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Current Opinion in Insect Science

Anthropogenic noise affects insect and arachnid behavior, thus changing interactions within and between species

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Urbanization and the by-product pollutants of anthropogenic activity pose unique threats to arthropods by altering their sensory environments. Sounds generated by human activities, like construction and road traffic, can oversaturate or interfere with biotic acoustic cues that regulate important ecological processes, such as trophic interactions and the coordination of mating. Here, we review recent work exploring how anthropogenic noise impacts inter-intra-specific interactions in insects and arachnids. We outline empirical frameworks for future research that integrate three mechanisms by which anthropogenic noise alters behavior through interference with acoustic cues: masking, distraction, and misleading. Additionally, we emphasize the need for experimental designs that more accurately replicate natural soundscapes. We encourage future investigations on the effects of developmental exposure to noise pollution and the impacts of multiple interacting sensory pollutants on insect and arachnid behavior.

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Current Opinion in Insect Science 2021, **47**:142–153

This review comes from a themed issue on **Global change biology**

Edited by **Gina M Wimp** and **Shannon M Murphy**

https://doi.org/10.1016/j.cois.2021.06.005

Introduction

The by-products of urban expansion have diverse and pervasive effects on ecological interactions and evolutionary trajectories [1•,2•,3•]. One such by-product is anthropogenic sound — for example, noise produced by construction, transportation, and energy-generating infrastructure (Figure 1a). By altering local soundscapes [2•,4••,5••,6••,7], anthropogenic noise can impart physiological, behavioral, survival, and reproductive costs to insects and arachnids [4••,8••,9•,10,11]. Given the crucial role that sound plays in shaping arthropod behavior and physiology (including regulating general activity patterns, predator–prey interactions, and mating interactions), anthropogenic noise is likely to alter the nature of arthropod interactions through changes to individual behavior, and can consequently alter the outcomes of ecological interactions [3•,4••,12•,13,14•,15••,16].

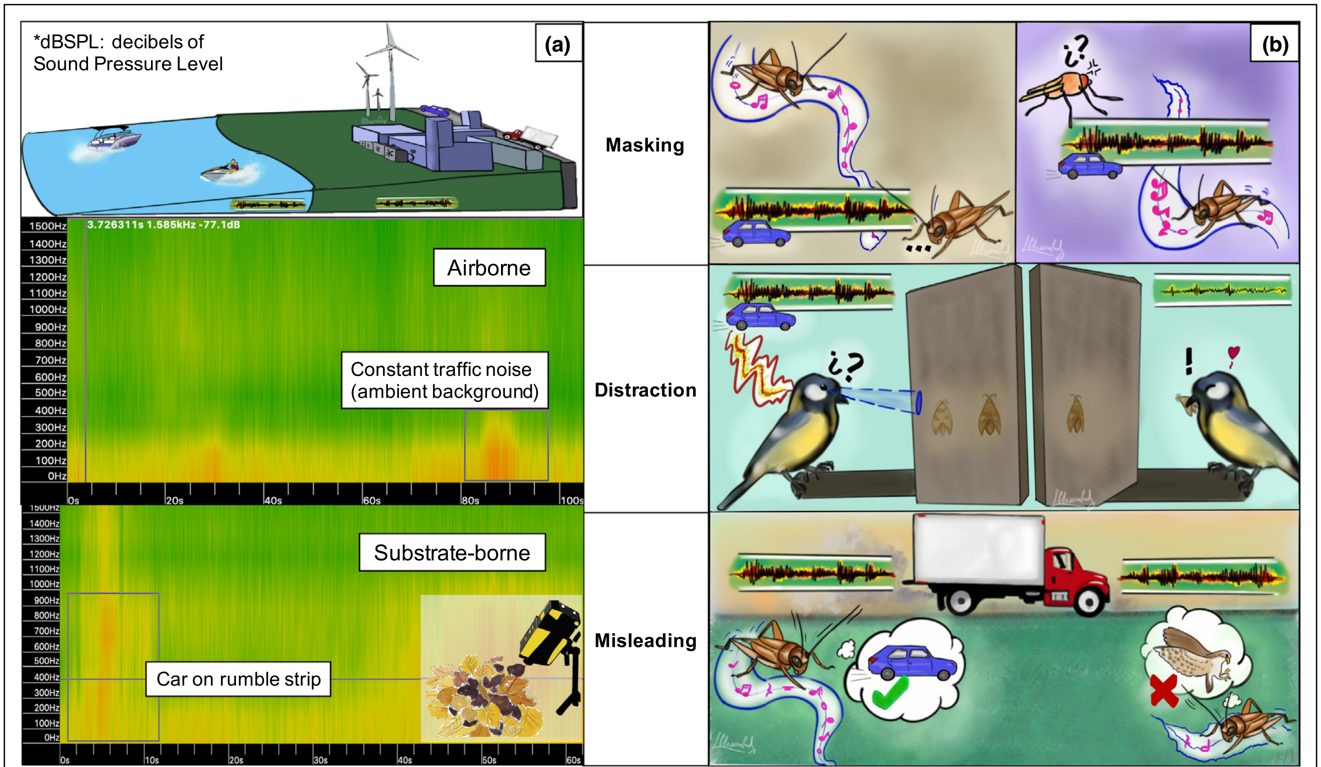
In this review, we synthesize recent work exploring how anthropogenic noise impacts insect and arachnid behavior. We review how anthropogenic noise can alter the detection and processing of acoustic cues and signals in ways that change the nature of inter-specific and intra-specific interactions. We also cover how anthropogenic noise alters habitat use and activity patterns in ways that modify the likelihood of these interactions occurring. We discuss the resulting consequences for predator–prey interactions and the coordination of mating, with a focus on research published over the last two years. Our review includes suggestions for standardizing and improving the accuracy of field-based sound recordings and acoustic playback studies. Lastly, we outline avenues of future research including work to examine how noise pollution during development influences adult behavior, and expanding research to include testing the effects of multiple sensory pollutants on multisensorial taxa.

