CHAPTER 2

Noise pollution

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Overview

Anthropogenic (human-made) noise pervades all ecosystems across the globe. Human activities both increase the amount of noise and generate sounds with different characteristics to those occurring naturally, meaning that wildlife now faces novel and unprecedented acoustic challenges compared to pre-industrial times. Behavioural changes are the most widespread response to noise pollution because such changes can result from even moderate noise levels occurring far from a source; they are also the most well-studied. Here, I begin with an overview of the different behavioural responses generated by anthropogenic noise. I then describe reasons why we see variation in these responses—within and between species, and across time—and the consequences for individual fitness, populations, communities, and ecosystems. Throughout, I provide examples illustrating the diverse range of taxa affected. Finally, I discuss what we still need to learn about noise impacts and the importance of implementing and testing mitigation and management strategies.

2.1 Anthropogenic noise: sources and problems

Terrestrial and aquatic environments across the globe have become substantially noisier since the Industrial Revolution because of sounds produced by human activities (Barber et al. 2010; Buxton et al. 2019; Duarte et al. 2021). Major sources of anthropogenic (human-made) noise on land include transportation networks, resource extraction, and urban development, whilst commercial shipping, recreational boating, offshore construction, habitat exploration, and energy production all generate noise in aquatic habitats. In some cases, such as the use of seismic surveys and sonar arrays, humans produce sounds deliberately. Many other human activities, such as vehicle use, pile-driving, and infrastructure operation, produce noise as an unintended by-product. Anthropogenic noises range on a continuum from intermittent sounds to those of a more continuous nature, but they also vary in many other characteristics, including frequency, rise time, duty cycle, impulsiveness, and source level (Francis and Barber 2013; Duarte et al. 2021). Crucially, though, all human sources not only increase the amount of noise in an area but also produce sounds with different acoustic features to those generated by the physical environment (abiotic sounds) and by organisms (biotic sounds) (Hildebrand 2009). For instance, much anthropogenic noise is a predominantly chronic disturbance with the sound energy concentrated at low frequencies (typically below 2 kHz); such sounds can readily permeate the environment across time and space. Animals in the natural world are therefore experiencing a very different soundscape, and thus a novel acoustic challenge, to that which existed in pre-industrial times.

In the last two decades, there has been a huge increase in research investigating the impacts of anthropogenic noise on wildlife (reviewed in Kight and Swaddle 2011; Francis and Barber 2013; Morley et al. 2014; Shannon et al. 2016; Duarte et al. 2021). High-intensity sound can cause death, physical damage, and hearing loss, whilst noises from a variety of anthropogenic sources have been shown

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Table 2.1 Four reasons why noise can cause behavioural changes; these are not mutually exclusive

Mechanism	Explanation
Acoustic masking	Noise can increase the threshold for detection or discrimination of important sounds of similar frequencies (Moore 2012). Masking can be complete, when an acoustic signal or cue is not detected at all, or partial, when the acoustic signal or cue is detectable by the listener but the content is hard to understand.
Perception as a threat	Noise may be perceived as a threat and thus generate responses (e.g. fleeing, hiding, additional vigilance) similar to those seen in a predation context (reviewed in Francis and Barber 2013).
Distraction	Noise can divert an individual's finite attention away from their primary task or goal, interfering with biologically important decision-making (Chan and Blumstein 2011). Stimuli from one modality (in this case, sound) can therefore interfere with the processing of information obtained in other modalities (e.g. visual or olfactory cues and signals).
Generation of stress	Noise can induce physiological stress as evidenced by, for instance, increases in the production of the steroid hormones cortisol, corticosterone, and aldosterone (Kight and Swaddle 2011). Elevated stress can, in turn, lead to behavioural changes; short-term stress may be beneficial (e.g. priming an animal to avoid a dangerous area) but chronic stress can have detrimental consequences.

to affect animal physiology, development, and behaviour. Behavioural impacts are likely the most temporally and spatially widespread because they can result from even moderate noise levels occurring at large distances from a noise source. Moreover, they are the most well-studied of responses and are particularly important because behavioural alterations represent the first line of defence for organisms in a changing world (Candolin and Wong 2012). Anthropogenic noise can affect animal behaviour in four main ways, which are not mutually exclusive: it can mask other sounds, be perceived as a threat, act as a distraction, and cause stress (Table 2.1). Thus, anthropogenic noise can hinder the processing of acoustic information (so-called unimodal effects), affect the detection and use of information in other sensory modalities (cross-modal interference), and generate a wide range of other behavioural changes.

In this chapter, I begin with an overview of the different behavioural responses generated by anthropogenic noise. Our understanding of noise impacts has come from a variety of complementary research approaches—including studies conducted in captivity and the wild, studies comparing areas with different noise levels, and studies where noise levels have been manipulated—which vary in their behavioural and acoustic validity, as well as the level of experimental control, but all add valuable knowledge. I then discuss reasons why we see variation in behavioural responses—both within and between species, as well as across time—and what the consequences are for individual fitness, populations, communities, and ecosystems. Throughout, I provide specific examples illustrating the diverse range of taxa known to be affected (Figure 2.1). I also provide some case studies of species that have each been used as model organisms to investigate several different questions relating to noise pollution. Finally, I look to the future—both in terms of what we still need to learn about noise impacts, including their mechanistic underpinnings and their effects in a multi-stressor context (see also Chapter 10), and the importance of implementing and testing mitigation and management strategies such that we can reduce the impact of this globally pervasive pollutant.

2.2 Behavioural responses to anthropogenic noise

Many behavioural studies investigating the impacts of anthropogenic noise have focused on the responses of individual animals, as this is logistically the simplest scenario to consider. But there is also increasing evidence that social interactions, both between members of the same species and between different species, can be affected. It is important to note, though, that noise does not always have a discernible effect—for instance, there was no detected adjustment in the vocalizations of harbour seals *Phoca vitulina* or Pacific chorus frogs *Pseudacris regilla* to compensate for noise-induced masking (Nelson et al. 2017; Matthews et al. 2020).

