

Chapter 1

Man-Made Sounds and Animals



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Abstract The world is full of sounds of abiotic and biotic origin, and animals may use those sounds to gain information about their surrounding environment. However, it is becoming increasingly clear that the presence of man-made sounds has the potential to undermine the ability of animals to exploit useful environmental sounds. This volume provides an overview of how sounds may affect animals so that those interested in the effects of man-made sounds on animals can better understand the nature and breadth of potential impacts. This chapter provides an introduction to the issues associated with hearing and man-made sound and serves as a guide to the succeeding chapters. Chapters 2, 3, 4 and 5 cover the basic principles of sound and hearing, including an introduction to the acoustic ecology of the modern world in which man-made sounds have become very prominent. They also address how noisy conditions may hinder auditory perception, how hearing adaptations allow coping under acoustically challenging conditions, and how man-made sounds may damage the inner ear. The role of sound propagation in affecting signals and noise levels is treated for both terrestrial and aquatic habitats. This chapter also provides an overview of hearing and the effects of sound on particular taxa, which are the focus of Chaps. 6, 7, 8, 9, and 10. Those chapters address the concepts and insights in five different vertebrate taxa: fishes, amphibians and reptiles, birds, terrestrial mammals, and marine mammals. The overall aim of this volume is to stimulate and guide future investigations to fill in taxonomic and conceptual gaps in the knowledge about how man-made sounds affect animals.

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1.1 Introduction to the Volume

1.1.1 *The Problem*

The past decades have seen increased interest in questions concerning the effects of man-made sounds on animals (e.g., Fletcher and Busnel 1978; Popper and Hawkins 2012, 2016). The overall issue, however, is not new, especially with regard to the potential effects of sound on humans. Indeed, a few years ago, the World Health Organization published a report on the topic (World Health Organization 2011), and the issue of potential effects of noise on humans has been the subject of much research and regulation (e.g., Le Prell et al. 2012; Murphy and King 2014). Moreover, it is now quite clear that many of the issues associated with the potential effects of man-made sound on humans (Miedema and Vos 2003; Basner et al. 2014) apply equally to animals (Francis and Barber 2013; Shannon et al. 2016).

The increased concern about the effects of man-made sounds on animals arises from the substantial increase in environmental noise produced by everything from roadway traffic to airplane overflights and from vessel noise to offshore exploration for oil and gas (Andrew et al. 2002; Mennit et al. 2015). The nature of these sounds varies dramatically, from the brief or intermittent high-impact signals produced by destruction or construction activities to the continuously increased background sound levels due to gradually fluctuating amounts of car and vessel traffic (e.g., Singh and Davar 2004; Hildebrand 2009).

The potential effects on animals (as on humans) also vary rather substantially, from immediate death due to overexposure from extremely intense sounds to changes in physiological stress levels that may or may not have long-term consequences. The potential effects may also range from temporary or permanent hearing loss to behavioral changes that result in animals interrupting activities or leaving their normal home range (Kight and Swaddle 2011; Popper and Hawkins 2016).

Additionally, more subtle man-made sounds may make biologically important signals or cues inaudible due to masking or may undermine optimal reception by distraction, which are effects that may have indirect but severe, detrimental consequences (Slabbekoorn et al. 2010; Shannon et al. 2016). Not being able to hear or pay sufficient attention to conspecific communication signals may mean missing important social aggregations or mating opportunities. Failing to recognize acoustic cues from the surrounding habitat may also result in the inability to find shelter or the right migratory route. Not hearing prey may prevent animals finding food. Not detecting a predator may even lead to sudden death.

The distribution and probability of potential effects on free-ranging animals can be viewed from different perspectives as reflected in the diversity in schematic

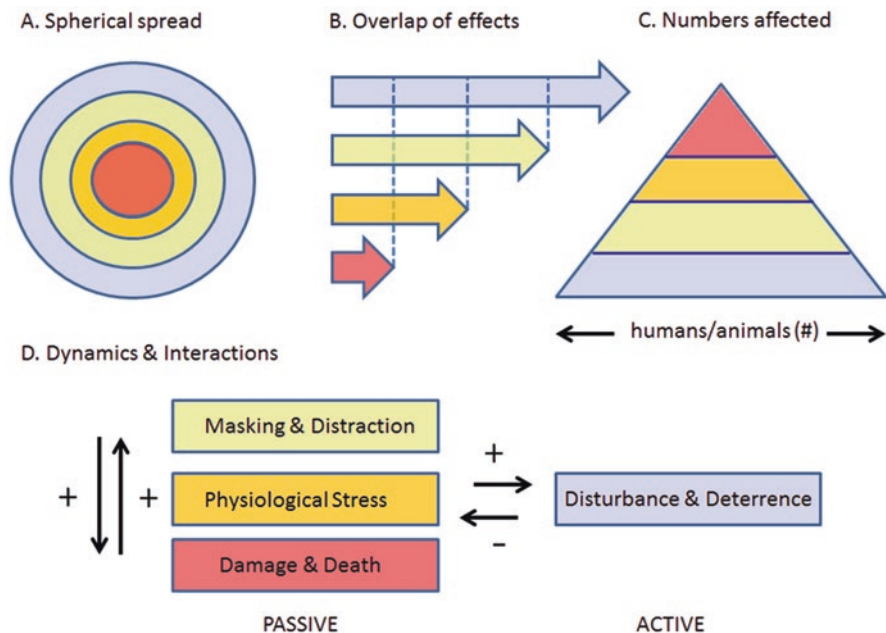


Fig. 1.1 Schematic illustrations providing insight into the nature of potential impact of man-made sounds on animals and emphasizing different aspects. **A:** noise impact severity is likely to decrease with distance away from the sound source in all directions due to propagation loss of sound energy via spherical spread (based on Richardson et al. 1995). **B:** the variety of potential effects accumulates with proximity to the sound source because the effects typically do not exclude each other but exhibit zones of overlap (see Hawkins and Popper, Chap. 6). **C:** a pyramid of noise-induced health effects, with the growing severity of the effect toward the top segment and the growing number of individuals that are likely to be affected toward the bottom segment (Babisch 2002). **D:** some potential effects are an inherent and passive consequence of sound exposure, whereas others depend on an active response of the animal itself (from Slabbekoorn 2012). Many potential effects are likely to be positively correlated (*up and down arrows and arrow to the right*). If exposure causes severe impact in one direction, it will likely do so in the other. However, a negative correlation may arise by negative feedback (*arrow to the left*) when an active behavioral response makes animals less vulnerable in other ways

