A phantom road experiment reveals traffic noise is an invisible source of habitat degradation

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Decades of research demonstrate that roads impact wildlife and suggest traffic noise as a primary cause of population declines near roads. We created a "phantom road" using an array of speakers to apply traffic noise to a roadless landscape, directly testing the effect of noise alone on an entire songbird community during autumn migration. Thirty-one percent of the bird community avoided the phantom road. For individuals that stayed despite the noise, overall body condition decreased by a full SD and some species showed a change in ability to gain body condition when exposed to traffic noise during migratory stopover. We conducted complementary laboratory experiments that implicate foraging-vigilance behavior as one mechanism driving this pattern. Our results suggest that noise degrades habitat that is otherwise suitable, and that the presence of a species does not indicate the absence of an impact.

traffic noise pollution | songbird migration | habitat degradation | foraging-vigilance trade-off | perceived predation risk

Human infrastructure shapes animal behaviors, distributions, and communities (1, 2). A meta-analysis of 49 datasets from across the globe found that bird populations decline within 1km of human infrastructure, including roads (2). Observational studies of birds near roads implicate traffic noise as a primary driver of these declines (3). Road ecology research has also shown negative correlations between traffic noise levels and songbird reproduction (4, 5). Birds that produce low frequency songs, likely masked by traffic noise, show the strongest avoidance of roads (6).

There is now substantial evidence that anthropogenic noise has detrimental impacts on a variety of species (3, 7–10). For example, work in natural gas extraction fields has demonstrated that compressor station noise alters songbird breeding distribution and species richness (11–13). However, explicit experiments would help to further rule out other characteristics of infrastructure, such as visual disturbance, collisions, chemical pollution, and edge effects, which might be driving these patterns (3). In addition, although these studies implicate noise as a causal factor in population declines, many individuals remain despite noise exposure (3), but at what cost? Proposed causes of decreased fitness for birds in noise include song masking, interference with mate evaluation, nonrandom distribution of territorial individuals, disruption of parent-chick communication, reduced foraging opportunities, and/or alterations in the foraging/vigilance trade-off (3, 4).

Here we parse the independent role of traffic noise from other aspects of roads experimentally by playing traffic sounds in a roadless area, creating a 'phantom road'. We focus on birds during migratory stopover, because energy budgets are streamlined; foraging, vigilance, and rest dominate activity (14). To meet the amplified physiological needs of sustained nocturnal migratory flights, birds must increase foraging during periods of stopover while maintaining appropriate vigilance levels (14, 15). Any interference with foraging will decrease stopover efficiency and thus reduce migration speed, a likely surrogate for fitness (14), thereby increasing exposure to significant mortality risks during what can be the most perilous stage of a migratory bird's life cycle (16). Anthropogenic noise might disrupt the foraging-vigilance tradeoff by acting as a form of perceived predation risk (17, 18) or by reducing sensory awareness via distraction or acoustic masking (3, 19). Using the "phantom road" experimental approach, we previously conducted count surveys of bird distributions at this site, finding a decrease in overall bird numbers of more than 25% (20). We hypothesized that the subset of birds choosing to stay at the site would experience other negative effects of traffic noise, and we predicted that the birds that remained would exhibit lower body condition and reduced ability to increase body condition (i.e., reduced stopover efficiency) in noise.

To test these predictions we used an array of speakers to recreate the soundscape of a ~0.5 km section of highway along a ridge in southwest Idaho. This approach enabled us to turn the traffic noise *on* and *off* throughout fall migration at our phantom road site, and compare it with a nearby quiet control site, creating a modified before-after-control-impact design (Fig. 1). Alternating noise on/off every four days, we sampled a different set of migrants during each block as birds arrived and departed from the stopover site (*SI Text*). We measured sound levels (hourly level-equivalent, or LEQ) continuously during the season using acoustic recording units placed at mist net locations (Fig. 1*A*). We compared mist-net capture rate (birds/net/hr) across site (control vs. phantom road) and noise treatment (on vs. off) to investigate whether birds were leaving or staying when exposed to traffic noise (*SI Text*). Similar to our survey work (20), our best-fitting model indicated that capture rate decreased by 31% during phantom traffic noise playback, demonstrating that anthropogenic noise, independent of other road forces, fundamentally shapes bird distributions. However, 69% of birds remained despite the noise (Table S1, Dataset S1, and *SI Text*).

