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Report

Noise Pollution Changes Avian Communities and Species Interactions

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Summary

Humans have drastically changed much of the world's acoustic background with anthropogenic sounds that are markedly different in pitch and amplitude than sounds in most natural habitats [1–4]. This novel acoustic background may be detrimental for many species, particularly birds [1]. We evaluated conservation concerns that noise limits bird distributions and reduces nesting success via a natural experiment to isolate the effects of noise from confounding stimuli and to control for the effect of noise on observer detection biases [5]. We show that noise alone reduces nesting species richness and leads to different avian communities. Contrary to expectations, noise indirectly facilitates reproductive success of individuals nesting in noisy areas as a result of the disruption of predator-prey interactions. The higher reproductive success for birds within noisy habitats may be a previously unrecognized factor contributing to the success of urban-adapted species and the loss of birds less tolerant of noise. Additionally, our findings suggest that noise can have cascading consequences for communities through altered species interactions. Given that noise pollution is becoming ubiquitous throughout much of the world, knowledge of species-specific responses to noise and the cumulative effects of these novel acoustics may be crucial to understanding and managing human-altered landscapes.

Results and Discussion

Nearly anyone who has been near a busy roadway, an airport, or industrial equipment can attest to the intensity of sounds produced by human activities. Many of these anthropogenic sounds can be physically harmful or distracting to humans or wildlife and are considered noise pollution (hereafter referred to as noise). Noise, characterized by high amplitudes and low spectral frequencies, is typical to habitats in and around human-altered landscapes [1–4, 6–8]. These acoustics have emerged swiftly on a global scale; therefore, noise presents an evolutionarily novel source of acoustic interference for many species and a potentially significant force influencing the ecology and evolution of many animals [1]. Because of their reliance on acoustic communication, birds have been viewed as especially vulnerable to the novel acoustics of noise [1–4]. Specifically, noise may disrupt acoustic communication [1–4, 6], interfere with detection of warning signals [1, 3], and elevate stress levels [1, 9].

To date, noise has been associated with declining bird densities [10–14], prompting conservation concerns that many species may be excluded from otherwise suitable habitat as a result of ecological sensitivities or intolerance to noise [1–4]. Additionally, individuals that settle in noisy habitats may have reduced reproductive success because noise interferes with detection of approaching predators [1, 3]. Despite previous links between noise and bird declines, evidence demonstrating a direct negative influence of noise on birds has been equivocal because previous efforts have employed methods with insufficient controls over other stimuli associated with noise, such as the physical alteration of habitat, community location at habitat edges versus interior habitat, or visual disturbance presented by moving traffic or equipment [1, 3, 15]. These uncontrolled variables could also explain observed bird declines. Additionally, these previous studies have not accounted for the negative influence of noise on the observer's ability to detect birds [5]. We tested conservation concerns that noise results in declines in bird densities, community species richness, and reproductive success via a unique study design that controlled for the effects of stimuli often associated with noisy habitats and detection problems caused by noise. We show how noise, in the absence of other influential stimuli, can have either a negative or an indirect positive effect on birds as a result of altered species interactions produced by species-specific responses to noise (Figure 1A).

Nesting Community Richness and Community Composition

We located and monitored nests for three breeding seasons at our study sites among the scattered natural-gas extraction infrastructure within pinyon (*Pinus edulis*)-juniper (*Juniperus osteosperma*) woodlands of northwestern New Mexico. Our design provided a natural experiment that permitted isolation of noise as a single experimental stimulus. Treatment sites included woodland habitat adjacent to natural gas wells with noise-producing compressors, which aid in extraction and transportation of gas through pipelines and run 24 hours a day, 365 days a year, aside from periodic maintenance and during our two-hour nest searching efforts and surveys. Woodland habitats adjacent to natural gas wells that lacked noise-generating compressors were used as control sites (see Figure S1 available online). We measured noise amplitudes at nests and throughout sites to characterize differences in the acoustic background between treatment and control sites (Figures S2 and S3). Given that noise can reduce avian detection probabilities [5] and may hamper researcher ability to locate nests, we turned off all compressors (n = 9) during nest searching efforts for the first two years of the study and for half of all treatment sites (n = 5 turned off; n = 5 left on) in the third year.