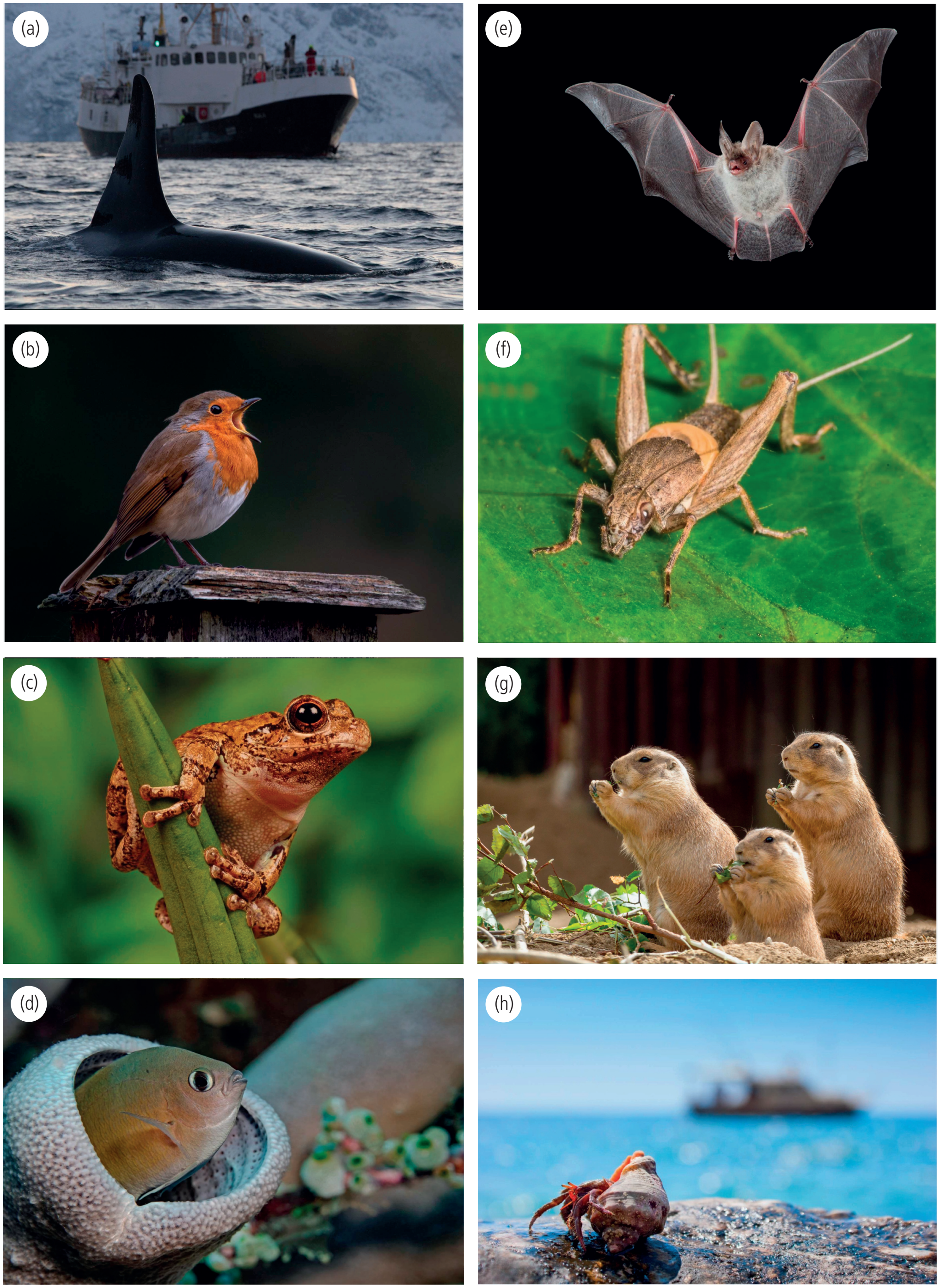

Figure 2.1 Animals from all major taxa have been shown to change their behaviour in response to anthropogenic noise. For example: (a) orcas *Orcinus orca*, (b) European robins *Erithacus rubecula*, (c) gray treefrogs *Hyla versicolor*, (d) ambon damselfish *Pomacentrus amboinensis*, (e) greater mouse-eared bats *Myotis myotis*, (f) field crickets *Gryllus campestris*, (g) prairie dogs *Cynomys ludovicianus*, and (h) hermit crabs *Pagurus bernhardus*.

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Such examples are likely under-represented in the literature due to the general publication bias towards research with statistically significant findings.

Animals may respond to increased noise in an area by moving away, but those remaining may exhibit important changes to individual behaviours, such as vigilance, foraging, movement, orientation, navigation, and settlement. Several studies have indicated noise-avoidance behaviour by different taxa: for example, seismic survey activity led to an 88% decrease in sightings of baleen whales and a 53% decrease in sightings of toothed whales (Kavanagh et al. 2019), whilst the creation of a 'phantom road' with an array of loudspeakers playing traffic noise resulted in a 31% decrease in migrating birds in a roadless area of the USA (Ware et al. 2015). For many animals, though, avoidance of noisier areas is not a possibility—a species might not be capable of relocating, the relevant area may hold critical resources, and/or there may be no viable alternative to move to—and there is strong evidence that those remaining can be negatively affected. For instance, anthropogenic noise can cause individuals to become more vigilant, as seen in white-crowned sparrows *Zonotrichia leucophrys*, prairie dogs *Cynomys ludovicianus*, and dwarf mongooses *Helogale parvula* (Shannon et al. 2014; Ware et al. 2015; Figure 2.2). Increased vigilance can reduce time available for foraging (Shannon et al. 2014; Ware et al. 2015), but foraging can also be affected directly: for example, traffic noise decreases the foraging efficiency of greater mouse-eared bats *Myotis myotis* and three-spined sticklebacks *Gasterosteus aculeatus* (Siemers and Schaub 2011; Voellmy et al. 2014). In terms

