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#### **REVIEW**



# Coping with a changing soundscape: avoidance, adjustments and adaptations

Dominique A. Potvin<sup>1</sup>

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Abstract Since the industrial age, background anthropogenic noise has become a pervasive feature of many habitable environments. This relatively recent environmental feature can be particularly challenging for organisms that use acoustic forms of communication due to its propensity for masking and decreasing the potential acoustic space of signals. Furthermore, anthropogenic noise may affect biological processes including animal interactions, physiological and behavioural responses to stimuli and cognitive development. However, animals' cognitive abilities may enable them to cope with high levels of anthropogenic noise through learning, the employment of acoustic and behavioural flexibility as well as the use of multi-modal sensory systems. We are only just beginning to understand how neural structures, endocrine systems and behaviour are mechanistically linked in these scenarios, providing us with information we can use to mitigate deleterious effects of pervasive noise on wildlife, along with highlighting the remarkable adaptability of animals to an increasingly anthropogenic world. In this review, I will focus mainly on birds, due to the amount of literature on the topic, and survey recent advancements made in two main spheres: (1) how anthropogenic noise affects cognitive processes and (2) how cognition enables animals to cope with increasingly noisy environments. I will be highlighting current gaps in our knowledge, such as how noise might impact behavioural traits such as

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predation, as well as how noise causes physical damage to neurotransmitters and affects stress levels, in order to direct future studies on this topic.

**Keywords** Anthropogenic noise · Communication · Bioacoustics · Urban ecology

#### Introduction

The effect of anthropogenic noise on animals is currently a hot topic, especially in the behavioural literature. Researchers around the globe are investigating how humans are changing natural acoustic environments and implications for the conservation of species and for biological processes as a whole. Fields as diverse as evolutionary biology, neurology and physics are all contributing to a growing body of literature on the subject. However, most of the research into how animals cope with rising levels of anthropogenic background noise tends to focus solely on adjustments to behaviours, and more specifically, communication patterns. Interestingly, noise has the potential to impact many facets of animal life history and physiology, including cognitive processes. This review aims to focus on the impacts of anthropogenic noise on animal cognition, including the underlying neurobiological, physiological and consequential behavioural changes we see in animals in an increasingly noisy world.

Noise, of course, is a natural part of most landscapes: environments often consist of soundscapes made up of both abiotic (e.g. water, wind) and biotic (e.g. animals) sources of sound. Any sounds that are part of the landscape yet not necessarily directly relevant as sources of information can be termed "background noise". For animals relying on acoustic signals, such noise may have implications for



<sup>☐</sup> Dominique A. Potvin dominique.potvin@anu.edu.au

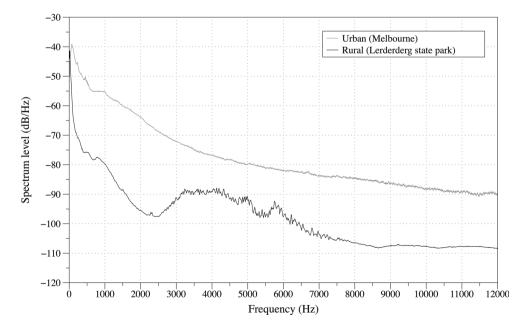
Research School of Biology, Australian National University, Canberra, ACT 0200, Australia

communication, the severity of which will depend on the energy present in the noise, as well as the acoustic abilities of the species or individuals in question. Given that effective acoustic communication involves the transmission of information via sound energy through the environment, a soundscape may impact the fidelity of a signal as well as the distance it is able to travel. There is evidence that many animals have been adapting acoustic communication characteristics over many generations for effective transmission through their local environments (Acoustic adaptation: Morton 1975). A now classic case of acoustic adaptation has been found in populations of satin bowerbirds (Ptilonorhynchus violaceus) across the continent of Australia, which lower the complexity of their vocal signals in denser habitats due to the tendency of trees to degrade complex signals resulting in loss of information (Nicholls and Goldizen 2006).