How anthropogenic noise affects insect and arachnid behavior

Noise pollution affects cue detection and processing

Noise pollution often produces low frequency (i.e. low pitch), high amplitude (i.e. loud) sounds that overlap with biotic cues and can travel great distances through air and substrate media (Figure 1a) [3•,4••,5••,6••,8••,9•]. For instance, transportation systems produce noise with frequency ranges of 10–10 000 Hz (and sometimes up to 50 000 Hz), with particularly high amplitudes at frequencies that arthropods rely on (typically ≤1000 Hz; Figure 1a) [4••]. As a result, anthropogenic noise can hinder the ability of arthropods to detect and process cues and signals that are used to make behavioral decisions during inter-specific and intra-specific interactions [4••,7,10,12•,17,18•,19,20•]. Following years of insightful

Figure 1



Current Opinion in Insect Science

(a) Noise pollution alters the soundscapes of terrestrial and marine environments [3•,6••] and covers a broad range of amplitudes across spatiotemporal scales (≤70–150 dBSPL; ∼63K–200M, with particularly high amplitudes at the low frequencies that arthropods rely on (≤1000 Hz) [4••]. The frequency composition and amplitude ranges of anthropogenic noise in the environment (color intensity: red higher amplitude levels). Recordings were done in an urban park in Saint Louis, MO at a 100 meters from the road. Airborne recordings made at nighttime with an Audio-Technica AT2022 Stereo Condenser Microphone and a SONY PM10 hand recorder. Substrate-borne recording collected from leaf-litter substrate during rush hour with a Polytech PDV100 laser vibrometer. **(b)** Three main mechanisms through which acoustic noise can impact the accuracy of cue and signal detection and processing: masking, distraction, and misleading [5••,21••]. Masking from noise pollution reduces the ability and accuracy of parasitoids to detect their host cues. Distraction alters how predators processes the target cue/signal by shifting their attention to the external stimuli and decrease foraging success on cryptic prey (e.g. noise pollution) [22•]. Noise pollution effect can mislead cue processing when interpreted as a natural cue and unexposed individuals may associate the external stimulus with a potential predator and alter the signaling effort, while experienced individuals may benefit [14•].

findings, researchers have outlined three main mechanisms through which acoustic noise, and other anthropogenic by-products, can impact the accuracy of cue and signal detection and processing: masking, distraction, and misleading (Figure 1b) [5••,21••]. The isolated and combined effects of these mechanisms can alter the nature of the interactions and the outcomes of predator-prey interactions and mating coordination [10,18•,22•,23••].

Masking occurs when the noise source shares similar sound energetic properties (e.g. frequency ranges and/or amplitudes) and occurs simultaneously with biotic sounds [5••,7,24]. This overlap impairs the ability for individuals to successfully detect and respond to biological cues and signals (Figure 1b) [20•,21••,22•,25•]. Masking has been well-studied in birds, frogs and bats under predation and foraging contexts [22•,26], and in mate signaling and detection contexts [7,27–31]. Despite the diverse and complex multi-trophic interactions that occur within arthropod food webs, studies on the effects of noise pollution in insects and arachnids have been largely limited to orthopterans, and to the effects of masking noise on the detection and processing of mate signaling (Figure 1b) [32•,33–35,36•], but see [13,16,37••,38•].

Distraction involves sudden shifts in an individual's attention from a target source to the noise source (e.g. a shift from a biotic cue/signal to a sensory pollutant), and alters how a receiver processes the target cue/signal [3•,5••,7,10,19,21••,39•]. For prey, this may alter their ability to properly perceive threats [33], and for predators, distraction may reduce foraging efficiency (Figure 1b) [13,22•]. Although distraction by sensory pollutants may be an important driver of how insects and arachnids process stimuli, we are unaware of any recent empirical evidence directly testing the effects of this phenomenon in insects and arachnids [21••].

Misleading occurs when an anthropogenic stimulus is detected as a natural cue and triggers a (typically) maladaptive response [21••,40]. For example, individuals typically unexposed to anthropogenic noise may associate acoustic products of human activity (e.g. truck sounds) with potential predatory threats and alter their behavior unfavorably (see *Noise pollution alters habitat use and activity patterns*) (Figure 1b) [21••]. Given that behavior is also influenced by natural abiotic cues (e.g. wind, rain, and even geology [15••,21••,38•,41•,42]), we need more work addressing maladaptive responses to stressors like noise pollution that may mimic those cues [21••,23••,25•].

Empirically testing and quantifying how inter-specific and intra-specific interactions change in response to anthropogenic noise can sometimes be limited by the experimental complexity of standardizing, isolating, and combining multiple sensory interferences. However, researchers are beginning to develop methods that will allow us to better address masking, distraction, and misleading in an integrated way (see [5••,8••,23••,24,38•,43]) to determine the extent to which noise pollution impacts ecological and evolutionary processes [1•,3•,4••,5••,11,12•,18•,44••].

Noise pollution alters habitat use and activity patterns

In addition to sharing acoustic space with other species that use similar signaling properties, insects and arachnids may also compete with anthropogenic by-products [45]. For instance, the peak activity of crepuscular species can overlap with the hours of peak traffic and human activity (depending on seasonality and geographical region) (Figure 2a) [3•]. To avoid overlap with anthropogenic noise, animals may exhibit shifts in spatiotemporal activity patterns, habitat use, and navigation [8••]. For example, individuals might alter their circadian rhythms to avoid the sensory interference from anthropogenic activity patterns (Figure 2a) [4••,5••,15••].

A rather astonishing animal response to noise is the shifting of microhabitat use to occupy substrates better suited for increasing performance under noisy conditions. This idea remains understudied across a wide range of taxa. However, there is evidence that arachnids and predatory insects can learn to eavesdrop on vibrational cues (e.g. spiders readily exploit the vibrational cues produced by their prey when foraging [46•]), and may exploit particular substrata to increase prey cue detection and capture [4••,43]. Any changes in spatiotemporal habitat use in response to anthropogenic noise can also alter which species or individuals overlap in niche space and interact with one another [4••]. For example, crickets living near roads and construction zones benefitted from reduced signaling competition with conspecifics and reduced predation relative to crickets living farther from the road (Figure 2b) [14•,36•]. At the same time, birds that use acoustic cues to detect arthropod prey shift away from noisy roadsides and may reduce the abundance and species richness of grasshoppers at sites farther from roads (Figure 2b) [8••]. Thus, shifts in spatiotemporal niches—by insect and arachnids or their predators—may ultimately alter patterns of species richness and abundance [8••,10,11,19,47]. Addressing the trade-offs between the costs and benefits of remaining at noisy sites versus shifting away to quieter areas occupied by predators that also avoid noisy conditions would provide a better understanding of community-level responses and species spatial distribution driven by noise pollution [10,21••].