Contrary to previous reports of reduced densities of birds as a result of road noise [10–13, 16], we found no difference in community nest density between treatment and control sites ($t = -0.38$, $df = 52$, $p > 0.70$; Figure 1B). Despite no difference in nest density, we observed 21 species nesting at treatment sites and 32 species nesting at control sites. Rarefaction and nesting species richness estimates from EstimateS species richness estimation software (http://purl.oclc.org/estimates)

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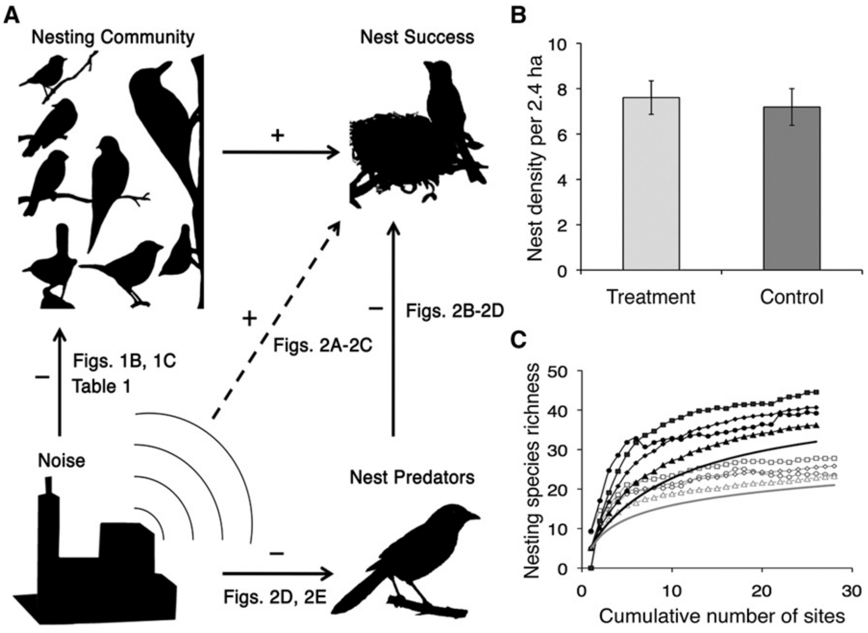

Figure 1. Influence of Noise on Nesting Community, Nest Density, and Nesting Richness at Treatment and Control Sites

(A) Interaction web showing the pathway by which noise negatively influences species richness of the breeding community but indirectly facilitates avian reproduction because fewer nests fail as a result of predation. The plus or minus signs refer to the direction of the effect for each interaction. Figure and table numbers indicate which figures or tables present data supporting each pathway step. Noise negatively influences the nesting communities' species richness and also a major nest predator, the western scrub-jay (*Aphelocoma californica*). Because the scrub-jay has reduced occupancy rates in noisy areas, fewer nests fail as a result of predation. These changes brought about by noise result in an indirect positive effect on nest success (dashed line).

(B) There was no difference in mean nest density between treatment and control sites. Results are shown as mean ± standard error of the mean (SEM).

(C) Rarefaction and richness estimate curves reflect the observed difference in nesting species richness, with higher estimates of nesting species richness at control sites (black lines and solid symbols) than at treatment sites (gray lines and open symbols). Richness estimates are denoted as follows: solid lines = rarefaction (Sobs), diamonds = first-order jackknife, squares = second-order jackknife, circles = Chao 1, triangles = bootstrap. (See http://purl.oclc.org/estimates for explanations and calculations of estimators.)

supported the observed richness difference between the two site types (Figure 1C). This difference was reflected by species that were unique to one of the two site types: nests of 14 species were found only at control sites, yet nests of 3 species were found only at treatment sites.

