The costs of chronic noise exposure for terrestrial organisms

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Growth in transportation networks, resource extraction, motorized recreation and urban development is responsible for chronic noise exposure in most terrestrial areas, including remote wilderness sites. Increased noise levels reduce the distance and area over which acoustic signals can be perceived by animals. Here, we review a broad range of findings that indicate the potential severity of this threat to diverse taxa, and recent studies that document substantial changes in foraging and anti-predator behavior, reproductive success, density and community structure in response to noise. Effective management of protected areas must include noise assessment, and research is needed to further quantify the ecological consequences of chronic noise exposure in terrestrial environments.

Anthropogenic noise and acoustic masking

Habitat destruction and fragmentation are collectively the major cause of species extinctions [1,2]. Many current threats to ecological integrity and biodiversity transcend political and land management boundaries; climate change, altered atmospheric and hydrologic regimes and invasive species are prominent examples. Noise also knows no boundaries, and terrestrial environments are subject to substantial and largely uncontrolled degradation of opportunities to perceive natural sounds. Noise management is an emergent issue for protected lands, and a potential opportunity to improve the resilience of these areas to climate change and other forces less susceptible to immediate remediation.

Why is chronic noise exposure a significant threat to the integrity of terrestrial ecosystems? Noise inhibits perception of sounds, an effect called masking (see Glossary) [3]. Birds, primates, cetaceans and a sciurid rodent have been observed to shift their vocalizations to reduce the masking effects of noise [4–7]. However, compromised hearing affects more than acoustical communication. Comparative evolutionary patterns attest to the alerting function of hearing: (i) auditory organs evolved before the capacity to produce sounds intentionally [8], (ii) species commonly hear a broader range of sounds than they are capable of producing [9], (iii) vocal activity does not predict hearing performance across taxa [9,10], (iv) hearing continues to function in sleeping [11] and hibernating [12] animals; and (v) secondary loss of vision is more common than is loss of hearing [13].

Masking is a significant problem for the perception of adventitious sounds, such as footfalls and other byproducts of motion. These sounds are not intentionally produced and natural selection will typically favor individuals that minimize their production. The prevalence and characteristics of adventitious sounds have not been widely studied [14–16], although their role in interactions

Glossary

Alerting distance: the maximum distance at which a signal can be perceived. Alerting distance is pertinent in biological contexts where sounds are monitored to detect potential threats.

Atmospheric absorption: the part of transmission loss caused by conversion of acoustic energy into other forms of energy. Absorption coefficients increase with increasing frequency, and range from a few dB to hundreds of dB per kilometer within the spectrum of human audibility.

Audible: a signal that is perceptible to an attentive listener.

A-weighting: A method of summing sound energy across the frequency spectrum of sounds audible to humans. A-weighting approximates the inverse of a curve representing sound intensities that are perceived as equally loud (the 40 phon contour). It is a broadband index of loudness in humans in units of dB(A) or dBA. A-weighting also approximates the shapes of hearing threshold curves in birds [20].

Decibel (dB): a logarithmic measure of acoustic intensity, calculated by 10 $\log_{10}$(sound intensity/reference sound intensity). 0 dB approximates the lowest threshold of healthy human hearing, corresponding to an intensity of 10^{-12} Wm^{-2}. Example sound intensities: −20 dB, sound just audible to a bat, owl or fox; 10 dB, leaves rustling, quiet respiration; 60 dB, average human speaking voice; 80 dB, motorcycle at 15 m.

Frequency (Hz and kHz): for a periodic signal, the maximum number of times per second that a segment of the signal is duplicated. For a sinusoidal signal, the number of cycles (the number of pressure peaks) in one second (Hz). Frequency equals the speed of sound ($\sim$340 ms^{-1}) divided by wavelength.

Ground attenuation: the part of transmission loss caused by interaction of the propagating sound with the ground.

Listening area: the area of a circle whose radius is the alerting distance. Listening area is the same as the 'active space' of a vocalization, with a listener replacing the signaler as the focus, and is pertinent for organisms that are searching for sounds.

Masking: the amount or the process by which the threshold of detection for a sound is increased by the presence of the aggregate of other sounds.

Noticeable: a signal that attracts the attention of an organism whose focus is elsewhere.

Scattering loss: the part of transmission loss resulting from irregular reflection, diffraction and refraction of sound caused by physical inhomogeneities along the signal path.

Spectrum, power spectrum and spectral profile: the distribution of acoustic energy in relation to frequency. In graphical presentations, the spectrum is often plotted as sound intensity against sound frequency (Figure 1, main text).

1/3 octave spectrum: acoustic intensity measurements in a sequence of spectral bands that span 1/3 octave. The International Standards Organization defines $1/3^{rd}$ octave bands used by most sound level meters (ISO 266, 1975). $1/3^{rd}$ octave frequency bands approximate the auditory filter widths of the human peripheral auditory system.

Spreading loss: more rigorously termed divergence loss. The portion of transmission loss attributed to the divergence of sound energy, in accordance with the geometry of environmental sound propagation. Spherical spreading losses in dB equal $20 * \log 10(R/R_0)$, and result when the surface of the acoustic wavefront increases with the square of distance from the source.

White noise: noise with equal energy across the frequency spectrum.

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Box 1. Geographic extent of transportation noise in the USA

Transportation noise is a near ubiquitous component of the modern acoustical landscape. The method used here to estimate the geographic extent of airway (Figure Ia,b), railway (Figure Ic) and roadway (Figure Id) noise in the continental USA is calculated using the average human 'noticeability' of noise. Noise was deemed noticeable when the modeled noise intensity from transportation [in dB(A)] exceeded the expected noise intensity as predicted from population density [also dB(A)]. Although noticeability is a conservative metric of the geographic extent of transportation noise, this analysis only indicates the potential scope of the problem. How anthropogenic noise changes the temporal and spectral properties of naturally-occurring noise (Figure 1, main text) and the life histories of individual species will be crucial components of a more thorough analysis.