Implications for inter-specific interactions in predator-prey and parasitoid-host contexts

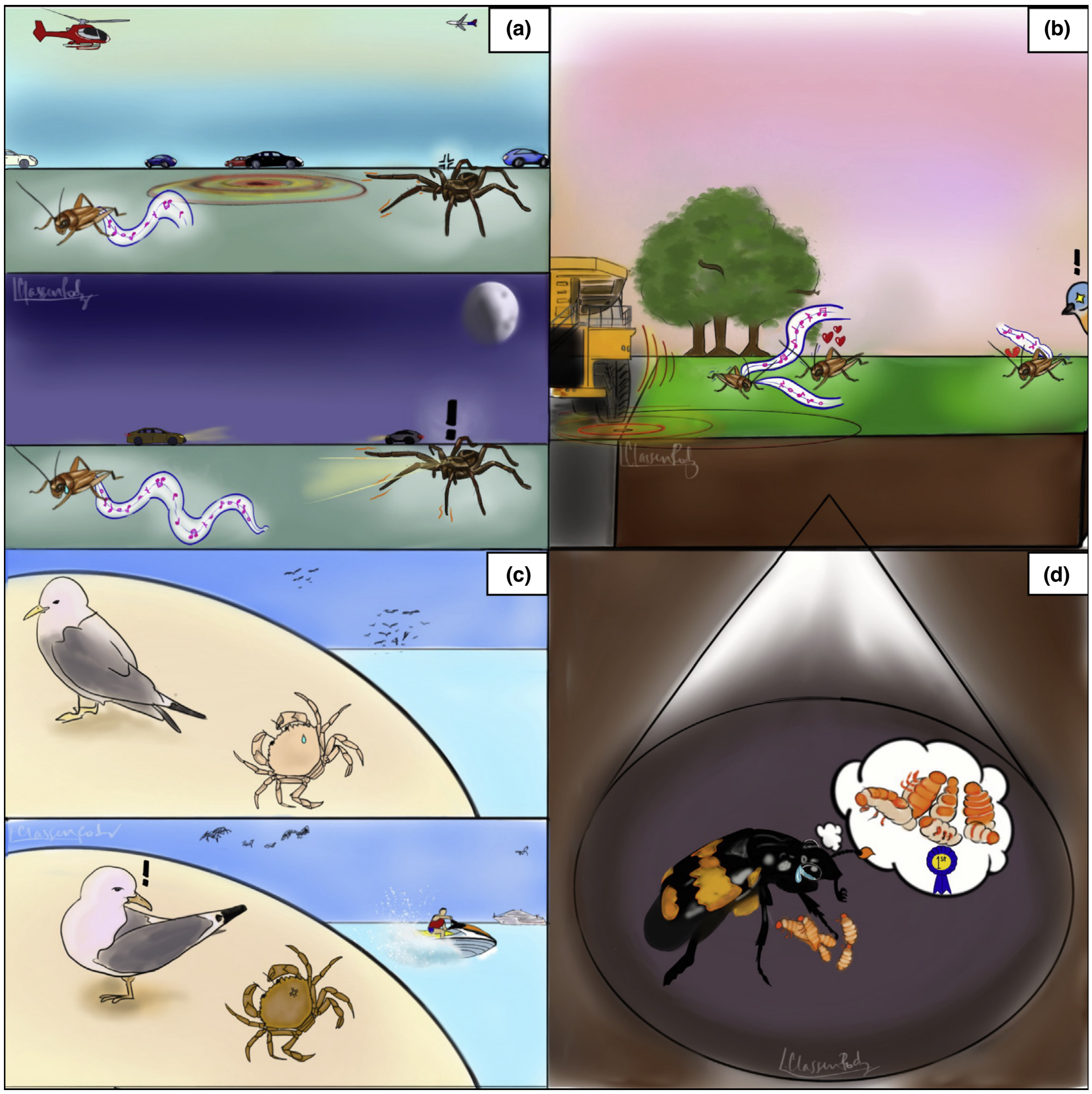
How noise pollution alters the nature of inter-specific interactions

Anthropogenic noise affects inter-specific interactions that have large effects on community dynamics and ecosystem functions [2•,5••,7,8••,10,11,23••], such as predator-prey and parasitoid-host interactions [8••,13,22•,38•]. In fact, evidence suggests that noise pollution can trigger trophic cascades throughout an entire community by modifying both predator and prey behaviors that determine the outcomes of predator-prey interactions [8••,9•,16,38•]. Many insect and arachnid species rely on acoustic cues (both airborne and substrate-borne) to detect, avoid, and deter predators and parasitoids, as well as to identify potential prey or hosts [4••,13,17,19,22•,43,48•]. By interfering with cue detection and processing, anthropogenic noise can greatly reduce the ability for, and accuracy with which, acoustically orienting predators and parasitoids respond to prey and host acoustic cues, benefitting prey (Figure 1b) [4••,9•,13,16,19,22•]. For example, adaptation of frogs (midge hosts) to urban areas may ultimately allow the frogs to avoid being parasitized by midges, which are sensitive to noise pollution [19]. However, noise pollution can similarly hinder the ability of prey and hosts to detect and avoid predators and parasitoids (Figure 1b) [46•]; this remains untested for the majority of insect and arachnid taxa. One interesting avenue to pursue is how noise pollution and predation pressure can impact the efficiency of anti-predator mechanisms and potentially trigger the evolution of diverse antipredator strategies, as seen in non-insect arthropods (e.g. shore crabs (Figure 2c) [49].

How noise pollution alters the likelihood of outcomes

We previously discussed how anthropogenic noise can alter habitat use and activity patterns, and consequently alter which organisms interact in a shared acoustic space (see *Noise pollution alters habitat use and activity patterns*), such individual changes in movement patterns are likely

Figure 2



Current Opinion in Insect Science

Noise pollution alters habitat use and activity patterns with implications for predator-prey and mating interactions. Examples include: **(a)** circadian rhythms may change to avoid sensory interference from anthropogenic activity [15••], **(b)** shifts in spatial distribution of predators away from noisy roadsides can decrease arthropod abundance and species richness at sites further from roads, leading to differential preferences for call characteristics under noise levels in road edges and urban environments [8••,12•,14•,34,36•,59], **(c)** ship noise during development can reduce anti-predator responses (e.g. camouflage), increasing predation likelihood [49], and **(d)** seismic disruption from noise pollution impacts parental care and brood size of ground dwelling arthropods sensitive to low-frequency vibrations [37••].
Artwork by Leticia Classen Rodriguez

to change encounter rates between predators and prey, or parasitoids and their hosts [4••,8••]. Noise pollution can alter functional responses for predators and prey. For example, noise can reduce predators' appetites through physiological effects that can trigger stress-induced hormonal changes [23••] and alter foraging activity [10,21••,22•,23••,25•]. Two illustrations of changes in the likelihood/outcome of predator-prey interactions in response to anthropogenice noise include reduced foraging of birds on cryptic moth prey (Figure 1b) [22•] and of insectivorous bats on their arthropod prey [50,51]. Future research will benefit from testing whether release from predation pressure outweighs the costs of remaining in noisy habitats where predators are less abundant (see *Effects of noise exposure during development*). Understanding the various mechanisms through which anthropogenic noise affects predator-prey and parasitoid-host interactions will allow researchers to better predict the extent of the effects of noise pollution on local populations and communities, and the consequences for local food webs [16].