representations (see Fig. 1.1). Increasing the distance from the source is almost always correlated with lower exposure levels, less severe effects, and less different overlapping effects (Richardson et al. 1995; Hawkins and Popper 2016). However, as severity goes down at the individual level, the potential effects at the community or even population level may go up as the number of individuals exposed becomes larger (Babisch 2002; Kunc et al. 2016). Some effects are an inherent consequence of passive exposure, whereas other effects only arise after an active decision by the animal itself (Slabbekoorn 2012). Furthermore, different overlapping effects may not only occur together, but they are also likely to covary and may have positive or negative feedback interactions.

1.1.2 Learning from Other Studies

Over the past several years, many investigators interested in the effects of man-made sounds on particular animal groups (e.g., fishes: Hawkins et al. 2015; marine mammals: National Research Council 1994, 2000) have come to realize that there is much to gain from studying the broader literature on hearing and on the potential effects of anthropogenic noise, including the effects of noisy indoor or outdoor conditions, on humans. It has also become clear that knowledge of the effects of sound on one group of animals (e.g., birds or frogs) can guide studies on other groups (e.g., marine mammals or fishes) and that a review of all such studies together would be very useful to provide a better understanding of the general principles and underlying cochlear and cognitive mechanisms that explain damage, disturbance, and deterrence across taxa.

The editors of this volume therefore decided that a comprehensive review would fulfill two major needs. First, it was thought to be important to bring together data on sound and bioacoustics that have implications across all taxa (including humans) so that such information is generally available to the community of scholars interested in the effects of sound overexposure and pollution. Second, the purpose of this volume is to bring together what is known about the effects of sound on diverse vertebrate taxa so that investigators with interests in specific groups can learn about the data from other species as well as about the experimental approaches used to obtain the data. Put another way, having an overview of the similarities and differences among various animal groups and insight into the “how and why” will benefit the overall conceptual understanding, applications in society, and future research.

Accordingly, this volume has two parts. Chapters 2, 3, 4, and 5 discuss the fundamental principles of sound and how noisy conditions may hinder auditory perception and how perceptual abilities, shaped over evolutionary time, can make the best of a potentially bad situation. In addition, damage to the inner ear after exposure to loud sounds for substantial periods is addressed, along with its consequences for hearing and conditions for complete or partial recovery of auditory function. How sounds propagate through the environment and how attenuation and degradation alter the signals from the senders and the cues from abiotic and biotic sources before they end up at the receivers are also covered.

In Chaps. 6, 7, 8, 9, and 10, the ideas and phenomena addressed in Chaps. 2, 3, 4, and 5 are applied to all major vertebrate taxa. To keep the length of this volume reasonable, it was decided to focus on vertebrates. However, it is recognized that many invertebrates detect sound and use their acoustic environment. This includes insects (Hoy et al. 1998; Montealegre-Z et al. 2012), crustaceans (Montgomery et al. 2006; Filiciotto et al. 2016), bivalves (Wilkens et al. 2012; Lillis et al. 2013), cephalopods (e.g., Mooney et al. 2010), and coral larvae (e.g. Vermeij et al. 2010). Several reviews have addressed these groups and what is known about the effects of man-made sounds although, in fact, very little is known about the effects on invertebrates and this is an area of growing interest and concern, particularly in the aquatic environment (Morley et al. 2014; Hawkins and Popper 2016).

Thus, the variety in hearing abilities and functions found among the vertebrate taxa is already impressive and a challenging but still reasonable and appropriate target for the current overview and integration. The variety of investigations addressed in this volume makes it clear that the basic ideas and principles discussed in the first chapters apply to all these vertebrate taxa treated later and to many invertebrate groups as well. This volume will hopefully stimulate and guide future investigations to fill in taxonomic and conceptual gaps in our knowledge.

1.2 Acoustic Ecology of the Modern World

1.2.1 *Perceiving the Auditory Scene*

Auditory challenges in human-altered environments may be novel selection pressures at an evolutionary timescale, and sound levels may often exceed typical naturally occurring ambient amplitudes. However, so-called competition for acoustic space in itself is not new, and the natural world surrounding animals (and humans) is full of sound (Brumm and Slabbekoorn 2005; Hildebrand 2009). The auditory senses that serve critical functions for survival and reproduction should therefore be regarded as shaped by selection under naturally fluctuating and often noisy conditions (Klump 1996; Wiley 2017). Sounds naturally occurring in the environment include abiotic sounds, generated by wind or rain and by rivers or oceans, and biotic sounds, generated by all members of more or less noisy local animal communities.

Habitat features above and below the water surface determine whether and how sounds originating at one point arrive at receivers and whether and how they may play a role in affecting their behavior (Wiley and Richards 1978; see Larsen and Radford, Chap. 5). Vegetation may attenuate and filter out or resonate and amplify particular frequencies. Sounds may be reflected by the ground below or the surface above, and reverberations may accumulate over distance and with habitat complexity. Industrialization and urbanization have not only added new, diverse sound sources to the modern world (Pine et al. 2016; Shannon et al. 2016) but also dramatic changes in propagation as a result of altered vegetation or novel obstacles and a multitude of reflective surfaces (roads, houses, and buildings; Warren et al. 2006).