The maps in Figure I reflect the following calculations: (i) noise calculations are county-by-county for a typical daytime hour; (ii) county population density is transformed into background sound level using an EPA empirical formula (see Ref. [84]); higher density implies higher background sound levels; (iii) the geographic extent of transportation noise is determined by calculating the distance from the vehicle track at which the transportation noise falls below the background sound level, multiplying twice that distance by the length of the transportation corridor in the county (giving a noticeability area), and comparing that area with the total area in the county to compute the percentage land area affected. A low percentage noticeability can result if either the population density is high or the number of transportation segments is low in the county. This analysis indicates that transportation noise is audible above the background of other anthropogenic noise created by local communities in most counties in continental USA. See Ref. [84] for more details.

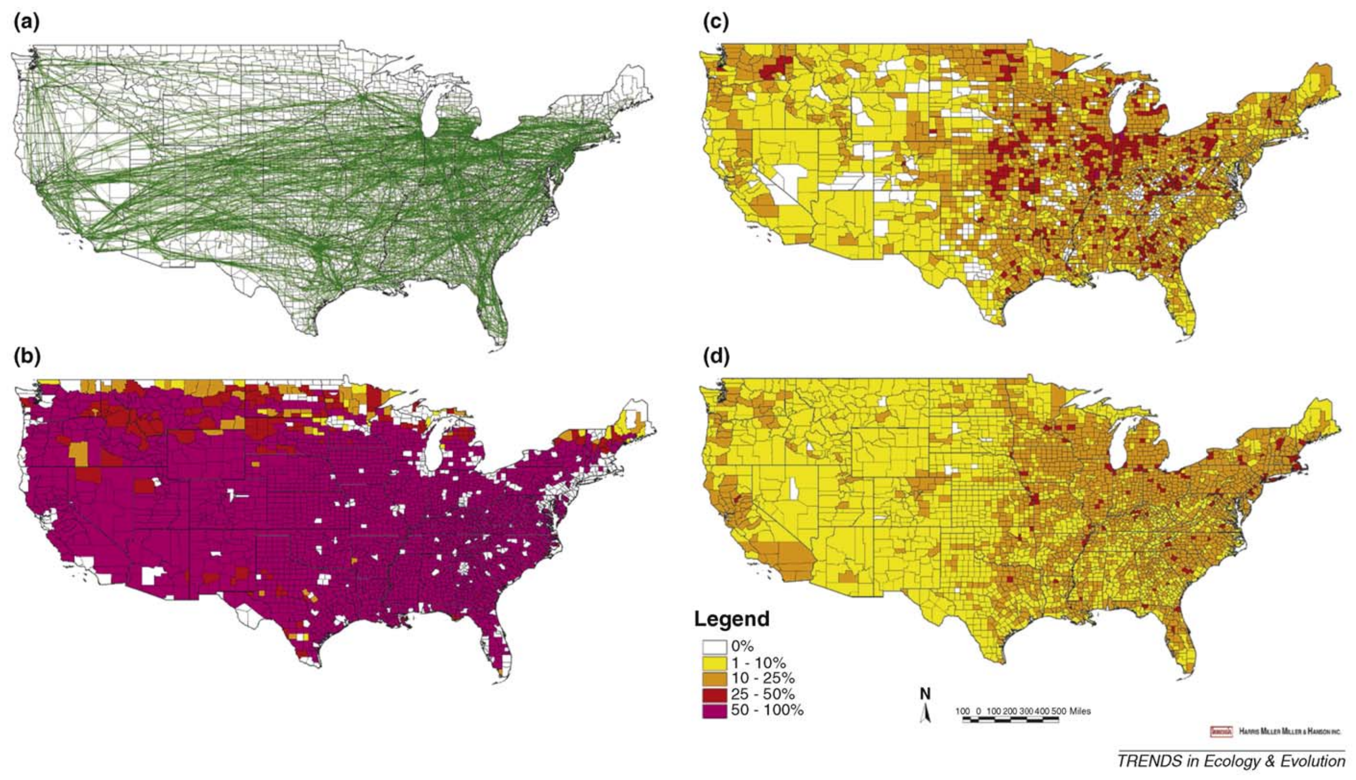

Figure I. Percent of US county areas in which transportation noise is noticeable. **(a)** Jet departures that occurred between 3 and 4 pm on Oct. 17, 2000, tracked to first destination. **(b)** Data from (a) were used to estimate the geographic extent of high altitude airway noise in the USA. The geographic extent of noise from railway and highway networks is depicted in **(c)** and **(d)**, respectively. The color-coded divisions (see legend; divisions increase in size as the percent increases) were chosen assuming that, as noticeability increases, so do estimate errors due to noticeability area overlap from different transportation segments. Adapted with permission from Ref. [84].

among predators and prey is unquestionable. In animal communication systems, both the sender and receiver can adapt to noise masking, but for adventitious sounds the burden falls on listeners.

Anthropogenic disturbance is known to alter animal behavioral patterns and lead to population declines [17,18]. However, animal responses probably depend upon the intensity of perceived threats rather than on the intensity of noise [19]. Deleterious physiological responses to noise exposure in humans and other animals include hearing loss [20], elevated stress hormone levels [21] and hypertension [22]. These responses begin to appear at exposure levels of 55–60 dB(A), levels that are restricted to relatively small areas close to noise sources [20].

The scale of potential impact

The most spatially extensive source of anthropogenic noise is transportation networks. Growth in transportation is increasing faster than is the human population. Between 1970 and 2007, the US population increased by approximately one third (http://www.census.gov/compendia/statab). Traffic on US roads nearly tripled, to almost 5 trillion vehicle kilometers per year (http://www.fhwa.dot.gov/ohim/tvtw/tvtpage.cfm). Several measures of aircraft traffic grew by a factor of three or more between 1981 and 2007 (http://www.bts.gov/programs/airline_information/air_carrier_traffic_statistics/airtraffic/annual/1981_present.html). Recent reviews of the effects of noise on marine mammals have identified similar trends in shipping noise (e.g. Refs [23,24]). In addition to transportation, resource extraction and motorized recreation are spatially extensive sources of noise on public lands.

