Invited Ideas

Toward a broader characterization of anthropogenic noise and its effects on wildlife

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Understanding how organisms respond to any environment requires a full characterization of how the environment varies over time and space. A rapidly growing literature on the influence of anthropogenic noise on wildlife, and in particular animal communication, has yet to fully describe this variation. Point measurements of amplitude, often separated in time and space from animal observations, and qualitative descriptions of noise inadequately capture variation, a bias that may limit deeper understanding of noise effects on wildlife. We suggest that a greater focus on temporal and spatial heterogeneity in noise amplitude, as well as additional properties of noise, including onset, consistency, regularity, and frequency range, is critical for continued advancement in this emerging field. Recordings of noise using calibrated systems allow researchers to measure a suite of noise properties simultaneously with animal observations. Not only will such an approach improve quantification of single metrics of noise, the noise data collected may then be analyzed in a multivariate framework, which will help us understand the full range of behavioral and physiological adjustments animals may make and their broader implications for wildlife health and conservation.

Key words: **anthropogenic noise, behavior, communication, environmental variation, measurement, sound pressure levels.**

INTRODUCTION

Anthropogenic or human-generated noise (hereafter noise) has increased worldwide over the last century (Barber et al. 2010; Frisk 2012). Noise may have widespread effects on wildlife both near and far from its source (or sources), with negative effects on animal health (e.g., Rolland et al. 2012), learning (e.g., Marler et al. 1973; Peters et al. 2012), predator detection (e.g., Chan et al. 2010), and communication (e.g., Slabbekoorn and Peet 2003; Wood and Yezerinac 2006; Francis, Ortega, et al. 2011; Hanna et al. 2011). Because noise may disrupt communication by overlapping or masking animal signals that occur in similar frequency ranges (Brumm and Slabbekoorn 2005), considerable attention has focused on shifts in signaling behavior in noise. Aquatic and terrestrial organisms, from fish to whales and grasshoppers to birds, alter the frequency, rate, and timing of signaling in response to noise (e.g., Fuller et al. 2007; Cunnington and Fahrig 2009; Gross et al. 2010; Hanna et al. 2011; Parks et al. 2011; Lampe et al. 2012; Picciulin et al. 2012; McLaughlin and Kunc 2013; Montague et al. 2013; Potvin and Mulder 2013).

Determining the nature and extent of the responses of wildlife to noise depends on our ability to quantify a feature of the environment that comes from diverse sources, including industrial machinery, resource extraction, recreation, and transportation. Although each source may be classified broadly as generating anthropogenic noise, the properties of noise emanating from them are not necessarily the same (Figure 1). Given the increasing importance of and attention to understanding the diverse effects of noise on animals, we advocate here for more detailed noise quantification to allow researchers to build on critical foundational studies (see also Read et al. 2014). We propose new questions regarding animal behavior permitted by detailed analyses of amplitude variation over time and space, as well as additional questions that may be explored by moving beyond the focus on amplitude. Noise is highly complex, and therefore, we also briefly touch on noise from a multivariate perspective (Figure 1). Fortunately, addressing these questions requires the relatively straightforward approach of recording noise simultaneously with behaviors of interest using calibrated microphone-recorder systems (Zollinger et al. 2012).