In a world full of sounds, there is much to learn about the surrounding environment if these sounds are detected, discriminated, and recognized (see Fig. 1.2) by the appropriate sensory and processing tools (see Dooling and Leek, Chap. 2; Dent and Bee, Chap. 3). Sound is not only highly suitable for eavesdropping on biologically relevant events (e.g., listening for cues of predators or prey) but also for communication among conspecifics (e.g., signals that have evolved by natural selection through the effects on mate attraction or competitor deterrence). For example, sound, unlike visual signals, is not hampered by lack of light or the presence of vegetation and other objects in the environment. Furthermore, although attenuation and degradation during propagation will limit the range of potential use, the resultant

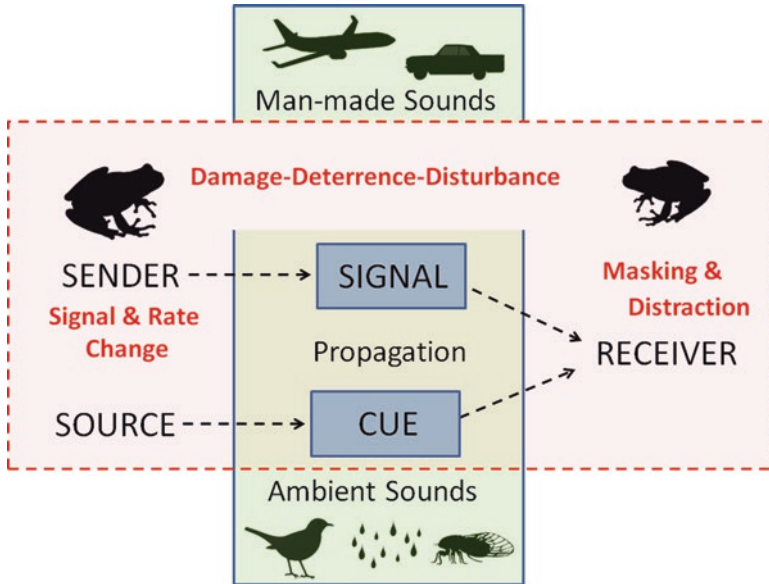


Fig. 1.2 Schematic illustration of the potential effects of man-made sounds in the context of senders and receivers of signals and cues, given the inherent degradation of perceptual potential due to propagation loss through the environment and the presence of natural ambient sounds of biotic and abiotic sources. Note that signals have evolved by natural selection and senders benefit from them being heard by receivers, which is not the case for cues. Man-made noise may cause damage, deterrence, and disturbance to senders and receivers. Senders may alter the acoustic structure of their signal or change the rate of calling or singing under noisy conditions, whereas receivers may be masked or distracted (i.e., informational masking) by the presence of man-made sounds

acoustic changes may also add information about the distance and direction of the sound source (Naguib and Wiley 2001).

Sound is obviously not the only medium by which animals and humans gather information about the world around them (Partan and Marler 1999; Munoz and Blumstein 2012). The visual, chemical, and tactile senses often serve in parallel in affecting auditory perception. Depending on the species, thermal, magnetic, and electrical senses may be added to the multimodal complexity of perceiving the world. Many signals or cues are explicitly multimodal, having, for example, an acoustic and a visual component, which may result in redundancy. This means that relevant information can still be extracted through one channel despite masking problems in the other, and animals have been shown to perceptually shift attention to the sensory information from the channel with the least interference (Pohl et al. 2012; Gomes et al. 2016). However, incoming stimuli in any channel may not only benefit an animal, but it may also interfere with the perception of information in another channel by attentional distraction or by general demands on processing capacity (Chan et al. 2010; Schlittmeier et al. 2015). The study of effects of man-made sounds on signal perception and animal performance is thereby an inherently multimodal discipline (van der Sluijs et al. 2011; Halfwerk and Slabbekoorn 2015).

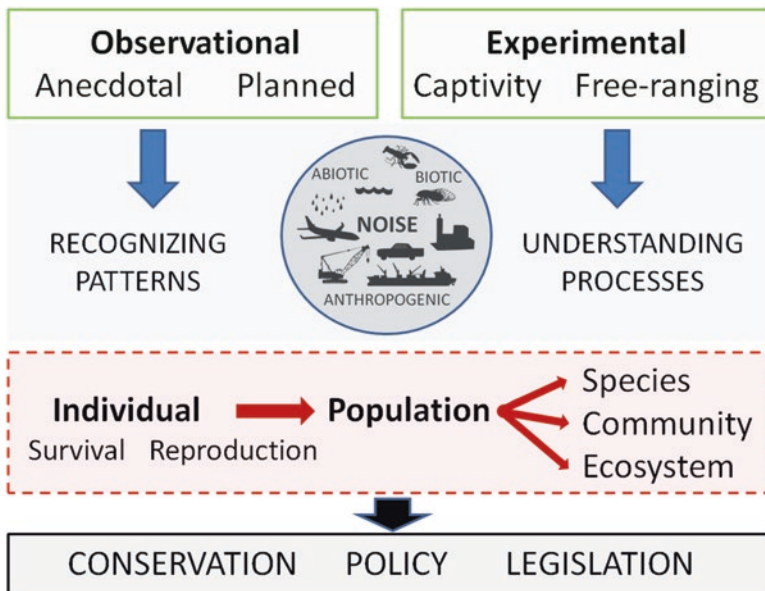


Fig. 1.3 Framework for the nature and contribution of noise impact studies on the understanding and mitigation of potential effects of man-made sounds on animals. Scientific investigations can be observational, ranging from anecdotal reports to planned and well-replicated sampling, or experimental, applying manipulations of sound conditions with replicated sampling and controls, either in captivity or on free-ranging animals in the wild. Observational studies provide correlational data and contribute most to recognizing patterns, whereas experimental data allow interpretations of causation and contribute most to understanding the processes. Both types of data can be combined with theoretical models for extrapolation across space or in time or for evaluation of critical parameters for the effects on survival and reproduction of individual animals. The effects on individuals will accumulate at the population level and potentially have consequences at the level of the species, community, or ecosystem, which can all be critical levels for conservationists, policy makers, and legislators

1.2.2 Studying the Potential Effects of Man-Made Sounds

The investigations into the potential effects of man-made sounds are diverse in terms of the types of studies, the types of effects, and the range of species (see Fig. 1.3). Research interest and awareness of potential problems often start with observational data and reports of anecdotal nature (something seen, somewhere, in some species). As an example, the issue of sonar impact on whale stranding started as anecdotal observations. However, after many observations, it has become clear that sonar use may indeed be associated with stranding whales, but it also has become equally clear that strandings can also happen without any sonar and not all sonar use leads to strandings. Thus, strandings may be caused by but are not inherently linked to sonar use (D’Amico et al. 2009; Zirbel et al. 2011).