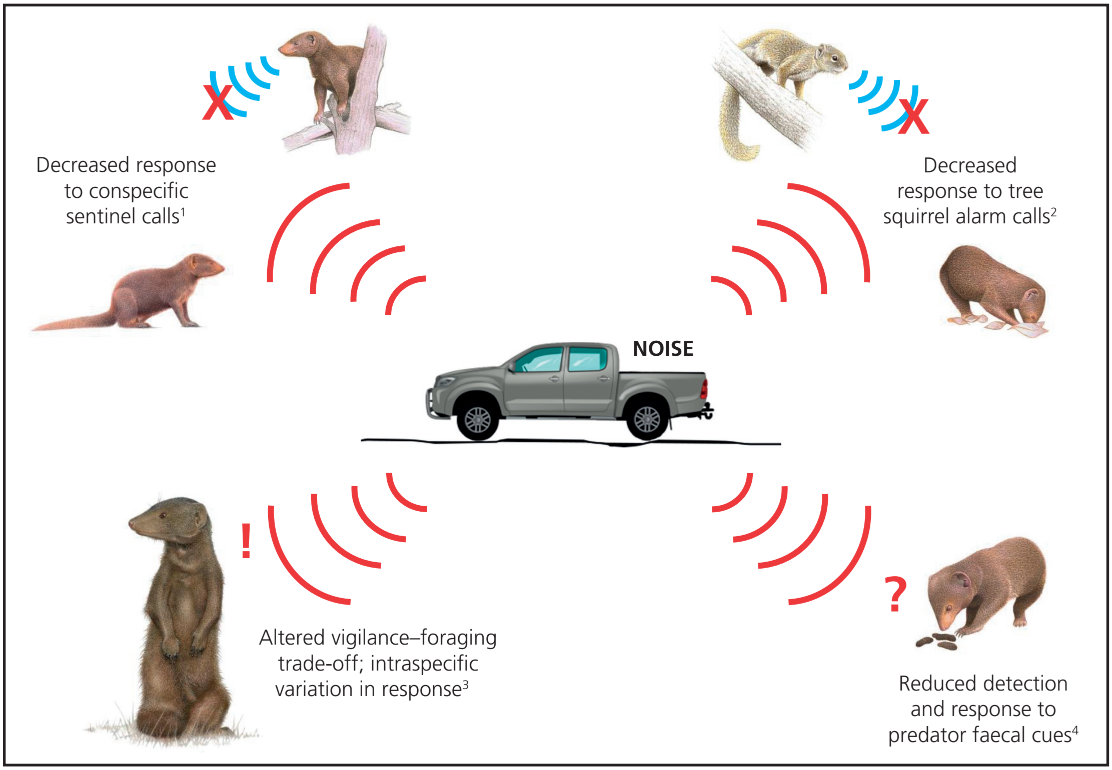

Figure 2.2 Impacts of traffic noise on the behaviour of dwarf mongooses *Helogale parvula*. [1]Kern and Radford (2016); [2]Morris-Drake et al. (2017); [3]Eastcott et al. (2020); [4]Morris-Drake et al. (2016).

Original artwork: Martin Aveling (@AvelingArtworks)

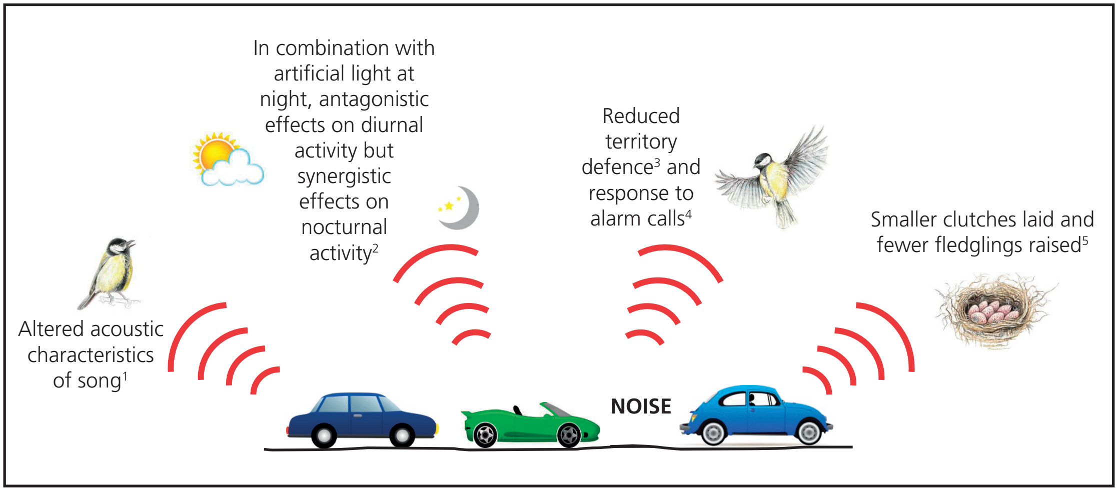

Figure 2.3 Impacts of traffic noise on the behaviour of great tits *Parus major*. [1]Slabbekoorn and Peet (2003); [2]Dominoni et al. (2020); [3]Mockford and Marshall (2009); [4]Templeton et al. (2016); [5]Halfwerk et al. (2011).

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of movement, various fish and squid move lower in the water column and swim faster in response to seismic airgun noise; these behavioural changes may reduce foraging opportunities and increase energy expenditure (Fewtrell and McCauley 2012). Noise can also affect the perception of environmental cues that individuals use to inform key life-history processes. For instance, the orientation, habitat-selection, and settlement decisions of larval coral reef fishes and invertebrates may suffer in areas with increased noise from human activities (Holles et al. 2013; Lecchini et al. 2018). Such impacts on individual behaviour may often be underpinned by noise-induced interference with cognitive performance; resource-assessment decisions in hermit crabs *Coenobita clypeatus*, foraging-task success in zebra finches *Taeniopygia guttata*, and predator learning in Ambon damselfish *Pomacentrus amboinensis* are all affected detrimentally by additional noise (Walsh et al. 2017; Ferrari et al. 2018; Osbrink et al. 2021).