Systematic monitoring by the Natural Sounds Program of the US National Park Service (http://www.nature.nps.gov/naturalsounds) confirms the extent of noise intrusions. Noise is audible more than 25% of the hours between 7am and 10pm at more than half of the 55 sites in 14 National Parks that have been studied to date; more than a dozen sites have hourly noise audibility percentages exceeding 50% (NPS, unpublished). Remote wilderness areas are not immune, because air transportation noise is widespread, and high traffic corridors generate substantial noise increases on the ground (Box 1). For example, anthropogenic sound is audible at the Snow Flats site in Yosemite National Park nearly 70% of the time during peak traffic hours. Figure 1 shows that typical noise levels exceed natural ambient sound levels by an order of magnitude or more.

Roads are another pervasive source of noise: 83% of the land area of the continental US is within 1061 m of a road [25]. At this distance an average automobile [having a noise source level of 68 dB(A) measured at 15 m] will project a noise level of 20 dB(A). This exceeds the median natural levels of low frequency sound in most environments. Trucks and motorcycles will project substantially more noise: up to 40 dB(A) at 1 km. Box 2 provides a physical model of the reduced listening area that can be imposed by these louder background sound levels.

Acoustical ecology

Intentional communication, such as song, is the best studied component of the acoustical world, and these signals are often processed by multiple receivers. These communication networks enable female and male songbirds, for example, to assess multiple individuals simultaneously for mate choice, extra-pair copulations and rival assessment [26]. Acoustic masking resulting from increasing background sound levels will reduce the number of individuals that comprise these communication networks and have unknown consequences for reproductive processes [27].

Reproductive and territorial messages are not the only forms of acoustical communication that operate in a network. Social groups benefit by producing alarm calls to warn of approaching predators [28] and contact calls to maintain group cohesion [29]. A reduction in signal transmission distance created by anthropogenic noise might decrease the effectiveness of these social networks. The inability to hear just one of the alarm calling individuals can result in animals underestimating the urgency of their response [30].

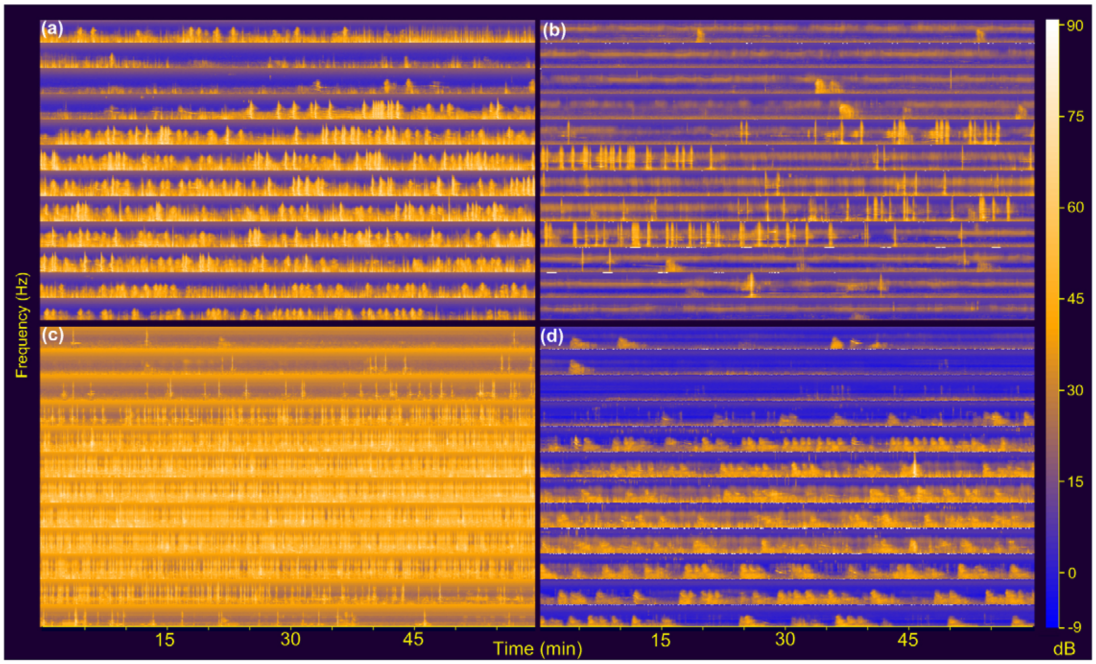

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Figure 1. 24-hour spectrograms of Indian Pass in Lake Mead National Recreation Area **(a)**, Madison Junction in Yellowstone National Park **(b)**, Trail Ridge Road in Rocky Mountain National Park **(c)**, and Snow Flats in Yosemite National Park **(d)**. Each panel displays 1/3 octave spectrum sound pressure levels, with two hours represented horizontally in each of 12 rows. The first three rows in each panel represent the quietest hours of each day, from midnight to 6 am. Frequency is shown on the y axis as a logarithmic scale extending from 12.5 Hz to 20 kHz, with the vertical midpoint in each row corresponding to 500 Hz. The z axis (color) describes sound pressure levels in dB (unweighted); the color scaling used for all four panels is indicated by the color bar on the right hand edge. The lowest 1/3 octave levels are below 0 dB, the nominal threshold of human hearing. White dots at the upper edge of some rows in the panels on the right side denote missing seconds of data. Low-frequency, broadband signatures from high altitude jets are present in all four panels. Distinct examples are present just before 6 am in (a), near 12:45 am in (b) and (c), and between midnight and 12:30 am in (d). Fixed wing aircraft signatures (tonal contours with descending pitch) are present in (a) and (d), with a good example at 1:15 am in (d). Broadband signatures with very low frequency tonal components in (a) are due to low-altitude helicopters, that are prominent from ~7 am until 8 pm. Another prominent helicopter signature is at 11:30 am in (d). (b) illustrates snowmobile and snowcoach sounds recorded ~30 m from the West Entrance Road in Yellowstone. (c) illustrates traffic noise recorded 15 m from Trail Ridge Road in Rocky Mountain National Park, during a weekend event featuring high levels of motorcycle traffic. Background sound levels at the Rocky Mountain site were elevated by sounds from the nearby river.