In addition to the difference in richness between treatment and control sites, we detected clear differences in the composition of the nesting communities at each site type. Analysis of similarity (ANOSIM) indicated that the nesting species composition at treatment and control sites was significantly dissimilar ($R = 0.19$, $p < 0.001$). This difference can be attributed to the difference in nesting species richness between noisy treatment and control sites, but also to the presence of indicator species for each site type [17]. The black-chinned hummingbird (*Archilochus alexandri*) and house finch (*Carpodacus mexicanus*) were strongly associated with treatment sites (Dufrêne-Legendre indicator species analysis: black-chinned hummingbird indicator value (IV) = 0.66, $p = 0.001$; house finch IV = 0.49, $p = 0.001$). This strong association was reflected by the relative abundance of each of these species at treatment sites: 36 (92%) of 39 black-chinned hummingbird nests and 29 (94%) of 31 house finch nests were at treatment sites. These species also accounted for a large proportion of the treatment-site nesting community. Black-chinned hummingbird nests accounted for 17% and house finch nests accounted for 14% of all nests at treatment sites. In contrast, nests of these species were uncommon at control sites, each representing fewer than 3% of all control-site nests. The mourning dove (*Zenaida macroura*) and black-headed grosbeak (*Pheucticus melanocephalus*) were strongly associated with control sites (mourning dove IV = 0.41, $p = 0.001$; black-headed grosbeak IV = 0.19, $p = 0.025$). Twenty-two (97%) of 23 mourning dove nests and all black-headed grosbeak nests ($n = 5$) were located at control sites. Mourning dove nests represented 12% and black-headed grosbeak nests represented 3% of the control-site nesting community.

Besides the presence of noise, there were minor, albeit insignificant, differences between site types in terms of number of pinyon trees and amount of bare ground (Table S1). These two variables had no effect on nesting patterns in terms of nest density or density of nesting species (see Figure S4). There were no additional differences in habitat features between treatment and control sites that would explain selection for treatment or control sites in each species' nest placement (Table S1).

We also detected avoidance of noise in terms of nest placement within treatment sites. Gray flycatchers (*Empidonax wrightii*), gray vireos (*Vireo vicinior*), black-throated gray warblers (*Dendroica nigrescens*), and spotted towhees (*Pipilo maculatus*) all nested significantly farther away from the well pad at treatment sites than at control sites, suggesting avoidance of noise generated at treatment-site well pads (Table 1). Nests parasitized by the brown-headed cowbird (*Molothrus ater*) were also significantly farther away from the well pad at treatment sites than at control sites (Table 1). No species nested closer to the well pad at treatment sites than at control sites.

Table 1. Species Nesting Significantly Farther from the Plot Origin at Treatment Sites Than at Control Sites

Species	Treatment	Control	t	p
Gray flycatcher (n = 67)	261.6 ± 16.3	206.4 ± 14.7	2.51	0.015
Gray vireo (n = 14)	275.3 ± 14.5	187.2 ± 33.8	2.40	0.043
Black-throated gray warbler (n = 11)	285.7 ± 9.8	188.5 ± 24.8	3.66	0.006
Spotted towhee (n = 33)	267.7 ± 25.3	157.4 ± 22.5	3.26	0.003
Cowbird-parasitized nests (n = 21)	297.5 ± 22.1	171.7 ± 30.3	3.36	0.003
Nests of all species (n = 400)	221.6 ± 7.6	200.5 ± 7.7	1.96	0.052

Results are presented as mean nest distance (m) from origin ± SEM. t values were determined by two-tailed Welch two-sample t test. Nests of all species were pooled, uncorrected for the number of nests for each species.

Our results confirm the conservation concern that noise negatively affects breeding bird communities through a reduction in nesting species richness, but the decline in richness was not reflected by a reduction in nest density of the breeding community as a whole. Rather, we documented a change in the composition of the community, with species-specific responses to the noise disturbance that ranged from positive to negative but were predominantly negative. Although the negative influence of noise on birds has been implicated in a number of studies [10–14, 16, 18, 19], findings have primarily been restricted to studies using surveys of individuals [10–14, 16, 18], often under conditions in which evidence for the effect of noise on birds is weak because of effects of uncontrolled confounding stimuli or potential detection errors (but see [14] for analytical methods for dealing with differences in detection probability). Because we were able to control for the effects of other influential stimuli and detection biases, our results provide especially strong evidence that noise alone reduces habitat quality for numerous species. Yet two species were much more common at noisy treatment sites than at control sites, prompting a need to identify whatever mechanism is causing the different responses among species.