Social interactions between conspecifics are crucial for many aspects of animal life and may be disrupted by anthropogenic noise (reviewed in Fisher et al. 2021). Perhaps most obviously, acoustic communication can be affected; such communication is often vital for survival and reproductive success, with numerous studies demonstrating that the behaviour of receivers is compromised by noise pollution. For instance, additional-noise playback reduced the anti-predator responses of wild superb fairy-wrens *Malurus cyaneus* and great tits *Parus major* to alarm calls indicating danger (Zhou et al. 2019; Figure 2.3). Use of other vocal information about predation risk can also be affected, as seen in the responses of dwarf mongooses to the surveillance calls of sentinels (Figure 2.2). From a reproductive perspective, noise has been shown to impact negatively the acoustic attraction or detection of potential mates by, for example, gray treefrogs *Hyla chrysoscelis* and field crickets *Gryllus bimaculatus* (Bee and Swanson 2007; Bent et al. 2018), territory defence in red-mouthed gobies *Gobius cruentatus* and great tits (Sebastianutto et al. 2011; Figure 2.3), and the provision of parental care by blue tits *Cyanistes caeruleus* to offspring that communicate their need through begging calls (Lucass et al. 2016). More generally, calculations of acoustic-transmission distances suggest that acoustic signals of, for instance, marine mammals and fish likely have a reduced range of effect in noisier areas (Putland et al. 2017). Consequently, many species exhibit changes in their acoustic behaviour to maintain detection and information flow. For example, a wide variety of invertebrates, anurans, birds, and both terrestrial and marine mammals alter the amplitude, frequency, rate, and duration of vocalizations, as well as where and when they vocalize, when competing with anthropogenic noise (reviewed in Kunc and Schmidt 2020; Duquette et al. 2021).

In addition to effects on communication, or as a consequence of them, noise pollution might impact group formation, social decision-making, and interactions between members of the same and different groups. For instance, both tufted titmice *Baeolophus bicolor* and Carolina chickadees *Poecile carolinensis* increased their grouping (reduced nearest-neighbour distances) and rates of social interactions in traffic noise, potentially to enhance communication and information transfer (Owens et al. 2012). In the group-living cichlid *Neolamprologus pulcher*, additional-noise playback not only affected individual behaviours (e.g. reduced nest digging and defence against egg predators) but caused increases in the amount of aggression and submission exhibited among group members (Bruintjes and Radford 2014). Alterations in social interactions between conspecifics can, in turn, affect social organization with respect to dominance hierarchies, collective behaviour, and mating systems (reviewed in Fisher et al. 2021). For instance, since noise can impact communication and social recognition, there are likely knock-on consequences for collective action and social coordination. As one example, groups of juvenile seabass *Dicentrarchus labrax* exposed to pile-driving playback became less cohesive, less directionally ordered, and were less correlated in speed and directional changes (Herbert-Read et al. 2017). Understanding how noise affects social interactions is crucial because many animals rely on such behaviours for their survival and reproductive success, and any potential impacts could have fundamental ecological and evolutionary implications.

Anthropogenic noise can also affect interspecific interactions, be that use of heterospecific cues or direct encounters between species. Since many animals eavesdrop on heterospecific acoustic signals (e.g. alarm calls), noise may mask this information, as demonstrated in northern cardinals *Cardinalis cardinalis* and dwarf mongooses (Grade and Sieving 2016; Figure 2.2). Similarly, there may be masking of acoustic cues indicating the presence of predators or prey. For instance, because greater mouse-eared bats find ground-running arthropods by listening for the faint rustling sounds created as these species move, prey detection is compromised by anthropogenic noise (Siemers and Schaub 2011). Moreover, there may be disruption to the use of information in other sensory modalities: for example, dwarf mongooses are less likely to respond appropriately when encountering predator faeces if they are exposed to traffic-noise playback (Figure 2.2). In terms of direct interactions, acoustic communication between different species (e.g. prey signalling their quality to predators) may be negatively affected by anthropogenic noise (Brumm and Slabbekoorn 2005). Beyond communication, there can be changes in both mutualistic interactions (e.g. between cleanerfish and clients) and those of an antagonistic nature (e.g. between predators and prey). For instance, bluestreak cleaner wrasses *Labroides dimidiatus* were less cooperative towards their client fish species when exposed to motorboat noise (Nedelec et al. 2017), whilst several species, including hermit crabs and Ambon damselfish, respond less often and less rapidly to simulated predators when experiencing additional noise (Chan et al. 2010; Simpson et al. 2016). Thus, in conflict scenarios and under certain circumstances, one party in an interspecific interaction may actually benefit from the additional noise. Indeed, anthropogenic environments could even provide new opportunities for species (reviewed in Fleming and Bateman 2018). But the 'winners' and 'losers' in any dyadic interaction influenced by noise will depend on the relative hearing sensitivities and noise tolerances of the species involved (see below).

2.3 Variation in behavioural responses

As research on the impacts of anthropogenic noise has expanded, it has become increasingly clear that there is extensive variation in behavioural responses. This variation occurs both between and within species, as well as over different time frames (i.e. initial responses can change over hours, days, or weeks of repeated exposure, and there can be adaptation across generations). Understanding such variation is crucial for improving the management of captive animals, the monitoring of wild populations, the modelling of species responses, and the mitigation of noise-pollution effects on wildlife.

Differences are expected between species in their behavioural responses to anthropogenic noise for a variety of reasons. Some studies have tested explicitly how different species respond to the same noise source. For instance, Voellmy et al. (2014) showed that whilst both European minnows *Phoxinus phoxinus* and three-spined sticklebacks consumed fewer prey when there was additional noise, the reason differed: minnows shifted their activity away from foraging behaviour (exhibiting greater inactivity and more social behaviour), whereas sticklebacks maintained foraging effort but made more mistakes. Studies comparing terrestrial areas with natural variation in noise levels, and those that experimentally applied traffic noise to roadless areas, have both demonstrated that bird species differ in their avoidance of noise and in their behavioural responses if they remain in noisier sites: some species were adversely impacted while others were not affected at all (Senzaki et al. 2020a, b). Interspecific differences might arise because of variation in, for example, hearing ability, physiological stress response, existing vocal repertoire, anti-predator strategies, and diet. For instance, Pieniazek et al. (2020) found a general trend for freshwater fish with more sensitive hearing to exhibit a greater decrease in foraging during boat-noise exposure. Senzaki et al. (2020a, b) found that those bird species most likely to abandon noisy areas have low-frequency acoustic signals; relative effects of noise on reproductive timing and hatching success were dependent on interspecific differences in vocalization frequency, nesting location, and diet. Such differences will likely affect community composition and structure both directly, through differences in the relative success of each species when disturbed, and indirectly, through altered interactions between species (see later).

