

Sound attenuation in forest and roadside environments: Implications for avian point-count surveys

Author(s): Daniel A. Yip, Erin M. Bayne, Péter Sólymos, James Campbell, and Darren Proppe

Source: *The Condor*, 119(1):73-84.

Published By: American Ornithological Society

<https://doi.org/10.1650/CONDOR-16-93.1>

URL: <http://www.bioone.org/doi/full/10.1650/CONDOR-16-93.1>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.



RESEARCH ARTICLE

Sound attenuation in forest and roadside environments: Implications for avian point-count surveys

Daniel A. Yip,^{1*} Erin M. Bayne,¹ Péter Sólymos,^{1,2} James Campbell,¹ and Darren Proppe³

¹ Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

² Alberta Biodiversity Monitoring Institute, University of Alberta, Edmonton, Alberta, Canada

³ Department of Biology, Calvin College, Grand Rapids, Michigan, USA

* Corresponding author: dayip@ualberta.ca

Submitted May 19, 2016; Accepted November 18, 2016; Published February 1, 2017

ABSTRACT

Point counts are one of the most common ways of collecting data to determine the relative abundance of birds. Many studies and monitoring programs, including the North American Breeding Bird Survey, use relative differences in counts of birds to assess changes in abundance over time and space. Many factors influence whether relative differences in counts of birds between various environmental conditions are reflective of actual differences in bird density. A major assumption of relative abundance is that birds with different song frequencies and amplitudes are heard at the same distances in different environmental conditions. We compared sound transmission in forest habitats and along low-use forestry roads, and calculated detection radius for different species to test the assumption that differences in bird counts between forest interior and roadside locations reflect actual differences in bird abundance. A playback–recording experiment was used to broadcast sounds through forest interior, along a forest edge, and down forestry roads in conifer and deciduous forests to determine whether sound propagation differed across environments. Sound attenuated significantly faster in forests than along roads or forest edges. Similarly, the distance at which bird songs could be detected was significantly shorter in forest than along the road or forest edge for 20 of 25 species. We found the area surveyed to be up to twice as large on road compared to within forests, which suggests that roadside surveys might inflate avian density estimates in comparison to off-road counts. Local atmospheric conditions also influenced detection probability, but the magnitude of the effect was weaker than the land-cover effect. Major differences in detection between roads and interior forest suggest that comparisons of surveys conducted along roadsides and in forest areas should be done carefully if the goal is to make direct comparisons of abundance.

Keywords: bioacoustics, detection distance, detection radius, roadside survey, survey bias

Atténuation sonore dans les milieux boisés et les bords de route : conséquences sur les relevés aviaires par points d'écoute

RÉSUMÉ

Les points d'écoute sont l'un des moyens les plus courants pour recueillir des données afin de déterminer l'abondance relative des oiseaux. Plusieurs études et programmes de suivi tels que le Relevé des oiseaux nicheurs de l'Amérique du Nord utilisent la différence relative dans les relevés d'oiseaux pour évaluer les changements d'abondance dans le temps et l'espace. Plusieurs facteurs ont une influence sur le fait que les différences relatives dans les relevés d'oiseaux effectués dans diverses conditions environnementales reflètent de réelles différences de densité aviaire. Une importante hypothèse de l'abondance relative est que les oiseaux ayant différentes fréquences et amplitudes de chant sont entendus aux mêmes distances dans différentes conditions environnementales. Nous avons comparé la transmission des sons dans des habitats forestiers et le long de chemins forestiers peu utilisés, puis calculé des rayons de détection pour différentes espèces afin de vérifier l'hypothèse que les différences entre les relevés d'oiseaux effectués à l'intérieur de la forêt et ceux sur les bords de route reflètent de réelles différences dans l'abondance aviaire. La repasse de chants a été utilisée pour émettre des sons à l'intérieur de la forêt, le long d'une lisière boisée et le long de chemins forestiers situés dans des forêts résineuses et feuillues afin de voir si la propagation des sons différait entre les milieux. Les sons étaient atténués significativement plus rapidement dans les forêts que le long des chemins ou des lisières boisées. De même, la distance à laquelle les chants d'oiseaux pouvaient être détectés était significativement plus courte dans la forêt que le long des chemins ou des lisières boisées pour 20 des 25 différentes espèces d'oiseaux. Nous avons trouvé que la zone inventoriée était jusqu'à deux fois plus grande sur les chemins en comparaison de l'intérieur de la forêt, ce qui suggère que les relevés le long de chemins peuvent gonfler les estimations de densité aviaire en comparaison des relevés hors route. Les conditions atmosphériques locales ont également influencé la probabilité de détection mais l'ampleur de l'effet était plus faible que l'effet de la couverture du territoire. Les différences majeures de détection entre les chemins et l'intérieur de la forêt suggèrent que la comparaison entre les

relevés effectués le long des chemins et ceux effectués dans les milieux forestiers devrait être réalisée avec précaution si le but est de faire une comparaison directe de l'abondance.