Implications for intra-specific interactions in mating contexts

How noise pollution alters the nature of intra-specific interactions

Anthropogenic noise affects intra-specific interactions associated with mating — including courtship and mate location — by altering the signaling environment and signal perception by receivers [52•]. As a result, noise pollution can have dramatic impacts on lifetime reproductive success [18•]. The coordination of mating depends broadly on acoustic communication in many arthropods (e.g. Refs. [12•,17,20•,21••,25•]. Seven orders of insects detect and use far-field airborne sound (Figure 1) [4••,38•] and over 90% of acoustically communicating insects use substrate-borne sound or a combination of substrate and airborne sounds to communicate species identity, location, quality, and fighting ability (amongst other things) (Figure 1b) [4••,12•,20•,37••,41•,53]. Evidence for effects of noise on arthropod reproductive behavior comes primarily from work with orthopterans, and has collectively demonstrated that noise pollution affects signals, signaling behavior, courtship, mate location, and even investment in reproductive organs (Figure 3a) [10,14•,15••,18•,32•,33–35,41•,54].

One particularly common response to anthropogenic noise is changes in animal signals [10,12•,21••]. Insects and arachnids, however, may be less able to alter signals in response to anthropogenic noise than vertebrates. Many insects and arachnids produce sound using stridulation, which involves rubbing hardened, ridged body structures together (e.g. a file and scraper mechanism) [20•]. The frequency (pitch) of the sound produced depends on the shape of the structural traits rubbed together and the geometry of resonators that project the sound produced. Thus, changes in the frequency components of signals may be far more restricted and less plastic in arthropods than they are in vertebrates [4••,34]. However, grasshoppers from noisy roadside habitats and cicadas living in more metropolitan areas produce calls with elevated frequency components, suggesting some long-term effects of living in noisy habitats on the spectral components of calls are possible, similar to findings in vertebrate taxa [36•,55,56]. Additionally, insects and arachnids can readily modify temporal components of calls and signaling behavior in response to noise pollution (also seen in avians), and do so in both non-adaptive and seemingly adaptive ways [20•,21••]. For instance, under anthropogenic noise, male tree crickets (*Oecanthus* spp.) shortened their calls and reduced signaling effort, while bladder grasshoppers (*Bullacris unicolor)* called less and increased the intervals between calls [15••,36•,54,57]. Reduced signaling effort likely decreases mate attraction and could harm fitness at noisy sites. Recent avian research suggests that anthropogenic sound may also affect territory defense signals and behavior (intrasexual competition) [14•,30], but to our knowledge, it has yet to be tested if arthropod competition is similarly affected.

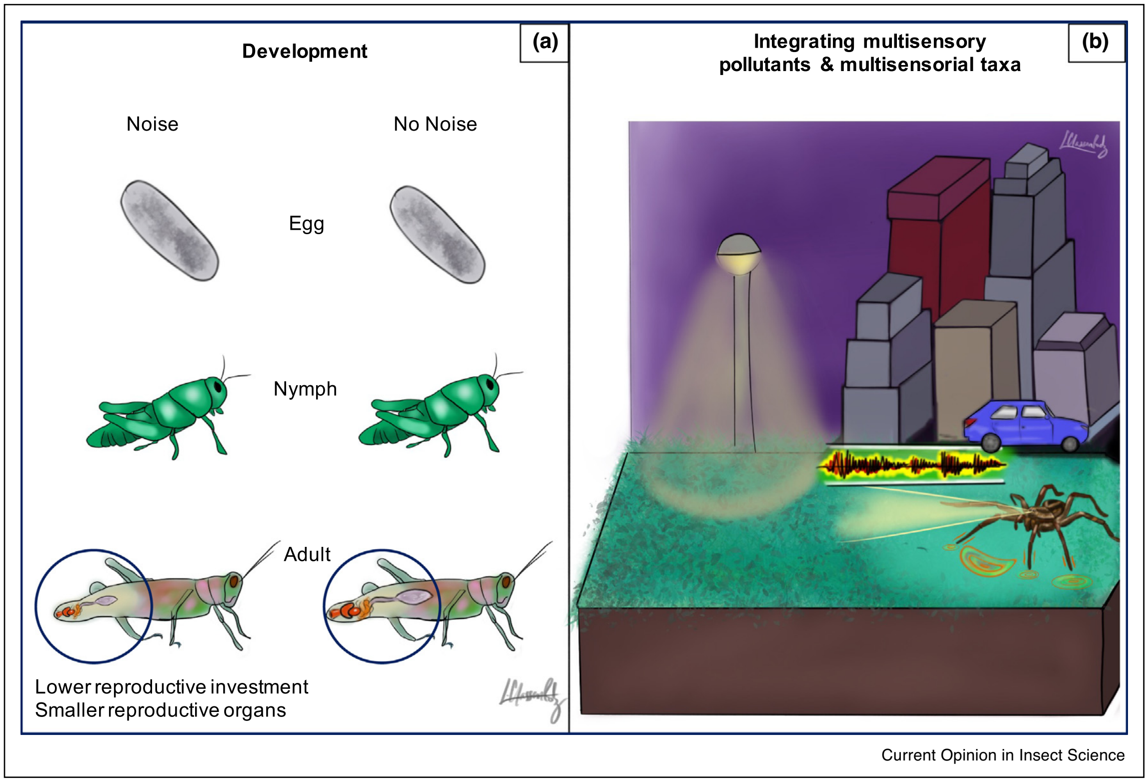
Other documented signaling responses to anthropogenic noise appear to be adaptive [20•]. Bladder grasshoppers, for instance, call later in the night at relatively noisier sites, which may allow them to take advantage of the relatively lower noise levels at those times (Figure 2a) [15••]. Similarly, male crickets living on habitat edges decreased chirp rates in response to passing cars, but males closer to the road decreased their chirp rate less than those living farther from the road [14•]. Thus, regular exposure to traffic sounds may decrease animals' sensitivity to this common anthropogenic disturbance (Figure 2b) [14•]. Additionally, while literature on the impacts of noise on insects that use substrate-borne communication is not as well developed as that on airborne acoustic signals (but see Refs. [4••,21••,58•], recent work in neotropical katydids suggests that even wind-induced environmental noise can modify the diel distribution (daily patterns) of signaling and frequency of tremulations produced [41•]. Therefore, it stands to reason that katydids and other insects and arachnids might exhibit similar types of responses to anthropogenic noise as well.

