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ABSTRACT: Many species are currently experiencing anthropogenically driven environmental changes. Among these changes, increasing noise levels are specifically a problem for species using acoustic signals (i.e., species relying on signals that use the same sensory modality as anthropogenic noise). Yet many species use other sensory modalities, such as visual and olfactory signals, to communicate. However, we have only little understanding of whether changes in the acoustic environment affect species that use sensory modalities other than acoustic signals. We studied the impact of anthropogenic noise on the common cuttlefish *Sepia officinalis*, which uses highly complex visual signals. We showed that cuttlefish adjusted their visual displays by changing their color more frequently during a playback of anthropogenic noise, compared with before and after the playback. Our results provide experimental evidence that anthropogenic noise has a marked effect on the behavior of species that are not reliant on acoustic communication. Thus, interference in one sensory channel, in this case the acoustic one, affects signaling in other sensory channels. By considering sensory channels in isolation, we risk overlooking the broader implications of environmental changes for the behavior of animals.

Keywords: animal communication, noise pollution, environmental change, phenotypic plasticity, *Sepia officinalis*.

Introduction

Animal communication plays a crucial role for many species, because it is used in different contexts (e.g., sexual selection, parental care, and predator-prey interactions; Bradbury and Vehrencamp 2011). Communication in its simplest form involves a sender producing a signal that conveys information and a receiver making a decision on how to respond to that signal (Bradbury and Vehrencamp

2011). Thus, for an individual, it is vital that the signal is transmitted effectively across the environment to the receiver. To maintain signal efficiency, species use a variety of different sensory modalities to communicate, depending on the environment they inhabit. However, many species are currently experiencing anthropogenically driven environmental changes, including noise altering acoustic environments in both aquatic and terrestrial ecosystems (Malakoff 2010; Slabbekoorn et al. 2010).

Changes in the acoustic environment are a specific problem faced by species that use acoustic signals (i.e., those that rely on signals that use the same sensory modality as anthropogenic noise). For example, anura and birds adjust their acoustic signals when experimentally exposed to increased noise levels (e.g., Halfwerk and Slabbekoorn 2009; Cunnington and Fahrig 2010; Gross et al. 2010; Verzijden et al. 2010). In these cases, animals modify their acoustic signals in response to changes in the acoustic environment within one sensory modality. Yet many species use other sensory modalities, such as visual and olfactory signals, to communicate (Bradbury and Vehrencamp 2011). However, whether changes in the acoustic environment affect species that use sensory modalities other than acoustic signals is still unknown.

Cephalopods use complex visual signals, including the alteration of body coloration and patterning (Tinbergen 1939; Hanlon and Messenger 1988, 1996). Additionally, they use a mechanosensory receptor system of epidermal head and arm lines, which allows them to detect local water movements, including those caused by sound waves transmitted underwater (Sundermann 1983; Budelmann and Bleckmann 1988). The perception of local water movements can be enhanced by raising their first pair of arms, and there is no evidence that cephalopods communicate by sound (Budelmann et al. 1991; Hanlon and Messenger 1996; Vermeij 2010). If species that do not rely on acoustic

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communication respond to anthropogenic changes in their acoustic environment, noise pollution could have far-reaching consequences by affecting not only species that use acoustic signals but also those that communicate by other means.

To test whether anthropogenic noise affects animals that do not rely on acoustic communication, we exposed common cuttlefish (*Sepia officinalis*) to an experimental noise-polluted environment. We examined whether cuttlefish changed their visual and tactile behavior in response to changes in their acoustic environment by exposing them to anthropogenic noise. To exclude the possibility that the presence of the loudspeaker alone or any other acoustic stimuli elicits the same behavioral response, we exposed the same individuals to a control playback consisting of waves breaking in the surf zone. We predicted that individuals exposed to anthropogenic noise should adjust their behavior to changes in their acoustic environment. Furthermore, if individuals responded more strongly to anthropogenic noise than to the control playback, we could conclude that anthropogenic noise, and not merely any change in the acoustic environment, affects behavior.