Mots-clés : biais du relevé, bioacoustique, distance de détection, rayon de détection, relevés le long de chemins

INTRODUCTION

One of the largest datasets available to ornithologists in North America is the Breeding Bird Survey (BBS). Many advances in our knowledge of birds have come from the BBS (U.S. Geological Survey 2009). However, there is concern that the roadside nature of this survey may provide biased estimates of bird abundance and trends in comparison to non-BBS monitoring and research done off-road (Bart et al. 1995, Keller and Scallan 1999, Lawler and O'Connor 2004), particularly when combining both types of data for analysis. Roadside habitats differ from forest interior habitats in ways that could alter our understanding of avian abundance and diversity patterns. It is known that roadside habitats often have differences in vegetation composition and structure (Keller and Scallan 1999), physical characteristics (road salts, sediments, etc.; Trombulak and Frissell 2000), and levels of ambient noise (Parris and Schneider 2008) in relation to forest interior. Traffic volume can also vary; to control for this, BBS surveys are often conducted along relatively low-use and secondary roads where alterations to the environment by traffic are minimized (Droege 1990). However, studies of sound transmission suggest that the distance at which sounds can be detected will vary between open and closed (more dense) environments (Fricke 1984). If that is the case, roadside surveys, such as those utilized by the BBS, may be confounded, in comparison to off-road surveys, by the open linear environments that necessarily define roads.

Attenuation and degradation of acoustic signals are directly related to the distance the signal must travel. Wiley and Richards (1982) state that under free field conditions, all sounds are expected to attenuate at ~ 6 dB each time the distance between the source and the observer is doubled (inverse distance law). Free field conditions are rarely met outside of the laboratory, because the composition of the sound path can result in attenuation in excess of what is predicted by the inverse distance law. Several factors can affect excess attenuation. Scattering and reverberation effects are greater when vegetation is present and thus could increase the attenuation of sound (Wiener and Keast 1959, Richards and Wiley 1980, Yang et al. 2013). Although scattering can reduce the transmitting energy of any frequency, this effect is especially significant for higher-frequency sounds, because shorter wavelengths are less able to pass around obstructing objects than sounds produced at lower frequencies (Piercy et al. 1977). Roadsides are more open along their path, so the acoustic environment could differ greatly from that of forest

interior. In addition to lower vegetation density along transmission paths, roadsides differ in surface composition characteristics. Decreased porosity on roads can decrease attenuation by lowering the impedance characteristics of the road surface (Aylor 1972). Finally, local atmospheric conditions can vary when comparing roadside to interior locations. Environmental gradients such as wind and temperature can differ between roadsides and interior areas and are often stronger in open areas, which can result in higher attenuation (Wiener and Keast 1959, Morton 1975, Trombulak and Frissell 2000). Overall, differences between roadside and forest areas suggest that the distance across which bird vocalizations transmit could differ considerably between them, potentially leading to biased estimation of avian abundance in studies combining roadside and non-roadside data.

To evaluate whether the distance over which sounds could be detected differed between sounds produced along open transmission paths parallel to the road, forest edge, and forest transmission paths perpendicular to roads, we played back and rerecorded a series of pure tones and different bird songs along forestry roads in boreal conifer and deciduous forest stands. These roads were selected because they are relatively free of confounding variables found along most roads (e.g., noise, traffic, surrounding development). Differing vegetation structure can influence sound (Aylor 1972); thus, we chose 2 of the main forest types in the boreal forest. A common assumption is that the detection area is circular. If transmission is altered along roadways in comparison to interior areas, we predicted that directionally dependent differences in detectability between forest interior, forest edge, and road transects would be observed. We had 3 objectives: (1) to measure how sound attenuation is influenced by roads and forest type, by calculating excess attenuation for each type of transmission path; (2) to determine whether sound transmission of birdsong is differentially affected by roads and by forest type, by determining the distances at which sounds can be detected by observers listening to sound playbacks and the environmental factors that influence them; and (3) to calculate the effective area surveyed and develop statistical correction factors to standardize count data obtained from on- and off-road sites.