How noise pollution alters the likelihood of mating outcomes

Anthropogenic noise can negatively affect the ability for receivers to locate potential mates, much as it can reduce the detection of predators and prey. Orthopteran species have shown an array of responses to varied noise conditions. In the field cricket *Gryllus bimaculatus*, for instance, mate searching females were less likely to approach male calls while exposed to traffic noise [33] (Figure 1b). In other studies, however, receivers were able to respond just as quickly to male signals in the presence of masking traffic noise as they were in its absence (Figure 2b) [35,36•]. After locating potential mates, exposure to traffic noise may also change the process and outcome of mating decisions. For example, female field crickets spent less time attending to (and presumably assessing) male calls before approaching them closely under anthropogenic noise conditions [33]. For the grasshopper *Chorthippus biguttulus* and the cricket *G. bimaculatus*, different noise conditions led to different preferences for call characteristics, suggesting that sexual selection may proceed differently in urban environments [34,59].

Lastly, substrate-borne interference generated by anthropogenic activity appears to impact reproductive success by disrupting seismic communication important for

Figure 3



Future directions for research on the impacts of noise pollution on arthropods include **(a)** considering developmental experience (e.g. potential impacts of developing in noise on reproductive organs at adulthood) [32•] and **(b)** multiple sensory integration and pollutants in urban environments (e.g. light pollution and noise pollution) [2•,5••,10,21••,44••,63–65].

ground dwelling arthropods (e.g. in the presence of seismic noise burying beetles, which stridulate during parental care, produced smaller broods with lower mass (Figure 2d) [37••]). Again, however, research on substrate-borne vibrations lags behind that of far-field airborne sound in this context. This is an exciting area for future research.

Challenges in experimental design

Potential challenges for replicating methodological approaches

For new researchers entering the field, it is important to determine (i) what acoustic components of noise pollution to address, and (ii) what equipment is necessary to measure and calibrate specific acoustic components during field recordings and acoustic playbacks. Furthermore, given that soundscape patterns occur at multiple spatiotemporal scales and arthropods display behavioral variation depending on their sensory environment [4••,11], (iii) establishing the desired spatiotemporal resolution for soundscape recordings and behavioral assessments will be important for sampling efforts and replication, [4••,5••,10]. However, (iv) to overcome these challenges it is important to also be thoughtful about the budgets required to fully rectify these challenges.

(i) What specific acoustic components of noise pollution to study, and (ii) What equipment is needed to accurately record and broadcast sound

The physics of sound recording and playbacks demands specialized equipment and routine calibration. Thus, researchers need to consider the reproducibility of recording in the environment, calibraiton, and playbacks in experimental design for noise-exposure experiments. However, these types of details are sometimes overlooked and ambiguous when provided in descriptions of methods. We provide suggestions for methods and reporting here. Behavioral ecologists would benefit from establishing standard methods for reporting sound value units of arthropod responses under validated calibration protocols and with properly calibrated equipment to increase the relevance of behavioral responses and acoustic analysis to environmental conditions (e.g. Refs. [4••,10,23••,60•]), For example, proper calibration requires using the same devices used for recording sound or the correct conversion between types of measurements (e.g. accelerometers measure particle acceleration and laser vibrometers measure the particle velocity) [60•]. It also requires selecting the appropriate distance between speakers and animal subjects [14•] and calibrating amplitudes and frequency spectra to better replicate field conditions [60•]. Engineering challenges arise in attempts to replicate airborne sounds for playback experiments: researchers often lose power in the lower frequency ranges, which are biologically relevant to most arthropods. In an extreme example, normal speakers are not able to reproduce frequencies lower than 60 Hz, and even high-quality subwoofers can only replicate frequencies as low as 30 Hz, thus poetntially excluding biologically relevant frequency components of anthropogenic noise. The required modifications to overcome this shortcoming unfortunately may require additional engineering experience and additional budgetary investment [60•]. A quick solution to some of these challenges is to always account for the devices' manufacturing specifications throughout the recording, calibration, and playback process (e.g. microphone pre-amplifier, analog and digital filtering, maximum amplitude, frequency ranges, and so on). Knowing each device's specifications is useful when determining what frequency ranges and amplitude levels to study, how devices process sound (e.g. particle velocity/voltage, decibels in sound pressure, etc.), and what devices will be able to record and replicate those ranges and levels without distorting the sound ('clipping') or damaging the device.

Another common challenge for acoustic playback studies is the quantification and control of substrate-borne stimuli produced by building vibrations—which can interfere with experiments when experimental set-ups are not properly isolated—and vibrations transduced from the airborne playback to the substrate where the animals are being tested [16]. The effects of the substrate-borne components of noise pollution are vastly understudied, mainly due to the budget limitations inherent in recording, calibrating, and replicating seismic conditions accurately. However, many insects and arachnids use substrate-borne vibrations to detect cues, and we are thus likely to fall short of a complete understanding of how noise pollution alters behavior and trophic interactions by underestimating the effects of substrate-borne noise [16].

(iii) Establishing the desired spatiotemporal resolution for soundscape recordings and behavioral assessments

We often overlook the complexity of assessing population and community level responses to noise pollution. We know soundscape patterns occur at varying spatiotemporal scales and that arthropods display behavioral variation depending on their sensory environment (Sensory Drive). It is important to keep in mind the resolution and scale of our studies to match those relevant to the animals for sampling and replicating efforts, and to accurately draw conclusions [4••,5••,10,11].

(iv) Reducing budgets needed for noise pollution research

Conducting acoustic research is not cheap, and for many researchers this is the main barrier limiting research, specifically when designing studies across large spatiotemporal scales [61••]. While there is a high variation in the type and quality of sound equipment, much of it is inaccessible for new researchers in the field (e.g. graduate students and underrepresented researchers). In general, we advocate for research to develop techniques that reduce the costs associated with recording and playback protocol for noise pollution studies. We encourage researchers with available equipment and funding opportunities to continue validating the quality of sampling and calibration of low-cost open-source solutions (e.g. AudioMoth recorders and portable oscilloscopes using Arduinos, respectively) in relation to the performance of more expensive equipment as a means to standardize accessible acoustic monitoring for researchers with limited funding and facilitate monitoring efforts for conservation goals (e.g. Refs. [60•,61••]).

Future directions

To push forward our understanding of the mechanisms through which anthropogenic noise affects animal behavior and ecological interactions, we must first establish rigorous standards to guarantee the quality and repeatability of findings for basic research and conservation management. We have highlighted some recommendations for standardizing field recordings, calibrating acoustic playbacks, and establishing standards regarding the reporting of parameters (see *Challenges in Experimental Design*) [23••]. We also advocate for controlled laboratory experiments paired with field enclosure studies and community monitoring to capture the mechanisms and full effects of anthropogenic noise on predator-prey and mating interactions (e.g. Ref. [8••]).