After initial anecdotal reports and initial observations, it is important to design a sampling scheme for planned comparisons, with replication of observations at the level of the question (Slabbekoorn and Bouton 2008; Slabbekoorn 2013). If the question is whether man-made sound in one habitat type makes animals behave differently from animals in another habitat type, one should not replicate by sampling multiple individuals at one site of each habitat type but by sampling individuals at multiple sites of each habitat type. For example, to test for noise-dependent song frequency use, great tit (*Parus major*) recordings were collected at 10 city sites and 10 rural sites (Slabbekoorn and den Boer-Visser 2006; see also Halfwerk, Lohr, and Slabbekoorn, Chap. 8). Planned comparisons with a similar replication design have also been reported for sound-dependent monitoring studies on diversity and density (Bayne et al. 2008; Goodwin and Shriver 2011).

The above observations should provide insights into patterns that then raise questions about underlying processes. Experimental studies can then be launched as the next step to proving causation. In such experiments, a single factor can be manipulated, keeping all other factors constant or left varying in the same way as they would have without the experiment. In such a design, a treatment effect provides proof for a causal relationship. Experiments can be conducted in captivity, such as when bats are shown to forage preferentially in a relatively quiet compartment of an aviary instead of an experimentally elevated noisy compartment (Schaub et al. 2008; see also Slabbekoorn, McGee, and Walsh, Chap. 9). They can also be conducted outside at the waterside for frogs or in natural bird territories (Sun and Narins 2005; Halfwerk and Slabbekoorn 2009). Again, if the question requires it, sampling should be replicated on a geographic scale (cf. Mockford and Marshall 2009; LaZerte et al. 2016).

Studies in captivity are often limited in terms of the spatial or social restrictions such that animals may not show a natural behavior or be in a behavioral or physiological state associated with a specific context because it only occurs in free-ranging conditions (Calisi and Bentley 2009; Neo et al. 2016). Studies in captivity also often use a specific subset of test animals raised in captivity or accidentally caught or stranded, which raises uncertainty about generalizability. However, captive studies also have advantages in that the test animals are typically well known (e.g., background, age, size, condition, coping style), available in sufficient numbers for replication, and selected for homogeneity in groups to compare. This type of study is therefore often suitable for investigating processes in the laboratory environment that explain patterns that occur in natural conditions, whereas absolute numbers or the nature of response patterns should not be extrapolated to the natural conditions of free-ranging animals in the wild (Slabbekoorn 2016).

In addition to the limitations mentioned above for studies in captivity, there are also possible difficulties with the acoustic test conditions of captive studies. Reverberant bird cages, speaker limitations in spectrum or level, or sound field conditions in fish tanks can make sound exposure very artificial and unlike anything animals would experience in the wild (Duncan et al. 2016; Rogers et al. 2016; see also Hawkins and Popper, Chap. 6). This obviously makes extrapolation of data

problematic. A similar extrapolation problem also applies to tests done at a single natural location in the wild with unique features or with a single, highly specific sound stimulus (Slabbekoorn and Bouton 2008). However, captive and single-location studies can be useful for investigating mechanisms and help answer fundamental questions. Inherently, studies of different types, on either animals spatially and behaviorally restricted in captivity or free ranging in the natural environment of their own choice in the wild, will never yield straightforward answers to the big questions by themselves. They just provide parts of the grand puzzle that requires complementary insights of both types of study (Slabbekoorn 2016).

Eventually, conservationists, policy makers, and legislators are interested in effects, not at the individual level but at the population or community level (New et al. 2014; Kunc et al. 2016). Detrimental effects of any kind can potentially affect an individual and determine its fitness through an impact on survival and reproductive output. The accumulated effects on all exposed individuals will translate into population-level consequences, which are of interest for the conservation of species, communities, or ecosystems. The societal relevance of sound impacts on animals in nature, farms, zoos, and laboratories is not only providing funding opportunities but is also guiding research interests. This sometimes results in unrealistic targets, such as single dose-response curves for a particular taxonomic group expressed in a sound unit unable to cover the necessary acoustic parameters required for impact assessment (Neo et al. 2014; Farcas et al. 2016). However, it is also the responsibility of scientists to identify such issues and comment on whether applications are appropriate and to gather the information and understanding required for societal needs.

1.2.3 Acoustic Deterrence by Man-Made Sounds: Foe or Friend?

A large part of the literature on the potential effects of man-made sounds on animals concerns behavioral changes and spatial responses in particular, such as moving away or acoustic deterrence (see Fig. 1.4). The sound-induced effects on decisions about movement probably involve a trade-off between reasons to stay and reasons to leave. An animal may stay as it exploits local resources related to feeding or breeding when it is familiar with local risks. However, the sense of fear for predation may be elevated by an unfamiliar sound. The decision about exchanging familiar conditions and certain resources for an unfamiliar and uncertain destiny may be detrimental but will vary with species and context. Furthermore, after repeated or continuous exposure to a sound, animals may habituate and respond less to the same stimulus if they do not experience direct negative consequences (Bejder et al. 2006; Neo et al. 2016). Alternatively, if there is some sort of negative reinforcement, animals may also exhibit sensitization and respond more strongly to subsequent exposure to the same stimulus (Götz and Janik 2011).