Individuals of the same species also differ in myriad ways, so variation in their behavioural responses to the same noise exposure is expected (reviewed in Harding et al. 2019). One source of intraspecific variation is differences in intrinsic characteristics such as age, sex, dominance status, personality, body size, and condition. For example, younger birds of various species showed greater avoidance than older individuals when exposed to traffic-noise playback (McClure et al. 2017), whilst European eels *Anguilla anguilla* in poorer condition exhibited a noise-induced reduction in responses to a simulated predatory strike that was not apparent in better-quality individuals (Purser et al. 2016). Intraspecific variation in responses to noise might also be the consequence of differences in extrinsic factors, including environmental or social context, prior experience of noise, and the presence and magnitude of additional stressors. For instance, traffic-noise playback did not affect the song-bout duration of tree frogs *Hyla arborea* singing alone but did lead to an alteration by those singing in a chorus (Lengagne 2008), and there was a synergistic effect of artificial light at night and noise on great tit nocturnal activity but an antagonistic effect of the two stressors on diurnal activity (Figure 2.3). A systematic review of the literature revealed that only 10% of papers examining noise impacts tested experimentally for intraspecific response variation, but that 75% of those considering intraspecific variation reported significant effects (Harding et al. 2019). Varied responses among conspecifics may affect relative mortality risk and the ability to emigrate or react flexibly, will determine the evolutionary potential of post-disturbance populations, and could have far-reaching consequences for communities and ecosystem functioning (see later).

Behavioural responses to noise can also vary in time frame, from initial individual plasticity through to evolutionary change across generations (see Tuomainen and Candolin 2011). The first response of individual animals to any environmental change is often a plastic alteration in behaviour. This flexibility has been demonstrated by numerous experimental studies where animals in a variety of taxa changed their behaviour in response to anthropogenic-noise playback. As just two examples, Amazonian treefrogs *Dendropsophus triangulum* altered their call rate, whilst silvereyes *Zosterops lateralis* adjusted their call frequency, amplitude, and duration, when experiencing noise playbacks (Kaiser and Hammers 2009; Potvin and Mulder 2013). However, there are differences in the capacity for such behavioural plasticity: some species may have limited vocal flexibility, for instance, if their songs or calls have little existing variation in frequency (Brumm and Slabbekoorn 2005). The initial reaction of individuals to noise may change through learning (LaZerte et al. 2016) or because repeated or chronic exposure leads to either increased (e.g. through sensitization or reduced tolerance) or decreased (e.g. through desensitization, increased tolerance, or habituation) responses (Nedelec et al. 2016; Neo et al. 2018). For instance, whilst juvenile threespot dascyllus *Dascyllus trimaculatus* initially hid more in the coral reef when exposed to motorboat-noise playback, they no longer did so after one or two weeks of exposure (Nedelec et al. 2016). Behavioural responses can also change over time through innovations and cultural inheritance, via social transmission of new behavioural patterns within and across generations (Tuomainen and Candolin 2011). Ultimately, there may be evolution of behavioural responses (i.e. genetic change over generations). For instance, the minimum frequency of white-crowned sparrow songs in a particular population increased over a 35-year period as urban noise increased (Luther and Derryberry 2012). Even if initial behavioural plasticity does not buffer a species fully against the challenges of anthropogenic noise, it might give the population additional time to adapt genetically to the new acoustic environment.

2.4 Consequences of behavioural changes

Behavioural changes in response to noise ultimately matter only if there are fitness consequences for individuals. Noise can directly affect fitness (e.g. causing mortality, or through physiological and developmental impacts), but the focus in this chapter is on how behavioural responses can lead to fitness consequences. Any such impacts on survival and reproductive success can have a profound influence on the persistence and evolution of populations, which, in turn, can alter community composition and structure, as well as the functioning of whole ecosystems.

Behavioural responses to noise can either be maladaptive or adaptive (reviewed in Tuomainen and Candolin 2011). Maladaptive responses are those that lead to a decrease in an individual's fitness, either because previous behavioural patterns continue but these are now detrimental in the changed environment, or because the behavioural alterations exhibited have negative consequences for survival or reproductive success. For example, if animals continue to produce vocalizations that are now masked by anthropogenic noise (Brumm and Slabbekoorn 2005), there could be a decreased likelihood of attracting a mate or of hearing the needs of offspring. If acoustic cues indicating viable or healthy habitat are masked (Holles et al. 2013; Lecchini et al. 2018), animals may end up in poorer-quality areas with potential reductions in fitness. In terms of behavioural changes, if noise leads to unnecessary increases in vigilance (Shannon et al. 2014; Ware et al. 2015), for instance, the resulting reduction in time available for activities such as foraging or parental care could, in principle, increase the risk of starvation for adults or young. By contrast, some noise-induced changes are viewed as adaptive; that is, they (likely) increase the survival and reproductive success of individuals. For example, vocal adjustments in the amplitude, temporal structure, frequency, and complexity of vocalizations are argued to improve signal detection and discrimination in noisy areas (Brumm and Slabbekoorn 2005), and are thus suggested to have benefits in terms of territory defence, mate attraction, anti-predator behaviour, and parental care. However, such vocal adjustments might also result in many direct or indirect fitness costs due to, for instance, reduced transmission distances, increased risk of predation or parasitism, altered energy budgets, and loss of vital information (reviewed in Read et al. 2014). As with all behavioural ecology, there are likely trade-offs between costs and benefits.