Significance

Using landscape-scale traffic noise playbacks to create a "phantom road," we find that noise, apart from other factors present near roads, degrades the value of habitat for migrating songbirds. We found that nearly one third of the bird community avoided the phantom road. For some bird species that remained despite noise exposure, body condition and stopover efficiency (ability to gain body condition over time) decreased compared with control conditions. These findings have broad implications for the conservation of migratory birds and perhaps for other wildlife, because factors driving foraging behavior are similar across animals. For wildlife that remains in loud areas, noise pollution represents an invisible source of habitat degradation.

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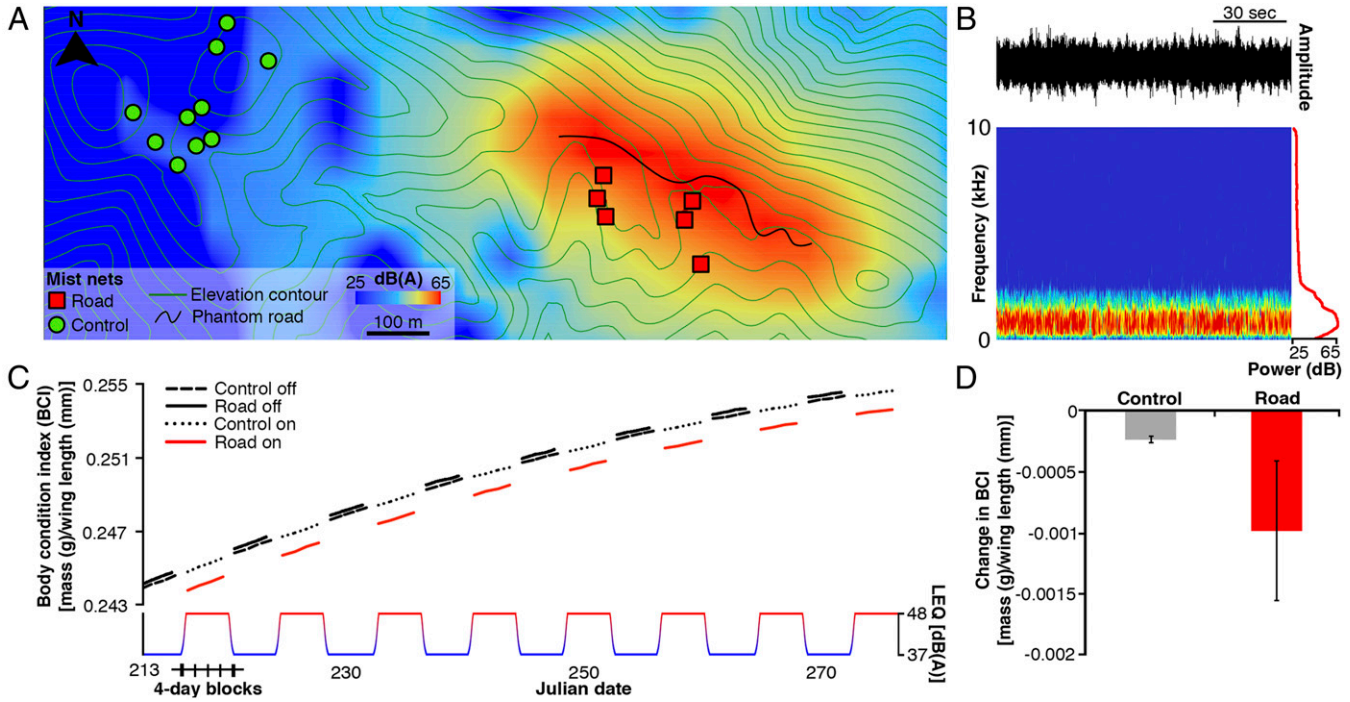

