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An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road

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Many authors have suggested that the negative effects of roads on animals are largely owing to traffic noise. Although suggestive, most past studies of the effects of road noise on wildlife were conducted in the presence of the other confounding effects of roads, such as visual disturbance, collisions and chemical pollution among others. We present, to our knowledge, the first study to experimentally apply traffic noise to a roadless area at a land-scape scale—thus avoiding the other confounding aspects of roads present in past studies. We replicated the sound of a roadway at intervals—alternating 4 days of noise on with 4 days off—during the autumn migratory period using a 0.5 km array of speakers within an established stopover site in southern Idaho. We conducted daily bird surveys along our 'Phantom Road' and in a nearby control site. We document over a one-quarter decline in bird abundance and almost complete avoidance by some species between noise-on and noise-off periods along the phantom road and no such effects at control sites—suggesting that traffic noise is a major driver of effects of roads on populations of animals.

1. Introduction

Roads are prevalent across vast stretches of the Earth and 83% of the USA is within 1 km of a road [1]. Although some studies have shown positive effects of roads on wildlife, the cumulative effects across taxa are overwhelmingly negative (reviewed by [2]). A recent meta-analysis of 49 datasets including 234 species of mammals and birds across four continents demonstrated that bird and mammal populations decline within 1 and 5 km of human infrastructure—including roads—respectively [3]. Despite myriad studies regarding the effects of roads on wildlife, the primary mechanism underlying these effects remains unknown. Effects of roads include habitat fragmentation, road mortality, sensory disturbance and chemical pollution, among others (reviewed by [2]). Therefore, a given road probably impacts wildlife in several ways—making it exceedingly difficult to estimate the strength of any single effect.

Several lines of evidence suggest that traffic noise is a major factor explaining declines in populations of wildlife near roads. Perhaps the best tests of the effects of noise on animal distributions come from studies of noise produced by natural gas compressors. For example, Bayne et al. [4] found a one-third reduction in songbird density at noisy gas compressor stations in Canada compared with nearby well pads that were almost identical in habitat, but were much quieter. Francis et al. [5] used a similar system of noisy gas compressors and quiet well pads in New Mexico to show that species richness of birds is greatly reduced at noisy sites, with 14 species avoiding areas surrounding gas compressors. Evidence from gas fields indicates that species remaining in noisy areas are those that vocalize within frequencies less masked by anthropogenic noise [6,7]—a phenomenon probably occurring in areas exposed to traffic noise. For example, birds that vocalize at frequencies similar to those of road noise are more likely

to avoid roads than species that vocalize at higher frequencies [8,9]. Species of frogs, birds and mammals are known to change the characteristics of their vocalizations in the presence of traffic and other anthropogenic noise, presumably to avoid the effects of masking (reviewed by [10]).

Behavioural evidence and studies of other anthropogenic noise sources suggest that road noise should be a major driver of observed road effects. However, although road ecology studies attempting to directly address the effect of traffic noise on wildlife have suggested that noise is a major cause of negative effects, they are typically conducted in the presence of other effects of roads [11]. For instance, Halfwerk et al. [12] demonstrated that great tits (Parus major) have reduced reproductive success in areas exposed to high levels of road noise. Several studies from The Netherlands have shown that bird distributions near roads are negatively associated with noise levels (reviewed by [2]). A study in the USA [13] found that distributions of grassland birds were negatively associated with traffic volume (vehicles per day)—an effect that was attributed to increased noise levels. However, Summers et al. [11] found that the effect of distance to a road was stronger than the effect of noise level and suggested that road mortality, not noise, was probably underlying the negative effects of roads. As Summers et al. [11] suggest, these past studies attempting to assess the effects of road noise on wildlife are certainly informative, but are confounded by other effects which are present at any road. Put another way, the current study paradigm in road ecology of comparing roadless areas to sites near roads or using observational data to examine correlations between road noise and animal abundance is perhaps yielding diminishing returns.

Noise playback is an effective method of testing the effects of noise in the absence of other factors but has been underused in road ecology because of the difficulty of applying noise across a landscape [14]. Recently, however, experimental application of noise has become more common in studies of road ecology. For example, Crino et al. [15] used playback to examine the effects of road noise on stress in nestling white-crowned sparrows (Zonotrichia leucophrys). Arroyo-Solís et al. [16] experimentally demonstrated that the spotless starling (Sturnus unicolor) and the house sparrow (Passer domesticus) shift the timing of their morning songs in response to urban noise. Blickley et al. [14] used experimental playback to test the effects of noise on the distribution of the greater sage-grouse (Centrocercus urophasianus)—demonstrating reduced lek attendance at sites experimentally exposed to road and gas-compressor noise. Here, we assess the effects of road noise in the absence of the other effects of roads by adding road noise to a roadless landscape—allowing us to experimentally test the effects of road noise on an entire community of migrating birds. We applied noise using a 0.5 km array of speakers—which we term the 'phantom road'—situated at an autumn migratory stopover site in the Boise Foothills in southwestern Idaho. We use a modified before–after-control-impact experimental design to assess changes in the abundance of migrating birds near the phantom road with the speakers turned on and off in repeating 4 day intervals in relation to a nearby control site.