NOISE VARIES OVER TIME

In most environments, noise is highly variable over time. Different sources may have very different temporal patterns of noise production (Figure 1A–C), and in complex landscapes with multiple
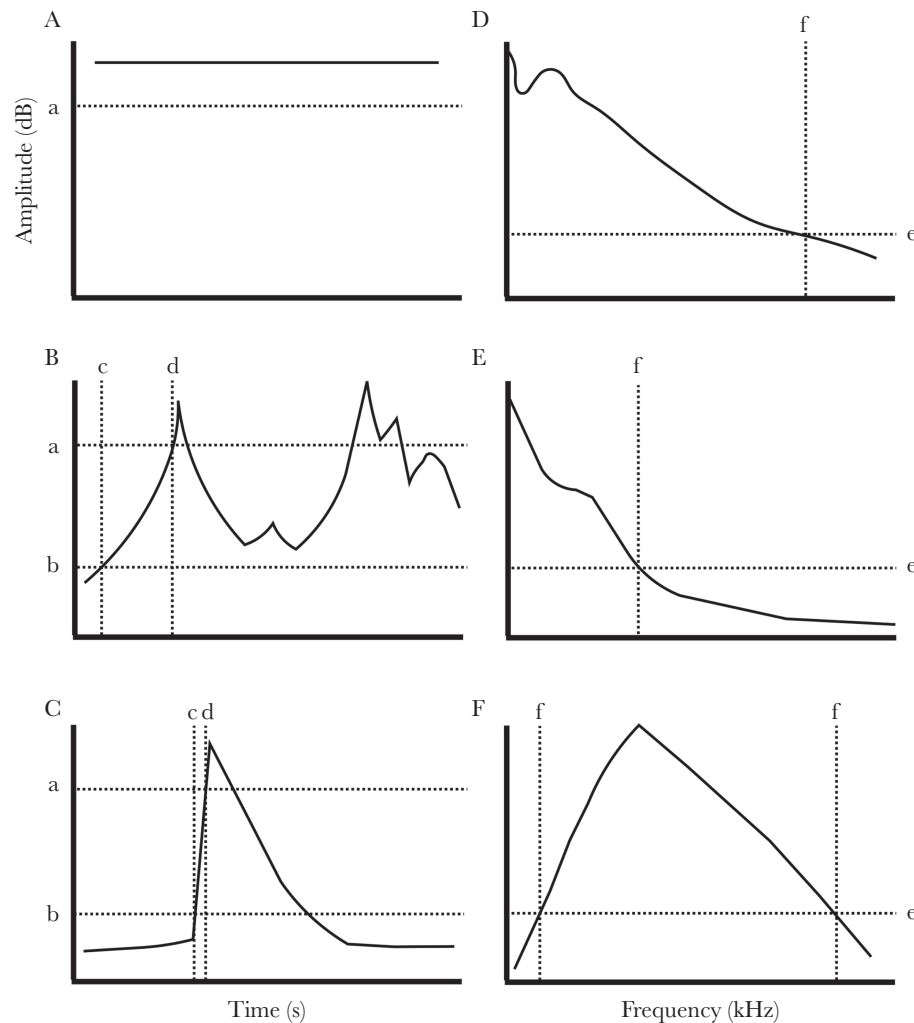
Figure 1

Hypothetical amplitude envelope models (A–C) and power spectra (D–F) generated by different noise sources, illustrating 5 characteristics of noise. Note that maximum amplitude is similar across these 3 examples, whereas time-averaged amplitude measurements (e.g., equivalent continuous SPL, L_{eq}) would likely differ; however, other characteristics of noise, which vary considerably, are not captured with amplitude measurements alone. A and D illustrate high-amplitude, sustained, and broadband noise (e.g., an air conditioner or a well compressor). B and E illustrate noise with amplitude that varies from low to high values, with relatively slow onset of noise to maximum amplitude and an amplitude that exceeds threshold values with some regularity (e.g., vehicular traffic). The frequency range of noise in B and E is narrower than in D. C and F illustrate a high-amplitude noise with rapid onset in a low-noise environment. The noise has a much more rapid onset than decay, occurs only once, and has a broad frequency range (e.g., a shotgun blast). In A–C, the line indicated by "a" represents a threshold energy value used to calculate noise consistency (the proportion of time that noise exceeds the threshold) and regularity (the pattern with which noise exceeds threshold values). In B and C, lines a and b represent maximum and minimum threshold energy values, respectively, that would be used to delineate the beginning (c) and end (d) of the onset of noise, from which duration of onset or slope (change in amplitude per unit time) could be calculated from these values (decay could be calculated in a similar way). Onset could not be calculated in A. In D–F, line e indicates a baseline energy threshold below which anthropogenic noise is not distinguishable from ambient noise. The frequency range of noise is then indicated by line f, at which amplitude exceeds the baseline value. Spatial variation in noise characteristics is not illustrated but could be included by recording noise sources using a microphone transect or array.

sources, all of which may have different properties, the sound environment may vary substantially over time. Yet characterizations of amplitude, including qualitative descriptors (noisy vs. quiet), point measurements of amplitude in decibels (dB), and time-averaged values (e.g., L_{eq}), fall short of capturing this heterogeneity. This may limit understanding of the responses of animals to noise; do animals respond to average noise amplitude, variability of amplitude over time, or other noise properties? Quantifying noise in greater detail in combination with quantification of temporally matched behaviors is critical in this emerging field and will contribute to a broader understanding of animal responses to environmental change.