Fig. 1. Phantom road playback causes songbird body condition decline. (*A*) Estimated sound levels [dB(A) 1 h LEQ: The level of a constant sound over a specified time period that has the same energy as the actual (unsteady) sound over the same interval] during periods when speakers were on: from August through October 2012–2013 in the Boise Foothills, Idaho. Sound level was modeled using NMSim (Wyle Laboratories) (20). Circles (control) and squares (road) represent capture sites. With the noise on, mean sound levels at the phantom road capture sites increased by 11 dB(A) to 48 dB(A) (SE = 0.3), whereas the control site averaged 2 dB(A) louder with noise on (mean± SE; 41 dB(A) ± 0.2). With noise off, sound levels averaged 39 dB(A) (SE = 0.2) at the control capture sites and 37 dB(A) (SE = 0.3) at the phantom road. Elevation contours are 50 m. (*B*) A 2-min sample of the phantom road file displayed as an oscillogram, a spectrogram and a power spectrum. (*C*) Predicted values for body condition index (BCI) as birds add fuel throughout fall migration. Estimates are based on the AIC-best model for BCI for all captures combined, with species as a random intercept. A consistent full SD change in BCI is evident during each noise-on block (pattern of noise on blocks displayed along the *x* axis) throughout the migratory period. (*D*) Predicted mean change in BCI at the control and phantom road sites between noise off and noise on periods across the entire study. Error bars represent SE. These differences in BCI (and associated error) are derived from the average of the predictions presented in *C*.

Focusing on birds exposed to a gradient of sound levels, we examined differences in body condition index (BCI) of newly captured birds. BCI is a size-adjusted metric of body mass calculated as mass (g)/natural wing chord (mm). Small changes in BCI represent large differences in condition (21). During migration, high body condition signifies birds with the energy stores needed for long migratory flights (15). The best-fitting model showed that as noise exposure increased, overall BCI of the bird community remaining at the road site decreased (Fig. 1*C*, Table S1, Datasets S1 and S2, and *SI Text*). In fact, BCI in noise declined by a full SD compared with the community mean in control conditions. In the absence of noise, BCI of the songbird community at the phantom road site did not differ from the values at the control site, indicating both were suitable stopover locations (Fig. 1*C*). Models for individual species showed 5 of 21 species significantly decreased BCI in noise. Iterative exposure to noise during the multiple stopovers of saltatory migration may ultimately result in mortality (16) or, in a better case scenario, reduced fitness manifested from slower migration speed (14) which would likely impact fitness and survival in the subsequent life history stage (22).

Because we turned the phantom road off overnight to match typical diel traffic patterns, it is likely that nocturnal migrants (the majority of species in this study; see ref. 23) chose to land at our site when it was quiet, before the phantom road playbacks began in the morning. In effect, diurnally varying traffic noise might function as an ecological trap (24) for migrants. Although staying in traffic noise has a cost, the energetic outlay for individuals to leave a given site might be even greater. Birds with low body condition are less likely to embark on migratory journeys than those in good condition, and depending on the suitability of surrounding habitat, it may not be worth the risk to disperse once landed (25). We cannot differentiate whether the lower BCI we documented in traffic noise is the result of (*i*) higher body condition birds leaving the population or (*ii*) birds losing body condition over the duration of noise exposure. We saw both reduced mean body condition and reduced bird numbers, suggesting that at least some birds with the energetic stores to migrate chose to leave the site and escape the costs of remaining in noise (25).

To examine if the birds that remained in noise were suffering reduced ability to add migratory fuel (i.e., increase BCI), we regressed BCI of new captures against time of day to estimate stopover efficiency. Comparing stopover efficiency of individuals between sites provides an essential metric to compare the relative value of stopover habitat (*SI Text*). The best-fitting model for the entire songbird community included noise intensity level [dB(A)] although the confidence intervals overlapped zero (*SI Text*). For nine individual species, the best-fitting model included a noise variable, however the confidence intervals overlapped zero for all but 3 of these species (Table S1).