In addition to methodological advances mentioned above, we highlight two avenues of future research to pursue in light of the importance of the sensory environment for sensory systems (Sensory Drive Hypothesis), and the use of multimodal signals and cues by many insects and arachnids. First, we urge researchers to invest in studying how anthropogenic sound experienced during development affects adult behavior, as exposure to noise can affect ecological and evolutionary responses to urbanization. These types of developmental studies are often easier to perform with insects and arachnids compared to vertebrates due to the efficacy of rearing many arthropods. Second, we encourage tackling how anthropogenic sensory pollution affects taxa that sense in multiple modalities or are exposed to noise in multiple sensory modalities in urbanized environments.

The effects of noise exposure during development

Many of the examples we have highlighted throughout this review demonstrate the immediate effects of the local soundscape on animal behavior. However, prior exposure to anthropogenic noise also appears to impact fitness-related adult traits (Figure 3a) [36•,62••]. Learning, developmental plasticity, and parental effects may exhibit adaptive patterns in response to previous exposure to different noise conditions that prepare animals to live and reproduce in anthropogenically disturbed environments [14•,63].

Although research in insects and arachnids to date has rarely addressed the consequences of development under anthropogenic noise, the few existing examples suggest that early exposure to noise pollution can influence adult traits (Figure 3a) [35]. One study found developmental plasticity in signaling in response to anthropogenic noise (grasshoppers reared under noise produced higher-frequency songs as adults [57]). Another study found fairly dramatic changes in female latency to begin mate searching and to locate a male song when exposed to traffic noise playbacks during development (Figure 1b Masking) [35]. Some limited evidence even supports the idea that exposure to anthropogenic noise during development may alter investment in reproductive organs. Male field crickets exposed to chronic masking traffic noise from birth had smaller reproductive organs at adulthood (Figure 3a) [32•]. Here, the authors suggested that, if anthropogenic sound masks the field cricket mating songs, noise may alter the perception of the density of available mates and competitors, and thus the perceived risk of sperm competition. Similar effects might alter the detection of predators, prey, and parasitoids, and thus the perceived risk of predation or availability of food, leading to mismatches between the environment and fitness-related adult traits (e.g. altered anti-predator strategies (Figure 2d; [49])). Conducting research on multiple arthropod groups and in many geographical regions may provide additional insight into whether responses across taxa and seasons are consistent, what the potential neurological and physiological responses to developmental noise exposure are [4••,25•], and how often behavioral patterns are correlated with the acoustic environment during development [7].

Multiple sensory integration and pollutants in urban environments

Most studies to date have focused on the effects on single pollutants or environmental stressors [5••,64] despite the common co-occurrence and covariance of multiple sensory pollutants in urbanized areas (e.g. noise, light, chemicals (Figure 3b) [5••,63]), but see [5••,18•,19,44••,65–67]). However, insects and arachnids use multi-sensory cues for decisions ranging from navigation [68•] to foraging and mediating predator-prey interactions [46•,69,70] and mating interactions [18•,71]. Broadly across animals, the presence of multi-sensory cues can increase the accuracy with which animals monitor their environments to make adaptive decisions [44••,68•,72]. Under varying conditions, the nature of multi-sensory cue interactions (i. e. if the information provided via cues from different modalities is redundant, additive, or interactive [10,71]) is likely to shape how multi-sensory pollution impacts behavior (Figure 3b). [65]. Redundant information across cues/signals from different sensory modalities can make shifts to rely more on a quieter sensory channel relatively straightforward when some sensory pollutants vary in their effects (e.g. Refs. [10,65]). However, when the effects of sensory pollutants are additive, antagonistic, non-linear or interactive, switching reliance on one sensory channel to another will not be as effective [5••,65]. Increased noise in one sensory channel could also impair perceptual processing capabilities in other channels, potentially even more so for predators that rely on multimodality to eavesdrop on signaling prey [73,74]. We encourage expanding and amplifying the foundation built by researchers in the last two years to understand how anthropogenic noise and other sensory interfering stimuli (i.e. natural abiotic noise and artificial light) can impact ecological interactions by altering behavior [5••,21••,43]. This is a field that is likely to grow rapidly in the coming years, as the fields of behavioral ecology, signal detection theory, and perceptual decision-making all move towards frameworks that incorporate multiple sensory modalities [4••,71,74] and pollutants and, as a result, research results can be applied to more realistic scenarios [5••,18•,44••,62••,75].

Conclusion

In the last couple of years, the majority of research on how anthropogenic noise affects behavior, reproductive success, and community structure has focused on vertebrate communities with far fewer empirical studies conducted across diverse arthropod taxa, despite the demonstrated importance of such work [11,13,33,35]. Currently, much of the evidence on how anthropogenic noise affects particularly predatory–prey interactions derives from assays focusing on changes in niche use or abundance of interacting species, rather than from experiments that directly test how noise affects the likelihood and nature of interactions to generate observed patterns (see Refs. [4••,7,9•,10,11,20•,21••]). The examples we have outlined in this review suggest a proliferous field that will benefit from direct tests of the mechanisms through which anthropogenic pollution can alter predator-prey and mating interactions. This venture should consider sensory ecology, movement ecology, and quantification of arthropod responses to noise across both ecological and evolutionary time scales. Here, we also call for the establishment of field standards that take into careful consideration the particular challenges replicating noise experienced by animals in the field [5••] and the associated budgetary constraints faced by many researchers.

Despite being in early stages, the current body of work promises creative and collaborative avenues of research addressing the important goal of a more wholistic approach to monitoring the impacts of anthropogenic noise on arthropod interactions. Furthermore, this research will allow researchers to better hypothesize ecological and evolutionary consequences triggered by our rapidly changing world.

Conflict of interest statement

Nothing declared.

Acknowledgements

We thank Noah Leith, Rowan McGinley, Dave Daversa, Brett Seymoure, Michael Moore, and the University of Denver's DUEEBs group for providing constructive feedback on this manuscript. Many of our recommendations for the establishment of field standards have emerged through conversations on experimental design challenges and practices with Reginald Cocroft. Saint Louis University Research Institute funding to KDF. Saint Louis University Diversity Fellowship to LCR.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

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2. • Buxton RT, Seymoure BM, White J, Angeloni LM, Crooks KR, Fristrup K, McKenna MF, Wittemyer G: **The relationship between anthropogenic light and noise in U.S. national parks**. *Landscape Ecol* 2020, **35**:1371-1384

Here, the authors overlaid existing geospatial models of anthropogenic light and noise with landscape predictors of national parks across the continental U.S. Their models predicted a low correlation between anthropogenic light and noise except parks with higher road density and within urban areas, while parks further from urban areas and with roads present had a greater probability of higher divergent light and noise exposure (e.g. high light and low noise). The authors conclude by outlining implications and ongoing challenges in conservation and management face as current research is starting to address the interactive and independent effects of multiple co-occurring and diverging anthropogenic stressors.