Many behavioural studies speculate about potential fitness consequences, but caution is needed, especially when extrapolating from demonstrations that acute noise exposure causes short-term responses. That is because there may be compensation in quieter periods or reduced noise impacts with repeated or chronic exposure, and even long-standing behavioural changes may not actually affect survival or reproductive success. Ideally, what is needed are studies that explicitly examine behaviour and quantify the resulting fitness consequences (Kunc et al. 2016); such work is relatively rare and mostly focused on reproductive success. For example, traffic noise resulted in female great tits laying smaller clutches and pairs raising fewer fledglings, likely due to masking of acoustic communication (Figure 2.3). Similarly, ash-throated flycatchers *Myiarchus cinerascens* had lower reproductive success if their nests were exposed to noise, in this case due to higher rates of abandonment at the incubation stage (Mulholland et al. 2018). Spiny chromis *Acanthochromis polyacanthus* brood-guarding males exposed to motorboat-noise playback reduced feeding and offspring interactions, resulting in a lower likelihood of offspring survival (Nedelec et al. 2017). In a study that combined laboratory and field experiments, a reduced response to predatory threats by Ambon damselfish translated into a higher mortality rate when faced with predatory dusky dottybacks *Pseudochromis fuscus* (Simpson et al. 2016). There is also considerable correlational evidence that the use of military sonar likely causes behavioural changes that lead to fatal mass strandings in a variety of cetaceans (Nowacek et al. 2007).

Anthropogenic noise can change populations both in terms of the abundance of a species and also its composition. In general, if individuals avoid noisier areas, or if they remain but respond maladaptively and suffer reductions in survival or reproductive success (see above), local population declines can result. Conversely, some species may increase in abundance if they are released from competitive or predation pressure due to noise-induced declines in others (Francis et al. 2009; Senzaki et al. 2020b). But intraspecific variation in responses to noise may also lead to changes in population structure. For instance, McClure et al. (2017) found age differences in noise-avoidance responses to a phantom road—first-year birds responded more strongly than adults, potentially because of different foraging–predation trade-offs and site-selection decisions—resulting in changed population demographics. More generally, whilst initial behavioural responses to human-induced environmental change may help to maintain a viable population and facilitate adaptation to new conditions, they also mean that there will likely be a greater proportion of individuals capable of rapid change moving forward. The genetic make-up of the population will have changed, with noise altering the evolutionary potential of a post-disturbance population (Tuomainen and Candolin 2011). It is also possible that avoidance behaviour could result in reduced genetic connectivity of the population, if it becomes fragmented, increasing the risk of inbreeding and thus lost genetic variation (see Brook et al. 2002). Long-term studies of population consequences of noise are rare, so predictive modelling is especially important. Such modelling can include determining how noise propagates across landscapes and its likely effect on populations (Barber et al. 2011; Mortensen et al. 2021).

Changes in populations can have direct and indirect consequences for communities (Kok et al. 2023). For example, studies of arthropods, anurans, and birds have found noise-induced changes in community composition (Bunkley et al. 2017; Grace and Noss 2018; Senzaki et al. 2020a). Most obviously, if a species declines in number, or even goes locally extinct, due either to avoidance behaviour or strong negative fitness impacts of noise, then it will be less represented in the community (Ware et al. 2015; Senzaki et al. 2020a, b). At the same time, there may be increases in the prevalence of some species if they gain through behavioural interactions with another species that is more susceptible to noise. For instance, this can happen where a predator benefits at the expense of a prey species whose anti-predator responses are compromised by noise, as found in the dottyback–damselfish predator–prey relationship (Simpson et al. 2016). Likewise, hosts may benefit if their parasites are compromised by noise, as is the case with frog-biting midges *Corethrella* spp. being unable to detect their túngara frog *Engystomops pustulosus* hosts (McMahon et al. 2017). There can also be indirect, knock-on consequences arising from a noise-induced change in the local abundance of a species. For instance, if avian pollinators or seed-dispersers move away from noisy areas, then there can be negative consequences for the plant and tree species that rely on them (Phillips et al. 2021). Conversely, if nest-predators are less common in noisy areas, then reproductive success of their prey can increase (Francis et al. 2009). Similarly, noise may change the balance of interspecific competitive interactions in favour of one species: for example, shore crabs *Carcinus maenas* are less likely to aggregate at a food source if it is noisy, resulting in reduced competition for sympatric common shrimps *Crangon crangon* (Hubert et al. 2018). Moreover, there can be carryover effects into other areas: for example, grasshoppers and odonates were less common at sites where their avian predators had moved when avoiding noise elsewhere (Senzaki et al. 2020b). Thus, there can be 'winners' and 'losers' within communities exposed to anthropogenic noise, and noise pollution can reverberate through wider communities by disrupting or enhancing interspecific interactions and ecological services.

2.5 The future

2.5.1 Greater understanding of noise impacts

Compared to 20 years ago, we now have a much greater understanding of the impacts of anthropogenic noise on wildlife. But there are still important gaps in knowledge where additional work is crucial. I highlight three general ones here, which are not mutually exclusive: expansion in scope, mechanistic underpinnings, and multistressor effects.

Behavioural studies of the impacts of anthropogenic noise would benefit from an expansion in various respects. First, there is still a taxonomic bias towards vertebrates in general (Morley et al. 2014) and to birds and marine mammals in particular (Shannon et al. 2016; Jerem and Mathews 2020). Second, most field studies have been conducted in Europe or North America, and there is a relative dearth of work both in nations with developing or emerging economies, and in rural areas likely to experience imminent major increases in urbanization (Jerem and Mathews 2020). Ideally, there would therefore be both a taxonomic and geographic expansion in knowledge, especially in biodiversity hotspots that likely have little prior exposure to anthropogenic noise and thus where new human activities might have the greatest initial effect. Third, as indicated earlier, additional work would usefully explore variation in responses to noise—for instance, how members of the same species are affected by different noise sources, and how the same noise source can have different impacts on individuals of the same and different species—and what causes this variation (see Harding et al. 2019). Using existing studies to extrapolate likely effects of noise will always be difficult but is made especially challenging at present because our understanding of intraspecific and interspecific variation is so limited. Fourth, there is a need for more research that measures the longer-term effects of noise exposure, including quantifying survival and reproductive success, because there can be changes in behaviour with chronic exposure and, ultimately, individual fitness consequences underpin population viability. Finally, further investigation of how interspecific interactions are affected by noise would be beneficial. Assessment is needed of the benefits and costs to both parties (e.g. predator and prey, host and parasite, two competitor species), not only because this is important in its own right—all animals interact with others throughout their lives—but because it is a stepping-stone to understanding the community-level effects. Whilst early studies of impacts of anthropogenic noise on wildlife understandably focused on short-term effects of acute exposures, the goal now is a more holistic knowledge from individuals to ecosystems.