For MacGillivray's warblers, the best-fitting model showed that stopover efficiency substantially decreased with increasing decibel levels. MacGillivray's warblers did not show reduced capture rates in noise, and were the species that showed the strongest negative responses for both BCI and stopover efficiency, indicating that individuals stayed but did poorly in noise (Fig. 2*A* and Tables S1 and S2). In contrast, Cassin's finches had significantly increased stopover efficiency in noise and a decreased capture rate (Fig. 2*B* and

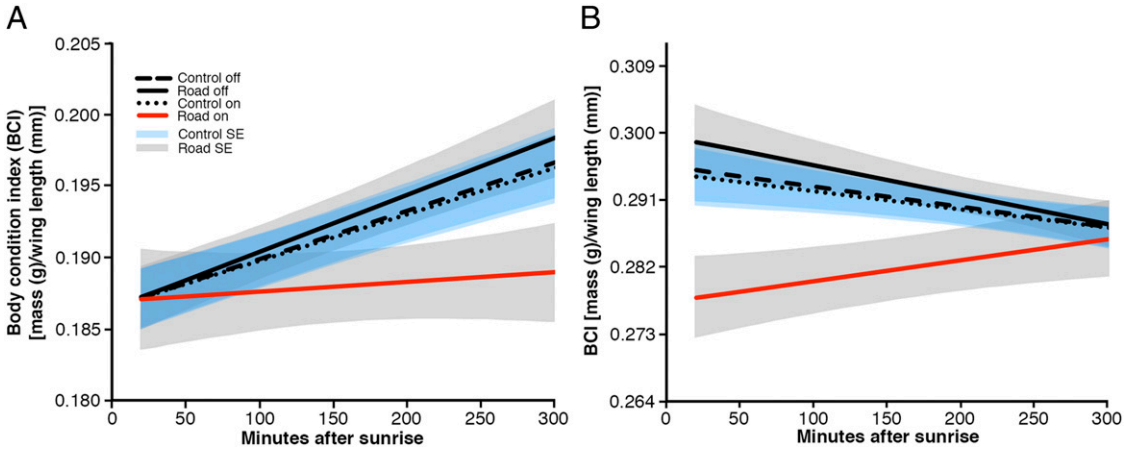

Fig. 2. Stopover efficiency is altered in noise. Predicted values for stopover efficiency for MacGillivray's warblers (*A*) and Cassin's finches (*B*). Estimates were made using average day of season using the AIC-best model for BCI for all captures combined. Values were predicted by inputting average dB(A) levels for each site. Values are shown for the control site noise off [avg. 42 dB(A)], control site noise on [43 dB(A)], phantom site noise off [40 dB(A)], and phantom site noise on [51 dB(A)]. Blue shading represents SE for the control site whereas gray shading represents SE for the phantom road.

Tables S1 and S2). This increase in stopover efficiency might reflect decreased competition for food resources in noise. Although stopover efficiency was increased in noise (Fig. 2*B*), Cassin's finches showed lower initial BCI in traffic noise (Fig. 2*B*), perhaps indicating individuals with higher BCI left the site during noise exposure. The best models for spotted towhees showed a reduced capture rate and also indicated different stopover efficiencies between on-off periods at the control and road sites with efficiency being negatively affected by noise along the phantom road (Fig. S1 and Tables S1 and S2).

It seems that for species impacted by noise, different strategies exist for managing the consequences, which might be based on differences in life history traits such as territoriality during stopover, migratory strategy, or flocking behavior. Our species-specific results show that birds may stay and incur a cost of remaining in noise (e.g., MacGillivray's warblers), or choose to leave (e.g., Cassin's finches). Leaving the noisy area may allow some species to avoid the costs of noise or a species may still experience the impacts of noise despite some individuals leaving (e.g., spotted towhees). Together, our observations of overall changes in the BCI of the entire bird community and of several individual species, as well as the changes in stopover efficiency of spotted towhee and MacGillivray's warbler, demonstrate that addition of traffic noise alone, without the other variables associated with actual roadways, can significantly decrease the value of a stopover site.