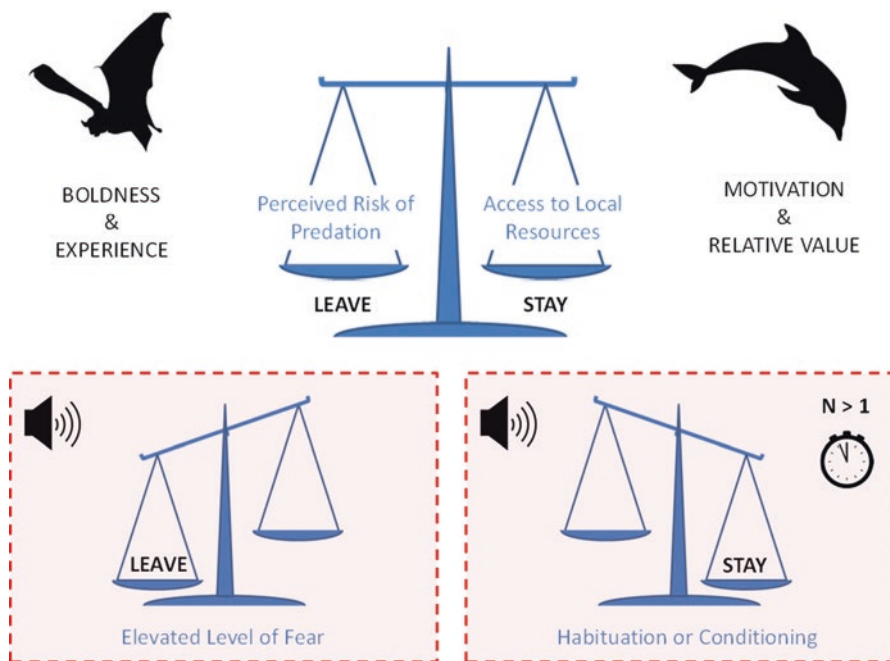


Fig. 1.4 Balance of decision making about spatial behavior in the context of exposure to man-made sounds. Whether an animal leaves or stays in a particular area likely depends on evaluation of the costs and benefits as determined by the perceived risk of predation (Frid and Dill 2002) as well as access to local resources (Sutherland 1983). Hunger or reproductive state may affect the motivation to stay or leave and particularly bold or experienced animals may be less easily frightened than shy and naive animals. The expectations about the relative value of local resources versus those likely to be encountered when leaving will also affect the balance. Exposure to man-made sound may shift the balance to “LEAVE” due to elevated fear or anxiety and make animals move away from the source (*bottom left*). Repeated or long-term exposure to man-made sound (*bottom right*) may cause the balance again to shift back to “STAY” due to habituation. Association between sound and beneficial conditions may result in conditioning and even attract animals toward the sound source (e.g., “dinner bell effect”)

It is also important to realize that species vary in relative site fidelity depending, for example, on their degree of territoriality. And some species are bolder than others and perhaps more resistant to noise pollution than others (cf. Møller 2010; Sol et al. 2013). This means that one has to exercise caution in extrapolating from one species to another because relative tolerance or quick habituation to man-made sounds may reflect a lack of threat from noise pollution in one species but not in another (Tablado and Jenni 2015). Furthermore, it is also possible that relatively resistant species are the same everywhere and that effects of man-made sounds at a community level are not simply reflected in local species diversity. Urban bird communities are, for example, often relatively species rich but typically concern the same set of species in cities that can be far apart. The so-called urban homogenization thereby entails a diversity decline across large areas (McKinney 2006; Slabbekoorn 2013).

One potential problem is that man-made sounds could deter animals from staying in a particular place. At the same time, that sounds can deter animals can be an effective tool to move pest animals from places at which they are not wanted. The need to move pest animals from certain places is widespread. For example, sounds may be useful in moving animals from gardens, agricultural fields, aquacultural facilities, and fishing nets. Animals may become threats to aircraft due to collision, spread disease, or induce direct physical harm or even death to domestic animals or humans themselves. In these cases, the potential deterrent effect of sound exposure to animals may or may not be harmful to the animals but often concerns an application to the benefit of humans. However, experience shows that acoustic deterrent devices currently on the market vary dramatically in effectiveness, in part because animals are flexible and adaptable. The two different types of studies on the deterrent effects of man-made sounds on animals (i.e., as a useful tool or a conservation or welfare problem, as a friend or foe) could possibly benefit from some integration and collaboration.

A few examples from the applied literature on deterrent devices in a wide variety of taxa clearly show several aspects that reflect the studies and insights addressed in this volume. Swaddle et al. (2016), for example, reported positive results in keeping starlings (*Sturnus vulgaris*) away from an airfield using a “sonic net” of sound overlapping their species-specific spectral range. This success is not necessarily the case for all attempts of acoustic deterrence because some species habituate quickly and sometimes people just select inappropriate sound stimuli. Jenni-Eiermann et al. (2014), for example, studied feral pigeons (*Columba livia*) as pests in terms of potential damage to buildings and as hazards to public health. The birds did not show any effect of an ultrasonic deterrent device; there were no changes in corticosterone levels of caged pigeons and no deterring effect on free-ranging pigeons. This should not have been a surprise because ultrasonic sounds are inaudible to humans but are also well above the sensitive range for pigeons.

Deterrent efficiency is reported to vary among species or with the spectral match between sound stimulus and hearing range. Domestic cats, for example, were shown to vary dramatically among and within individuals in their response to an audible (for them) ultrasonic device and did not necessarily avoid the area covered acoustically (Mills et al. 2000; Nelson et al. 2006). Moreover, badgers (*Meles meles*) were not frightened by an acoustic deterrent device and were even reported to be attracted by the sound to sites when it was associated with bait (Ward et al. 2008). Apparently, there are factors that vary among (e.g., age, boldness, strength) and within (e.g., over time, across motivational states, or after experience) individuals that help shape decisions about responses to man-made sounds. Natural recordings of predators or conspecific calls of distress are sometimes better deterrents (e.g., Spanier 1980; Ramp et al. 2011), although occasionally the opposite is found (Yokoyama and Nakamura 1993). It is also true that multimodal stimuli may be most effective and delay habituation best (Lecker et al. 2015).