In general, species-specific responses to noise remain poorly described, and the mechanisms responsible for these responses are largely unknown [1–4, 6]. Species' avoidance of noisy habitat may be a result of ecological intolerances of noise or species' inability to effectively communicate through the din of human activities [1–4, 6, 18, 19]. Vocal frequency characteristics of indicator species suggest that the latter may have occurred at our sites. The two control-site indicator species have vocalizations characterized by low frequencies: mourning dove vocalizations have an emphasized frequency (i.e., the frequency at which the vocalization has the highest amplitude) near 527 Hz [20], and black-headed grosbeak notes range from 1.5 to 4.0 kHz [21]. These frequency ranges overlap with most anthropogenic noise (<2.0 kHz) and are within the frequency range of noise produced at our treatment sites (<5 kHz; Figure S2). Acoustic masking likely limits these species to control sites where their vocalizations can be heard. In contrast, treatment-site indicator species have vocalization frequencies that may escape the masking effects of noise or are capable of adjusting vocal signals in response to noise. Black-chinned hummingbird vocalizations span 1.5–12.0 kHz but generally have the most energy above 5 kHz [22], and house finches are known to sing with higher minimum frequencies in response to urban noise [23]. Signal adjustments may not permit house finches to escape masking effects of noise entirely but might shift signals to higher frequencies at which compressor noise has less acoustic energy (Figure S2).

Signal plasticity or use of frequencies above those dominated by noise may facilitate black-chinned hummingbirds and house finches in their ability to inhabit noisy areas, yet these attributes do not explain each species' preference for treatment sites over control sites in their nest site selection. To our knowledge, this is the first evidence demonstrating that some species select for noisy habitats over quiet habitats, and this finding provides an intriguing focus for future research. These species may use noise as a settlement cue in habitat selection; however, in light of our evidence documenting an altered community structure plus higher nest success and lower levels of predation in noisy areas (see below), the possibility exists that these species are responding indirectly to noise via factors such as lower interspecific competition pressure or additional cues representative of predation risk. Further research is needed to identify mechanisms responsible for settlement in noise areas and the potential tradeoffs associated with living in noisy conditions, such as declines in feeding rates [24, 25].

Influence of Noise on Nest Success

To determine whether noise negatively influences nest success, we monitored all nests until they fledged or failed. Nest predation was the major cause of nest failure (76% of all failures) throughout the study area, followed by abandonment (13%) and brown-headed cowbird brood parasitism (9%). In terms of apparent (observed) nest success, and counter to expectations, 13% of nests with known outcomes at treatment sites (n = 205) failed to predation, and 32% of nests with known fates (n = 174) were depredated at control sites ($\chi^2_1 = 12.1$, $p < 0.001$). We further estimated nest success in terms of daily nest survival (DNS), calculated via the logistic-exposure method [26], and used likelihood-ratio tests to assess model performance. For the nesting community as a whole, the DNS model with the inclusion of a site-type covariate was significantly better than a constant DNS model (likelihood-ratio test, $\chi^2_1 = 18.3$, $p < 0.001$). DNS was higher at treatment sites (0.989, 95% confidence interval [CI]: 0.981–0.994) than at control sites (0.974, 95% CI: 0.969–0.980; $\beta_{\text{treatment}} = 0.85 \pm 0.20$ standard error [SE]), reflecting the difference in predation. Assuming a 23-day nest cycle, the predicted nest success from these DNS estimates was 22% higher at treatment sites than at control sites (Figure 2A). Inclusion of those habitat features that differed slightly between treatment and control sites (amount of bare ground and number of pinyon trees) did not improve DNS model performance over the model with the site-type covariate. (For likelihood-ratio test results, see Supplemental Data.)