We chose to apply our study design to migrating birds for two reasons. First, because migrating birds stay at stopover sites for short durations, the bird community is constantly changing. This constant change in the bird community means that as we turn the phantom road on and off over the course of the migratory period we sample different individuals and populations of birds. Second, populations of migratory birds have declined sharply in recent decades [17–20] and identification, preservation and maintenance of stopover habitat is a research priority [21–24]. To our knowledge, the effects of anthropogenic noise on birds during migration have never been examined. Accordingly, our study fills an important gap in our knowledge of the use of stopover habitat. We therefore test the hypotheses that animals avoid roads because of disturbance by noise and that anthropogenic noise degrades migratory stopover habitat. We predicted that fewer birds would be present near the phantom road when speakers were turned on than when they were off, and that bird abundance would be negatively correlated with sound levels.

2. Material and methods

(a) Phantom road

We constructed the phantom road on an east–west oriented ridge extending southeast from Lucky Peak, Idaho roughly 0.8 km from the Idaho Bird Observatory's field site. This ridge was typical of most ridges along the Boise front in that the vegetation on north-facing slopes was dominated by mature Douglas fir forest (Pseudotsuga menziesii), whereas on the south-facing slopes bitter and choke cherry bushes (Prunus virginiana and emarginata) were prevalent on drainages and sagebrush steppe dominated ridges. We erected 15 pairs of speakers in Douglas fir trees along the crest of the ridge—with one speaker oriented towards the evergreen forest, and the other oriented towards the cherry/sage. Each set of speakers was approximately 4 m above the crest of the ridge. We amplified the speakers (Dayton Audio—Springboro, OH, USA—RPH16 Round 16' PA Horns paired with MCM Electronics—Centerville, OH, USA—40 W midrange compression drivers (± 5 dB(A), 400–3000 Hz)) with Parts Express (Springboro, OH, USA) 2 W x 2channel, 4-ohm, Class D amplifiers and played back sound files (MP3, 128 kbps) using Olympus (Center Valley, PA, USA) LS-7 and Roland (Los Angeles, CA, USA) R-05 audio players. We powered amplifiers and audio players with arrays of LiFePO$_4$ (Batteryspace, CA, USA) batteries housed in waterproof plastic containers. The geometry of a sound source can have profound impacts on the scale of noise exposure—point sources (e.g. generators, gas-compressor stations, a single car) lose sound energy at approximately 6 dB per doubling of distances, whereas line sources (e.g. a busy roadway, train) fall off at approximately 3 dB per doubling of distance. We therefore placed speakers roughly 30 m apart to ensure that, when playing noise, the individual speaker point sources fused into a line-source at our bird count locations. The phantom road was therefore roughly 0.5 km in length (figure 1a).