In support of our field results, we conducted a controlled laboratory study to test whether traffic noise alters the foraging-vigilance tradeoff in songbirds and could thus mechanistically underpin our field data (*SI Text*). We focused on the second most common species from our field study, white-crowned sparrow (*Zonotrichia leucophrys*), a species that also decreased BCI in noise, to investigate the reduction in foraging and increase in vigilance implied by our community-wide body condition analysis. We quantified head-down duration (i.e., foraging) and head-up rate (i.e., vigilance), because these are known measures of avian visual vigilance that change when auditory surveillance is limited and that correlate with food intake and ability to detect predator attacks (26). We also measured feeding duration (no. seconds per 8-min trial spent feeding) to quantify overall feeding bout duration. Using the same playback file as our field experiment, we played 61 dB(A) and 55 dB(A) traffic noise treatments, plus a silent control track [32 dB(A)] to foraging sparrows (n = 20). White-crowned sparrows decreased foraging by ~8%, increased vigilance levels by ~21%, and decreased feeding duration by ~30% when exposed

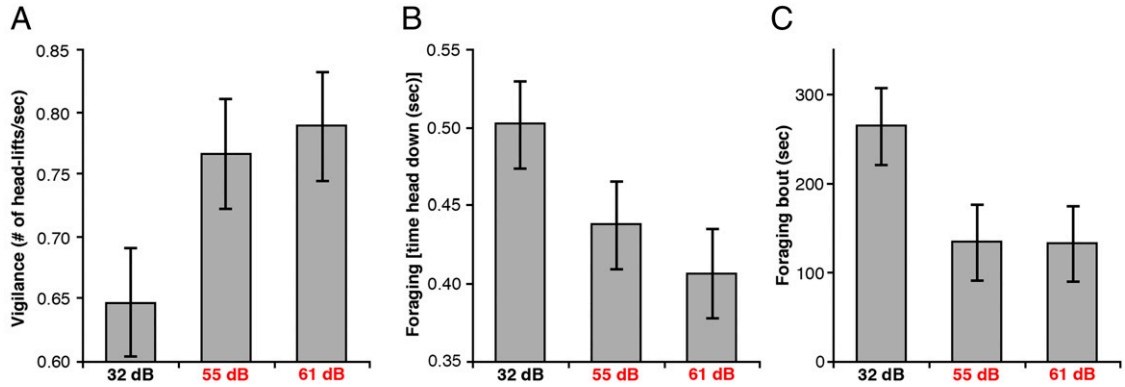

Fig. 3. The foraging/vigilance trade-off is altered in noise. White-crowned sparrows foraging in traffic noise at 61 and 55 dB(A) had reduced foraging rates (*A*), increased vigilance (*B*), and decreased foraging bout duration (*C*) compared with trials in ambient conditions [32 dB(A)]. Data are means ± SE. [Mean head up rate (head lifts/s) for 61 dB(A) = 0.79 ± 0.06, 55 dB(A) = 0.77 ± 0.05, 32 dB(A) = 0.65 ± 0.05. Mean head down duration (s): 61 dB(A) = 0.41 ± 0.03, 55 dB(A) = 0.44 ± 0.04, 32 dB(A) = 0.50 ± 0.04. Mean foraging bout duration (s): 61 dB(A) = 159.25 ± 28.0 55 dB(A) = 147 ± 32.5 32 dB(A) = 228 ± 33.7]. Birds showed more head lifts/s (β = 0.005 ± 0.002), decreased the amount of time spent with their heads down searching for seeds (β = −0.003 ± 0.001), and decreased total feeding duration (β = −4.589 ± 1.944; Movies S1 and S2) during noise playback compared with ambient conditions.

to traffic noise [61 dB(A); Fig. 3, Movies S1 and S2, and Dataset S3]. Vigilance behavior of individuals did not change based on the number of trials experienced, indicating birds did not habituate to the noise (*SI Text* and Table S2). During energetically demanding periods in a bird's life, increasing vigilance can reduce survival because of increased starvation risk (27). In contrast to song masking, which can be partially overcome by frequency shifting (28), release from masking is not possible for auditory cues necessary for aural vigilance (7). With limited auditory information, animals must resort to other methods such as visual scans to compensate for the increase in perceived predation risk, perhaps driven by masking of communication calls and predator-generated sounds (26, 29).