For a fuller understanding of the behavioural impacts of anthropogenic noise, we need more detailed studies of the mechanistic underpinnings. At one level, 'mechanism' can refer to whether a behavioural response results from masking, distraction, threat, and/or stress (Table 2.1). Studies explicitly teasing apart which of these is the underlying reason for a noise-induced change in behaviour are currently rare (Zhou et al. 2019). Another mechanistic level concerns physiological, neurological, developmental, cellular, immunological, and genetic processes (Kight and Swaddle 2011). Whilst an extensive literature exists on how these might be affected by different environmental noises, a more integrated, interdisciplinary approach marrying such research with behavioural work would be of benefit. There is also a need to establish more fully the interplay between the sound-detection capabilities of a species and the acoustic characteristics of noise sources that cause (detrimental) impacts (Kunc et al. 2016); establishing the link between hearing mechanisms and vulnerability to noise. Understanding the mechanisms of noise impacts is important because it can help not only to predict effects but also, potentially, to propose successful mitigation methods and noise-management plans (Kight and Swaddle 2011; Francis and Barber 2013).

Anthropogenic noise is rarely, if ever, isolated from other forms of human disturbance, but there is a dearth of studies investigating multi-stressor effects on behaviour (reviewed in Halfwerk and Slabbekoorn 2015; Chapter 10). Major sources of human-made noise often generate other stressors too: for instance, urbanization concurrently modifies temperature, light, and noise levels, whilst roads and their associated traffic don't just add noise to the environment but also artificial light, chemical pollution, and the risk of collisions. More generally, animals do not experience anthropogenic noise in isolation, but must simultaneously cope with other major disturbances (e.g. climate change, habitat destruction, ocean acidification). The effects of multiple stressors could be additive, multiplicative, synergistic, or antagonistic, or one stressor could dominate another (Halfwerk and Slabbekoorn 2015; Harding et al. 2019). Attempting to extrapolate likely combined responses from single-stressor studies is difficult because, whilst populations might show no adverse effects from individual pollutants, the addition of another stressor may cause a markedly different response or take individuals beyond their physiological limit (Côté et al. 2016). Furthermore, other anthropogenic changes can affect noise-pollution levels and thus their effects: for instance, ocean acidification results in decreased water pH, which reduces sound absorption, whilst increasing temperatures lead to a reduction in the speed at which sound travels through the ocean (Kunc et al. 2016). Studies investigating how other stressors modify the impacts of anthropogenic noise on wildlife are therefore crucial but are currently rare (for exceptions, see McMahon et al. 2017; McCormick et al. 2018a; Senzaki et al. 2020a).

As much as possible, any such future research needs to record and to make available accurate and relevant measures of sound sources; without this information, comparisons between studies are challenging (see McKenna et al. 2016). In terms of relevance, those recordings need to be of sound pressure, particle motion, and/or vibrations depending on the species in question. Full reporting of acoustic metrics includes, for instance, information on natural and playback power spectra or frequency (e.g. range and peak levels), equipment specifications, and reference levels; ideally, sound files would be publicly shared (see Jerem and Mathews 2020). As with any research field, and with anthropogenic noise studies to date, a range of data-collection approaches will continue to be beneficial because that provides a complementary understanding of different aspects of noise effects. For example, tight control of extraneous variables might only be possible in captive situations, but then there are the inherent limitations relating to restrictions on how animals can and do behave, as well as the sound field generated (especially in aquatic studies in small tanks). Field studies can provide both acoustic and ecological relevance, but are logistically often much more challenging. To isolate the importance of noise per se, experimental (or pseudo-experimental) tests are required. Ideally, there might be a combination of different approaches in the same study—the most appropriate will depend on the exact question being asked—although cost and feasibility will also play a part in the decision-making.

2.5.2 Mitigation and management

Noise pollution is unusual in the sense that it does not linger in the environment once the source is removed (compared to, for instance, chemical pollution). Also, noise levels can be potentially lessened much more quickly than other pollutants, as evidenced during lockdowns associated with the COVID-19 pandemic (Lecocq et al. 2020; March et al. 2021). Moreover, it is plausible to reduce the effects of noise pollution on a local scale (compared to, for instance, climate warming), with potentially short- and long-term benefits. Whilst there is increasing evidence that various mitigation options—both technological and behavioural—lead to less noise entering the environment, it is crucial to test explicitly whether there are improvements for wildlife and then to scale-up for longer-term and broad-scale management plans.

Technological innovations can help to lessen noise from human activities and its impact on wildlife in various ways. First, there can be reduction of noise generated by the source: for instance, engineering of quieter engines, propellors, tyres, road surfaces, and pile-driving foundations. Some experimental work has shown that this can be beneficial to animals: for example, the negative impacts of two-stroke motorboat engines on the behaviour of Ward's damselfish *Pomacentrus wardi* were lessened or eliminated by replacement with four-stroke engines, which are more fuel-efficient and quieter (McCormick et al. 2018b). Similarly, the use of electric engines rather than petrol-driven ones reduced avoidance behaviour in various terrestrial mammals (Yosef et al. 2021). A second type of technological mitigation involves the inclusion of sound barriers, such as baffles alongside roads and bubble curtains around pile-driving units, to reduce the sound energy propagated into the environment. As one example, using bubble curtains around the monopiles in a windfarm construction project resulted in an approximate halving of the displacement distance of harbour porpoises *Phocoena phocoena*, thus minimizing the temporary loss of habitat for these animals (Dähne et al. 2017). A third means by which technology can lessen anthropogenic noise impacts is through either the 'soft start' of noisy activities or the use of acoustic deterrent devices (ADDs). The purpose of both is to reduce the likelihood of animals being in the vicinity of high-intensity human-made noises, thus mitigating exposure levels without changing the sound field itself. For instance, reductions in initial piling energy and pre-exposure to ADDs reduced the likelihood of harbour porpoises being present in zones where the noise would cause injury (Thompson et al. 2020). As yet, studies directly testing such benefits are relatively rare; technological mitigation measures are also expensive and time-consuming, so alternatives need consideration.