Acoustic adaptation over generations is one mechanism by which the acoustic properties of a signal might change over time to become more efficient or effective in a noisy environment. Additionally, within an individual's lifetime strategies for increasing signal quality may be similarly employed over a shorter term. Immediate adjustments to current acoustic surroundings allow animals to cope with noise and effectively send or receive signals (or acoustic cues, e.g. from a predator or prey item), especially when noise levels might be variable or unpredictable. An increase in the active space of a signal (the distance a signal can travel) can be achieved by avoiding certain highenergy frequencies present in the environment. This can be done by signalling at either a higher or lower frequency to avoid masking, one of many strategies—including precise timing of signals—employed by old-world frogs competing for acoustic space in a species-rich community (Garcia-Rutledge and Narins 2001). Of course, a more immediate strategy is to signal more loudly (i.e. with more energy) when background noise increases; a psychoacoustic phenomenon known as the Lombard effect (Lombard 1911). Many species—from domestic cats (Felis catus) to Japanese quail (Coturnix coturnix japonica) and humansdemonstrate this reactive behaviour by communicating louder when they detect an increase in background noise (Brumm and Zollinger 2011). Such strategies are particularly important when the noise profile of a natural environment undergoes a major shift, as when a species colonizes a new environment. The spectral (frequency) divergence of acoustic signals to avoid masking has been observed, for example, when a new species of Darwin's finch settled a new island previously inhabited by heterospecific finches (Grant and Grant 2010).

Since the industrial age, humans have altered existing natural soundscapes to an extent whereby effects are almost ubiquitous. Anthropogenic noise sources are not only pervasive in human-dominated areas, but also reach uninhabited areas, due to our tendency to build and use infrastructure such as roads or flyways within or surrounding naturally conserved landscapes. Anthropogenic noise differs from natural background noise in certain key characteristics. It contains much more energy, and this energy as well as frequency can be either quite variable over time (as with airports, or roads that experience peak hours) or consistent (as with industrial noise or city centres; Bucur 2006; Warren et al. 2006). Such noise, including that from air and road traffic, has a very specific energy spectrum with most of the energy concentrated at low frequencies (Fig. 1). As a result, many landscapes are

**Fig. 1** Typical noise profiles (morning hours, between 0600 and 1000) of an urban park (Melbourne, Australia) and a rural park (Lerderderg State Park, Australia). Spectrum level refers to the energy present in the background noise at each frequency (*x* axis). Figure taken from Potvin et al. (2014)





quickly becoming homogeneous not only in structure (for example, the replacement of woodlands, swamps and pastures with urban infrastructure) but also in soundscape (i.e. the replacement of diverse natural sounds with stereotypical anthropogenic noise). It should be noted that stereotypical anthropogenic noise can have implications for previously undisturbed biotic communities even in the absence of pervasive physical urban landscape changes, for example, in cases where oil pipeline compressors or other industrial infrastructure passes through natural areas (Habib et al. 2007; Ware et al. 2015).

When animals are faced with new industrial, traffic or other anthropogenic noise sources as a consequence of human development, there are three main strategies for an individual or population to maintain efficiency in the communication of acoustic information or mitigate other negative effects of noise: (1) avoidance of the noise source either temporally or spatially; (2) immediate or short-term modification of acoustic signals made in the presence of noise (i.e. flexibility or plasticity); or (3) long-term (cross-generational) selection of a portion of existing acoustic signals that are most efficient in the current noise environment (i.e. adaptation). Of course, these strategies are not necessarily mutually exclusive. For example, individual animals may signal louder when needed (immediate flexibility), but also produce some particular signals that travel better in a noisy environment than others, and that are therefore selected for over generations (cross-generational adaptation; Luther and Baptista 2010; Luther and Derryberry 2012; Potvin and Parris 2013). Additionally, in some cases noise may not only impact signal transmission, but also have detrimental effects on the auditory, neural or endocrine systems of individuals (Blickley and Patricelli 2010; Iyengar and Bottjer 2002; Kight and Swaddle 2011; Kujala and Brattico 2009; Wright et al. 2007; Zevin et al. 2004). In these cases additional strategies to those above may be required, to ensure survival of individuals and populations—further detail regarding such effects and strategies will be discussed below.