METHODS

Field Playbacks

The research was conducted near Calling Lake, Alberta, Canada (55.21°, -113.19°), between July 22 and August 24,



FIGURE 1. Sampling design schematic for our experiments near Calling Lake, Alberta, Canada, July 22–August 24, 2014. Wildlife Acoustics SM2 recorders were placed on the forest edge (1) and on the road (2), and playbacks were conducted to both recorders simultaneously along a transect following the forest edge. For forest playbacks, recorders were placed within the interior forest (3) and playback transects ran perpendicular to the road.

2014. We conducted 600 playback trials at 30 different distances (“stations”) between the recorder and the playback unit. Ten transects each were placed along forestry roads, along forest edges, and within forest interior ≥ 50 m from the road (Figure 1). Forest transects were located perpendicular to roads in sites where the vegetation path represented a single forest class. In this region, tree diversity is low and forest stands are often composed of a single species. Half of the transects were in deciduous-dominated forest (defined as $\geq 65\%$ deciduous) where the dominant species was Quaking Aspen (*Populus tremuloides*), and the other half were in coniferous-dominated forest (defined as $\geq 65\%$ coniferous) where the dominant species was White Spruce (*Picea glauca*) or Black Spruce (*P. mariana*). Dominance was determined by estimating forest composition at 4 points per transect every 250 m.

Each playback was done between 0800 and 2000 hours MST during late summer to reduce the chance of recording actual bird sounds. Average wind speed, temperature, and humidity were recorded using a handheld weather monitor (Kestrel 4000) for the duration of each playback. Wind speeds at the start of each trial were ≤ 2 on the Beaufort scale; average (\pm SD) wind speed was 1.3 ± 1.4 km hr⁻¹. Average temperature was $24.7 \pm 5.1^\circ\text{C}$, and average relative humidity was $58.3 \pm 14.1\%$. The date and order (forest vs. road) of playback at each site were selected by alternating between forest and road transects. Roads were low-use (< 1 vehicle hr⁻¹) dirt or gravel forestry roads. Recordings were done in absence of vehicle traffic.

We broadcast 36 known sounds from an Alpine digital CD receiver (CDE-122) connected to an Alpine 6.5 inch

speaker and tweeter set (SPR-60) contained within a wooden box ($25 \times 29 \times 38$ cm) at 30 standardized distances ranging from 12 to 1,312 m, measured using GPS (GARMIN GPSmap 78, accuracy ± 3 m) at each transect. The speaker was placed so that it directly faced the recorder at a height of 1.5 m, a height similar to those used in other avian playback studies (Maynard et al. 2012, Koloff and Mennill 2013, Sandoval et al. 2015). At each site, a Song Meter SM2+ Automated Audio Recorder (Wildlife Acoustics, Maynard, Massachusetts, USA) was set to continuously record (sampling rate = 44.1 kHz, bit depth = 16, WAV format). Recording units were located at the forest edge and at the road, and the speaker was moved to each distance interval for playback. “Forest edge” was defined as the transition between the mature trees and the ditch of the road where the forest ended with a distinct edge. “Road” was defined as the transition between the ditch and the road surface. For the road and forest edge transect, the playback unit was placed at the forest edge and broadcast to both road and forest edge recorders simultaneously. For forest transects, the recording and playback unit were located separately within a continuous stand of deciduous or coniferous forest to best simulate a bird calling from within an interior forest environment.

Playbacks at each station consisted of a 5:10 min sequence beginning with an escalating series of 1 s pure (sine wave) tones following half-octave intervals (1,000, 1,414, 2,000, 2,828, 4,000, 5,656, and 8,000 Hz). We used Adobe Audition CS6 (Adobe Systems, San Jose, California, USA) to generate these sounds. These tones were followed by a series of vocalizations of boreal bird and amphibian species selected to represent a range of frequencies and song complexities, including (in no particular order) Clay-colored Sparrow (*Spizella pallida*, CCSP), Black-and-white Warbler (*Mniotilta varia*, BAWW), Lincoln’s Sparrow (*Melospiza lincolnii*, LISP), Brown-headed Cowbird (*Molothrus ater*, BHCO), Red-breasted Nuthatch (*Sitta canadensis*, RBNU), Bay-breasted Warbler (*Setophaga castanea*, BBWA), Dark-eyed Junco (*Junco hyemalis*, DEJU), White-throated Sparrow (*Zonotrichia albicollis*, WTSP), Cape May Warbler (*Setophaga tigrina*, CMWA), Common Raven (*Corvus corax*, CORA), Belted Kingfisher (*Megasceryle alcyon*, BEKI), Olive-sided Flycatcher (*Contopus cooperi*, OSFL), Pine Siskin (*Spinus pinus*, PISI), Tennessee Warbler (*Oreothlypis peregrina*, TEWA), Warbling Vireo (*Vireo gilvus*, WAVI), Rose-breasted Grosbeak (*Pheucticus ludovicianus*, RBGR), Ovenbird (*Seiurus aurocapilla*, OVEN), Yellow Rail (*Coturnicops noveboracensis*, YERA), Northern Saw-whet Owl (*Aegolius acadicus*, NSWOW), Boreal Owl (*Aegolius funereus*, BOOW), Great Gray Owl (*Strix nebulosa*, GGOW), Long-eared Owl (*Asio otus*, LEOW), Barred Owl (*Strix varia*, BADO), western toad (*Anaxyrus boreas*, WETO), and Canadian toad (*Bufo hemiophrys*, CATO). We used a 2 s interval between calls