Consideration of temporal variation in noise presents an opportunity to study phenotypic plasticity, the ability of individuals (their genotypes) to produce different phenotypes in response to variation in the environment. Animals from diverse taxa show population-level adjustments of signals in noise (e.g., Slabbekoorn and Peet 2003; Sun and Narins 2005; Parks et al. 2011; Lampe et al. 2012), with experimental playbacks providing critical evidence of plasticity: on average, individuals change signal structure when constant high-amplitude noise is played (e.g., Lengagne 2008; Halfwerk and Slabbekoorn 2009; Gross et al. 2010; Montague et al. 2013). The nature of signal plasticity, however, remains unclear: are all

individuals plastic and if so, do they express plasticity to the same degree? Given rapid fluctuations in noise amplitude (Figure 1B,C), can animals adjust their signals as rapidly? Answers to these questions require detailed quantification of noise amplitude over time in combination with measurement of temporally matched signals (e.g., Parks et al. 2011). This approach offers many advantages, from better description of noise amplitude fluctuation over time (Figure 1B–F) to questions regarding fitness costs of signaling (if individuals adjust to noise at the time of signaling, is this a mechanism to minimize potential costs of signaling in noise?). Importantly, individual plasticity can occur without population-level adjustments (Nussey et al. 2007; Job JR, Kohler SL, Gill SA, in preparation), suggesting that exploration of population-level responses is only the first step in understanding animal communication and species persistence in noise.

Although the focus of most research to date, amplitude levels at any given moment are just one way noise varies over time. We consider 3 other temporal properties of amplitude. Noise onset is the time for noise to reach a maximum threshold amplitude from a minimum threshold value (or the slope of energy of the attack, Figure 1B,C). Noise may have a rapid onset (Figure 1C; e.g., a shotgun blast or car horn) or a more gradual onset and fading such as that from the intermittent passage of vehicles at a given location (Figure 1B). We predict that noise with different onset characteristics will affect animals in different ways (e.g., Lengagne 2008; McLaughlin and Kunc 2013) and that a threshold onset value might exist below which startle responses and behavioral disruption may not occur.

Noise consistency is the proportion of time with which noise levels exceed a defined amplitude value (Figure 1A–C). A noise that is highly consistent would be detected above a threshold most of the time (Figure 1A), whereas noise that is transitory with low consistency would exceed this threshold infrequently (Figure 1C). A critical and challenging question links amplitude values with threshold responses by wildlife: can threshold limits of noise be developed, similar to annoyance curves established for humans (e.g., Ouis 2001)? We so far lack such values for wildlife, but these would be informative for maintaining habitat that is appropriate for them. For example, intermittent road noise had a greater effect on lek attendance than constant noise from natural gas drilling (Blickley et al. 2012); whether this is a general pattern across animals requires additional study.

Finally, regularity refers to the temporal pattern with which noise exceeds an amplitude threshold, ranging from a regular occurrence with low temporal variation between successive thresholds to irregular patterns with high variation between successive peaks (Figure 1B; note that we prefer regularity rather than predictability—cf. Francis and Barber 2013—as the latter implies perception that may or may not exist). Regularity might influence whether animals habituate or become more sensitive to noise over time. Studies should investigate whether noise with high regularity is perceived as predictable by animals, with habituation more likely compared with irregular and unpredictable noise to which animals may become more sensitive. As animals habituate to noise, their tolerance of it may increase, whereas the opposite would occur through sensitization (Bejder et al. 2009). Marine mammals, for example, become increasingly tolerant of noise over the course of experimental noise trials on one day only to be less tolerant by the next, suggesting habituation to noise occurred in the short-term only (Kastelein et al. 2006).