Much of the research into the effects of anthropogenic noise on animals—and their resulting responses—has been performed on birds, especially passerines (as reviewed in Barber et al. 2010; Blickley and Patricelli 2010; Brumm and Slabbekoorn 2005; Francis and Barber 2013; Kight and Swaddle 2011; Rabin et al. 2003; Slabbekoorn and Halfwerk 2009). Birds are particularly suitable models for such studies because of their use of acoustics as part of many essential reproductive and survival processes, including various forms of communication and predator—prey interactions. They also allow for comparative studies on community compositions (Francis et al. 2011; Peris and Pescador 2004; Slabbekoorn and Halfwerk 2009). The

neural mechanisms underlying their behaviours are also well described: we have a good understanding of cognitive processes such as song learning in passerines (Brainard and Doupe 2002), and how these relate to the ecology of species, allowing us to test specific hypotheses about how noise affects biology, potential coping mechanisms and responses. For example, many songbirds use syllables or memes that are population-specific and geographically variable; investigations into how the use of these memes change over time as noise levels change can reveal how noise might select for certain acoustic patterns (Luther and Derryberry 2012). In addition, the ability of passerines to learn song has been of particular interest, since it highlights the possible importance of behavioural flexibility in coping with new acoustic environments. It should be noted that research into the effects of anthropogenic noise on many other taxa is gaining ground, especially with marine mammals (Tyack and Janik 2013), invertebrates (Morley et al. 2014) and anurans (Narins 2013). However, as earlier stated, much of this review will focus on avian research, simply due to the current state of the field. Although this is not-by far-the first examination of the impacts of noise on animal behaviour, especially birds (see references above), previous reviews focus predominantly on behaviour and ecology of species or wild populations. There is a prominent gap in the literature collating research from studies focusing on internal mechanisms—especially the role of cognition—that underlie the behavioural changes we observe in wild animals occupying noisy environments. The remainder of this review, therefore, first investigates ways in which noise affects individuals and populations in terms of cognitive processes and their development, and subsequently highlights the role of cognition in helping animals cope with anthropogenic soundscapes.

## Part 1: How anthropogenic noise affects cognitive processes

While many studies have documented the effects of anthropogenic noise on signalling, far fewer have investigated the potential consequences of noise on cognitive processes. Elevated background noise such as that made by anthropogenic sources is predominantly associated with chronic behavioural effects (as opposed to acute effects, often caused by loud, short-term disturbances; Blickley and Patricelli 2010; Dooling 2011). The internal mechanisms providing the causal link between behavioural changes and chronic background noise are still under investigation, however. Chronic loud noise can impact the ability to hear by inducing either temporary or permanent threshold shifts (PTS)—a process whereby the eardrum is damaged, effectively narrowing the level at which sounds can be



perceived (Dooling 2011; Dooling and Saunders 1974; Hashino et al. 1988). This may affect the ability of animals to hear, interpret and make decisions based on acoustic information. I propose that such damage may also contribute to findings of urban birds as being less "reactive" to disruptive stimuli—a result most often attributed solely to habituation, but still yet without a definitive, mechanistic explanation (Møller et al. 2015; Valcarcel and Fernandez-Juricic 2009). Research into how PTS might affect vigilance, reactivity, boldness or shyness would therefore be valuable in this context. To test this, a study comparing audiograms of wild birds from urban and rural environments could examine any differences in auditory thresholds based on environment, to detect impairments in urban birds. One can do this either behaviourally or with auditory brainstem responses—and subsequently test personality or behavioural reactivity to both visual (control) and auditory stimuli.