to avoid signal overlap. This sequence was broadcast at a sound pressure level (SPL) of 90 dB (re 20 μ Pa), which we normalized using the peak amplitude (maximum volume) of each sound in Adobe Audition CS6 and calibrated using a handheld sound-level meter (Sper Scientific 840018) measuring the 1,000 Hz tone 1 m from the speaker (based on fast-time A-weighting).

Sound Processing

Recorded playbacks were isolated from continuous recordings using Audition, and individual sounds from each sequence were clipped into individual sound files ($n = 27,143$) using an automated script and the “textgrid” function in Praat 5.4.06 (Boersma and Weenink 2015). These clips were randomized and pooled in sets of 10 sounds with 2 s spacing to create a single sequence of randomized sounds using an automated batch script. These sequences were given to 6 observers, who identified any detectable sounds simultaneously by (1) sight, using visual scanning of spectrograms in Adobe Audition (window type: Blackman-Harris; window length: 2048); and (2) sound, using standardized volume levels and headphones. Volume levels were selected to maximize amplitude and detections while avoiding any risk of hearing damage. Fifteen percent of sounds were blank ambient background sound consisting of low levels of wind and vegetation noise normally present in recordings to control for false positive identifications. Randomization of sounds removed an observer’s ability to predict which sounds would occur in what order, although observers were aware of all possible species that could be presented.

The inverse distance law predicts that SPLs will attenuate at a specific rate (Berg and Stork 2004). However, vegetation can alter attenuation rate. We measured relative SPL of the pure tones ($n = 5,656$) using a batch-process selection-table function in Raven Pro 1.4 (Charif et al. 2010). We calculated averaged background noise levels within the same bandwidth of each measured tone at hourly intervals for each site ($n = 5$) to determine the baseline power level of each transect. We removed data at distances where the SPL of pure tones dropped to the levels of ambient background noise. While it is still possible to detect sounds below this level, it is no longer possible to measure SPL. Measurements were conducted on a selection of 0.4 s duration and 100 Hz bandwidth for each clip (i.e. for 1,000 Hz: 950–1,050 Hz selection) by calculating power spectral density summed over the frequency range of the selection (window type: Hann; window length: 256). We chose a shorter section of each pure tone and avoided doing measurements at the onset or end to avoid acoustic distortion. We then calculated excess attenuation, compared to the attenuation predicted from the inverse

distance law, using

$$\text{EXCESS}_{\text{SPL}} = (\text{SPL}_{12.5} - \text{SPL}_i) - \left(20 \cdot \log_{10} \left(\frac{d_i}{12.5} \right) \right) \quad (1)$$

where $\text{SPL}_{12.5}$ is the SPL at 12.5 m, SPL_i is the SPL for i distance, and d_i is the distance i (in meters) at which each tone was recorded. We used SPL at 12.5 m as a reference value because it was the closest distance measured, and we calculated excess attenuation for each distance beyond 12.5 m for each individual transect.

Sound Attenuation and Excess Attenuation

We used Akaike’s Information Criterion (AIC; Burnham and Anderson 2002) to rank linear mixed models (lmer function, lme4 package in R; Bates et al. 2015; see [Supplemental Materials](#)) that predicted the effect of distance, frequency, transect and vegetation type, and weather on sound attenuation and excess attenuation. We ranked models with all tones pooled together to investigate the effect of frequency between different tones. We also tested models for each individual tone to investigate effects on sound by the environment for each frequency separately. Site was included as a random effect. The best model for each tone was selected using the lowest AIC_c and ΔAIC_c values ([Supplemental Material Table S2](#)). For model selection where $\Delta\text{AIC}_c < 2$, we selected the most parsimonious model as our best model (Arnold 2010). We found a strong negative correlation between humidity and temperature ($r = -0.77$). Humidity was weighted higher during preliminary model selection, so temperature was dropped from our full models to avoid issues with collinearity, given that both variables influence attenuation (Harris 1966). Log-transformed distance had higher model weight in preliminary analyses and was included over untransformed distance in subsequent analyses. We reported marginal R^2 values (R^2_m) to provide information on variation due to fixed effects, and conditional R^2 values (R^2_c) to provide information on variation due to fixed and random effects for each final model (Nakagawa and Schielzeth 2013; r.squaredGLMM function, MuMIn package, Bartoń 2015).