NOISE VARIES OVER SPACE

The amplitude of noise varies on both small (e.g., Díaz et al. 2011; Ríos-Chelén et al. 2013) and large spatial scales (e.g., Matsinos et al. 2008; Krause et al. 2011; Bormpoudakis et al. 2013; Kuehne et al. 2013), reflecting both the properties of noise from a given source as well as factors influencing sound transmission (a topic beyond the scope of this article). Do animals respond to spatial variation in noise? Given large-scale heterogeneity, animals might avoid high-noise habitat (e.g., Forman and Deblinger 2000; Habib et al. 2007; Goodwin and Shriver 2011; Naguib 2013). Even on smaller spatial scales, animals experience significantly different noise environments (e.g., Díaz et al. 2011; Ríos-Chelén et al. 2013), which may influence selection of habitat. Individuals may preferentially select lower over higher noise sites (McClure et al. 2013) or could adjust the location of signaling based on noise variation within territories or display sites (Blickley et al. 2012; Halfwerk et al. 2012; McLaughlin and Kunc 2013; Polak 2014). Thus, in addition to adjustments of signal structure, signaling location may be modified to minimize masking by noise, with the possibility of complex spatial–temporal interactions affecting signal structure and signal location in completely unexplored ways. An enticing prospect is that multiple solutions to the problem of signaling in noise exist and species could differ in the solutions they employ. In addition to spatial variation in amplitude, investigations could also consider spatial variation in onset, consistency, and regularity, with an important challenge of addressing how the combination of these different properties of temporal heterogeneity play out across various spatial scales.

BEYOND AMPLITUDE

Up to this point, we have considered how variation in the amplitude of noise may affect animals, but properties in spectral dimensions are important as well. A fundamental spectral property is frequency range, defined as the range of frequencies occupied by noise and represented as minimum and maximum frequencies (e.g., 1–2 kHz) at which noise exceeds ambient noise levels (Figure 1D–F). This property is often assumed rather than directly assessed (but see, e.g., Cunnington and Fahrig 2009; Francis, Ortega, et al. 2011; Parks et al. 2011), yet frequency range varies among noise generated by different sources (e.g., Cunnington and Fahrig 2009 vs. Parks et al. 2011) and may exceed the range usually considered as characteristic of noise (0–2 kHz; see e.g., Francis, Paritsis, et al. 2011). Frequency range is critical for understanding whether noise may mask signals (i.e., frequency overlap, Francis and Barber 2013) and, therefore, whether we expect behavioral adjustment by signalers. It is also critical from the receiver's perspective: can signals be detected in noise (just noticeable differences), and more importantly, do receivers discriminate among signals in noise (just meaningful differences; Klump 1996; Dooling and Blumenrath 2013)?

The answers to these questions depend on the animal's auditory systems, which are complex and variable across taxa (and beyond the scope of this article; see excellent chapters in Brumm 2013). Here, we consider auditory sensitivity, which refers to the frequencies at which the auditory system is most sensitive or "tuned." The auditory systems of fish (Ladich 2013) and amphibians (Vélez et al. 2013) are tuned to relatively low frequencies (<3 kHz) compared with birds (1–6 kHz for songbirds) and marine mammals (1 kHz—ultrasonic range; Dooling and Blumenrath 2013; Finneran and Branstetter 2013). Tuning of auditory systems, often to the

frequencies found in the species' signals, may limit the capacity of organisms to detect at least some frequencies of anthropogenic noise; thus, we must be cautious to avoid bias in thinking that when we detect noise, so too do the animals we study. Further, the ability to discriminate slight changes in amplitude is highly variable among animal groups, and small changes of only a few decibels may not be meaningful to some animals (Dooling and Blumenrath 2013).

An open question is whether noise, even if it is not audible, could still significantly affect animal behavior and physiology. Anthropogenic noise generates vibrations that propagate through substrates, both natural and artificial (Wu and Elias 2014). Arthropods (Cocroft and Rodríguez 2005) and amphibians (Schwartz and Bee 2013) use vibrations for prey and predator detection, and mate attraction, functions that may be disrupted by human-generated sources of vibration (Wu and Elias 2014). Vibrations affect heart rate and sleep (e.g., Croy et al. 2013; Smith et al. 2013) and increase activation of the stress axis (Raff et al. 2011). To our knowledge, studies on the physiology of wild animals have not been undertaken, and in general, the effect of vibrations from anthropogenic noise on the behavior of wild animals is poorly understood.