A common assumption made in many studies investigating noise and cognition is that noise is a physiological (as well as environmental) stressor. However, the link between noise, elevated glucocorticoids and cognition is still as yet primarily theoretical. Recently, there has been an increase in the number of studies investigating the effects of chronic noise on circulating stress-related hormones. The stress response—including chronic or acute elevations in glucocorticoids—is an important strategy for animals to cope with external negative circumstances and enables an individual to function in periods of stress by entering an emergency life history stage. However, elevated levels of glucocorticoids have detrimental long-term effects, especially on cognition, learning and brain development (Buchanan et al. 2004; Conrad 2010; Lupien et al. 2009; Spencer and MacDougall-Shackleton 2011). Thus, it appears logical that chronic noise—as a stressor—might impact brain development and cognition negatively, if an animal perceives the noise as a stressor—similar to parasitic infection, unpredictable food supply or increased predator risk (Martin et al. 2011)—and responds by increasing circulating stress hormones over an extended period. Unfortunately, although the connection between stress and brain development—especially in birds—has been reasonably well established (reviewed in Spencer and MacDougall-Shackleton 2011), the connection between noise and glucocorticoid levels remains much less clear, due to limited investigation and controversial results.

Both observational and experimental studies show conflicting results when attempting to link long-term glucocorticoid levels to anthropogenic background noise. Field studies have associated chronically elevated glucocorticoid levels with anthropogenic background noise in whales (Rolland et al. 2012), frogs (Kaiser et al. 2015; Tennessen et al. 2014) and birds (Blickley et al. 2012b). However, this

relationship is not observed in all taxa and has not been found experimentally in either fish or birds (Crino et al. 2013; Grunst et al. 2014; Potvin and MacDougall-Shackleton 2015a; Spiga et al. 2012). Indirectly, noise may affect long-term brain development in juveniles by affecting parental behaviours such as feeding (Potvin and Mac-Dougall-Shackleton 2015b; Schroeder et al. 2012) which may result in nutritional stress (Nowicki et al. 1998). However, this connection is as yet conjectural. Performing parallel captive experiments within the same laboratory comparing the effects of nutritional stress with possible effects of chronic anthropogenic background noise on glucocorticoid levels, brain development and song learning would be useful. Establishing an association between noise and brain development as being mediated by chronically elevated stress responses has been a challenge, and one that may need this type of experimental evidence to hold weight.

Attempts to investigate neural mechanisms underpinning observed behavioural changes associated with changing acoustic environments are currently underway. Currently, most of the research into how chronic noise affects the auditory pathway, brain development and morphology has been performed on humans and to a lesser extent, rats (Cui et al. 2009; Ising and Kruppa 2004). Research on humans has predominantly focused on behavioural symptoms that are used to infer underlying physiological changes; however, there is some direct evidence that chronic noise exposure increases circulating levels of glucocorticoid hormones (Evans et al. 1998; Ising and Braun 2000). More specifically, both lower attention spans and speech control abilities have been found in human patients with chronic background noise exposure (Isling and Kruppa 2004; Kujala and Brattico 2009). In rats, detailed work has been performed on how chronic elevated background noise can affect neural pathways. For example, chronic noise has been shown to affect the hippocampus, namely through increasing excitotoxicity (glutamate levels), and reducing expression of NMDA receptors, with consequences for spatial memory (Cui et al. 2009). In addition, rats treated with chronic noise have demonstrated weight loss (Alario et al. 1987), sleeplessness (Rabat et al. 2005), anxiety and depression (Naqvi et al. 2012). Changes in these behaviours are thought to be related to changes in the activation of neurotransmitters including levels of serotonin, dopamine, norepinephrine and epinephrine (Naqvi et al. 2012; Ravindran et al. 2005). However, again, a comprehensive explanation as to how and why noise affects neurotransmitters is still lacking. Unfortunately, the effects of how chronic noise affects brain pathways associated with cognitive abilities such as learning, communication and memory are thus still largely unknown, and further research—especially on other taxa—is warranted.