Acoustic deterrence has also been applied in the aquatic environment, mainly to marine predators and fishes, although not without problems and often only with very limited success (Bomford and O'Brien 1990; Popper and Carlson 1998).

Man-made sounds are, for example, used not only in the context of bycatch and depredation problems but also to keep animals away from potentially harmful human activities such as explosions or pile driving. The so-called “pingers” have been shown to work for some, but not all, marine mammal species, although habituation may limit long-term applications (Cox et al. 2001; Rankin et al. 2009). The application has also raised concerns about unwanted side effects such as hearing loss in target species (Brandt et al. 2013; see also Saunders and Dooling, Chap. 4). Furthermore, acoustic deterrent devices may even become a sort of “dinner bell” when animals learn that the sound is not associated with any danger but with an exceptional aggregation of food (Carretta and Barlow 2011; Schakner and Blumstein 2013). Obviously, more studies are often needed to initially design and repeatedly improve such applications. Fundamental insights about the impact of man-made sounds on animals, as addressed in the following chapters, may serve as a guide and inspiration.

1.3 Chapter Contents

1.3.1 *Basic Principles for Impacts of Noisy Conditions*

Chapters 2, 3, 4, and 5 focus on the basic principles that are applicable to all animal groups, including humans (see Fig. 1.5). Although there is a wide variety of the potential effects of man-made sounds, only directly auditory phenomena (related to hearing and damage to the ear) are treated but not the more indirect consequences of exposure (physiological stress, behavioral deterrence, and disturbance). Many animals use sounds to detect predators and prey and to find partners or deter competitors, all critical matters for survival and reproduction. Thus, it makes sense to consider the impacts of noise pollution in the typical framework used for acoustic communication, with a sender generating a signal (or a source generating a cue) that propagates through the environment before it reaches receivers. Aspects of hearing such as masking and distraction are restricted to the receiver side, whereas damage to the ear can apply to both senders and receivers and thereby affect the production and perception of signals for communication. The fact that signal production can also be affected by noisy conditions without any physical hearing damage will only be addressed in the taxonomically organized chapters that follow after this part of the book.

Chapter 2 by Robert J. Dooling and Marjorie Leek and Chap. 3 by Micheal L. Dent and Mark A. Bee address hearing complications and perceptual strategies under challenging conditions in terms of noisy and complex acoustic environments. As mentioned in Sect. 1.2.1, the natural world is often very noisy so the complications that occur and the strategies used by animals are not novel or special for man-made sounds. Long evolutionary histories and strong selection pressures for hearing particular sounds against a naturally noisy background explain the auditory phenomena

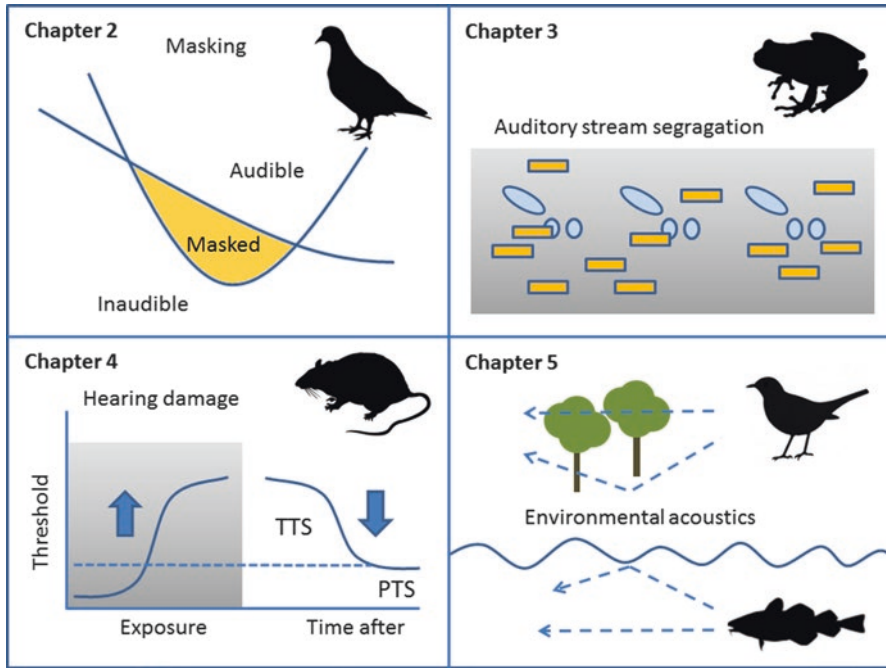


Fig. 1.5 Overview of the core concepts addressed in Chaps. 2, 3, 4, and 5. Chapter 2 by Dooling and Leek: auditory masking, reflected by a hearing curve of detection threshold across frequencies, overlaid by a noise masker with an energy bias toward low frequencies. Chapter 3 by Dent and Bee: auditory stream segregation, depicted by a repetitive, biologically relevant signal amid a scattered background of irrelevant sounds. Chapter 4 by Saunders and Dooling: temporary threshold shifts (TTS) and permanent threshold shifts (PTS) in the auditory detection threshold after exposure for a particular duration. Chapter 5 by Larsen and Radford: environmental acoustics in air and in water, where absorption, scatter, and reflections by objects and surfaces in animal surroundings affect propagation of sounds in a variety of ways. The animal silhouettes reflect potential model species, but the phenomena apply across taxa

reviewed and the wide variety in hearing capacities across animal taxa. In Chap. 4 by James C. Saunders and Robert J. Dooling, acoustic overexposure is addressed, which is obviously less of a natural phenomenon and a matter of physical trauma that is of interest especially in the context of artificial sound impact assessments. Chapter 5 by Ole Næsbye Larsen and Craig Radford is not about hearing or damage but about attenuation and degradation, which are fundamental principles for all sounds propagating through an environment.