3. • Proulx R, Waldinger J, Koper N: **Anthropogenic landscape changes and their impacts on terrestrial and freshwater soundscapes**. *Curr Landscape Ecol Rep* 2019, **4**:41-50

Review that quantifies the direct effects of anthropogenic landscape alterations on the intensity and propagation of sounds, and the indirect effects on wildlife behavioral responses to novel acoustic habitats by modifying landscape structure and species distribution patterns. The authors conclude by recommending further research addressing the effects of anthropogenic sounds on species' sensorial traits as a framework to scale and link individual responses to community responses and better predict anthropogenic impacts on ecosystems.

4. •• Raboin M, Elias DO: **Anthropogenic noise and the bioacoustics of terrestrial invertebrates**. *J Exp Biol* 2019, **222**:jeb178749

Literature review on the impacts of airborne and substrate-borne anthropogenic noise on terrestrial invertebrates and propose a framework that addresses the trade-offs and adaptative responses to noise pollution, especially under multimodal contexts. The authors recommend expanding the focus of noise pollution propagation across mediums in order to create a moreholistic understanding and effective mitigation strategies.

5. •• Dominoni DM, Halfwerk W, Baird E, Buxton RT, Fernández-Juricic E, Fristrup KM, McKenna MF, Mennitt DJ, Perkin EK, Seymoure BM *et al.*: **Why conservation biology can benefit from sensory ecology**. *Nat Ecol Evol* 2020, **4**:502-511

The authors outline an integrated framework that addresses the multiple ways sensory pollutants can impact animal sensory ecology, physiology, and life history; and how these three mechanisms (masking, distracting and misleading) present the ecological consequences and implications for conservation.

6. •• Duarte CM, Chapuis L, Collin SP, Costa DP, Devassy RP, Eguiluz VM, Erbe C, Gordon TAC, Halpern BS, Harding HR *et al.*: **The soundscape of the Anthropocene ocean**. *Science* 2021, **371**:eaba4658

The authors review the impacts of increased anthropogenic noise on ocean soundscapes and the impacts it has on marine animals at multiple levels, including their behavior, physiology, and, survival. They outline recent evidence of the changes and impacts, as well as discuss conservation and management practices that can mitigates the impacts on marine habitats and wildlife.

7. Rosa P, Koper N: **Integrating multiple disciplines to understand effects of anthropogenic noise on animal communication**. *Ecosphere* 2018, **9**:e02127 http://dx.doi.org/10.1002/ecs2.2127.

8. •• Senzaki M, Kadoya T, Francis CD: **Direct and indirect effects of noise pollution alter biological communities in and near noise-exposed environments**. *Proc R Soc B* 2020, **287**:20200176

The authors quantified the impacts of noise on birds, grasshoppers and odonates by experimentally applied traffic noise pollution to multiple roadless areas (phantom roads). Acoustically oriented birds, including grasshoppers and odonates without acoustic receptors, were found in reduced species richness and/or abundance; as well as in different community compositions in experimentally noise exposed and adjacent areas. Their results suggest that noise pollution can indirectly affect acoustically oriented animals, even those found in quieter adjacent areas, through cascading effects across biological communities.

9. • Kunc HP, Schmidt R: **The effects of anthropogenic noise on animals: a meta-analysis**. *Biol Lett* 2019, **15**:20190649

The authors used a multi-level phylogenetically controlled meta-analysis under a holistic framework that accounts for phylogeny contribution on the response variation to noise. They found that noise affects many amphibian, arthropod, bird, fish mammal, mollusc and reptilian taxa, but phylogeny has a low contribution to the variation in response to noise.

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11. Bunkley JP, McClure CJW, Kawahara AY, Francis CD, Barber JR: **Anthropogenic noise changes arthropod abundances**. *Ecol Evol* 2017, **7**:2977-2985 http://dx.doi.org/10.1002/ece3.2698 2045-7758.

12. • Broder ED, Elias DO, Rodríguez RL, Rosenthal GG, Seymoure BM, Tinghitella RM: **Evolutionary novelty in communication between the sexes**. *Biol Lett* 2021, **17**:20200733 http://dx.doi.org/10.1098/rsbl.2020.0733.

13. Phillips JN, Ruef SK, Garvin CM, Le M-LT, Francis CD: **Background noise disrupts host–parasitoid interactions**. *R Soc Open Sci* 2019, **6**:190867 http://dx.doi.org/10.1098/rsos.190867.

14. • Gallego-Abenza M, Mathevon N, Wheatcroft D: **Experience modulates an insect's response to anthropogenic noise**. *Behav Ecol* 2020, **31**:90-96

The authors ran behavioral playback experiments testing responses to anthropogenic noise mediated by previous experience. All tested individuals responded to broadcasted traffic noise, with males closest to the road decreasing their chirp rate less than individuals calling further from the road. Their results suggest that behavioral plasticity may be shaped by experience to environmental stressors.

15. •• Sathyan R, Couldridge V: **The effect of anthropogenic noise and weather conditions on male calls in the bladder grasshopper *Bullacris unicolor***. *Bioacoustics* 2021, **30**:110-123

The authors assessed call parameter variation in the bladder grasshoppers inhabiting two sites in close proximity to each other that differed in their noise levels. They monitored calling activity with passive passive acoustic recorders and recorded weather conditions.They found that the total number of calls detected decreased with anthropogenic noise and the timing of their calls shifted to later in the night at the noisier site. Weather conditions, particularly temperature, had a significant influence on call parameters.

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pollution and weakens a trophic cascade. *Ecol Evol* 2018, **8**:7649-7656 http://dx.doi.org/10.1002/ece3.4273 2045-7758.

17. Morley EL, Jones G, Radford AN: **The importance of invertebrates when considering the impacts of anthropogenic noise**. *Proc R Soc B* 2013, **281**:20132683 http://dx.doi.org/10.1098/rspb.2013.2683.

18. • Candolin U, Wong BBM: **Mate choice in a polluted world: consequences for individuals, populations and communities**. *Phil Trans R Soc B* 2019, **374**:20180055
The authors discuss the impacts pollution has on communication and behaviors involved in different stages of mate choice, and how it has further impacts on individual fitness, population dynamics, and community structure and function. Lastly, the authors recommend that an improved understanding of the cascading effects of pollution is needed for more effective conservation and management practices.