We applied noise along the phantom road at 4 day intervals—alternating between noise-on and noise-off periods throughout autumn migration. We alternated every 4 days because almost all species stopover at our site for fewer than 8 days on average during autumn migration [25]. Therefore, individual birds were probably only present during one noise-on and one noise-off period, and thus each set of noise-on/off periods was probably independent. Alternating between noise-on and noise-off periods also ensured that noise-on and noise-off periods were not correlated with potentially confounding factors, such as seasonally variable phenology of migrating birds, fruit or insect availability and weather fronts. We attempted to mimic normal traffic patterns by beginning noise playback at 04.30 and ending it at 21.00 local time each day during noise-on blocks. We gradually increased the volume of the noise over
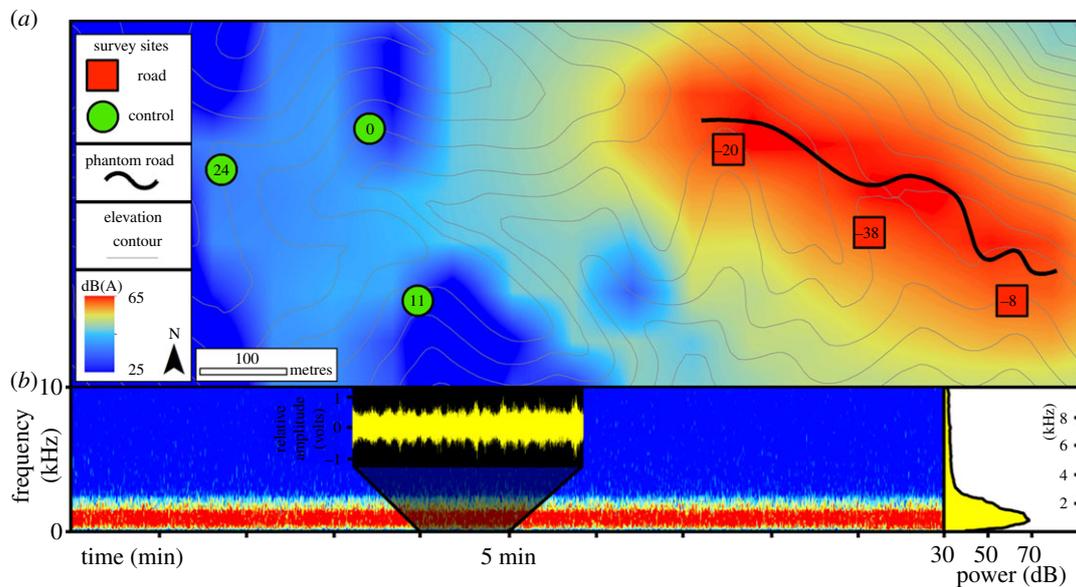
Figure 1. (a) Estimated background sound levels (dB(A) 1 h LEQ) during periods when speakers were turned on at our study site in the Boise Foothills in south-western Idaho. Background sound level was modelled using NMSIM (Noise Model Simulation; Wyle Laboratories, Inc., Arlington, VA) where inputs were chosen to match observed values at point count locations. Numbers represent the per cent change in birds present at a survey site between 4 day noise-on and noise-off periods which alternated continuously from 19 August through to 9 October 2012. (b) Ten minute spectrogram, 1 min waveform and power spectrum of noise file (recorded 35 m from the phantom road at a point count location) played from 04.30 to 21.00 along the phantom road during noise-on periods.

30 min in the morning so as not to elicit a startle response from any birds along the phantom road and also gradually decreased the volume over 15 min at the end of each noise-on day.

(b) Playback files

We played traffic noise recorded within Glacier National Park. To create the playback file, we combined files of 12 individual cars recorded at known distances, decibel levels and speeds. We choose car pass-by events based on clarity of recording, decibel level and speed. We created a 1 min file of 12 car pass-by events and repeated this file without shuffling. Because any possible habituation would have only reduced our ability to detect distributional changes, we see this as a minor concern. Our playback file therefore contained 720 pass-by events per hour of cars travelling at approximately 45 miles h^{-1}—traffic levels and speeds found along roads in some of the most visited national parks, national forests and other protected areas globally. Our playback file further simulated the frequency profile of typical traffic noise with most of the energy of the noise between 0 and 3 kHz with a peak around 1 kHz (figure 1b). We manipulated the source level of each set of speakers to produce a background decibel level of roughly 55–60 dB(A) hourly level-equivalent (LEQ) at each of the three point count locations along the phantom road. Hourly LEQ values are the level of a constant sound over an hour that has the same energy of the actual, fluctuating energy over that hour [26]. The background noise level during noise-on periods therefore approximated the thresholds hypothesized by Reijnen *et al*. [27] at which road noise negatively affects densities of birds (also see [26]).

(c) Bird counts

We placed point count locations along the phantom road within the centres of three patches of cherry shrubs. We surveyed patches of cherry shrubs because they contain the highest diversity and abundance of birds of any habitat-type within our study site during migration [28]—allowing us to maximize sample size while examining the effects of noise on the high-quality stopover habitat. Each point count location was at least 150 m from the nearest other location, and between 30 and 50 m from the nearest

speaker. Because patches of cherries were within drainages, each point count location was also separated from the other locations by ridges, meaning that an observer was unlikely to detect birds in patches of cherries other than the one they were currently surveying. We also placed control point count locations at three locations roughly 0.8 km away from the phantom road, also within patches of cherries separated by ridges (figure 1). Control point count locations were placed on sites with roughly the same slope and aspect and at roughly the same distance to forest as sites along the phantom road and all point count locations were within 100 m in elevation of each other. We therefore made every effort to ensure that control and experimental sites were placed within the same habitat mosaic and within similar microhabitats.