Our behavioral investigations in the laboratory offer compelling evidence that the body condition changes measured in the field were due at least in part to a change in foraging and vigilance behavior, but our field results could be due to a combination of factors that also deserve consideration. For example, noise might also increase physiological stress levels (ref. 30, but see ref. 31) that could cause additional declines in body condition. However, we view it as unlikely that noise can cause a stress response independent of a change in behavior. In addition, noise might indirectly change foraging rates through alterations in prey search time, sleep, or territoriality. For instance, our phantom road might have disrupted foraging behavior by reducing the acoustic detectability of insect prey (32) or reducing insect numbers. We did not test for changes in insect abundance or distribution, but because we found noise impacts on a mixed community of both frugivorous and insectivorous birds (Table S1 and Dataset S1), it seems unlikely that altered insect numbers explain a significant component of the observed patterns. Effects were consistent between the 4-d noise-on blocks throughout migration, despite documented seasonal variation in fruit and arthropod availability at the site (33), so it is more likely that changes in bird behavior drove these responses. Our experimental design was not able to determine whether noise disrupts territoriality or dominance hierarchies during stopover. However, both territorial and nonterritorial species showed negative effects of noise (23) (Table S1 and Datasets S1 and S4). We expect that a subset of these indirect effects plus the behavioral changes quantified in the laboratory contributed to the body condition declines seen in our field experiment. Because provisioning is a constant requirement for birds throughout the year, other effects of noise that occur outside of migration (e.g., refs. 4 and 5) would be in addition to, rather than instead of, the impacts we document here.

Previous work that failed to find a change in animal distributions near roads or other infrastructure has assumed a lack of negative impacts from loud human activities (2, 3). Our results demonstrate that individuals may remain in an area with high levels of noise yet suffer significant costs. We found that different species chose different strategies: to either leave noisy areas, or stay and perhaps incur the costs of noise (Fig. 1, Fig. S2, and Table S1). We exposed the bird community at our phantom road to sound levels similar to some suburban neighborhoods [~55 dB(A) hourly LEQ] (34). Many protected areas and high-value habitats are currently exposed to these levels, and would benefit from noise relief measures (35, 36). The impact of noise reaches far beyond the physical footprint of human infrastructure. Unlike other aspects of roads, noise impacts can be minimized without removing the road itself. Substrate alteration and speed limit reduction on existing roads can significantly lower decibel levels (34).

Our results reveal the need for attention to noise impacts beyond distributional shifts (3). For individuals that remain in areas disturbed by loud human activities, noise pollution represents an invisible source of habitat degradation that has been largely ignored: Traffic noise degrades habitat value but leaves no physical signs of change. Stopover habitat loss and degradation have been identified as major contributing factors to migratory songbird declines worldwide (37, 38). Migrants are exposed to an unknown risk landscape at stopover sites and must therefore rely heavily on increased vigilance to compensate (39–41). Unlike resident species, successful conservation of migratory species requires protection of habitats in breeding, wintering, and stopover locations (41). In addition, reduction in condition or delay in migration could have carry-over effects into the overwintering or breeding seasons (42). Further understanding of anthropogenic noise's impact on body condition is key, as it is an important predictor of fitness across taxa and life stage (22). When managing natural systems, we should ensure that the habitat we protect remains of high quality, including the quality of the acoustic environment.

All birds caught during this project were mist-netted and banded under the Intermountain Bird Observatory's federal permit (22929) and Idaho Department of Fish and Game permit (764–13-000039). All experiments were approved by Boise State University's Institutional Animal Care and Use Committee (006-AC12-007 and 006-AC13-002).

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