19. McMahon TA, Rohr JR, Bernal XE: **Light and noise pollution interact to disrupt interspecific interactions**. *Ecology* 2017, **98**:1290-1299 http://dx.doi.org/10.1002/ecy.1770 00129658.

20. • Römer H: **Insect acoustic communication: the role of transmission channel and the sensory system and brain of receivers**. *Funct Ecol* 2020, **34**:310-321
The author provides examples for active mechanical processes in insect sensory receptors that influence the responses to external stimuli for adaptive strategies. They conclude by describing the advantages of having access to simple nervous systems and with the combined use of a variety of behavioural tests, can allow new insights into acoustic communication and its evolution.

21. •• Velilla E, Halfwerk W: **Adjustments to facilitate communication in noisy environments**. In *Encyclopedia of Animal Behavior,* edn 2. Edited by Choe JC. Academic Press; 2019:598-605
The authors review the various ways in which animals are affected by noise in their living environment and outline how they can cope with it. Highly recommended.

22. • Halfwerk W, van Oers K: **Anthropogenic noise impairs foraging for cryptic prey via cross-sensory interference**. *Proc R Soc B* 2020, **287**:20192951
Empirical study that addressed how noise affects a predator's foraging performance when foraging on cryptic prey. Noise significantly increased approach and attack latencies depending on the level of crypsis, with increased latencies for more cryptic prey targets than for conspicuous targets. Their results suggest that noise can interfere with the processing of visual information, such as cryptic prey, and could potentially influence important evolutionary consequences (e.g. arms race).

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Authors review the strategies to cope with natural sources of noise and provide a framework for the quantitative and mechanistic understanding of how noise has shaped populations and communities in the past.

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32. • Bowen AE, Gurule-Small GA, Tinghitella RM: **Anthropogenic noise reduces male reproductive investment in an acoustically signaling insect**. *Behav Ecol Sociobiol* 2020, **74**:103 http://dx.doi.org/10.1007/s00265-020-02868-3 0340-5443, 1432-0762.

33. Bent AM, Ings TC, Mowles SL: **Anthropogenic noise disrupts mate searching in *Gryllus bimaculatus***. *Behav Ecol* 2018, **29**:1271-1277 http://dx.doi.org/10.1093/beheco/ary126 1045-2249.

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35. Gurule-Small Gabrielle A, Tinghitella Robin M: **Developmental experience with anthropogenic noise hinders adult mate location in an acoustically signalling invertebrate**. *Biol Lett* 2018, **14**:20170714 http://dx.doi.org/10.1098/rsbl.2017.0714.

36. • Duarte MHL, Caliari EP, Scarpelli MDA, Lobregat GO, Young RJ, Sousa-Lima RS: **Effects of mining truck traffic on cricket calling activity**. *J Acoust Soc Am* 2019, **146**:656-664
The authors analyzed the mining noise effects on the acoustic communication of three species of crickets in an Atlantic Forest area in southeastern Brazil. Their results showed how crickets shift their auditory signaling emission patterns, such as decreasing their signaling effort, in response to temporal and spectral overlap with truck traffic. Their results supported the testing hypothesis, that anthropogenic activities (like mining) can trigger differences in the call spectral characteristics emitted by populations living in sites close and distant from the anthropogenic source.

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The authors examined the sensitivity of the Nicrophorus marginats burying beetle to substrate-borne vibration and their vulnerability to seismic noise. They observed the timing of stridulation during reproduction, measured the neural responses to substrate-borne vibrations, and measured beetle reproduction in the presence and absence of seismic noise.

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39. • Slabbekoorn H: **Noise pollution**. *Curr Biol* 2019, **29**:R957-R960 http://dx.doi.org/10.1016/j.cub.2019.07.018 09609822.

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The authors determined the effects of wind on the production of tremulatory signals in the neotropical katydid by recording signaling activity and natural wind variation in the field, as well as experimentally tested katydid response to varying levels of artificial wind during their most active signaling time. Wind levels coincided with peak signaling period for male katydids, and males produced significantly fewer tremulations when exposed to wind rather than acoustic noise or silence, suggesting that katydids are able to time their vibratory signaling both in the short-term and long-term to favorable sensory conditions.

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The authors review the benefits that sensory ecology can bring to wildlife conservation and management through case studies across major taxa and sensory modalities.

45. Fenoglio MS, Calviño A, González E, Salvo A, Videla M: **Urbanisation drivers and underlying mechanisms of terrestrial insect diversity loss in cities**. *Ecol Entomol* 2021, **46**:757-771.

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A synthesis and review of the current knowledge and empirical evidence on substrate vibrations as a readily available information source to eavesdroppers (e.g. predators and parasitoids) that shapes predator-prey behavior and interactions. Overall, generalist arthropod predators can intercept signals emitted by insects to obtain information about prey availability and use that information when making foraging decisions. Therefore, the longer individuals advertise themselves and the higher the amplitude of their vibrational signals, the higher the predation risk. The authors conclude by suggesting that the eavesdropping and exploitation of vibrational signals are major evolutionary drivers of inter-specific variation in communication and trophic interactions.

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The authors present neurophysiological recordings of net-casting spiders in response to acoustic stimulation from sound-sensitive areas in the brain and isolated forelegs. The author's demonstrate Deinopis have a broad range of auditory sensitivity (100–10 000 Hz) and can detect auditory stimuli at 2 m from the sound source, and at or above 60 dB SPL.

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The authors dicuss the concepts and basic terminology in the field of vibroscape and provide guidelines on how experimental approaches and analysis for the study and recording of vibroscape in the field.

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The authors provide a method for thoroughly conducting calibrated and high-fidelity vibrational playbacks using consumer audio equipment and custom-written signal processing software.

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The authors describe the hardware build of the low-cost, small, full-spectrum recorder (AudioMoth) and provide the open-source information for the device.

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Systematic literature search for empirical evidence of intra-specific variation in responses to anthropogenic noise. The authors outline the intrinsic (e.g. body size, condition, sex, and personality) and extrinsic (e.g. environmental context, repeated exposure, prior experience, and multiple stressors) factors that influence response to an environmental stressor. They find that only 10% experimentally test intra-specific variation, and stress the need to improve our husbandry, monitoring, and management of wildlife, as well as including the framework in noise pollution mitigation management.

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Review on present the current knowledge of multimodal cue use during orientation and navigation in insects. The authors highlight examples from sensorimotor behaviours in various insect taxa including species that

migrate seasonally over large distances, and demonstrate how multiple cues are combined behaviourally and what potential trade-offs insect be confronted when using different modalities.

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