We conducted point counts at all point count locations along the phantom road and at the control site daily within 5 h after sunrise following a modified protocol of the Rocky Mountain Bird Observatory (D. J. Hanni, C. M. White, R. A. Sparks, J. A. Blakesley, G. J. Levandoski, J. J. Birek 2009, unpublished report). At each point count location, observers conducted three consecutive 5 min point counts [29]. For each individual bird detected during a point count, observers recorded the species and the minute in which it was first detected, as well as the method of detection (visual, call or song). Observers also recorded the distance to a bird when it was first detected using a laser range-finder. To increase our ability to obtain an accurate distance measurement, observers performed point counts in 4 m tall towers which allowed them to more easily detect a bird above the dense shrub layer. Observers also recorded temperature, wind speed (Beaufort Scale) and per cent cloud cover upon arriving at each survey location. Because detection of birds varies by both time and date, we shuffled the order in which points were surveyed every day. We alternated which site (control or phantom road) was surveyed first every 8 days, coinciding with the changes in noise-on/off blocks. Furthermore, the order of point count locations surveyed within each site was randomly determined for each day.

Two trained observers conducted point counts during our study, with one observer conducting all counts on a given day. Because probability of detection is probably different between observers, we scheduled observers so that they surveyed the

same number of days during the season ($n = 26$) and both observers conducted at least one survey during each noise-on and noise-off block. Our sampling scheme therefore ensured that all locations were surveyed at different times of the morning by different observers throughout the study season.

Because background noise levels exceeding 45 dB have been shown to negatively affect the probability of detection of birds within 60 m [30], observers turned off the speakers surrounding individual point count locations before counts at sites near the phantom road during noise-on blocks. Observers only turned off speakers surrounding the location that they were currently surveying and turned them back on before moving to the next location. Turning off speakers in this manner ensured that dB levels were below 45 dB (confirmed by a dB metre) during point counts, and minimized the time speakers needed to be turned off during noise-on mornings.

(d) Analysis of background sound level

We determined the background sound levels of each point count location during noise-on and noise-off blocks using MP3 audio recordings [31]. During two full noise-on and noise-off blocks, we deployed an MP3 recorder (Roland R05 or R09 recording at 128 kbps) at each point count location, which continuously recorded background sound level during the entire blocks. We then used a custom programme (Damon Joyce, NPS, AUDIO2NVSPL) to convert the MP3 recordings into an hourly sound pressure level format, and then converted those values to hourly LEQ values in dB(A) using another custom programme (Damon Joyce, NPS, Acoustic Monitoring Toolbox). Finally, we averaged the hourly background LEQ during the hours of 05.00 through to 21.00 across the noise-on and noise-off blocks to create the noise-on and noise-off LEQs.

(e) Statistical analysis

To ensure that we only examined birds within the patches of cherries that we intended to survey, we truncated the data to include only birds detected within 50 m of the sample point. Although our sampling scheme was designed to minimize the effects of heterogeneity in probability of detection, we evaluated and corrected our counts for the possibility of imperfect detection using a removal model [32]. A removal model calculates the probability of detecting a present individual during a survey using the minute in which individual birds are detected during surveys. We implemented the removal model using the Huggins closed-capture setting in MARK [33] using the package RMark [34] in R [35]. We built models of detection including combinations of observer, noise-on versus noise-off, control versus experimental sites, and linear and quadratic effects of date. We also built a null model which only included the intercept and a global model that included all factors. We ranked and compared the models using Akaike's Information Criterion (AIC, [36]) corrected for small sample size (AICc, [37]). We then used the estimates from the highest ranked detection model to calculate the probability of detecting an individual if it was present during each survey and corrected the observed count of each survey for detection by dividing the observed count by the probability of detection during that survey [32]. Although inference from this study with and without a correction for detection is qualitatively similar, we present results of the detection-corrected analysis.

Once our counts were corrected for imperfect detection, we modelled the abundance of birds at our survey locations in response to site and seasonal differences as well as changes in background noise levels owing to the phantom road. We modelled abundance using linear mixed-effects models and controlled for the repeated sampling of sites using a random intercept for each point count location. We also controlled for possible temporal autocorrelation by including an autoregressive

error structure within each model. Furthermore, plots of bird abundance against background dB(A) levels revealed possible problems regarding heteroskedasticity among residuals. For each species, we therefore tested a null model which included a 'power of the covariate' error structure with dB(A) as the covariate against one with the default error structure. We then ranked the models with competing error structures using AIC and used the error structure within the AIC-best model within all subsequent models for that species. We also normalized abundance values before analysis using a natural log transformation.