Box 2. Physical model of reduced listening area in noise

The maximum detection distance of a signal decreases when noise elevates the masked hearing threshold. The masked detection distance: original detection distance ratio will be the same for all signals in the affected frequency band whose detection range is primarily limited by spreading losses. For an increase of N dB in background sound level, the detection distance ratio is: $k = 10^{-N/20}$. The corresponding fraction of original listening area is: $k = 10^{-N/10}$. A 1-dB increase in background sound level results in 89% of the original detection distance, and 79% of the original listening area. These formulae will overestimate the effects of masking on alerting distance and listening area for signals that travel far enough to incur significant absorptive and scattering losses. More detailed formulae would include terms that depend upon the original maximum range of detection.

Figure I illustrates the expected noise field of a road treated as a line source (equal energy generated per 10 m segment). An animal track is marked by ten circular features, that depict the listening area of a signal whose received level (expressed as a grey-scaled value for each possible source location) decreases with the inverse square of distance from the listener. The apparent shrinkage of the circles is due to masking by the increasingly dark background of sound projected from the road, just as noise would shrink the listening area. The circles span 9 dB in road noise level, in 1-dB steps from the quietest location (upper right) to the noisiest (at the crossing).

Masking effects are reduced with increasing spectral separation between noise and signal. The model presumes that the original conditions imposed masked hearing thresholds, so organisms that are limited by their hearing thresholds will not be as affected by masking. A diffuse noise source is illustrated, but the same results would be obtained if some spatial release from masking were possible, so long as the original conditions implied masked hearing thresholds (see Ref. [85] for a review of release strategies).

These measures of lost listening opportunity are most pertinent for chronic exposures. They imply substantial losses in auditory awareness for seemingly modest increases in noise exposure. Analyses of transportation noise impacts based on perceived loudness often assert that increases of up to three dB have negligible effects; this corresponds to a 50% loss of listening area.

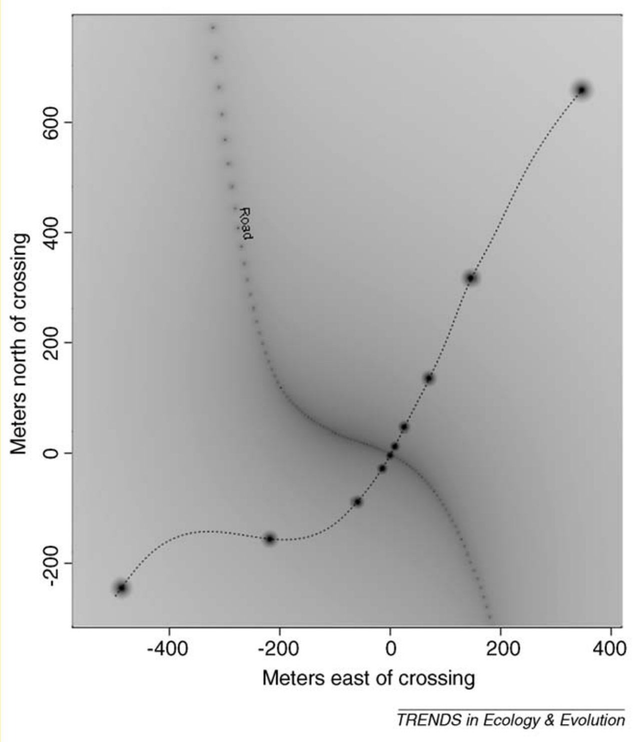

Figure I. A physical model of reduced listening area as an animal approaches a road.

Many vertebrate and invertebrate species are known to listen across species' boundaries to one another's sexual (e.g. Ref. [31]), alarm (e.g. Ref. [32]) and other vocalizations. Recent examples include gray squirrels, *Sciurus carolinensis*, listening in on the communication calls of blue jays, *Cyanocitta cristata*, to assess site-specific risks of cache pilfering [33]; and nocturnally migrating songbirds [34] and newts (Ref. [35] and Refs therein) using heterospecific calls to make habitat decisions. Reduced listening area imposed by increased sound levels is perhaps more likely to affect acoustical eavesdropping than to interfere with deliberate communication. The signaler is under no selective pressure to ensure successful communication to eavesdroppers and any masking compensation behaviors will be directed at the auditory system and position of the intended receiver rather than of the eavesdropper.

Acoustical communication and eavesdropping comprise most of the work in bioacoustics, but the parsimonious scenario for the evolution of hearing involves selection for auditory surveillance of the acoustical environment, with intentional communication evolving later [8]. Adventitious sounds are inadequately studied, in spite of their documented role in ecological interactions. Robins can use sound as the only cue to find buried worms [36]; a functional group of bats that capture prey off surfaces, gleaners, relies on prey-generated noises to localize their next meal [37]; barn owls (*Tyto alba*; [38]), marsh hawks (*Circus cyaneus*; [39]), and grey mouse lemurs (*Microcebus murinus*; [15] have been shown to use prey rustling sounds to detect and localize prey; big brown bats, *Eptesicus fuscus*, have the ability to use low-frequency insect flight sounds to identify insects and avoid protected prey [40]. In addition to prey localization, spectrally unstructured movement sounds are also used to detect predators. White-browed scrubwren (*Sericornis frontalis*) nestlings become silent when they hear the playback of footsteps of pied currawong, *Strepera graculina*, their major predator [41]; and tungara frogs, *Physalaemus pustulosus* avoid the wingbeat sounds of an approaching frog-eating bat, *Trachops cirrhosus* [42]. We are aware of only one study that has examined the role of adventitious sounds other than movement noises; African reed frogs, *Hyperolius nitidulus* flee from the sound of fire [43]. It is likely that other ecological sounds are functionally important to animals.

It is clear that the acoustical environment is not a collection of private conversations between signaler and receiver but an interconnected landscape of information networks and adventitious sounds; a landscape that we see as more connected with each year of investigation. It is for these reasons that the masking imposed by anthropogenic noise could have volatile and unpredictable consequences.