To more thoroughly examine the relationship between noise and nest predation, we estimated daily nest predation (DNP) by excluding all nests that failed for reasons other than predation and used only those nests that were successful or depredated. In this context, estimates of DNP were inverse measures of DNS. As expected, the DNP model including nest placement at treatment or control sites was an improvement over a constant DNP model (likelihood-ratio test, $\chi^2_1 = 27.0$, $p < 0.001$). DNP was much higher at control sites than at treatment sites (Figure 2B). In other words, probability of not being depredated was higher at treatment sites than at control sites (DNS $\beta_{\text{treatment}} = 1.14 \pm 0.24$ SE). Given that the composition of the breeding community differed at treatment and control sites, species-specific differences in DNP could potentially explain differences in nesting success between site types; therefore, we also used measured noise amplitudes at each nest to predict DNP for three species common to treatment and control sites and for the entire community. DNP models including amplitude were significantly better than constant DNP models (likelihood-ratio tests, community: $\chi^2_1 = 30.6$, $p < 0.001$; gray flycatcher: $\chi^2_1 = 7.0$, $p = 0.004$; spotted towhee: $\chi^2_1 = 3.5$, $p = 0.04$; chipping sparrow [*Spizella passerina*]: $\chi^2_1 = 4.2$, $p = 0.02$). Increases in noise amplitude resulted in lower DNP (i.e., the probability of a nest escaping predation increased) for all three species and for the pooled nesting community (Figure 2C). These results suggest that higher nest success at treatment sites can be attributed to noise rather than to different rates of nest success among species and that the difference results from reduced nest predation with increased noise amplitudes.

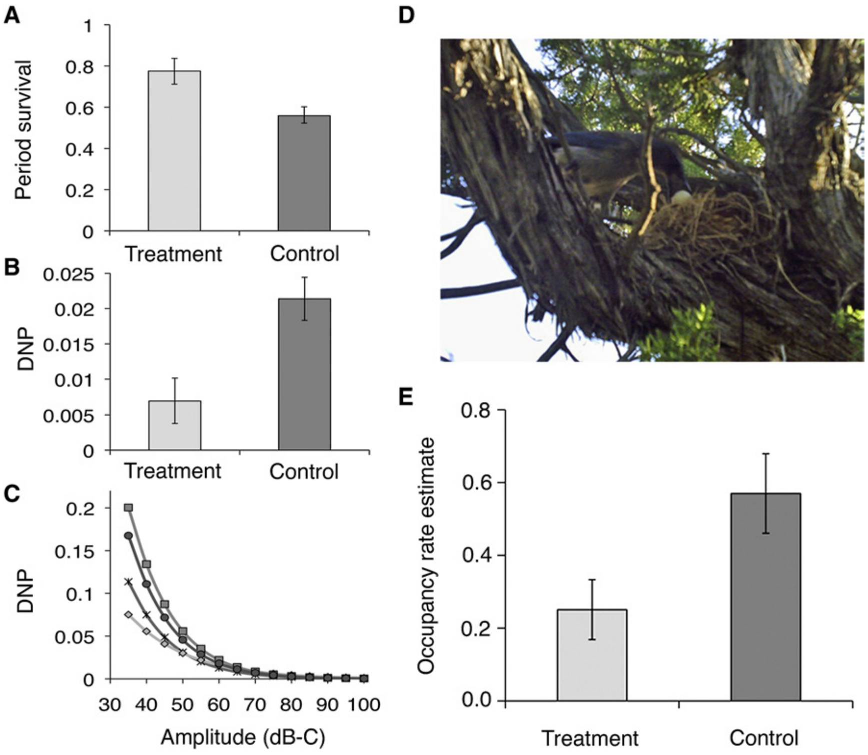

Figure 2. Influence of Noise on Nest Success, Nest Predation, and a Major Nest Predator, the Western Scrub-Jay

(A) Predicted nest success from daily nest survival (DNS) estimates was higher at treatment sites than at control sites for the entire nesting community. Error bars denote standard error (SE).

(B) Daily nest predation (DNP, the inverse of DNS) was calculated using only nests with known outcomes that were successful or failed as a result of predation (see Supplemental Data). DNP was higher at control sites than at treatment sites. Data are shown as DNP and SE.

(C) Increases in noise amplitude decreased DNP for the nesting community and individual species that nest at treatment and control sites (community: DNS $\beta_{dB} = 0.092 \pm 0.02$ SE; gray flycatcher: DNS $\beta_{dB} = 0.06 \pm 0.04$ SE; spotted towhee: DNS $\beta_{dB} = 0.10 \pm 0.07$ SE; chipping sparrow: DNS $\beta_{dB} = 0.10 \pm 0.045$ SE). Results are displayed as DNP. Xs denote nesting community; diamonds denote gray flycatcher; squares denote spotted towhee; circles denote chipping sparrow.