We built linear mixed-effects models representing several hypotheses regarding bird abundance. Each model included a random intercept for survey site. We constructed models representing several *a priori* hypotheses (see the electronic supplementary material, appendix S1). Several models included an interaction between factors indicating whether an observation occurred at the control site or along the phantom road and a factor representing noise-on and noise-off periods as well as their main effects. This interaction model represents the hypothesis that abundance along the phantom road changed between noise-on and noise-off periods while there was no difference in abundance between noise treatments at the control site. The main effect of site controls for potential differences in habitat between the control site and the phantom road. Several models contained the dB(A) levels recorded at each site during noise-on and noise-off periods—representing the hypothesis that bird abundance is linearly related to background sound levels. We also controlled for seasonal fluctuations in bird abundance by building models that contained linear and quadratic effects of Julian date. All mixed models were built in R using the package nlme [38] and were fit using maximum likelihood. Because models within $\Delta AIC < 2$ are considered to receive equal support as the best models [39], we considered there to be an effect of noise on bird abundance if models within $\Delta AIC < 2$ contained either an interaction between site and noise factors, or the covariate for background dB(A) levels with 85% CIs of these terms excluding zero [40]. Because of convergence and over-fitting problems inherent with small sample sizes, we only analysed data for species with more than 50 detections.

3. Results

We recorded 8078 detections of birds of 59 species within 50 m of bird survey locations (table 1). Twenty-two species were detected more than 50 times and those species constituted 91% of the total detections within 50 m of the observer (table 1). We integrated a total of 120 h of background noise levels for noise-on and noise-off blocks, separately at each survey site. The noise-on LEQ at point count locations near the phantom road averaged 55 (s.e. = 0.6) dB(A) and was 11 (s.e. = 2.6) dB(A) greater than the average noise-off LEQ along the phantom road. Whereas, noise-on LEQ at control locations averaged 41 (s.e. = 1.8) dB(A) and was 1 (s.e. = 0.2) dB(A) greater than the noise-off LEQ. The range of hourly LEQ values ($L_{min}-L_{max}$) during noise-on periods were 31 (s.e. = 4.8)–51 (s.e. = 0.7) at control survey locations and 36 (s.e. = 2.5)–63 (s.e. = 1.3) at road survey locations. Whereas during noise-off periods hourly LEQ values ranged from 31 (s.e. = 4.8) to 45 (s.e. = 0.2) at control survey locations and 32 (s.e. = 6.1)–52 (s.e. = 2.5) at road survey locations. The slightly higher background sound level during noise-off periods near the phantom road compared with control sites was probably owing to wind exposure. Overall, our study design produced a gradient of sound levels ranging from roughly 37 to 57 dB(A) under which birds were sampled.

Table 1. Common name, scientific name and number of encounters of birds detected within 50 m of point count locations within the Boise Foothills of southern Idaho 19 August through 9 October 2012. (Unidentified birds are not listed.)

common name	scientific name	no. encounters
American robin	Turdus migratorius	1452
ruby-crowned kinglet	Regulus calendula	890
spotted towhee	Pipilo maculatus	877
dark-eyed junco	Junco hyemalis	600
white-crowned sparrow	Zonotrichia leucophrys	583
yellow-rumped warbler	Setophaga coronata	564
red-breasted nuthatch	Sitta canadensis	560
Cassin's finch	Haemorhous cassinii	274
Cassin's vireo	Vireo cassinii	193
cedar waxwing	Bombycilla cedrorum	181
pine siskin	Spinus pinus	173
western tanager	Piranga ludoviciana	148
chipping sparrow	Spizella passerina	143
mountain chickadee	Poecile gambeli	129
MacGillivray's warbler	Geothlypis tolmiei	119
Townsend's solitaire	Myadestes townsendi	81
yellow warbler	Setophaga petechia	76
lazuli bunting	Passerina amoena	64
golden-crowned kinglet	Regulus satrapa	62
dusky flycatcher	Empidonax oberholseri	59
Townsend's warbler	Setophaga townsendi	52
evening grosbeak	Coccothraustes vespertinus	51
brown creeper	Certhia americana	49
Wilson's warbler	Cardellina pusilla	49
black-headed grosbeak	Pheucticus melanocephalus	39
black-capped chickadee	Poecile atricapilla	35
warbling vireo	Vireo gilvus	31
northern flicker	Colaptes auratus	30
orange-crowned warbler	Oreothlypis celata	28
Hammond's flycatcher	Empidonax hammondi	26
hermit thrush	Catharus guttatus	25

(Continued.)