Effect on Observer Detection

Generalized linear models (GLMs) were ranked using AIC_c for each species and tone to predict observer detection probability ([Supplemental Material Table S4](#)). We randomly partitioned data into 70% training data and 30% testing data and performed cross-validation on our models. These models predicted the probability of an observer detecting a given species or tone as a function of weather, distance, and transect type (road, forest edge, or forest) in each forest type (deciduous or coniferous).

Similarly, we modeled detection data with all species pooled and included the minimum frequency of each species to investigate a species-specific frequency effect. Minimum frequency is defined as the lowest frequency measured over the duration of each species-specific sound. Finally, we validated our best model for each species and tone by determining AUC (i.e. area under the curve) statistics and receiver operating characteristic (ROC) curves using our testing data (roc function, pROC package, Robin et al. 2011; [Supplemental Material Table S4](#)).

We performed a Monte Carlo simulation to determine whether statistical differences existed between detection distances in forests, forest edge, and roads, as well as between deciduous and coniferous forest types. This was done to determine the scale of effective detection radius (EDR) correction required between different combinations of transect and forest types (see below). We generated coefficients ($n = 1,000$) using maximum-likelihood estimates and variance-covariance matrix from the original model and calculated 90% confidence intervals of the predicted values for each species when making comparisons. If statistical differences did not exist between certain combinations of transect and forest, we assumed that correction was unnecessary.

We investigated differences in wind speed, relative humidity, and temperature at forest interior and roadside sites using a linear mixed model in R (R Development Core Team 2015; lmer function, lme4 package, Bates et al. 2015) to account for variation in site, date, and time. We used ordinal date and time on a continuous scale of minutes in relation to average sunrise time for the days of sampling. We included site as a random effect.

Calculating Correction Factors to Standardize Count Data

We developed correction factors for each species and tone by calculating a ratio of the effective area sampled in forest, on roads, and at forest edges ($A_{\text{Forest}} : A_{\text{Road}} : A_{\text{ForestEdge}}$). To do this, we followed a half-normal detection function often used in the distance sampling literature to calculate EDR (Sólymos et al. 2013). EDR is the parameter, τ , in the half-normal detection function: $p(d) = \exp(-d^2/\tau^2)$. EDR is defined as the distance at which the number of individual birds detected outside τ is equal to the number of missed individuals within τ . We ran our GLMs with a fixed intercept at zero, complementary log-log link (“cloglog”) function, and binomial distribution. Interaction with distance was included in models for all parameters of interest, but main effects were excluded to accommodate a fixed intercept. This allowed us to calculate EDR using a linear modeling framework. We transformed distance to $x = -d^2$ before modeling so that distance was a linear predictor. We estimated EDR for all species and tones on roads, on forest edges, and within forests by summing the

beta coefficients of variables related to distance in our best models (β). We calculated EDR using $\tau = (1/\beta)^{0.5}$. Finally, we determined the effective area sampled for the forest using the formula for area of a circle ($A_{\text{Forest}} = \pi \times \tau_{\text{Forest}}^2$). We presented 2 scenarios for effective area sampled on a road, a simple ellipse ($A_{\text{Road-ForestEdge}} = \pi \times \tau_{\text{Forest}} \times \tau_{\text{Road-ForestEdge}}$) and a more complicated equation ([Supplemental Material Figure S1](#)) taking into account the angle of detection and proportion of distance traveled through forest vs. road. The ratio of A_{Forest} to $A_{\text{Road-ForestEdge}}$ is the correction factor for a given species or tone, which can be used to multiply roadside or forest count data to allow for standardization ([Supplemental Material Table S9](#)).

RESULTS

Estimating Sound Attenuation and Excess Attenuation for Pure Tones of Different Frequencies

Relative SPL attenuated at a higher rate with increasing frequency when all tones were pooled (Figure 2). Relative SPL was also negatively influenced by distance for all tones. The top-performing model for each individual tone included $\log(\text{Distance})$ and transect while omitting weather variables, with the exception of the 8,000 Hz tone. Tones that were transmitted through forest attenuated at a higher rate than those transmitted along forest edges or roads in both coniferous and deciduous vegetation types (Figure 2). For the 8,000 Hz tone, wind negatively influenced relative SPL. For all models assessing influences on relative SPL, the R^2_{m} value was >0.71 and the R^2_{c} value was >0.77 ([Supplemental Material Table S2](#)).