(D) Baited artificial nests paired with motion-triggered cameras were used to identify common nest predators. Photograph shows a western scrub-jay removing an egg from an artificial nest at one of the study sites.

(E) The occupancy rate estimate for western scrub-jays was significantly lower at treatment sites than at control sites. Results are reported as the proportion of point-count stations occupied at treatment or control sites. Error bars denote SE.

Nest Predator Response to Noise

To account for differences in nest predation between sites, we hypothesized that common nest predators were absent from or less abundant at treatment sites than control sites. Using baited artificial nests paired with motion-triggered cameras, we identified the western scrub-jay (*Aphelocoma californica*) as the primary nest predator in our study area (Figure 2D). To determine whether there was any evidence that noise influences occupancy rates of this important nest predator, we used standard point-count surveys at treatment and control sites, with treatment-site compressors turned off. We estimated scrub-jay occupancy with Presence occupancy modeling software (http://www.mbr-pwrc.usgs.gov/software/presence.html) and found the inclusion of a noise covariate (noise-conditional model) to significantly improve occupancy estimations over a uniform occupancy model (likelihood-ratio test, $\chi^2_1 = 17.3$, $p < 0.001$). Scrub-jay occupancy rates determined from the noise-conditional model were 32% higher at control sites than at treatment sites (Figure 2E). This was the pattern we expected to see and supports the pattern of lower predation rates for nests at treatment sites.

Contrary to the concern that noise may negatively influence nest success [1, 3], our findings show that noise can have an indirect positive effect for individuals nesting in noisy areas. This result exemplifies the importance of examining the consequences of anthropogenic disturbance from a community-level perspective. In our study area, the decrease in nest predation was a result of the western scrub-jay's avoidance of noisy habitat. Scrub-jays' intolerance of noisy habitat, much like the intolerance of the control-site indicator species, may be a result of acoustic masking of its vocalizations, which include frequencies below 2 kHz [27]. Future research should consider the possibility that nest predators present in noisy areas, especially those that rely on acoustic cues to locate nests, may be less likely to locate nests because of the masking effects of noise, which would also lead to increased nest success of prey species with noise amplitude.

That noise changes patterns of nest predation has important implications for additional species interactions in noisy landscapes. For example, in our study area the scrub-jay is not only a major nest predator, it is also a key mobile link for pinyon pine through dispersal of its seeds [28, 29]. Scrub-jay avoidance of noisy habitats may have negative consequences for seedling recruitment that could result in decreased pinyon pine densities in noisy areas, potentially affecting many organisms and community dynamics that are dependent on pinyon pine [30, 31]. Knowledge of the full extent to which noise can trigger changes is urgently needed, given the rate at which natural habitat is being transformed by human activities. More insight on the cumulative consequences of noise pollution may be gained through studies that focus on species with important roles within communities across diverse habitat types.

Conclusions

The current study has important implications for both avian conservation and community ecology within human-altered landscapes. The change in the avian community is in line with earlier studies implicating the negative influence of noise on birds [8, 10–14]; however, we provide the first evidence of this trend while simultaneously controlling for confounding stimuli and potential noise-caused detection biases. This is the strongest evidence to date that noise negatively influences bird populations and communities, and acoustic masking may be a dominant mechanism precluding many birds from breeding in noisy habitats [1–4, 18, 19, 32, 33]. Because noise also indirectly facilitates reproductive success, species intolerant of noise may suffer from not only exclusion from noisy habitats that might be otherwise suitable but also higher rates of nest predation relative to species inhabiting noisy areas. If this phenomenon is common to noisy environments, it may help explain the high degree of success among urban-adapted species and the homogenization of avian communities in and around human-altered habitats [33, 34]. Perhaps more noteworthy, however, is that noise alone can disrupt species interactions, potentially influencing many organisms and processes indirectly. Noise pollution is becoming much more prevalent throughout much of the world. Knowledge of how species respond to this novel force, especially species with critical links within the ecosystem, may be crucial to maintaining biodiversity and ecological processes in the growing number of landscapes disrupted by our industrial clamor.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures, one table, and four figures and can be found with this article online at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01328-1.

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