Table 1. (Continued.)

common name	scientific name	no. encounters
Nashville warbler	Oreothlypis ruficapilla	24
Steller's jay	Cyanocitta stelleri	21
dusky grouse	Dendragapus obscurus	12
hairy woodpecker	Picoides villosus	10
house wren	Troglodytes aedon	9
mountain bluebird	Sialia currucoides	9
western wood-pewee	Contopus sordidulus	9
sharp-shinned hawk	Accipiter striatus	8
American goldfinch	Spinus tristis	5
calliope hummingbird	Selasphorus calliope	5
red crossbill	Loxia curvirostra	5
Swainson's thrush	Catharus ustulatus	4
Clark's nutcracker	Nucifraga columbiana	3
common raven	Corvus corax	3
white-breasted nuthatch	Sitta carolinensis	3
western flycatcher	Empidonax difficilis	3
black-billed magpie	Pica hudsonia	2
Bullock's oriole	Icterus bullockii	2
northern pygmy-owl	Glaucidium gnoma	2
American kestrel	Falco sparverius	1
black-chinned hummingbird	Archilochus alexandri	1
Brewer's sparrow	Spizella breweri	1
band-tailed pigeon	Patagioenas fasciata	1
Cooper's hawk	Accipiter cooperii	1
northern harrier	Circus cyaneus	1
olive-sided flycatcher	Contopus cooperi	1
red-tailed hawk	Buteo jamaicensis	1
varied thrush	Ixoreus naevius	1

The best models of detection for all birds together contained factors for observer and site (electronic supplementary material, appendix S1). Observer effects were apparent for six individual species (American robin, spotted towhee, white-crowned sparrow, red-breasted nuthatch, lazuli bunting and evening grosbeak) and site effects were apparent for five species (American robin, spotted towhee, red-breasted nuthatch, Cassin's finch and evening grosbeak; electronic supplementary material, appendix S1). Detection of five species varied between noise-on and noise-off periods (dark-eyed junco, white-crowned sparrow, Cassin's finch, and chipping sparrow), and interactions between noise and site as well as noise and observer were within the best models for two species
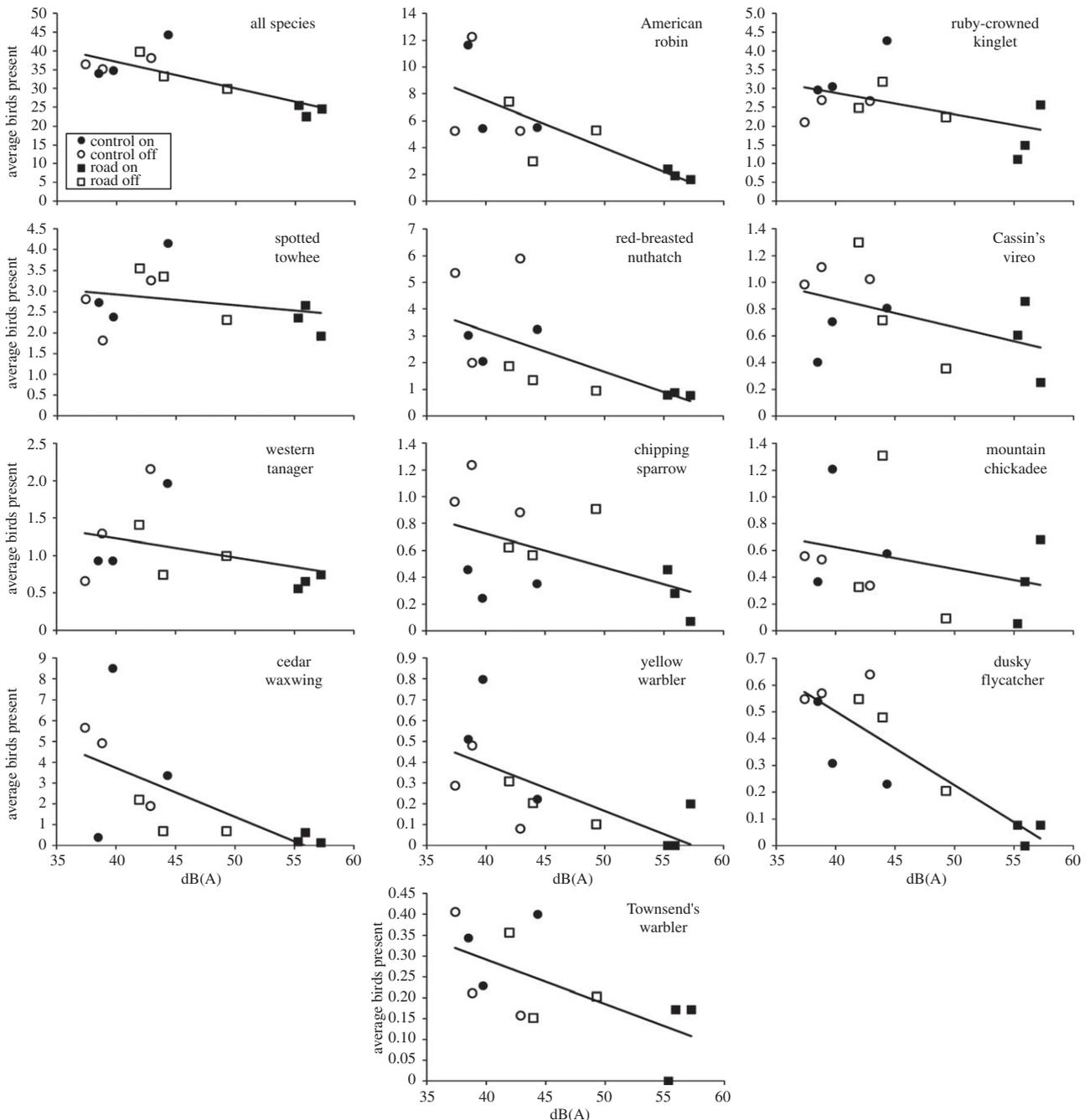
Figure 2. Average numbers of birds present per survey during noise-on and noise-off periods along the phantom road and at control sites in the Boise Foothills in southwestern Idaho. Only species with significant differences in abundance among treatments or background sound levels are shown.