Excess attenuation increased with distance at all frequencies and at higher frequencies with all tones pooled together. The top-performing model for each individual tone was the same as for relative SPL and included $\log(\text{Distance})$ and transect while omitting weather variables. At 8,000 Hz, the top-performing model included wind. Tones had higher excess attenuation when transmitted through the forest interior for both vegetation types (Figure 2). All tones transmitted along roads and forest edges initially had lower attenuation than expected from free field environments. At 8,000 Hz, wind increased rates of excess attenuation. For all models assessing influences on excess attenuation, the R^2_{m} value was >0.39 and the R^2_{c} value was >0.52 ([Supplemental Material Table S3](#)).

Estimating Effects of Transect Type and Weather on Detectability

Detectability declined with distance at different rates for different transect and forest-type combinations. Detectability decreased with increasing frequency (Figure 3). The top-performing model for each species varied. A global model including distance, transect type, humidity, and

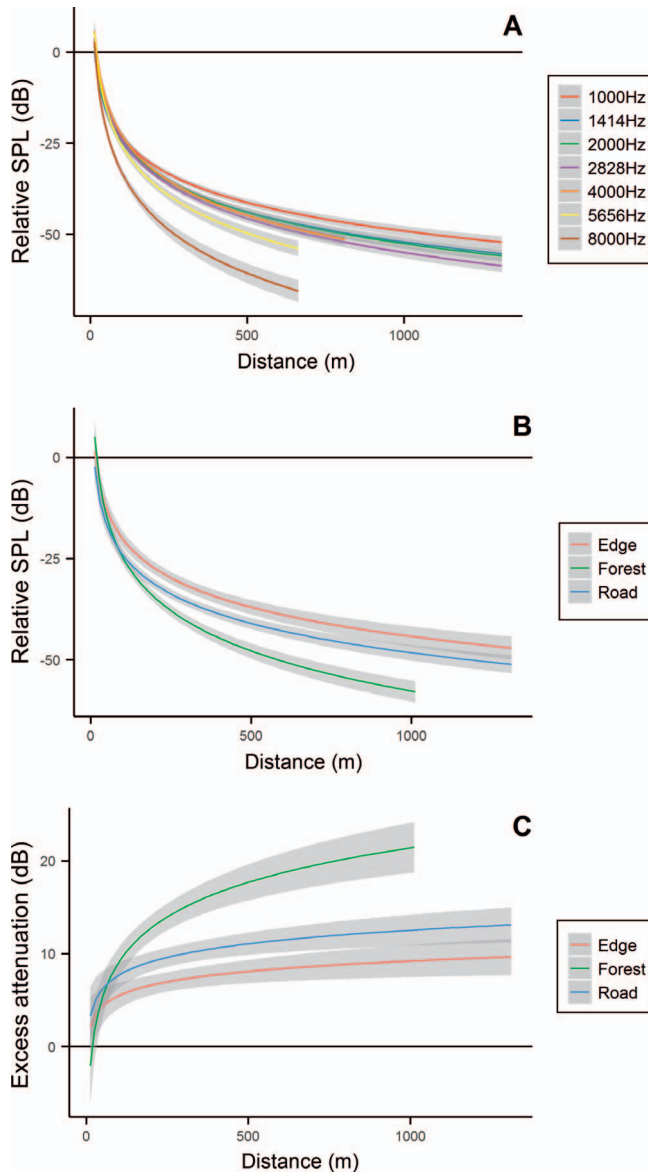


FIGURE 2. Predicted values for the effect of frequency on (A) attenuation of relative sound pressure level (SPL); (B) attenuation of relative SPL for a 1,000 Hz pure sine wave; and (C) excess attenuation from what is expected (from the inverse distance law) for a 1,000 Hz pure sine wave with distance, along different transects (edge, forest, and road) in our study area near Calling Lake, Alberta, Canada. Predictions were calculated from measurements of relative SPL and are presented with 95% confidence intervals. The reference value for relative SPL measurements was defined as the measured voltage for each transect at a distance of 12.5 m and theoretical slope backward fit to zero in the absence of data.

wind was the top-performing model for 13 species and 2 pure tones. A model excluding wind and humidity was selected for 12 species and 5 pure tones (BEKI, PISI, BBWA, TEWA, CMWA, LISP, YERA, WTSP, OSFL, RBGR, WAVI, and DEJU; 1,000, 1,414, 4,000, 5,656, and 8,000 Hz).

