also affect parasite transmission via effects on group cohesion [39]. For instance, noise pollution is reported to affect the vertical distribution patterns and schooling behaviour in a number of fish species [23,40–42]. If such effects would yield alterations in the average distances among individuals or groups of individuals, they could also influence the probability of horizontal parasite transmission, as known from studies on relative proximity of fish aggregations in aquaculture [43]. Another example of potential noise impact through effects on intraspecific interactions may be negative impacts of anthropogenic noise on grooming in mammals [44]. Grooming is known to prevent disease through ectoparasite removal [45], on top of a reduction in stress levels [46]. Noise may thus cause a reduction in parasite removal, through increased vigilance and disruption of grooming behaviours. On the other hand, the close proximity of individuals during grooming might facilitate the transmission of airborne parasite infective stages or parasites with faecal-oral transmission. If noise leads to an increase in vigilance and a decrease in grooming, the transmission of such parasites could be reduced. This is especially true if increased vigilance leads to increased inter-individual distance.

Many parasites rely on the predation of their intermediate hosts to infect the next host in their life-cycle [47], therefore any alteration of predator-prey interactions through noise pollution could potentially influence the trophic transmission of parasites. Interspecific interactions, such as foraging and predation, can be altered by noise pollution. This is especially true for animal species that are unable to flee from noisy sites and for predators that rely on acoustic cues to locate prey [22,48]. Different effects of noise pollution on animal foraging have been observed, such as masking of prey sounds [49], distraction of predators [50], and changes in predator diet composition [51], indicating that noise pollution effects on trophic transmission of parasites are likely.

Besides host behaviour, survival of the free-living infective parasite stages in aquatic environments might also be affected by noise pollution (also see [52]). The survival of infective stages of many metazoan parasites is known to be affected by a number of environmental disturbances [53,54], and noise pollution might have similar impacts. It remains unclear how small creatures may be affected by relatively long wave lengths, but loud seismic survey sound can kill zooplankton [55]. Furthermore, vessel propellers often generate additional sound on top of the engine, through so-called cavitation – implosion of vapour-filled bubbles resulting from pressure differences generated by the propeller movement through the water. Cavitation can reduce survival of free-living parasite stages [56,57], although, the role of cavitation sound in this is not yet investigated. Nevertheless, pistol shrimps are able to stun their tiny aquatic prey by cavitation sound [58], and there are multiple studies on zooplankton, which report reduced survival [59], retarded development, and higher rates of malformations [5,60] through noise impacts.

Finally, we believe that the probability of host exposure to parasites can be affected by noise pollution though an effect on host seeking behaviour of infective stages (c.f. [61,62]). Host seeking in free-living endohelminths may share features and sensitivities with small pelagic life cycle stages of sessile marine invertebrates, which are known to be guided by acoustic cues for settlement [60]. It is therefore possible that noise pollution can alter host finding strategies of parasites, and thereby alter the spatio-temporal overlap between hosts and parasites (c.f. [37]). Noise pollution also affects host seeking in terrestrial environments [36]. This could happen through direct interference or masking. Alternatively, acoustic noise in air, transferred to vibratory noise in the substrate [63], could mask host substrate vibrations used by some parasites and parasitoids [64,65].

Noise impacts on host susceptibility and parasite infectivity

At a second stage of the interaction between parasites and their hosts, noise pollution can affect successful infection after exposure. This depends on the interaction between host susceptibility, mainly determined by the immune response, and parasite infectivity. Significant effects of noise pollution on animal physiology are reported in 20% of all noise pollution studies [40]. Accordingly, anthropogenic noise pollution can cause physiological stress and consequently undermine the disease resistance via reduced efficacy of the immune response to parasite infection [66,67]. This reduced host resistance could be due to direct impacts on the immune system, but also through indirect impacts, via trade-offs in energy allocation. Similarly, on the parasite side, infectivity could also be reduced through physiological stress [68]. Thus, noise pollution has the potential to alter the establishment of parasites in their hosts in multiple ways.