In addition to affecting physiological mechanisms, chronic anthropogenic background noise may affect learning ability and cognition in a more direct way. If acoustic signals are required to be taught and learned or transmitted culturally through a population, theory dictates that those signals masked by anthropogenic noise may not be heard by a receiver, and therefore not be learned. Field studies provide some initial support for this hypothesis through the maintenance and loss of certain animal sounds in populations inhabiting noisy environments (Cardoso and Atwell 2011; Derryberry 2009; Luther and Baptista 2010; Potvin and Parris 2013). However, laboratory-based experimentation quantifying what sounds may or may not be learned in certain acoustic environments is in early stages.

In short, the study of effects of chronic anthropogenic noise on animal cognition is still very young. It should be noted that laboratory studies focusing on the effect of chronic noise are, of course, testing only the consequences of remaining in a noisy environment: studies on wild versus captive animals may show conflicting results simply because individuals are free to avoid noisy sites that may impact negatively on processes, if such impacts can be detected. Experimental studies linking anthropogenic noise with brain function in animals, being able to associate chronic noise with quantifiable stress responses and being able to measure how any of these effects ultimately affect behaviours in both the laboratory and in the wild will be valuable in the coming years.

#### Part 2: How cognition allows for coping

While chronic anthropogenic background noise can impact cognitive processes as outlined above, how these impacts translate to many of the behaviours we observe in wild populations living in disturbed areas is still relatively unknown. Regardless of the underlying physiological mechanisms, anthropogenic noise and especially sound masking can have consequences for many biological processes that use acoustic information. These include foraging for acoustically locatable prey (Siemers and Schaub 2011), hearing an approaching predator (Wignall et al. 2011) or intraspecific communication (reviewed in Barber et al. 2010; Francis and Barber 2013; Halfwerk and Slabbekoorn 2014; Slabbekoorn and Ripmeester 2008). These effects can have an impact on reproduction or survival to such an extent that behavioural changes are required-either on a short or long timescale—for population persistence (Blickley and Patricelli 2010; Francis and Barber 2013; Slabbekoorn and Ripmeester 2008). Cognition especially brain functions such as learning, perception and problem solving (e.g. figuring out how to make yourself heard or how to hear others in noisy areas)—can therefore be an important element of such changes and be a considerable advantage for animals to adapt to new acoustic environments. In particular, cognition may play an important role in three major responses that animals exhibit when faced with an increase in anthropogenic noise: avoidance, adjustment and adaptation.

#### **Avoidance**

Studies over the past two decades have revealed changing patterns—notably, the absence of many species—in the species composition of noisy sites. Anthropogenic noise has been found to contribute to low species richness, especially alongside roads (Arévalo and Newhard 2011; Francis et al. 2009, 2011; Proppe et al. 2013). For some species, this may be a result of higher mortality rates, although noise itself has not yet been found to cause direct mortality (except where predators are unable to be heard; Wignall et al. 2011). Body condition, by contrast, especially of juveniles, does appear to be affected in some species (Potvin and MacDougall-Shackleton 2015b; Ware et al. 2015), which may lead to observed patterns of reduced reproductive success in noisy sites (Halfwerk et al. 2011b; Schroeder et al. 2012). Habitat selection theory proposes that animals should avoid sites that are unsuitable for survival and/or reproduction (Hildén 1965). If true, affected populations would no longer remain in noisy environments. However, low survival and/or reproductive success are likely not the only—or even primary—causes of extirpation from noisy areas. If individuals demonstrate plasticity in their choice of habitat (i.e. if they are not compelled to be philopatric or do not have restricted mobility), then noise may simply act as a deterrent, indicating unsuitable habitat. The plasticity of traits (i.e. ability to express multiple phenotypes from a given genotype) has been cited as an important factor for whether animals are able to cope with changing environments (Chevin et al. 2010). While some organisms do not show plasticity in terms of habitat selection, most are able to make site decisions within certain ecological confines. Active avoidance of noisy sites is known to occur, such as when animals in a population disperse and form territories or leks away from noise sources (Blickley et al. 2012a; McClure et al. 2013; Tyack and Janik 2013; Ware et al. 2015). The exact reasons for this behaviour—how much of the noise is perceived and how it contributes to decision making about habitat or territory quality—can still only be speculated upon. There is the suggestion that perception of noise and human disturbance may be similar to the perception of chronic predator threat (Frid and Dill 2002); however, whether similar neural and physiological pathways (i.e. "fear" pathways) are indeed stimulated in both habitat