(white-crowned sparrow, Cassin's finch). Finally, detection of four species varied by the day of the season (ruby-crowned kinglet, cedar waxwing, pine siskin and yellow warbler).

Abundance of every species except evening grosbeak changed as the season progressed with either linear or quadratic effects of day of the season being within models ΔAIC < 2 and having confidence intervals excluding zero (electronic supplementary material, appendix S2). The best two models for the abundance of all birds within our study site received 99% of the model weight and contained a negative association with dB(A) and with the interaction between site and noise-on periods—indicating that when the noise was on, fewer birds were present near the phantom road (figure 2 and electronic supplementary material, appendix S2). Furthermore, over half of the individual species analysed responded negatively

to the noise produced by the phantom road with 13 of 22 species being negatively associated either with dB(A) levels, or the interaction between site and noise-on periods, or both (figure 2). Eight species did not seem to be affected by noise because their best models were either the null or only contained covariates relating to the day of the season (electronic supplementary material, appendix S2). Finally, only one species—the Cassin's finch—was positively associated with the interaction of site and noise-on periods—indicating a positive effect of noise on abundance of this species. The number of birds present along the phantom road during noise-on periods was 28% (s.e. = 8%) lower than that during noise-off periods. Whereas, the number of birds present at the control site during noise-on periods was 3% (s.e. = 7%) higher than that during noise-off periods (figures 1 and 2). Furthermore,

cedar waxwing and yellow warbler almost completely avoided the phantom road during noise-on periods (figure 2).

4. Discussion

This study is, to our knowledge, the first to experimentally demonstrate an effect of road noise on distributions of an animal community. To date, the most persuasive demonstrations of the effects of road noise on distributions of wildlife relied on comparing roadless areas to areas near roads [27,41–43]. Although suggestive, results from most road ecology studies are confounded by the other effects of roads such as collisions, visual disturbance and habitat alteration—and thus their interpretations have been questioned [11]. Our phantom road—an array of speakers broadcasting road noise into a roadless landscape—allowed us to isolate the effects of noise. The decline of bird abundance by over one-quarter along the phantom road, and the almost complete avoidance of two species by our treatments, suggests that road noise is a major driver of the documented effects of roads on wildlife. Therefore, our results experimentally validate the observational conclusions of past researchers—that negative effects of roads on animals can be driven by traffic noise (reviewed by [2]).

In addition, our study design of applying road noise using a line array of speakers and recording background sound levels using MP3 recorders yielded several benefits. We were able to quantify the bird community at the same sites under both noise-on and noise-off conditions instead of comparing sites that are always noisy to sites away from roads. Furthermore, our method of employing control sites, alternating between noise-on and noise-off blocks throughout the migratory period, and testing models which included covariates for day-of-season allowed us to assess and control for natural fluctuations in bird abundances and any potential differences in habitat among survey sites.

Accurate and thorough quantification of background sound levels is imperative for studies of effects of anthropogenic noise on animals [44]. Our use of MP3 recorders also allowed us to assess the LEQ over 16 days (two noise-on and noise-off blocks)—thereby performing, to our knowledge, the most thorough assessment of background sound levels in relation to distributions of terrestrial animals yet undertaken. For example, Summers et al. [11] quantified traffic noise over a 5 min period, Proppe et al. [45] quantified sound levels over four 11 min periods and several studies did not directly sample noise levels [13,41,43,44]. Because background sound level at a site can fluctuate strongly [26] and formulae estimating dB levels based on traffic volume ignore ambient sound levels, using continuous sound recordings provides a more accurate assessment of background sound levels. Our method of deploying MP3 recorders at survey sites is therefore efficient, thorough, accurate and cost effective [31].