An animal's immune response is a complex interplay between a myriad of proteins, but changes in the secretion of corticosteroids in vertebrates are particularly prominent under stress [69]. These hormones tend to enhance the immune response of individuals, to get them into 'a state of emergency' [70]. However, elevated levels of stress over longer periods of time is associated with deleterious effects, most notably a reduced immune response [69]. Accordingly, acute exposure to noise pollution could boost the immune response of vertebrates, but chronic exposure might undermine it and favour infections. Evidence for this hypothesis so far has been variable, as some species exposed to noise pollution showed an increase in immunocompetence [66], while it decreased baseline glucocorticoids [71] immunocompetence [72] in others. In the later, the apparent lack of a response may have been due to an overall delay in the development of the immune response [72]. Furthermore, if individuals spend considerable time in marginal habitats due to displacement by noise, this could influence their body condition, making them more susceptible to parasites [29]. At the same time, a reduction in parasite removal, as discussed in the previous section, combined with increased stress levels, could also increase susceptibility.

A small number of studies directly addressed the impact of noise exposure on parasite-host interactions after exposure. One of those, an experimental study on guppies (*Poecilia reticulata*), showed that acute exposure to elevated noise levels yielded higher levels of infection with the ectoparasite *Gyrodactylus turnbulli*. This contradicts the 'state of emergency'-hypothesis, however, chronic exposure led to lower infection rates and higher host mortality rates [73]. The noise exposure likely caused a stress response that prevented an effective barrier against the parasite, while the chronic noise exposure must have reduced the tolerance of hosts to infections. Another fish study, found no effect of chronic noise exposure on the infection with the gram-negative rod bacterium *Yersinia ruckeri,* causing enteric redmouth disease, in rainbow trout (*Oncorhynchus mykiss*) [74]. Trout were exposed to noise levels common in aquaculture which did not have an effect on hearing ability, growth and mortality rate, or the infection rate. However, a terrestrial study found that side-blotched lizards (*Uta stansburiana*) captured around wind farms (responsible for noisy conditions) harboured lower numbers of trombiculid mites (*Neotrombicula spp.*) compared to lizards from undisturbed areas [75]. This suggested that sound could play a role in either lizard host susceptibility or the establishment of the parasitic mite on the host. However, a number of confounding factors were present also in this correlative study.

Although plausible, there is little published evidence to date for infectivity or virulence of parasites to be impacted by noise pollution. For instance, loud sounds could impose a physiological cost on free-living infectious stages, as seen for extreme temperatures (e.g. [68]). Host seeking could be more time-consuming in noisy areas due to lower host densities and masking of cues, resulting in a depletion of resources and thereby reducing infectivity. Developing parasites might also suffer malformations due to noise pollution, as seen in planktonic larvae [76], which could also limit their ability to successfully infect their host. Accordingly, noise pollution might cause carry-over effects, with noise impact early in life affecting performance later in life [77], especially in parasite species with complex life-cycles. However, such carry-over effects largely remain speculative at the moment, as we still lack critical knowledge on environmental impacts on whole parasite life-cycles.

Post-infection combined impacts of noise pollution and disease

The third stage at which noise pollution can affect parasite-host interactions is through an impact on hosts or parasites after the latter has established itself [78,79]. The potential ways of impact from noisy conditions at this stage may be similar to those during the infection process. Reduced host resistance through direct effects on the immune system can affect host susceptibility and resistance to infection, but may also affect tolerance of infections via trade-offs in energy allocation [80]. Parasite infectivity during infection and virulence in hosts after infection can both be reduced through physiological stress in the parasite. Because many parasites have complex life cycles with multiple hosts, they may be even more susceptible to a wider range of environmental disturbances [13], including a negative effect of noisy conditions. However, the outcome of combined impacts (noise and disease) is not necessarily a straightforward summation of detrimental effects for the host.