types is yet to be shown. Tracking studies that are able to follow the movements of animals when making settlement decisions (Clobert et al. 2009) would be very useful in determining how individuals sense and use acoustic information when determining the relative attractiveness of noisy versus quiet sites.

Although spatial avoidance can alleviate some of the impacts of loud anthropogenic noise (especially long term), temporal noise avoidance is also employed by many animals. In the short term, individuals can decide to communicate during breaks in anthropogenic noise if the opportunity exists, a phenomenon known as "gap calling behaviour" as observed in frogs (Narins 2013; Sun and Narins 2005; Vargas-Salinas et al. 2014). Over a longer term, individuals may shift the daily timing of entire choruses to reduce masking by noise that fluctuates in energy: avian dawn choruses, for instance, have been shown to begin earlier to avoid traffic noise peaks (Arroyo-Solís et al. 2013; Fuller et al. 2007; Yang and Slabbekoorn 2014). It seems evident that animals are therefore able to perceive periods when anthropogenic noise is masking communication and are possibly making decisions regarding the best time at which to signal. This perception problem—often referred to as (or compared with) the "cocktail party problem" in humans—is solvable cognitively by both humans and animals using auditory scene analysis. This enables an individual to group sounds in order to segregate and discriminate informative and noninformative signals (for a more detailed description of processes, see Bee and Micheyl 2008). Cognitive ability and behavioural plasticity when making decisions on the current perceived soundscape can therefore allow animals to cope with increases in anthropogenic noise and associated challenges simply through spatial and temporal avoidance.

#### Adjustments

While avoiding an area with high levels of anthropogenic noise might be advantageous in some cases, it may not be advantageous in others nor may it be feasible. Rather, many organisms must cope with the challenges presented by a noisy environment using other strategies, often within their lifetime. Above, plasticity with respect to movement and temporal and spatial habitat selection was discussed. However, in cases where noise is unavoidable, other coping mechanisms may be necessary for survival and reproduction. Learning can be considered a form of behavioural phenotypic plasticity (Dukas 1998) and even the underlying neural changes associated with learning have been found to be phenotypically plastic (Nolfi et al. 1994). For this reason, cognitive ability—such as the ability to learn—may aid animals in coping with anthropogenic noise by

allowing them to adjust behaviours based on experience and environmental conditions. As with avoidance, making adjustments (e.g. to acoustic behaviours) to overcome the negative impacts of anthropogenic noise may occur at different timescales. Immediate assessment of the soundscape can help animals make decisions about adjustments that are required (e.g. for effective communication). As outlined above, many animals signal more loudly when background noise is present (Lombard effect: Zollinger and Brumm 2011). More recently, acoustic flexibility has also been found in other vocalization characteristics: animals may be able to adjust not only amplitude but also the frequency and duration of calls to avoid frequencies present in (and therefore masked by) anthropogenic background noise and to distinguish calls further from background noise (Bermudez-Cuamatzin et al. 2011; Brumm et al. 2004; Potvin and Mulder 2013). Immediate song-type switching has also been observed in songbirds when noise is present (Halfwerk and Slabbekoorn 2009). Instantaneous detection of acoustic environmental changes and the specific behavioural adjustments made in response is indeed effective in counteracting masking effects of noise, demonstrating the advantages of signalling flexibility (Parris and McCarthy 2013). Unfortunately, again, we do not know the specific neural mechanisms that underlie the process of environmental noise detection and signal adjustment: such real-time monitoring of brain activity, even if we know the brain areas involved, is difficult to perform, but may be possible with continuing technological advances.