Separating anthropogenic disturbance from noise impacts

Recent research has reinforced decades of work [44,45] showing that human activities associated with high levels of anthropogenic noise modify animal ecology: for example, the species richness of nocturnal primates, small ungulates and carnivores is significantly reduced within ~ 30 m of roads in Africa [46]; anuran species richness in Ottawa, Canada is negatively correlated with traffic density [47]; aircraft overflights disturb behavior and alter time budgets in harlequin ducks (*Histrionicus histrionicus*; [48]) and mountain goats (*Oreamnos americanus*; [49]); snowmobiles and off-road vehicles change ungulate vigilance behavior and space use, although no evidence yet links these responses to population consequences [50,51]; songbirds show greater nest desertion and abandonment, but reduced predation, within 100 m of off-road vehicle trails [52]; and both greater sage-grouse (*Centrocercus urophasianus*; [53]) and mule deer (*Odocoileus hemionus*; [54]) are significantly more likely to select habitat away from noise-producing oil and gas developments. Thus, based on these studies alone, it seems clear that activities associated with high levels of anthropogenic noise can re-structure animal communities; but, because none of these studies, nor the disturbance literature in general, isolates noise from other possible forces, the independent contribution of anthropogenic noise to these effects is ambiguous.

Other evidence also implicates quiet, human-powered activities, such as hiking and skiing, in habitat degradation. For example, a paired comparison of 28 land preserves in northern California that varied substantially in the number of non-motorized recreationists showed a five-fold decline in the density of native carnivores in heavily used sites [55]. Further evidence from the Alps indicates that outdoor winter sports reduce alpine black grouse, *Tetrao tetrix* populations [17] and data from the UK link primarily quiet, non-motorized recreation to reduced woodlark, *Lullula arborea* populations [18]. A recent meta-analysis of ungulate flight responses to human disturbance showed that humans on foot produced stronger behavioral reactions than did motorized disturbance [45]. These studies strengthen a detailed foundational literature suggesting that anthropogenic disturbance events are perceived by animals as predation risk, regardless of the associated noise levels. Disturbance evokes anti-predator behaviors, interferes with other activities that enhance fitness and, as the studies above illustrate, can lead to population decline [44]. Although increased levels of noise associated with the same disturbance type appear to accentuate some animal responses (e.g. Refs [44,48]), it is difficult to distinguish reactions that reflect increasingly compromised sensory awareness from reactions that treat greater noise intensity as an indicator of greater risk.

To understand the functional importance of intact acoustical environments for animals, experimental and statistical designs must control for the influence of other stimuli. Numerous studies implicating noise as a problem for animals have reported reduced bird densities near roadways (reviewed in Ref. [56]). An extensive study conducted in the Netherlands found that 26 of 43 (60%) woodland bird species showed reduced numbers near roads [57]. This research, similar to most road ecology work, could not isolate noise from other possible factors associated with transportation corridors (e.g. road mortality, visual disturbance, chemical pollution, habitat fragmentation, increased predation and invasive species along edges). However, these effects extended for over a mile into the forest, implicating noise as one of the most potent forces driving road effects [58]. Later work, with a smaller sample size, confirmed these results and contributed a significant finding: birds with higher frequency calls were less likely to avoid roadways than birds with lower frequency calls [59]. Coupled with the mounting evidence that several animals shift their call frequencies in anthropogenic noise [4–7], these data are suggestive of a masking mechanism.

A good first step towards disentangling disturbance from noise effects is exemplified by small mammal translocation work performed across roadways that varied greatly in traffic amount. The densities of white-footed mice, *Peromyscus leucopus* and eastern chipmunks *Tamias striatus* were not lower near roads and both species were significantly less likely to cross a road than cover the same distance away from roads, but traffic volume (and noise level) had no influence on this finding [60]. Thus, for these species, the influence of the road surface itself appears to outweigh the independent contributions of direct mortality and noise.

Recent findings on the effects of anthropogenic noise

Two research groups have used oil and gas fields as ‘natural experiments’ to isolate the effects of noise from other confounding variables. Researchers in Canada’s boreal forest studied songbirds near noisy compressor stations [75–90 dB(A) at the source, 24 hrs a day, 365 days a year] and nearly identical (and much quieter) well pads. Both of these installations were situated in two to four ha clearings with dirt access roads that were rarely used. This design allowed for control of edge effects and other confounding factors that hinder interpretation of road impact studies. The findings from this system include reduced pairing success and significantly more first time breeders near loud compressor stations in ovenbirds (*Seiurus aurocapilla*; [61]), and a one-third reduction in overall passerine bird density [62]. Low territory quality in loud sites might explain the age structuring of this ovenbird population and, if so, implicates background sound level as an important habitat characteristic. In addition to the field data above, weakened avian pair preference in high levels of noise has been shown experimentally in the lab [63]. These data suggest masking of communication calls as a possible underlying mechanism; however the reduced effectiveness of territorial defense songs, reduced auditory awareness of approaching predators (see Box 3 for a discussion of the foraging/vigilance tradeoff in noise), or reduced capacity to detect acoustic cues in foraging, cannot be excluded as explanations of the results.

A second research group, working within natural gas fields in north-west New Mexico, US, used pinyon, *Pinus edulis*-juniper, *Juniperus osteosperma* woodlands adjacent to compressor stations as treatment sites and woodlands adjacent to gas wells lacking noise-producing compressors as quiet control sites [64]. The researchers were able to turn off the loud compressor stations to perform bird counts, relieving the need to adjust for detection differences in noise [62]. This group found reduced nesting species richness but in contrast to Ref.

Box 3. Do rising background sound levels alter vigilance behavior?

Predation risk and human disturbance increase vigilance behaviors (e.g. Refs [50,86]), at a cost to foraging efficiency [87,88]. Habitat features that influence predator detection, such as vegetation height, predict predation risk [88]. If background sound level interferes with the ability of an animal to detect predators, risk can increase. Do animals perceive background sound level as a habitat characteristic that predicts predation risk? Two recent studies document increased vigilance behaviors in high levels of noise (Figure I). It seems probable that these increased anti-predator behaviors are the result of attempted visual compensation for lost auditory awareness. Evidence from ungulates near roads suggests this is the case (Figure II); however, the distinct contributions of traffic as perceived threat and traffic noise as a sensory obstacle are confounded in road studies. Experimental research with birds and mammals suggests that lost visual awareness owing to habitat obstruction reduces food-searching bouts and increases vigilance (reviewed in Ref. [89]). Although no evidence exists (but see Ref. [64]), if noise shifts the spatial distribution of foraging effort, then plant growth and seed dispersal could also be altered.