We believe that both synergistic and antagonistic effects exist between noise pollution and disease impacts on host mortality, development, and reproduction. Few empirical studies exist to confirm this, but some insight may come from investigations of multiple stressors which include either disease or noise pollution [81,82]. First, host mortality is tightly linked to parasite virulence through morbidity. Many parasites can alter host survival through reduced body condition and escape capacity, enhancing predation risk, or even inducing ‘suicidal’ behaviour, to aid in the completion of the parasite’s life-cycle [83–85]. Noise impact can have additive effects and worsen these patterns through physiological stress effects and further reduce host survival, as for instance seen in guppies infected with *Gyrodactylus* parasites under chronic noise exposure [73].

Alternatively, noise impact may also reveal antagonistic effects when comparing infected and non-infected hosts as seen in other cases of multiple stressors. For instance, nitrate run-off can be toxic to aquatic organisms, but in specific cases can also reduce *Gyrodactylus turnbulli* infections in guppies [86], showing the antagonistic interaction between pollution and parasites. Noisy conditions may disrupt the development of parasites within hosts, either resulting in reduced post-infection survival of the parasite, or a reduction in the output of infective stages. Both could also results in an overall decrease in parasite infections in the host population.

Host development can also be affected by parasite infections, and be modified by environmental factors such as food availability and potentially noise pollution. Three-spined sticklebacks (*Gasterosteus aculeatus*) experimentally infected with a cestode parasite (*Schistocephalus solidus*), gained weight more slowly compared to uninfected controls, revealing the detrimental impact on growth [87]. Energy allocation patterns were affected by trematode infection (*Echinostoma revolutum*) in a freshwater pond snail (*Limnaea elodes*), and depended on food availability [88]. Growth impacts were apparent with a low but not high protein diet, while survival was negatively affected by both parasite infection and shortage of food. Hence, noise pollution could worsen the ontogenetic challenge of infected individuals through a direct impact on the immune system through stress physiological effects [89], but also indirectly through an impact on reduced foraging efficiency [90,91] or elevated energy expenditure [92,93].

Finally, noise pollution and disease could also have combined effects on reproduction, since both can independently have negative effects on maturation and gonad development, and potentially alter behaviour that affects selection of breeding sites and sexual mates [24,94,95]. Noise pollution may reduce fitness for uninfected hosts – through mating with low-quality mates – and the overall population by enhancing parasite transmission and reproductive consequences of being infected. Parasite infections [96] and noise [5] can have negative impacts on reproductive outputs with delayed or reduced reproductive investments. At the same time, noise pollution can disturb foraging and thereby reduce parental investment [97] in species with parental care, which may be especially the case for infected individuals that already have higher energetic demands because of their infection. Together, this could lead to fewer offspring in the host population and a potential reduction in population size.

Besides the potentially synergistic or sometimes antagonistic effects of noise pollution and disease on hosts, it is possible that noise pollution can also be detrimental to the fitness of some parasites [13,98]. In particular, higher virulence, due to reduced host tolerance, could boost the immediate rate of transmission for parasites, but it might also lead to an overexploitation of the host resource [13]. The joined effects of noise pollution and disease could lead to the premature host death and an overall lower parasite spread across the host population. In some cases, noisy conditions could also improve the conditions for infected hosts, for instance when their predators depend on eavesdropping on acoustic cues. Masking of acoustic cues could raise the survival chances of infected prey and thereby extend the duration of infections and boost parasite fitness, similar to eutrophication mediated increases in *Ribeiroia* parasite fitness [81].

Concluding remarks and future perspectives

We provided an overview (Table 1) of the potential impacts of noise pollution on three main stages of parasite transmission and disease development: 1) pre-infection exposure probability, 2) infection upon exposure, and 3) severity of post-infection consequences. From this it becomes clear that noise pollution has the potential to significantly impact parasite-host interactions. Consequently, the disturbances caused by noise pollution are likely underestimated and significant effects of noise pollution on wildlife may be explained by its effect on wildlife diseases. However, the discussion above also indicates that our knowledge on noise pollution effects on wildlife diseases is very limited, as only very few parasite-host systems and a fraction of the proposed mechanisms have been studied.