As a potentially cheaper and faster way to reduce noise impacts, there is the option to change human behaviours such as slowing down traffic, moving sources further away from vulnerable areas, and stopping activities at crucial times (e.g. the breeding season or during migration). As with technological solutions, there is a need to test not only how such modifications decrease sound propagation but, crucially, whether there are discernible benefits to wildlife. Lockdowns used in an attempt to control the spread of COVID-19 reduced noise in urban areas considerably—for example, due to greatly reduced traffic and construction activity (Hasegawa and Lau 2022)—providing a 'natural' experiment. As a specific example of how that affected wildlife, white-crowned sparrows responded by producing higher-performance songs at lower amplitudes, effectively maximizing the salience of their vocalizations and the distance over which they communicated (Derryberry et al. 2020). Away from lockdowns, Nedelec et al. (2022) used field and laboratory experiments to test how limiting motorboat traffic, and associated noise, could potentially have a positive effect on coral reef fish reproductive success (Box 2.1a). Successfully lobbying for such changes in human behaviour is far from easy though. So, it may also be sensible to consider the potential for mitigating noise impacts on animals through the use of learning principles: using classical and operant conditioning to alter the behaviour of wildlife to minimize their risks (see Proppe et al. 2016). As one hypothetical example, which would need careful testing to determine the direct and indirect consequences, playback of a positive, biologically salient stimulus (e.g. conspecific song) could be paired with road noise to reduce fear responses induced by the latter (Proppe et al. 2016).

As we move forward with tests of mitigation measures, it must be kept in mind that the benefits might not always be immediate. Some species may have the capacity to exploit quieter soundscapes rapidly, with discernible behavioural changes. These may, in turn, translate into positive demographic effects and higher species diversity, but such consequences will take time to manifest. There may also be slower but equally important recoveries, so long-term monitoring is critical, especially when scaling-up from behavioural effects to those at the level of populations and communities (Phillips et al. 2021). Modelling of the projected impact of mitigation measures, in addition to noise propagation and its effects, is thus important too (Barber et al. 2011). Ultimately, national or international legislation limiting noise levels is required, but determining the most appropriate level is dependent on increasing our knowledge about variation in noise impacts between individuals, species, and habitats (Box 2.1b).

Box 2.1 Illustrations of how scientific studies are crucial for the design of suitable mitigation and management policies relating to noise pollution

(a) Changes in human behaviour to reduce noise pollution

Potentially the fastest way to reduce noise pollution in an area is through a change in human behaviour: a decrease in occurrence or spatial shift in the noise-producing activity. For this to be viewed as a viable option, studies are needed that test the benefits to wildlife. As a specific example, Nedelec et al. (2022) conducted a season-long field manipulation where they limited motorboat activity near some coral reefs in comparison to other reefs that received typical traffic levels. They coupled this fieldwork with a laboratory playback experiment to isolate the importance of reduced noise rather than other aspects of motorboat disturbance. Reducing noise resulted in greater reproductive success of the fish study species (spiny chromis *Acanthochromis polyacanthus*): individuals on the reduced-noise reefs were almost twice as likely as those at busier motorboat sites to have surviving offspring at the end of the breeding season, likely due to improvements in parental care. More such studies are required to build a convincing case that could then be used to persuade those engaged in a noise-generating activity (in this case, motorboat use) that a change in behaviour would be beneficial. In this particular instance, there is not necessarily the need for a human activity to cease; rather, some limiting of traffic speeds and/or proximity to vulnerable habitats would make a positive difference. Moving forward in this regard will require a delicate balancing of wildlife protection and human needs, but it will necessarily be best-informed by rigorous science.

(b) Noise levels in policy

If noise pollution is to be managed at a national or global scale, then policy-makers will need to set cumulative noise limits. One early example of this in relation to ocean anthropogenic noise was the Marine Strategy Framework Directive, which required members of the EU to attain noise levels 'that do not adversely affect the marine environment'. Of course, there is the immediate question about what those levels actually are; without defined targets, then coordinated, focused action is impossible. To manage noise pollution requires: (a) quantification of risk (e.g. production of risk maps and modelling of the population consequences arising from different noise scenarios); and (b) setting of scalable noise-budgets that are conveyed to decision-makers. Merchant et al. (2018) describe a possible framework: using noise-exposure curves to quantify the proportion of a habitat or population exposed, and thus associated exposure durations that would be deemed acceptable given current knowledge of impacts. This 'indicator' methodology can then be the basis for both location-based and ecosystem-based management measures. Merchant et al. (2018) showcase the applicability of this approach with two case studies, using data from an international assessment of cumulative impulsive noise activity in the North Sea to predict the risk to harbour porpoises *Phocoena phocoena* and to herring *Clupea harengus* spawning. One of the benefits of this risk-based approach is that it is flexible—new scientific knowledge about noise levels and their impacts on wildlife can be assimilated quickly, allowing adjustment to statutory commitments.

2.6 Conclusions

We have known for a long time that anthropogenic noise has a range of detrimental effects on humans. Research in the last two decades has demonstrated that non-human animals in all taxa also suffer from our noisy activities. These negative impacts on wildlife extend from individual and social behaviour to consequences for survival, reproductive success, population viability, community structure, and ecosystem functioning. But there is cause for cautious optimism. Animals have always lived in a world full of sound, so they are capable of adaptation when given the chance. Moreover, there are simple starting solutions that can help quickly and on a local scale. What is needed moving forward, therefore, is both an increasing understanding of the problems and increased testing and refining of mitigation and management policies. Mitigating and managing anthropogenic noise is important not only in its own right—it is a pollutant found in all ecosystems throughout the world—but because building resilience in this respect may help wildlife 'fight' against other human disturbances for which we do not necessarily have such potentially rapid solutions.

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