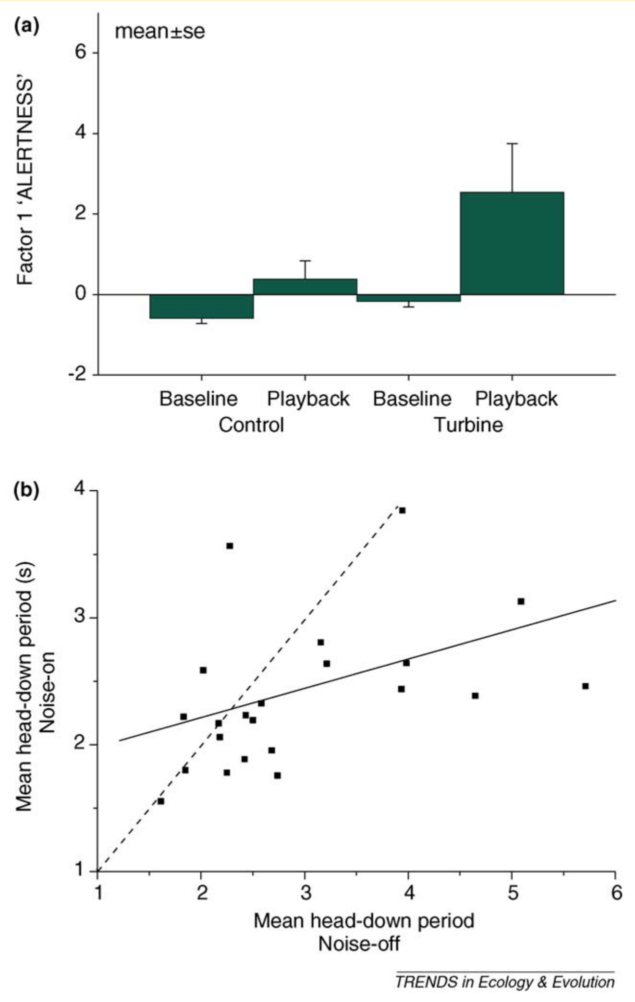

Figure I. Examples of increased vigilance behavior in noise. (**a**) When predator-elicited alarm calls are played back to California ground squirrels (*Spermophilus beecheyi*), adults show a greater increase in vigilance behavior at a site heavily impacted by anthropogenic noise, under power-generating wind turbines, than in a quiet control site [67]. (**b**) Further work on vigilance behaviors in noise comes from controlled, laboratory work with foraging chaffinches (*Fringilla coelebs*). In noise these birds decrease the interval between head-up scanning bouts, which results in fewer pecks and, thus, reduced food intake [90]. Dots depict the mean head-down period for each individual with and without white noise playback. Points below the dashed line (slope = 1) document individuals who increased scanning effort in noise. The solid regression line shows that the general trend was a more dramatic response from individuals with the lowest scanning effort. (a) adapted and (b) reproduced, with permission from Refs [67] and [90], respectively.

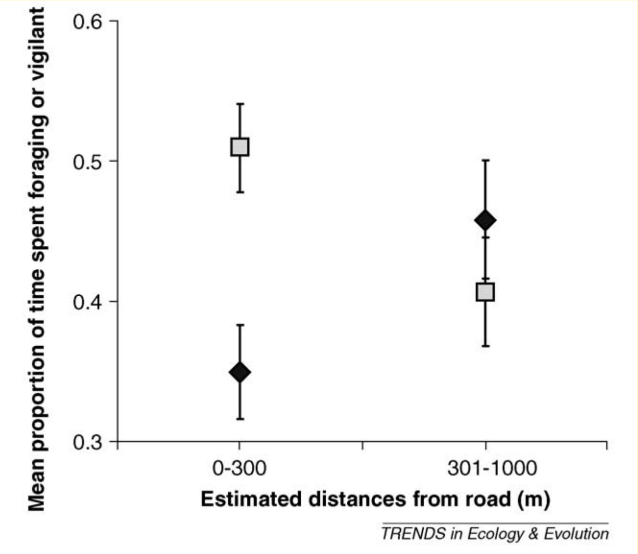

Figure II. An example of the foraging–vigilance tradeoff. Pronghorn (*Antilocapra Americana*) spend more time being vigilant (squares) and less time foraging (diamonds) within 300 meters of a road [86]. Future experiments should attempt to separate the roles of traffic as perceived threat and reduced auditory awareness on these tradeoffs. Reproduced, with permission, from Ref. [86].

[62], no reduction in overall nesting density. Unexpectedly, nest success was higher and predation levels lower in loud sites (also see Ref. [52]). The change in bird communities between loud and quiet sites appears to be driven by site preference; the response to noise ranged from positive to negative, with most responses being negative (e.g. three species nested only in loud sites and 14 species nested only in quiet, control sites). However, given the change in community structure, habitat selection based on background sound level is not the only interpretation of these data, as birds might be using cues of reduced competition pressure or predation risk to make habitat decisions [64]. The major nest predator in the study area, the western scrub jay, *Aphelocoma californica*, was significantly more likely to occupy quiet sites, which might explain the nest predation data [64]. It is probable that nest predators rely heavily on acoustic cues to find their prey. The study also found that the two bird species most strongly associated with control sites produce low-frequency communication calls. These observations suggest masking as an explanatory factor for these observed patterns. This work highlights the potential complexity of the relationship between noise exposure and the structure and function of ecological systems.

Adjusting temporal, spectral, intensity and redundancy characteristics of acoustic signals to reduce masking by noise has been demonstrated in six vertebrate orders [4–7,65]. These shifts have been documented in a variety of signal types: begging calls of bird chicks [66], alarm signals in ground squirrels [67], contact calls of primates [68], echolocation cries of bats [65] and sexual communication signals in birds, cetaceans and anurans [4–7,69]. Vocal adjustment probably comes at a cost to both energy balance and information transfer; however, no study has addressed receivers.