We here propose a few avenues for future studies that we consider to be most urgent. First of all, it will be important to determine how common noise pollution effects are via the three main routes that we have identified (see **Outstanding Questions** for specific question to be addressed). We believe experimental infection studies on parasite-host systems, with noise exposure as a treatment, will be most informative. These should consider realistic sound fields and address challenges with artificial sound exposure conditions in the lab [99]. Ideally these experimental studies will cover a large diversity of parasite-host systems from terrestrial and aquatic realms . These experimental lab studies could be coupled with correlative field studies, e.g. comparing infection levels and infection consequences between noisy and unaffected habitats, to inform about effects sizes under realistic conditions. Second, it will be important to investigate local exposure conditions, because various types of noise sources and varying magnitudes of noise exposure may have different impacts. For instance, acute and chronic exposure to the same noise source may initiate very different responses. This should also take into account the possibility of acclimatisation and the importance of inter-individual variation in responses among host individuals [100]. Finally, it will be important to investigate the consequences of noise pollution effects on wildlife diseases for the surrounding communities and entire ecosystems and what the repercussions are for resource management and nature conservation, for instance in form of possible mitigation measures. Accordingly, we encourage future projects on this topic to involve both stakeholders and policy makers.

Although the existing literature is very limited to date, it suggests that noise impacts on wildlife diseases exist and that they may have major repercussions for wildlife health, given the global increase in anthropogenic noise pollution. We therefore call for an urgent intensification of research efforts along the three major routes of noise impacts to identify noise pollution impacts via hosts and parasites and their role in the emergence of wildlife diseases.

Author contributions

AB came with the initial idea of linking noise pollution impacts with wildlife diseases and initiated this collaboration. BWB led the manuscript writing process. BWB, DWT, HS and AB conceived and developed the conceptual outline of the manuscript. BWB and AB contributed equally to the writing of the manuscript with guidance from DWT and HS. All authors reviewed the manuscript.

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Glossary

Anthropogenic noise: Sound produced by human activities, targeted (e.g. music and sonar) or as by-product (e.g. engine and construction sounds).

Disease: The collective symptoms of the parasite on the host, the can or cannot have impacts on host fitness.

Host: Organism that serves as a resource for a parasitic life-stage.

Infectious disease: Abnormal condition of an organism caused by an infection with pathogens/parasites that detrimentally affects its function.

Infective stages: Typically, free-living or on-host stages of parasites that have the potential to infect a host.

Infectivity: The ability of a parasite to infect and establish in a suitable host upon contact.

Noise pollution: Sound of anthropogenic origin that disturbs normal functioning of wildlife.

Parasite: Ecological term that denotes an organism living in or on an other organism (the host) on which it energetically depends, at the expense of the host.

Parasite-host interaction: Type of ecological species interaction in which parasites interact with their hosts (similar to predator-prey and competitive interactions).

Particle motion: Movement of particles in a medium (air, water) due to sound waves. The intensity of which is often measured in dB_{SVL} (sound velocity levels).

Pathogen: Medical or veterinarian term that denotes parasites that cause disease.

Sound pressure: Pressure deviations from the average in a medium due to sound waves. The intensity of which is often measured in dB_{SPL} (sound pressure levels).

Virulence: Scale of fitness reduction in the host caused by a parasite.