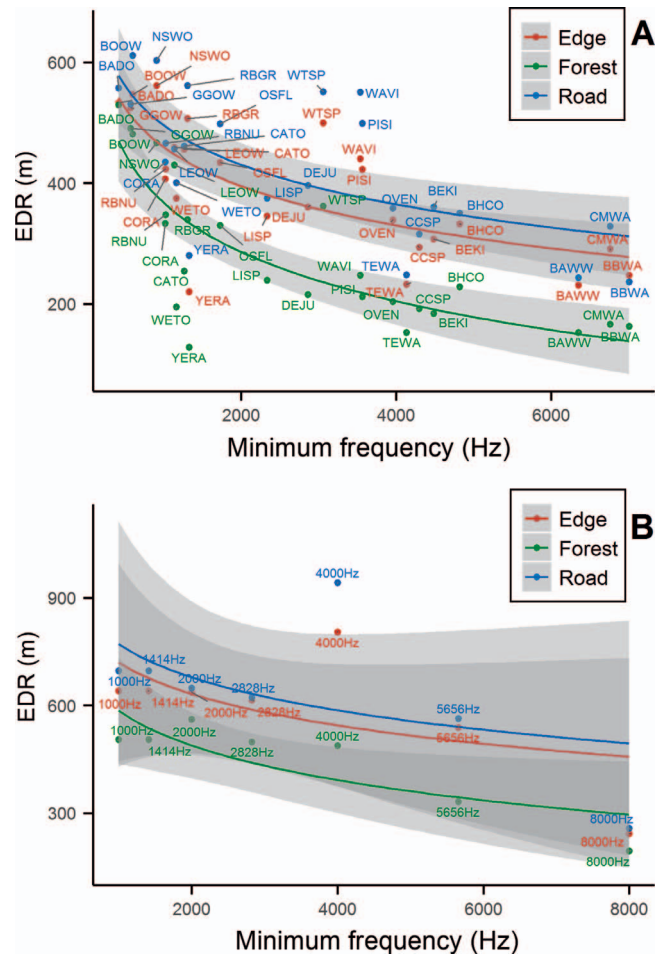


FIGURE 3. Influence of minimum frequency on effective detection distance (EDR, with 95% confidence intervals) for each (A) species and (B) tone along different transects (edge, forest, and road) near Calling Lake, Alberta, Canada, July 22–August 24, 2014.

Wind had a variable effect on detectability whereby 4 species appeared to be positively influenced (CCSP, BAWW, OVEN, and BHCO) and 9 species and 2 pure tones appeared to be negatively influenced (BOOW, NSW, LEOW, BADO, WETO, CORA, RBNU, GGOW, and CATO; 2,000 and 2,828 Hz). Humidity had a negative effect on detectability for 13 species and 2 pure tones (BOOW, NSW, LEOW, BADO, WETO, CORA, RBNU, BAWW, CATO, OVEN, LISP, GGOW, and BHCO; 2,000 and 2,828 Hz). The top model for 8,000 Hz included observer as an important parameter for detection probability.

Environmental gradients differed between roads and the forest interior. Mean (\pm SD) wind speed was lower within the forest (0.9 ± 1.1 km hr⁻¹) than on roads (1.8 ± 3.4 km hr⁻¹; Figure 4). Humidity decreased with time on roads and in forests but decreased faster on roads than in forests over the day (forest: $56.4 \pm 12.5\%$, road: $60.2 \pm 15.4\%$;