Masking also affects the ability of animals to use sound for spatial orientation. When traffic noise is played back to grey treefrog, *Hyla chrysoscelis* females as they attempt to localize male calls, they take longer to do so and are significantly less successful in correctly orienting to the male signal [70]. Similar studies with the European tree frog, *Hyla arborea* show decreased calling activity in played back traffic noise [71]. *H. arborea* individuals appear to be unable to adjust the frequency or duration of their calls to increase signal transmission, even at very high noise intensities (88 dB(A), [71]); although other frogs have been shown to slightly shift call frequencies upward in response to anthropogenic noise [69]. These are particularly salient points. It is likely that some species are unable to adjust the structure of their sounds to cope with noise even within the same group of organisms. These differences in vocal adaptability could partially explain why some species do well in loud environments and others do poorly [5,7,72].

Under many conditions, animals will minimize their movement sounds. For example, mice preferentially select quieter substrates on which to move [73]. Adventitious sounds of insects walking contain appreciable energy at higher frequencies (main energy ~3–30 kHz [16]) and are thus unlikely to be fully masked by most anthropogenic noise (<2 kHz [4–7]) but the spectral profile near many noise sources contains significant energy at higher frequencies (e.g. Ref [74]). Foundational work with owls and bats has shown that frequencies between approximately three and eight kHz are crucial for passive sound localization accuracy [38,75]. In fact, a recent laboratory study demonstrated that gleaning bats avoided hunting in areas with played back road noise that contained energy within this spectral band ([74]; Box 4).

Adapting to a louder world

Animals have been under constant selective pressure to distinguish pertinent sounds from background noise. Two

Box 4. Effects of acoustic masking on acoustically specialized predators

Laboratory work has demonstrated that gleaning bats (who use prey-generated sounds to capture terrestrial prey; Figure Ia) avoid noise when foraging (Figure Ib). Interestingly, treefrogs, a favorite prey of some neotropical gleaning bats, tend to call from sites with high ambient noise levels (primarily from waterfalls) and bats prefer frog calls played back in quieter locations [91]. Extinction risk in bats correlates with low wing aspect ratios (a high cost and low wing-loading morphology), a trait that all gleaning bats share [92]. A recent analysis indicates that urbanization most strongly impacts bats with these wing shapes [93]. However, low wing aspect ratio is also correlated with habitat specialization, edge intolerance and low mobility [92,93], obscuring the links between a gleaning lifestyle, louder background sound levels and extinction risk as urbanization reduces available habitat, fragments landscapes and generates noise concomitantly.

A radio-tag study showed that a gleaning bat, *Myotis bechsteinii*, was less likely to cross a roadway (three of 34 individuals) than was a sympatric open-space foraging bat, *Barbastella barbastellus* (five out of six individuals; [94]), implicating noise as a fragmenting agent for some bats. The latter species hunts flying insects using echolocation (an auditory behavior that uses ultrasonic signals above the spectrum of anthropogenic noise) [94]. Similar findings suggest acoustically mediated foragers are at risk: terrestrial insectivores were the only avian ecological guild to avoid road construction in the Amazon [95] and human-altered landscapes limited provisioning rates of saw-whet owls [96]. That these animals plausibly rely on sound for hunting might not be coincidental.

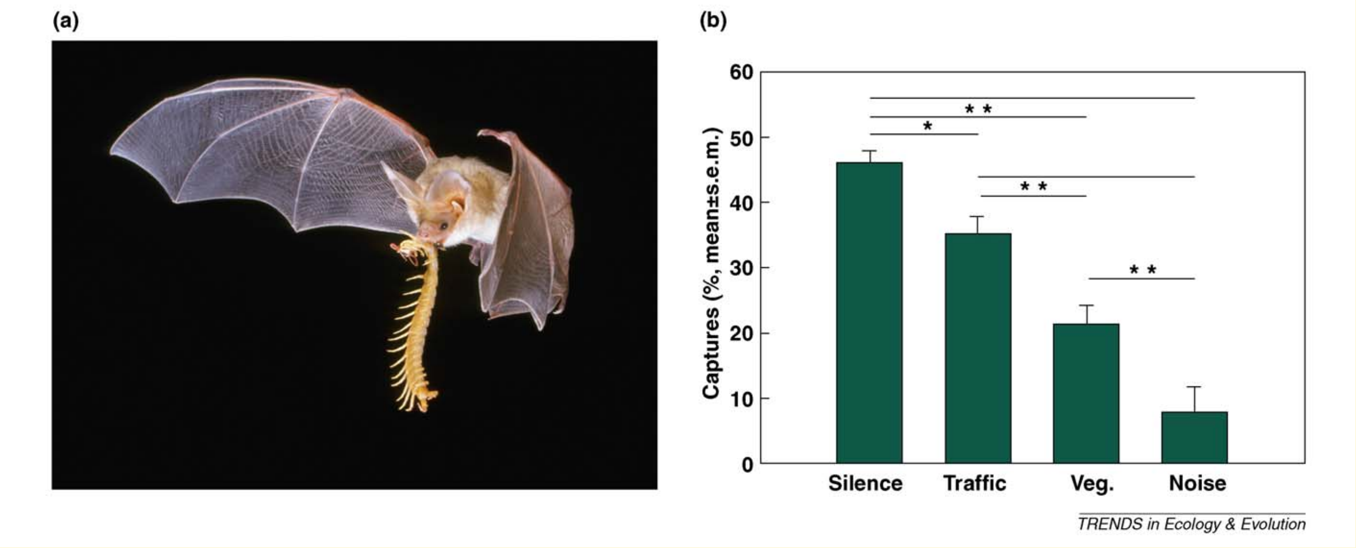

Figure I. Gleaning bats avoid hunting in noise. The pallid bat, *Antrozous pallidus* **(a)**, relies upon prey-generated movement sounds to localize its terrestrial prey. Recent work demonstrates that another gleaning bat, the greater mouse-eared bat, *Myotis myotis*, avoids foraging in noise [74]. **(b)** A laboratory two-compartment choice experiment showed that this bat preferred to forage in the compartment with played-back silence versus the compartment with played-back traffic, wind-blown vegetation or white noise. This pattern held true whether the percentage of flight time, compartment entering events, the first 25 captures per session or overall capture percentage were compared across silent and noise playback compartments. Asteriks indicate the results of post repeated-measure ANOVA, paired t-tests (**P<0.01, *P<0.05, N=7 bats). The differences between noise types (traffic, vegetation and white noise) probably reflect increased spectral overlap between prey-generated movement sounds and the spectral profile of the noise. Reproduced with permission from Scott Altenbach (a) and Ref. [74] (b).