Material and Methods

Study Species and Housing

Sepia officinalis eggs were collected from lobster pot lines off Weymouth, England; transported to aquarium facilities in Portaferry, Northern Ireland; and reared under standard laboratory conditions for 4–6 weeks after hatching (e.g., Forsythe et al. 1991, 1994). Animals were fed live mysid shrimps ad lib., with food supplies checked and topped up twice daily. Cuttlefish were exposed to only common aquarium noises until the start of the playback experiments. One week before experimentation, 30 cuttlefish were placed singly in isolated tanks (22 cm × 31 cm × 22 cm) supplied with flow-through seawater at local ambient temperature. To prevent sound from playbacks being transmitted to other tanks, all tanks rested on a 10-cm thick Styrofoam base, and each tank was isolated visually from neighboring tanks by 5-cm Styrofoam.

Playback Stimuli and Experimental Setup

First, we tested whether cuttlefish adjusted their behavior to anthropogenic noise, and second, whether the exposure to anthropogenic noise and a control sound led to different behavioral responses (cf. Gross et al. 2010). To avoid pseudoreplication, a new set of acoustic stimuli was created for each individual (Kunc et al. 2007a, 2007b; McMullen et al. 2014). The control playback consisted of recordings of waves breaking in the surf zone, and the anthropogenic

noise playback consisted of underwater engine noise from a small car ferry (MV *Portaferry II*, 312 gross tonnage). We chose ship noise, because it is the most common source of anthropogenic noise in the aquatic environment (Vasconcelos et al. 2007), and because most other anthropogenic noise is biased toward the lower frequency band (Hildebrand 2009). Therefore, ship noise represents a suitable stimulus to test the impact of anthropogenic noise on animals in the aquatic environment. Recordings of both types of stimuli were made with a hydrophone (HTI-96-MIN with preamplifier; manufacturer-calibrated sensitivity, −165 dB re: 1 v/μPa; frequency range, 2 Hz to 30 kHz) connected to a Marantz PMD660 recorder. The hydrophone and recorder were calibrated using a signal of known amplitude (for method, see Purser and Radford 2011). Averaged power spectra (fig. 1) were generated in AVISOFT SASLab (R. Specht, Berlin) using fast Fourier transform (FFT) analysis (FFT size 1,024; Hann evaluation window; spectrum level units normalized to 1 Hz bandwidth; 50% overlap, averaged from 5-s segments of multiple recordings).

The original recording of the ship noise, which was used as the anthropogenic noise stimuli, had a higher sound pressure level (SPL) than the waves breaking the surf zone, which was used as a control treatment (fig. 1). Therefore, to mitigate the difference in SPL, we standardized the stimuli to the peak amplitude using the "normalize" function in Audacity 1.2.6. (sample frequency: 44.1 kHz; sample format: 32-bit float). Rerecordings of the two stimuli in the tank showed that this successfully reduced the difference in SPL between the two stimuli (fig. 1; difference between original recordings: 48 dB; difference between tank rerecordings: 20 dB). The remaining differences in the recordings of the different stimuli are based on the spectral characteristics of the stimuli, which show similar patterns to the original recordings (frequency quartiles for the original anthropogenic recording: 25% = 417 Hz, 50% = 812 Hz, 75% = 22,358 Hz; frequency quartiles for the anthropogenic noise recorded in tank: 25% = 270 Hz, 50% = 656 Hz, 75% = 6434 Hz; frequency quartiles for the original control recording: 25% = 80 Hz, 50% = 370 Hz, 75% = 2,488 Hz; frequency quartiles for the control recorded in tank: 25% = 80 Hz, 50% = 140 Hz, 75% = 235 Hz).

The aim of our study was to test whether changes in one sensory channel (the acoustic channel, which was affected by adding anthropogenic noise) affect behavior in other sensory channels (the tactile and the visual channels). To rule out the possibility that individuals might respond to any change in their acoustic environment in a uniform manner, we compared the response to anthropogenic noise with response to the control treatment.