Adjustments may also be made over longer timescales and more closely resemble acclimation rather than automatic reactive flexibility. Learned behaviours, either through trial and error or imitation, for instance, may be very important in this context (Sol et al. 2013). For example, male songbirds use female responses to certain songs under different anthropogenic noise regimes to make decisions about which signal types to produce (Halfwerk et al. 2011a). Further studies showing changes in song over time possibly due to learning from conspecific responses are ongoing (Potvin and MacDougall-Shackleton 2015a). Phenotypic plasticity may also be advantageous in environment-dependent sexual selection under anthropogenic noise regimes (Montague et al. 2013). In particular, plastic or learned anti-predator behaviours in noisy environments are of particular interest to behavioural ecologists: animals living in noisy environments appear to have a lower threshold for fleeing from danger (Lowry et al. 2011; McGiffin et al. 2013; Meillère et al. 2015), although the exact role of noise as opposed to high human occupancy is still unclear in this context. More research is required investigating behaviours that may be acoustically sensitive—especially anti-predator behaviours, mating signals



and foraging—and how phenotypic plasticity might increase individual and population fitness in noisy environments, when avoidance is unachievable.

#### Adaptation

Cognitive abilities and behaviours are, as are all biological traits, subject to selection. In many cases, it is difficult to distinguish the extent to which behavioural characteristics are genetically heritable and are plastic or learned. In many cases, flexibility and learning may be adaptive traits in and of themselves. As yet the role of noise—especially anthropogenic noise—in directly selecting for genetically heritable traits (cognitive or otherwise) is almost completely unknown. There is some evidence that certain "personalities" or behavioural syndromes such as boldness and risk taking (Naguib et al. 2013; Owens et al. 2012) as well as tolerance of conspecifics (McCarthy et al. 2013; Owens et al. 2012) and humans (McGiffin et al. 2013) may be selected for in noisy environments. However, many of these studies fail to disentangle effects of urbanization/ human development and noise itself.

Acoustic adaptation—the selection process for effective acoustic signalling in certain environments (Morton 1975)—has been shown to occur over generations in disturbed areas. However, in most (if not all) cases this has been attributed to cultural, rather than genetic, evolution. Learned behaviours such as birdsong may change slowly over generations if certain acoustic features are more effective or better heard/learned than others in areas of high anthropogenic noise. Evidence for this process has been found by comparing the use of memes both temporally and spatially in different populations of passerines (Cardoso and Atwell 2011; Luther and Baptista 2010; Luther and Derryberry 2012; Potvin and Parris 2013). It is reasonable to expect that other learned behaviours might be similarly affected by noise across generations—however, again, research into these processes is young.

#### Conclusion

Noise is a natural part of any environment and has been an important element in shaping the acoustic behaviours of many animals. Since the industrial age, human-generated noise has been increasing in its impact in both energy and extent, so as to now be almost completely pervasive, even in the most remote habitats (Blickley and Patricelli 2010; Kight and Swaddle 2011; Wright et al. 2007). Recently, behavioural ecologists have become increasingly concerned with how cognitive processes are affected by this change in soundscape on both an intellectual and a practical level. The application of behavioural and cognitive

research to conservation priorities has also become clear: as animal communities change in highly disturbed areas, we have begun to understand what traits allow certain species to remain while others are extirpated. In this vein, research into how noise might act similarly to other chronic stressors or fear-inducing situations would be valuable. In addition, cognitive research into how noise affects physiological and neurological processes—including the impact of chronic noise on the development of brain structures such as the hippocampus and HPA axis—will aid in attempts to identify what aspects of noise are most harmful to both animals and humans, and hopefully lead towards mitigation. Progress in this field is ongoing, and our current knowledge provides a solid foundation from which to pursue many exciting opportunities.

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