Chapter 2 by Dooling and Leek addresses the phenomenon of masking of biologically relevant sounds with a focus on communication sounds. Masking can be defined as the interference of detection of one sound by another. The presence of man-made sounds, at levels above naturally present ambient noise, may result in increased hearing thresholds for detection, discrimination, and recognition of target sounds depending on the overlap in time and frequency. And in humans, there is

another level of hearing that is easy to determine: that of a comfortable listening level. Although this cannot be assessed directly for animals, comfortable listening can be inferred by the relationship between the different levels of hearing. Basic principles are largely shared between humans and nonhuman vertebrates, suggesting that human listeners might actually serve as a proxy for assessing whether a given noise is likely to be detrimental for animals. Laboratory studies on rodents and birds provide a clear picture of the critical features of cochlear processing that explain auditory performance under varying signal-to-noise ratios.

In Chap. 3 by Dent and Bee, the discussion goes beyond masking because they address perceptual mechanisms for extracting relevant signals from a background of potentially distracting sounds. They review how the auditory system is able to decompose the complexity of incoming sound stimuli from the auditory scene around the animal, typically a very heterogeneous scene in space and time. Studies on a wide variety of species, including insects, fish, frogs, birds, and nonhuman mammals, are reviewed. Dent and Bee provide clear evidence that the perceptual grouping of sounds as auditory objects is reminiscent of the perceptual grouping of visual objects, which is best known for humans and is based on Gestalt principles such as proximity, similarity, and continuation.

In Chap. 4, Saunders and Dooling address issues related to acoustic overexposure to sound levels that have the potential to damage the ear and auditory system. Although natural and man-made sounds rarely exceed levels or durations that result in physical injuries, exceptional overexposures can occur when animals are near blast explosions or pile driving or when animals remain for an extended period of time in close proximity to a noise source such as runways with jet aircraft or in waters with relatively long-term seismic surveys. Many comprehensive studies on several rodent species highlight the acoustic parameters that are important in causing damage to the inner ear and yielding temporary or permanent hearing loss (temporary [TTS] and permanent [PTS] threshold shifts).

In Chap. 5, Larsen and Radford cover the physical properties of air and water in terms of sound transmission. Sound properties of biologically relevant sounds and potential maskers are critical for acoustic receivers aiming at detecting signals and cues, but the signal-to-noise ratio matters only at the receiver and not at the source. Attenuation and degradation during propagation through the environment from source to receiver may alter perceptual opportunities and are of critical importance to understand the potential for detrimental effects of man-made sounds, which are affected in the same way as any other sound.

1.3.2 Taxon-Specific Insights for Sound Impact on Animals

After discussion of the basic principles applicable to all animals, Chaps. 6, 7, 8, 9, and 10 provide overviews of the concepts addressed and insights gained from five different taxonomic groups: fishes, amphibian and reptiles, birds, terrestrial mammals, and marine mammals. The chapters cover a wide variety of sensitivities,

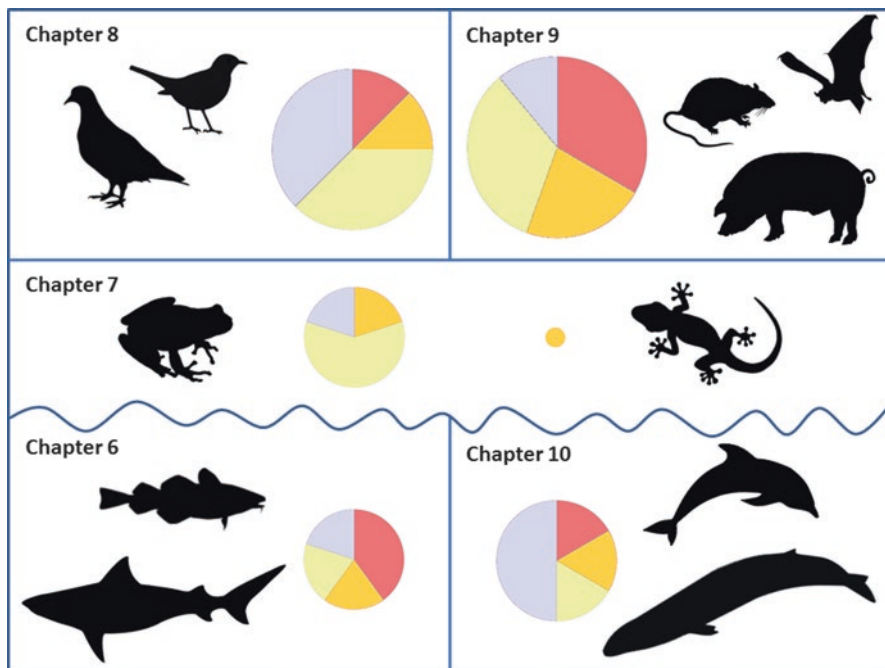


Fig. 1.6 Overview of the taxonomic groups of vertebrates discussed in Chaps. 6, 7, 8, 9, and 10 and an indication of the number of studies published on the effects of man-made sounds in these taxa. Relative size of the pie charts indicates a single or very few to hundreds of studies. The colors in the pie charts reflect the estimated proportion of studies addressing particular effects: *red*, damage and death; *orange*, physiological stress; *yellow*, masking and distraction; *lilac*, disturbance and deterrence. The pie charts are based on the material covered in these chapters: fishes, Chap. 6 by Hawkins and Popper; anurans and reptiles, Chap. 7 by Simmons and Narins; birds, Chap. 8 by Halfwerk, Lohr, and Slabbekoorn; terrestrial mammals, Chap. 9 by Slabbekoorn, McGee, and Walsh; marine mammals, Chap. 10 by Erbe, Dunlop, and Dolman

habitats, contexts, and conditions and include observational as well as experimental studies and investigations of animals in captivity and in the wild, in air and underwater. Despite the variety and number of species addressed, it should be realized that still only a limited subset of species has been investigated and the overall efforts and allocation strategies toward particular effects vary per group (see Fig. 1.6). It also becomes clear in these chapters that the basic principles discussed in Chaps. 2, 3, 4, and 5 are relevant to all species.