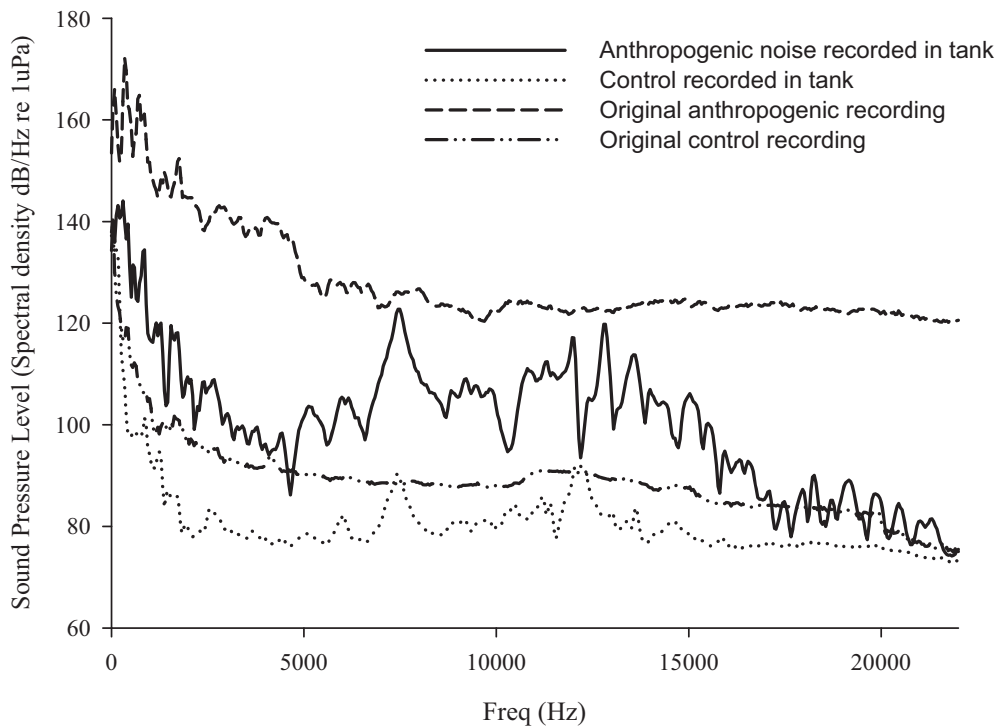Playbacks were conducted on 30 individuals in a ran-

Figure 1: Averaged power spectra for anthropogenic noise (ferry noise) and biological control (waves breaking in the surf zone) recorded in the wild and recorded in the experimental tank (fast Fourier transform size = 1,024; Hann evaluation window; spectrum level units normalized to 1 Hz bandwidth; 50% overlap; averaged from 5-s recordings). Freq = frequency.

domized order, and the two treatments were separated by 24 h to minimize habituation effects. Stimuli were played back through a UW30 underwater speaker (Lubell Labs) from a compact disk player connected to an amplifier (EAGLE TPA 30V). The speaker was mounted in a customized tank lid that allowed it to sit below the water line while keeping disturbance to a minimum.

Experimental Protocol

For each playback, individuals were observed for 210 s before the playback started (silence), which provided an individual's baseline level. Playback duration was 210 s, and we continued to observe subjects for another 210 s after playback (silence). For the first 30 s of the playback period, the noise level was increased gradually to avoid startling the cuttlefish. During each of the 210-s periods, we noted (i) the frequency of color changes, as a measure of visual signaling; (ii) the frequency of time individuals had their first pair of arms raised, as a measure of tactile signaling (cf. Hanlon and Messenger 1988); and (iii) the time spent swimming (in seconds), as a measure of activity.

Statistical Analyses

Statistical analyses were performed in IBM SPSS 19. To test whether cuttlefish changed their behavior during the anthropogenic noise playbacks, we used repeated measures ANOVA. To fulfill the assumptions of sphericity, the three behavioral measurements were transformed using root squared ($x + 10$). Data shown in the figures are raw data and are available in the Dryad Digital Repository: http://datadryad.org/resource/doi:10.5061/dryad.c6011 (Kunc et al. 2014). Treatment order had no significant effect on each of the behavioral responses and thus was excluded from the final models. To test whether cuttlefish changed their behavior differently from the baseline control observations to the two treatment observations, we calculated the differences of the transformed data in the frequency of color changes, in the time swimming, and in the frequency of arms raised per cuttlefish per interval and tested these values against each other using paired t-tests (cf. Gross et al. 2010). All tests were two-tailed.