Box 1. Sound features and noise pollution

Sound and perception

Sound originates from a source that vibrates and then travels as a wave through a medium. Sound concerns two aspects: acoustic pressure fluctuations and acoustic **particle motion**. Depending on their sensory capacities, organisms can sense either one or both of them. Sound may be informative to those animals with acoustic perception abilities and can provide insight into the presence and location of the associated sound source. Animals that have pairs of ears with eardrums (such as mammals, reptiles, and some insects) are able to detect and localize sound sources based on **sound pressure** information, depending on the sensitivity and relative distance between the ears. Animals with a gas-filled cavity living in water (such as fish with a swim bladder) are also able to perceive sound pressure. Creatures without such capacity are typically only sensitive to the particle motion aspect of sound through hair cells in their ears or elsewhere on their body. Acoustic pressure fluctuates in the medium along the axis of the travelling sound wave. Acoustic particle motion is a vector with the dominant direction along this same axis and thereby also provides directional cues to those with particle motion sensitivity.

Signals, cues, and noise

Sound can be a signal, cue, or noise, depending on the receiver, and its source. An acoustic signal for humans is an informative target sound for detection. Animal signals are informative sounds that play a role in communication, typically among members of the same species, and evolved for this purpose. Acoustic cues are sounds generated by abiotic conditions, such as wind or surf, that may provide useful environmental information, or by animals, but not deliberately so, and potentially detrimental to the source animal, for instance in the case of acoustic prey detection by a predator. Noise concerns all sounds that are not signals or cues, and that may mask signals or cues, and that may disturb and deter. A signal or cue for one species, may at the same time be noise for another. Signals used for communication between two individuals of one species may be a cue to another, and just noise for yet another species. Signal-to-noise levels at potential receivers are important determinants of masking problems. Noise pollution levels at potentially affected animals are important for disturbance and deterring effects.

Sound spectrum and noise impact

An important property of sound is the frequency. Animals can only exploit and respond to sound of frequencies they can perceive, even though they might be physically impacted by frequencies below or above the hearing range, including species that do not hear. Every hearing species has its own species-specific hearing curve, depicting variation in relative sensitivity across the spectrum. Wide and narrow, and high and low frequency ranges have evolved in different species in response to selection pressures related to the functionality of hearing in survival and reproduction as well as evolutionary constraints. Species with both sound pressure and particle motion sensitivity are expected to have distinct and partly overlapping sensitivity ranges for both aspects. High frequencies have short wave lengths and low frequencies have long wave lengths, which has consequences for hearing ability and potential impact, as organs and organisms smaller than the wave length are expected to remain unaffected by a passing sound wave. Hosts are likely to be hearing species and can be affected by sound pressure and/or particle motion, through disturbance, deterrence, and masking of signals or cues. Parasites may or may not have apparent hearing ability, and they are only likely to be affected by the particle motion aspect of sound, potentially through masking of cues, disturbance and deterrence.

Furthermore, hosts and parasites are likely to be differentially affected by sound related to frequency-dependent noise impact determined by species or organ size.