In Chap. 6, Anthony D. Hawkins and Arthur N. Popper address what is known about the effects of man-made sound on fishes. This group, which comprises more species than all of the other vertebrate groups combined, is characterized by relative low-frequency hearing abilities, a range that includes the acoustic energy produced by many man-made sound sources such as shipping, pile driving, and seismic exploration. The potential problems of man-made sounds for aquatic animals such as fishes have only recently attracted more attention, which may be due to challenges

for visual and acoustic observations in water. One prominent challenge in assessing problems is related to the fact that all fishes are sensitive to the particle motion component of sound, but only species with a swim bladder can detect sound. This requires adequate measurements and measurement conditions to get the appropriate insights into threshold levels for damage, deterrence, and other potentially detrimental effects. The current insights in this group come from a variety of test conditions, from fixed individuals in captivity to free-swimming individuals in semicaptive conditions to free-ranging fishes in natural water bodies. For many species including sharks (Casper et al. 2012), there is still limited insight into the effects of man-made sounds on behavior and physiology.

In Chap. 7, Angela Megela Simmons and Peter M. Narins address the literature on the effects of man-made sounds on amphibians, which include frogs and toads, salamanders, newts, and the caecilians (limbless amphibians). Frogs and toads are the most prominent species group in terms of vocal behavior and in terms of what is known about hearing and the detrimental effects from man-made noise. This species group also has a relatively long history of studies on noisy chorus conditions and problems for hearing under naturally challenging conditions. The often nocturnally active animals sometimes have to perform under already high biotic noise levels so that man-made sound is not likely to be an issue. However, many studies do suggest effects on distribution and behavior, aspects that are studied the most in this group, whereas the physical and physiological effects are much less investigated. Reptiles are also included in this chapter, but there are actually very few studies on noise pollution and sound exposure in turtles, tortoises, crocodylians, snakes, and lizards.

Birds are the subject of Chap. 8 by Wouter Halfwerk, Bernard Lohr, and Hans Slabbekoorn. The chapter discusses the relatively homogeneous and well-studied songbirds that comprise about half of the 10,000 bird species. Birds are particularly interesting because the typical spectral range of sensitivity is very similar to that of humans. Furthermore, the ability to regenerate hair cells after noise-induced inner ear trauma and (temporary) hearing loss has made birds an attractive model for medical investigations. Besides the laboratory work on damage and recovery and various aspects of masking, there is also a lot of work on wild birds. Birds that are territorial and vocally advertising are well suited for monitoring studies and experimental playback studies. Such investigations have yielded much insight into the effects of man-made sounds on distribution, density, and noise level-dependent signal changes and, recently, to some extent on physiological stress levels, behavioral performance, reproductive success, and ecological interactions. Nonsongbirds, including, for example, doves, parrots, grouse, and hearing specialists like owls, are much less well investigated for the effects of man-made sounds.

In Chap. 9, Hans Slabbekoorn, JoAnn McGee, and Edward J. Walsh address the wide-ranging hearing abilities as well as the wide-ranging types of investigations into the sound impact on the diverse group of terrestrial mammals. The species treated include placental mammals and marsupials as well as the primitive monotremes. Laboratory rodents have traditionally been the model for medical investigations into the auditory system of humans and there are many studies into the

fundamental understanding of hearing, hearing problems, and inner ear damage. There is also a lot known from this work on the nonauditory effects of loud and long overexposure, including aspects of brain development and physiological performance declines. Besides the lab work, terrestrial mammals have been investigated in farms and zoos, particularly for stress and behavioral changes related to noisy holding conditions and visitors. Furthermore, various studies have investigated the impact of traffic noise and industrial and recreational activities on the distribution and foraging activities of a diverse set of small-to-large mammal species in habitat types ranging from boreal pine forests to tropical rainforests. Bats, with their exceptionally high-frequency hearing ranges and echolocation abilities, form a special group that also has been investigated for the various effects of man-made sounds.

In Chap. 10, Christine Erbe, Rebecca Dunlop, and Sarah Dolman address marine mammals, including cetaceans (whales, dolphins, and porpoises) and sirenians (sea cows), that are fully aquatic and several marine carnivores (seals and walrus) that spend time both on land and in water. Like terrestrial mammals, the hearing ranges vary dramatically among species; they can go high in the ultrasonic range and many species echolocate. Marine mammals inhabit all of the world's oceans, including distant offshore waters where some species dive several kilometers deep and shallow coastal waters where the smaller species roam close to the surface. These habitat preferences will likely affect exposure probability. For example, close to the coast are many human activities and therefore more man-made sounds, whereas propagation of low-frequency sounds is more restricted in shallow waters. Furthermore, it is also important to understand whether species generate low-frequency, long-ranging calls like some baleen whales or high-frequency, short-range calls like those produced by many dolphins and porpoises. The conditions for collecting data are among the most challenging of any taxa, but many modern studies include advanced technology such as passive acoustic monitoring, tagged data loggers, and experimental exposure, complemented with studies on animals in captivity.

1.4 Inspiration and Guideline: Ready to Dive into the Book

The editors hope that the targets of this volume will be met and that both parts of the book and all chapters on the various taxonomic groups will be read with equal interest. The questions and issues range from the cellular to the community level and concern both fundamental and applied studies. Some issues and species groups have a relatively long history of investigation, whereas others have just recently come to the forefront and many others remain untouched. Consequently, although many topics are well explored, there are also many gaps in our understanding of how man-made sounds affect animals. It is therefore clear that the future will be bright and variable for studies of man-made sound impact and it is the hope of the editors that this volume serves as an inspiration and guide to that future.

Compliance with Ethics Requirements

Hans Slabbekoorn declares that he has no conflict of interest.

Robert J. Dooling declares that he has no conflict of interest.

Arthur N. Popper declares that he has no conflict of interest.

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