Results

Cuttlefish changed their behavior in response to anthropogenic noise, and their response also differed between

the anthropogenic noise and the control playback. Cuttlefish altered their visual displays by changing color more frequently during the anthropogenic noise playback compared with before and after the playback ($F_{2,58} = 18.31$, $P < 0.001$; fig. 2A). The increase in color changes was higher during the anthropogenic noise playback than during the control playback ($t_{29} = -3.9$, $P < 0.001$; fig. 2D). Individuals also spent more time swimming during the anthropogenic noise playback than before and after the playback ($F_{2,58} = 10.09$, $P < 0.001$; fig. 2B) and spent more time swimming during the anthropogenic noise playback compared with during the control playback ($t_{29} = -2.3$, $P < 0.032$; fig. 2E).

However, the change in the acoustic environment affected signaling not only in the visual channel but also in the tactile channel. Cuttlefish raised their first pair of arms more often during the anthropogenic noise playback compared with before or after the playback ($F_{2,58} = 19.92$, $P < 0.001$; fig. 2C). During the anthropogenic noise playback, cuttlefish raised their first pair of arms more frequently than during the control playback ($t_{29} = -6.7$, $P < 0.001$; fig. 2F).

Discussion

Our results provide experimental evidence that anthropogenic noise can affect behavior across sensory modalities. We found that cuttlefish immediately adjusted their behavior when they were exposed to anthropogenic noise, and their response to the noise and the control playback differed. The noise playback elicited a stronger response than the control playback of waves breaking in the surf zone. Cuttlefish in our experiment changed color more frequently, swam more, and raised their first pair of arms more often during high levels of noise than before or after the noise playback.

Adjustments in behavior may allow individuals to respond to interference in one sensory channel by changing behavior in another channel. However, individuals may only mitigate the effect of environmental changes, not fully compensate for them (Gross et al. 2010). A change in a species' environment, whether that change is natural or induced by humans, is a potential source of selection on traits important for fitness (Gienapp et al. 2008). For example, the crossmodal impact of noise on behavior may change the outcome of sexual selection in species that rely on visual signals. Cephalopods use complex visual signals in courtship and deterrence of rivals (Tinbergen 1939; Hanlon and Messenger 1988, 1996). Therefore, the increase in color changes observed in our experiment may affect both inter- and intrasexual selection. The crossmodal effect of noise on visual signals may also affect predator-prey interactions. The simplest and most common antipred-

predator strategy is to avoid being detected by predators (Bradbury and Vehrencamp 2011). The primary antipredator strategy of cephalopods is crypsis (i.e., blending into the background; Hanlon and Messenger 1996). Therefore, the increased frequency of color changes caused by noise affects the ability to be optimally camouflaged and may thus increase the risk of predation.

Regarding the behavioral adjustments observed in our experiment, a number of possible mechanisms may be involved. Anthropogenic noise can increase stress levels (Stansfeld and Matheson 2003; Wysocki et al. 2006; Kight and Swaddle 2011). When exposed to anthropogenic noise cuttlefish changed colors more frequently and swam more, suggesting an increase in stress levels. Such stress responses are found when cuttlefish are exposed to predators by changing their coloration (Langridge et al. 2007; Langridge 2009), and an increase in swimming suggests enhanced alarm or avoidance behavior (cf. Skalski et al. 1992; Slotte et al. 2004; Sara et al. 2007; Fewtrell and McCauley 2012). Moreover, noise can distract individuals (Chan et al. 2010a, 2010b), reducing the ability of an individual to maintain efficient crypsis, which may in turn lead to more color changes.