QUANTIFYING NOISE

Particularly in the study of terrestrial species, noise quantification has been limited through the use of sound pressure level (SPL) meters. SPL meters are useful to rapidly characterize the sound amplitude environment, but inexpensive versions do not permit more detailed analysis of prevailing sound. Measurements using low-cost SPL meters cover a wide frequency range (20–20 000 Hz); overall sound level is averaged over sampling time, and the ability to focus on amplitude at relevant frequency ranges may be limited. High-end units (>$5000) analyze amplitude in 1/1 and 1/3 octave frequency bands, allowing researchers to isolate bands most characteristic of noise at their site. Equally problematic, SPL meters are not always deployed simultaneously with focal animal observation, resulting in temporal mismatch of amplitude levels with animal behavior (see Pater et al. 2009; Ortega 2012 for further discussion of SPL meters).

A more refined approach avoids temporal mismatch of noise recordings and animal behavior (e.g., Slabbekoorn and Peet 2003; Wood and Yezerinac 2006; Holt et al. 2008; Ripmeester et al. 2010; Parks et al. 2011; Proppe et al. 2011). Paired systems of microphones and recording units can be calibrated (Zollinger et al. 2012) with an acoustic calibrator that generates a tonal sound set to standard amplitude and frequency (e.g., 94 dB at 1000 Hz; this technique presumes that the system is linear over the frequency range of interest). The generated sound is recorded using different gain settings on recording devices, resulting in specific dB–Volts to dB SPL conversion factors (known as calibration factors) for each setting. Calibrations may be performed in anechoic chambers, in an environment with very low ambient noise, or in the field if the calibrator fits snugly over the microphone (high-end systems only).

Calibration factors can be used in 2 ways. Sound analysis programs (e.g., AviSoft SASLab-Pro) allow researchers to enter calibration factors, which are used to set amplitude levels of recordings relative to 0 (rather than an arbitrary scale). Alternatively, script written in MATLAB can be used to sample recordings at researcher-specified time intervals (e.g., every 1 s or when behavior was observed) and overall, 1/1 or 1/3 octave frequency band level amplitudes can be extracted (e.g., Ripmeester et al. 2010; Parks et al.

2011). Calculation of 1/3 octave bands allows exploration of the effects of amplitude in particular bands on wildlife (e.g., Miksis-Olds and Tyack 2009). Low- and high-pass filters can be set to allow users to extract amplitude levels for frequency ranges relevant to the focal species (Job JR, Kohler SL, Gill SA, in preparation; see Cunnington and Fahrig 2009 for an alternative calibration method).

The distinct advantages of calibrated systems are the ability to extract amplitude at time scales relevant to the animal and the behavior of interest and the ability to compare amplitude levels across multiple time points and frequencies within a single recording, among recordings in a single study, and among different studies, which will be important for meta-analyses of animal responses to noise (see also Zollinger et al. 2012). Sound analysis programs allow calculation of power spectra, allowing researchers to visualize the relationship between amplitude and frequency (Figure 1D–F), as well as whether noise overlaps the signals of focal species, which is not always the case (e.g., Cunnington and Fahrig 2009; Francis, Ortega, et al. 2011). Moreover, researchers can measure properties of noise in addition to decibel levels, with the potential to explore the effect of noise in animals from a multivariate perspective. A deeper understanding of noise effects may be gained when multiple traits are simultaneously considered (Zollinger et al. 2012) using multivariate analyses (e.g., principal components analysis, discriminant function analyses) in addition to or instead of univariate approaches.

MOVING FORWARD

Clearly, the exact details regarding how noise should be sampled and quantified vary with the question of interest, the source of noise and its properties, and factors that influence the spatial spread of noise. However, based on the ideas presented here, we advocate for the following. First, sound field (s) should be quantified in advance of conducting the study to understand temporal and spatial variation in noise and noise properties. Second, during the study, noise should be recorded using calibrated microphone-recording unit systems. This is critical, as recordings permit 1) the generation of power spectra to visualize the spectral profile of a given noise source, which will inform communication researchers about the potential for masking by noise, 2) the calculation of the full suite of properties of noise (amplitude, frequency range, onset, consistency, and regularity) that may affect animals, and 3) simultaneous quantification of noise and animal behavior. By considering noise properties beyond amplitude and by pairing noise quantification and behavior, we may continue to build on critical foundational work and significantly advance understanding of the effects of noise on wildlife.

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