Box 5. Outstanding questions

- Multiple studies with birds have demonstrated signal shifts in anthropogenic noise that does not substantially overlap in frequency with the birds' song [4–7,72]. To what extent does low-frequency anthropogenic noise inhibit perception of higher frequency signals? Mammals appear more prone to the 'upward spread' of masking than do birds [85,97]. Noise commonly elevates low frequency ambient sound levels by 40 dB or more, so small amounts of spectral 'leakage' can be significant. Laboratory studies should be complimented by field studies that can identify the potential for informational or attentional effects [98]. This work should use anthropogenic noise profiles and not rely on artificial white noise as a surrogate. Furthermore, we suggest that future studies measure or model sound levels (both signal and background) at the position of the animal receiver (*sensu* Ref. [23]).
- What roles do behavioral and cognitive masking release mechanisms [85] have in modifying the capacity of free-ranging animals to detect and identify significant sounds? Only one study has examined the masked hearing thresholds of natural vocal signals in anthropogenic noise [97]. This work found that thresholds for discrimination between calls of the same bird species were consistently higher than were detection thresholds for the same calls [97]. This highlights the lack of knowledge concerning top-down cognitive constraints on signal processing in noise. Can noise divide attention and reduce task accuracy by forcing the processing of multiple streams of auditory information simultaneously [99]?
- Do animals exploit the temporal patterning of anthropogenic noise pollution (see Ref. [4])? Alternatively, what constitutes a chronic exposure and how does this vary in relation to diel activity schedules?
- Does noise amplify the barrier effects of fragmenting agents, such as roads [94,100]?
- What routes (exaptation, behavioral compensation, phenotypic plasticity and/or contemporary evolution) lead to successful tolerance of loud environments?
- What role does audition have in vigilance behaviors? Are visually mediated predators at an advantage in loud environments when prey animals rely upon acoustical predator detection?
- Do animals directly perceive background sound level as a habitat characteristic related to predation risk? A noise increase of 3 dB(A) is often identified as 'just perceptible' for humans, and an increase of 10 dB(A) as a doubling of perceived loudness. These correspond to 30% and 90% reductions in alerting distance, respectively. Do organisms assess reduced alerting distance by monitoring other acoustical signals?

examples include penguin communication systems being shaped by wind and colony noise [76] and frog systems driven to ultrasonic frequencies by stream noise [77]. A meta-analysis of the acoustic adaptation hypothesis for birdsong (the idea that signals are adapted to maximize propagation through the local habitat) found only weak evidence for this claim [78]. Physiological constraints and selective forces from eavesdropping could explain this weak relationship [78], in addition to variation of noise profiles across nominally similar habitat types (e.g. insect noise, [79]).

Phenotypic plasticity enables one adaptation to anthropogenic noise. The open-ended song learning documented in great tits, *Parus major* helps explain the consistent song shifts observed in all ten comparisons between urban and rural populations [72]. Contemporary evolution (fewer than a few hundred generations) has now been quantified in several systems [80] and we might anticipate similar microevolutionary changes in many species with rapid generation times that consistently experience acoustical environments dominated by noise, particularly in increasingly fragmented landscapes.

Perhaps the greatest predictors of the ability of a given species to succeed in a louder world will be the degree of temporal and spectral overlap of biologically crucial signals with anthropogenic noise (Figure 1), and their flexibility to compensate with other sensory modalities (e.g. vision) when auditory cues are masked. Given known sensory biases in learning [81], many animals will be constrained in their ability to shift from acoustical inputs to other sensory cues for dynamic control of complex behavioral sequences.

Conclusions and recommendations

The constraints on signal reception imposed by background sound level have a long history of being researched in bioacoustics, and it is increasingly clear that these constraints underlie crucial issues for conservation biology. Questions have been raised about the value of behavioral studies for conservation practice (for a review see Ref [82]), but ethological studies of auditory awareness and the consequences of degraded listening opportunities are essential to understanding the mechanisms underlying ecological responses to anthropogenic noise (Box 5). These studies are more challenging to execute than observation of salient behavioral responses to acute noise events, but they offer opportunities to explore fundamental questions regarding auditory perception in natural and disturbed contexts.

Chronic noise exposure is widespread. Taken individually, many of the papers cited here offer suggestive but inconclusive evidence that masking is substantially altering many ecosystems. Taken collectively, the preponderance of evidence argues for immediate action to manage noise in protected natural areas. Advances in instrumentation and methods are needed to expand research and monitoring capabilities. Explicit experimental manipulations should become an integral part of future adaptive management plans to decisively identify the most effective and efficient methods that reconcile human activities with resource management objectives [83].

The costs of noise must be understood in relation to other anthropogenic forces, to ensure effective mitigation and efficient realization of environmental goals. Noise pollution exacerbates the problems posed by habitat fragmentation and wildlife responses to human presence; therefore, highly fragmented or heavily visited locations are priority candidates for noise management. Noise management might also offer a relatively rapid tool to improve the resilience of protected lands to some of the stresses imposed by climate change. Shuttle buses and other specialized mass transit systems, such as those used at Zion and Denali National Parks, offer promising alternatives for visitor access that enable resource managers to exert better control over the timing, spatial distribution, and intensity of both noise and human disturbance. Quieting protected areas is a prudent precaution in the face of sweeping environmental changes, and a powerful affirmation of the wilderness values that inspired their creation.

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