In terrestrial species, recent research showed that behavioral plasticity allows individuals to respond to a novel acoustic environment by immediately adjusting their acoustic signals to increasing noise levels (Cunnington and Fahrig 2010; Gross et al. 2010; Verzijden et al. 2010; Bermudez-Cuamatzin et al. 2011; Hanna et al. 2011; McLaughlin and Kunc 2013; Montague et al. 2013). It has been suggested that species using acoustic signals as their main form of communication may suffer most from changes in the acoustic environment because of the increased interference in their communication channel (Rabin and Greene 2002; Rabin et al. 2003; Warren et al. 2006). Our results extend these findings by demonstrating that anthropogenic noise does not affect only behavior within the interfered sensory modality. Thus, the impact of anthropogenic-induced changes in the environment, by having a crossmodal impact on the behavior of species that rely on sensory channels other than the one with interference, may be more widespread than previously thought.

The crossmodal impact of anthropogenic noise was not limited to the visual channel alone; noise also affected the tactile channel. Cuttlefish detect local water movements with the epidermal head and arm lines (Komak et al. 2005), which are analogous to the lateral lines of fish (Budelmann and Bleckmann 1988). The increase in arm raising seen in this study suggests that an individual is in a heightened state of awareness that is caused by the constant water movements generated by the playback. Because cuttlefish rely on the epidermal lines for prey location, hunting, and capture (Budelmann et al. 1991), anthropogenic noise
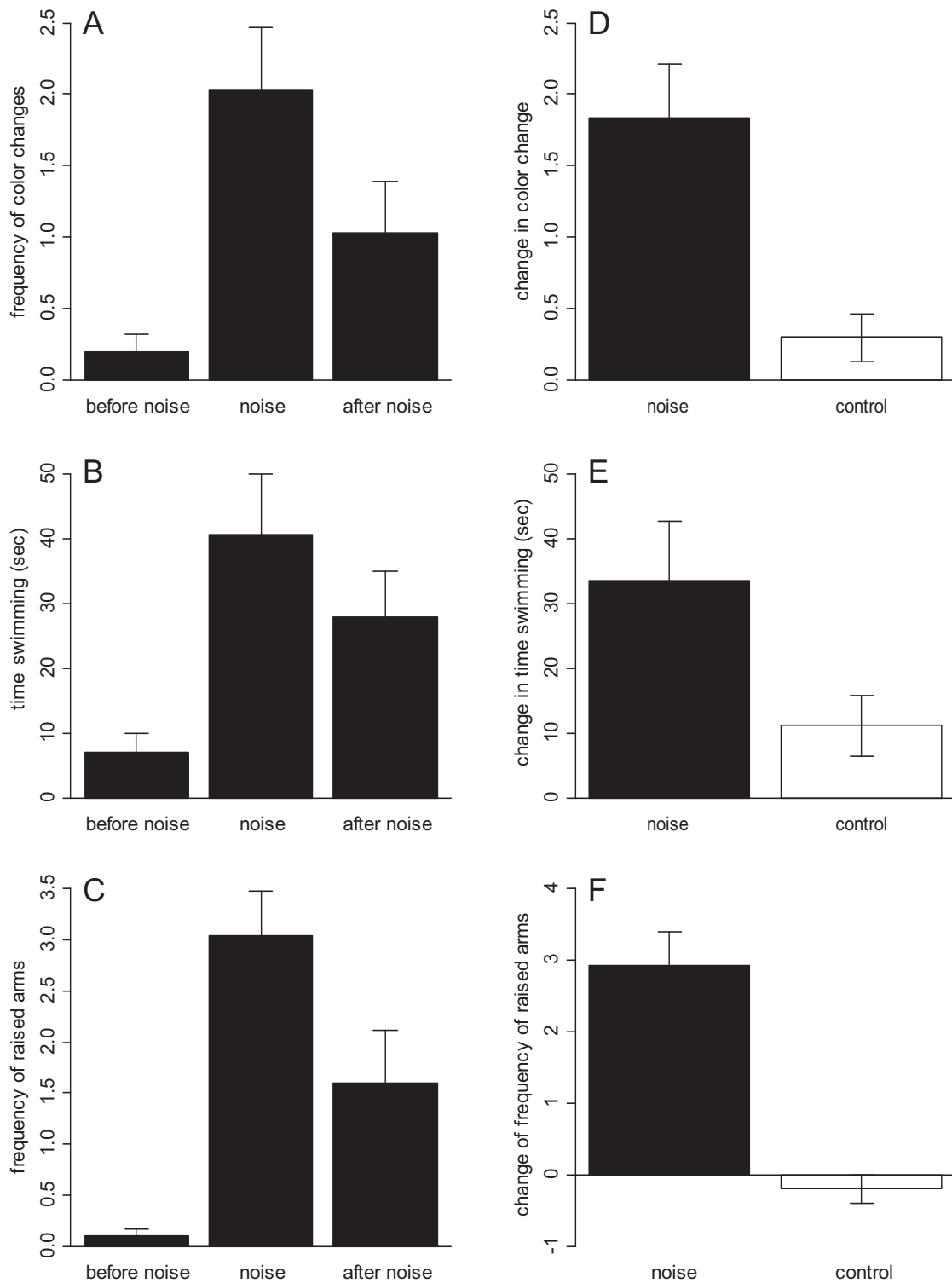
Figure 2: Mean ± SE (*A*) frequency of color changes, (*B*) time spent swimming, and (*C*) frequency of raised-arms behavior before, during, and after the ferry noise playback. Mean ± SE change in (*D*) frequency of color changes, (*E*) time spent swimming, and (*F*) frequency of raised-arms behavior from before to during the noise and control playback.