Although our results demonstrate that traffic noise can severely affect bird abundances, other effects of roads (reviewed by [2]) will probably add to or multiply the effects of noise. Negative effects of roads are also likely to be driven by different aspects of roads depending on the taxon examined [2], and therefore taxa other than birds may be less affected by noise. Furthermore, migrating birds might strongly avoid noise because of their inherent mobility—they can easily avoid a noisy site, given there are other suitable, quieter areas nearby. Therefore, territorial breeding birds or less mobile taxa may be less willing or able to avoid noisy areas. However, our results demonstrate that noise alone is enough to cause some birds to avoid a site—suggesting that road noise might be, in some instances, the main driver of the effects of roads on animals.

Populations of migratory birds are in decline for myriad reasons including loss and degradation of migratory stopover habitat [21,23]. In fact, migration might be the most dangerous time of a migratory bird's annual cycle. For example, 85% of the yearly mortality of the black-throated blue warbler (*Dendroica caerulescens*) occurs during migration [46]. We substantially depleted the population of migratory birds and caused entire species to almost completely avoid an otherwise high-quality stopover site [25,28,47] using only traffic noise—demonstrating that anthropogenic noise can alter the amount of habitat available to migratory birds during stopover. For example, the yellow warbler—a species with declining range-wide populations [48]—was essentially absent from sites near the phantom road during noise-on periods. Because 83% of the USA is within 1 km of a road [1], it is likely that noise-sensitive species such as the yellow warbler avoid substantial areas of otherwise suitable habitat simply because they are too loud. Even within protected areas, roads can produce sound exposures similar to those produced by our phantom road across large areas [26]. Anthropogenic noise should therefore be considered when preserving and managing habitat, including stopover habitat for migratory birds.

Of course, management actions should also be informed by identifying the mechanisms underlying avoidance of noisy sites [49]. Background noise may mask important sounds, such as con- and heterospecific songs and calls, as well as sounds made by both predators and prey [10]. Increases in background noise are therefore known to increase predator vigilance in California ground squirrels (*Spermophilus beecheyi*, [50]), pronghorn (*Antilocapra americana*, [51]) and chaffinches (*Fringilla coelebs*, [52]). Because increased predator vigilance generally leads to less food intake [51,52], it is possible that noise degrades stopover habitat because migrants are less able to gain fat needed to fuel migration, but more study is needed.

An animal's ability to vocalize within frequencies which are not masked by background noise probably influences its response to increased noise [10]. For example, Francis et al. [7] and Rheindt [9] demonstrated that birds with higher frequency songs are less likely to avoid sites exposed to gas-compressor and road noise, respectively—probably because they are less affected by masking at lower frequencies. Furthermore, Francis et al. [6] demonstrated that of two closely related tyrant flycatchers, one species shifted its song to a higher frequency in response to gas-compressor noise, but did not avoid noisy areas, whereas the other species did not shift its song but was less likely to occupy noisy sites—suggesting that tolerance of noise is influenced by the ability of a species to avoid masking of its song. It is likely that the differing responses to noise among species within our study are, in part, owing to different abilities to avoid masking. However, past work has focused on masking of songs, whereas the migrating birds that we surveyed sing infrequently and to varying degrees. Future work should therefore examine the effects of masking of conspecific calls and which species possibly shift call-frequency in the presence of noise. Further, in addition to masking, other effects of noise such as disturbance,

increased stress levels and distraction might have contributed to our results [49], and future studies should examine their relative contributions to changes in animal distributions.

Owing to logistical constraints regarding the difficulty of maintaining a phantom road, our design consisted of a single experimental and control site each containing three point count locations. That our point count locations were subsamples of the control and experimental sites might complicate the generalization of our results to other sites [53]. However, we took great care to ensure that our survey locations were as independent as possible—ridges separated survey locations and our analysis only included birds detected within 50 m. More large-scale playback studies are needed to assess the generality of our results among roads.

Generally, a deep understanding of large-scale ecological phenomena, such as those encountered in road ecology, requires both manipulative experiments and observational studies. Manipulative experiments provide strong inference into causal relationships that produce the widespread (in the case of road ecology, global) correlations demonstrated by observational studies [54,55]. Our study provides experimental

demonstration of one of the primary causes underlying the correlations presented in past studies of effects of roads on animals. Future studies should employ a system similar to our phantom road to examine the effects of noise on direct measures of habitat quality such as individual fitness as well as examine the effects of noise on other taxa.

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