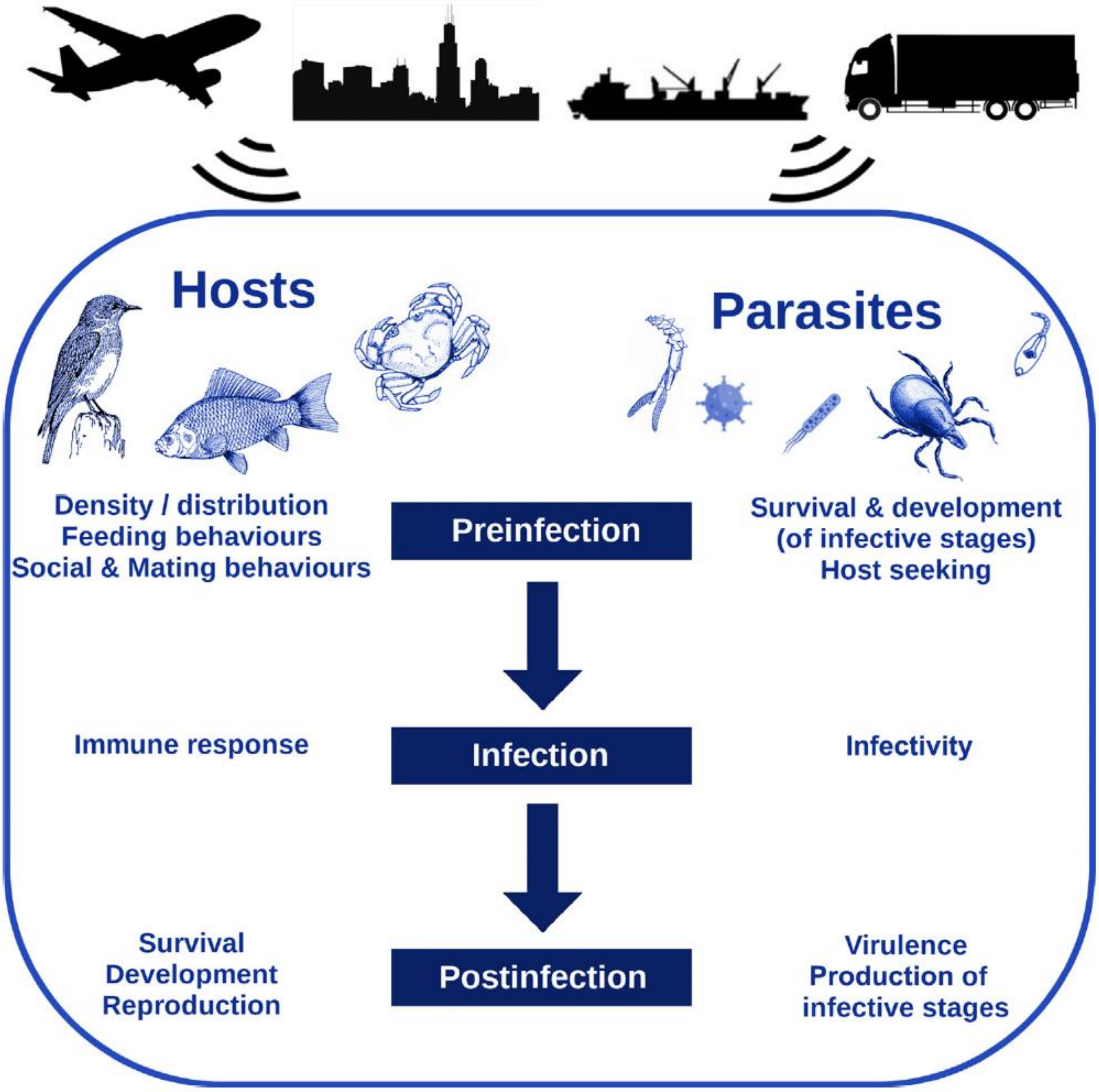

Figure 1. Graphical overview of the potential impacts of noise pollution on three stages of parasite-host interactions: pre-infection, the event of infection, and post-infection. The main factors with a critical impact on these stages and that are likely to be affected by noise pollution are listed per stage, for hosts (left) and parasites (right).

Table 1. Overview of the described effects of anthropogenic noise pollution on hosts and parasites. Different symbols indicate different types of effects; physiological stress (Triangle, ▲), masking, disturbance or deterrence (open circle, o), or direct damage to or death of the organism (square, ▪) through noise. The effect marked with [1] is restricted to terrestrial habitats, the effect marked with [2] is restricted to aquatic habitats. Effects marked with a asterisk (*) have been observed. In the study by Alaasam et al. [75] the mechanism leading to reduced infection rates is unknown.

	Hosts	Parasites
pre-infection	o Reduced/increased exposure through lower/higher host densities o Reduced parasite removal through grooming[1]	▲ Reduced development and survival[2] o Impaired host seeking o Disruption of trophic transmission
infection	▲ Increased susceptibility through reduced immune response	▲ Reduced infectivity through depletion of resources*
post-infection	▪ Increased mortality due to combined stressors ▲ Reduced reproductive output	▪ Reduced survival through depletion of resources* ▪ Over-exploitation of hosts