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might mask subtle cues, such as vibrations of potential predators or prey.

Anthropogenic noise may mask important auditory cues in the environment (e.g., Katti and Warren 2004; Brumm and Slabbekoorn 2005; Patricelli and Blickley 2006). Cuttlefish use a mechanosensory receptor system to detect local water movements. There is much debate regarding whether and how cephalopods detect sound per se (e.g., Packard et al. 1990; Hu et al. 2009; Mooney et al. 2010). Underwater acoustic stimuli have two components: particle motion and sound pressure, both of which can provide information to individuals (Radford et al. 2012). Most recent evidence suggests that squid, a closely related species, detect particle motion rather than pressure of a sound field (Mooney et al. 2010). In our setup, individuals were in the acoustic near field; therefore, particle motion cannot be estimated from the SPL, because the two are not proportionally coupled (Akamatsu et al. 2002). Therefore, an increase in SPL does not necessarily correspond with an increase in particle motion (Akamatsu et al. 2002). Because of the lack of commercially available equipment, particle motion was not measured. The differences in the response to the two stimuli are not necessarily due to differences in SPL or particle motion. However, the observed differences could be explained by the nature of the stimuli, which differ in time domain and spectral characteristics (cf. Gross et al. 2010). Indeed, our data suggest that cuttlefish are able to distinguish between different acoustic stimuli in their environment. Cuttlefish may habituate to anthropogenic noise over time, although this process would depend on the nature and characteristics of the signal in question. Additional studies conducted over different time scales are required to consider the longer-term consequences of these behavioral responses.

Our experiment was not designed to distinguish between the two components, particle motion and sound pressure, but rather to investigate behavioral responses to changes in the acoustic environment, which are often difficult to detect underwater. Experimental studies in a controlled environment provide a starting point to test whether anthropogenic noise affects not only species that rely on acoustic signals but also species that use other sensory channels as their main form of communication. Care must be taken when extrapolating results from tank-based experiments to meaningful implications for individuals living in the wild, because underwater acoustics are complex (Bruintjes and Radford 2013; Wale et al. 2013).

In conclusion, our results provide experimental evidence that anthropogenic noise has a marked effect on the behavior of a species that is not reliant on acoustic communication and that different types of background noise lead to different behavioral responses. Interference in one sensory channel, in this case the acoustic one, can affect behavior in other sensory channels. Thus, by considering sensory channels in isolation, we risk overlooking the broader implications of noise pollution.

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