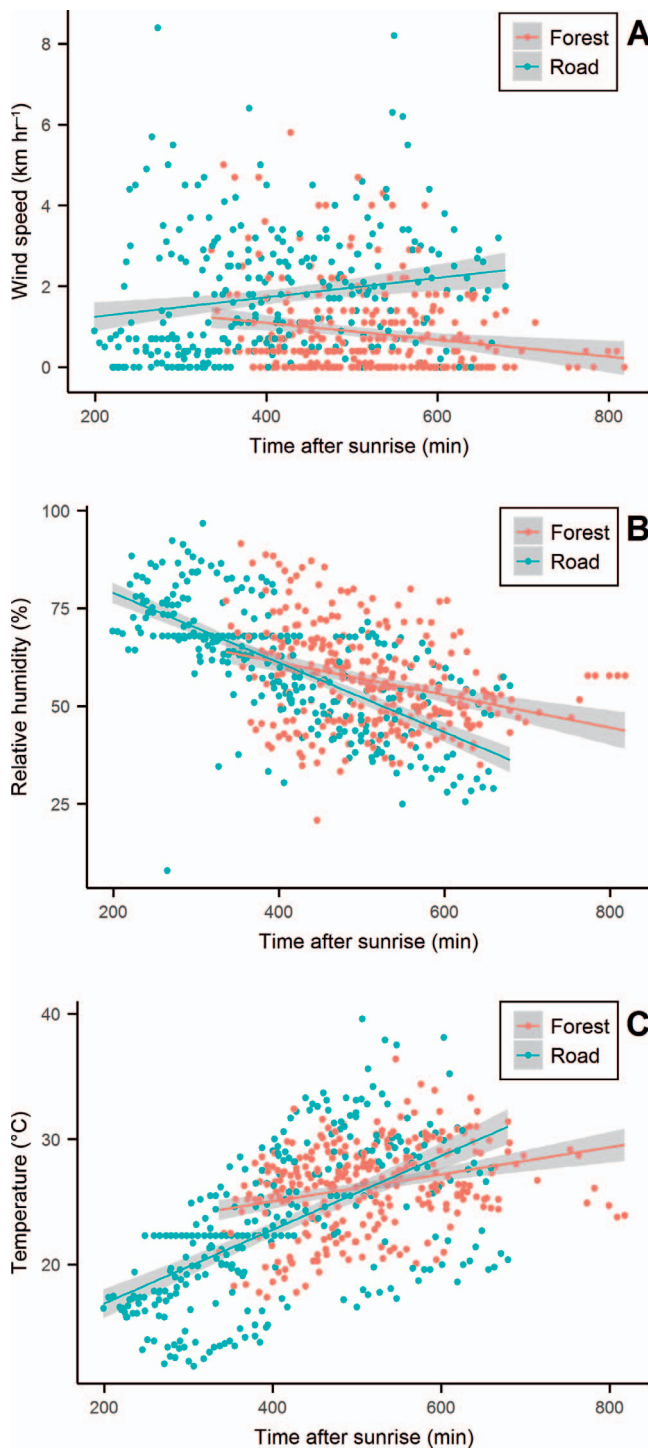


FIGURE 4. Regression lines (with 95% confidence intervals) for (A) wind speed, (B) relative humidity, and (C) temperature over time along forest and road transects near Calling Lake, Alberta, Canada, July 22–August 24, 2014. Time indicates elapsed time in minutes since average sunrise for the sample period.

Figure 4). We did not find strong support for a transect effect on temperature (forest: $26.3 \pm 3.4^{\circ}\text{C}$, road: $23.1 \pm 6.0^{\circ}\text{C}$) but observed a positive relationship with time of day (Figure 4).

We compared Monte Carlo 90% confidence intervals to investigate differences between each combination of transect and forest type. Probability of detection was higher on road compared to interior forest for every combination of forest type for almost all species (Figure 5). Similarly, we found detection to be higher for roads compared to interior forest, with the exception of the comparison between deciduous forest edge and deciduous interior forest. Comparisons for 9 species showed higher detectability on roads of both forest types vs. deciduous forest edges (BEKI, DEJU, LISP, OSFL, PISI, RBGR, TEWA, WAVI, and YERA). Five species differed between deciduous and coniferous forest edges (BEKI, DEJU, LISP, PISI, and RBGR; [Supplemental Material Table S10](#)). We found no differences between road transects or interior forest transects of different forest types, aside from some of the pure tones. Owls (NSWO, BOOW, GGOW, LEOW, and BADO) and lower-frequency pure tones (1,000, 1,414, 2,000, and 2,828 Hz) did not differ between any combination of transect or forest type. The AUC values for test data were >0.90 for most species ([Supplemental Material Table S4](#)). The lowest-frequency tones (1,000, 1,414, and 2,000 Hz) and the 4 owl species (BADO, GGOW, LEOW, and NSWO) had $0.90 > \text{ROC} > 0.80$. A single tone (2,000 Hz) had $0.80 > \text{ROC} > 0.70$ ($\text{AUC} = 0.7993$).

Estimating Effective Detection Radius, Effective Survey Area, and Corrections for Roads, Forest Edges, and Forests

We combined roads and interior forests of different forest types into single categories because we found no difference between forest types for both categories. Although we found differences with 5 species when comparing forest edge transects of different forest types, we collapsed them into a single category as well, to simplify effective area estimation, increase robustness of EDR estimates, and provide corrections for the “broadest” group possible to make it more applicable to researchers who wish to use our data. We then estimated EDR and effective survey area for the 3 transect types and calculated correction factors for comparing detections from different transects ([Supplemental Material Table S9](#)). A correction factor of 1 indicates that the transmission of vocalizations is not influenced by transect and that the same effective area is surveyed regardless of whether a point count is done at a roadside or in the forest interior. Deviations from 1 indicate increasing difference between transects. Calculated correction factors varied, depending on how strongly transmission of bird calls was influenced by being in the

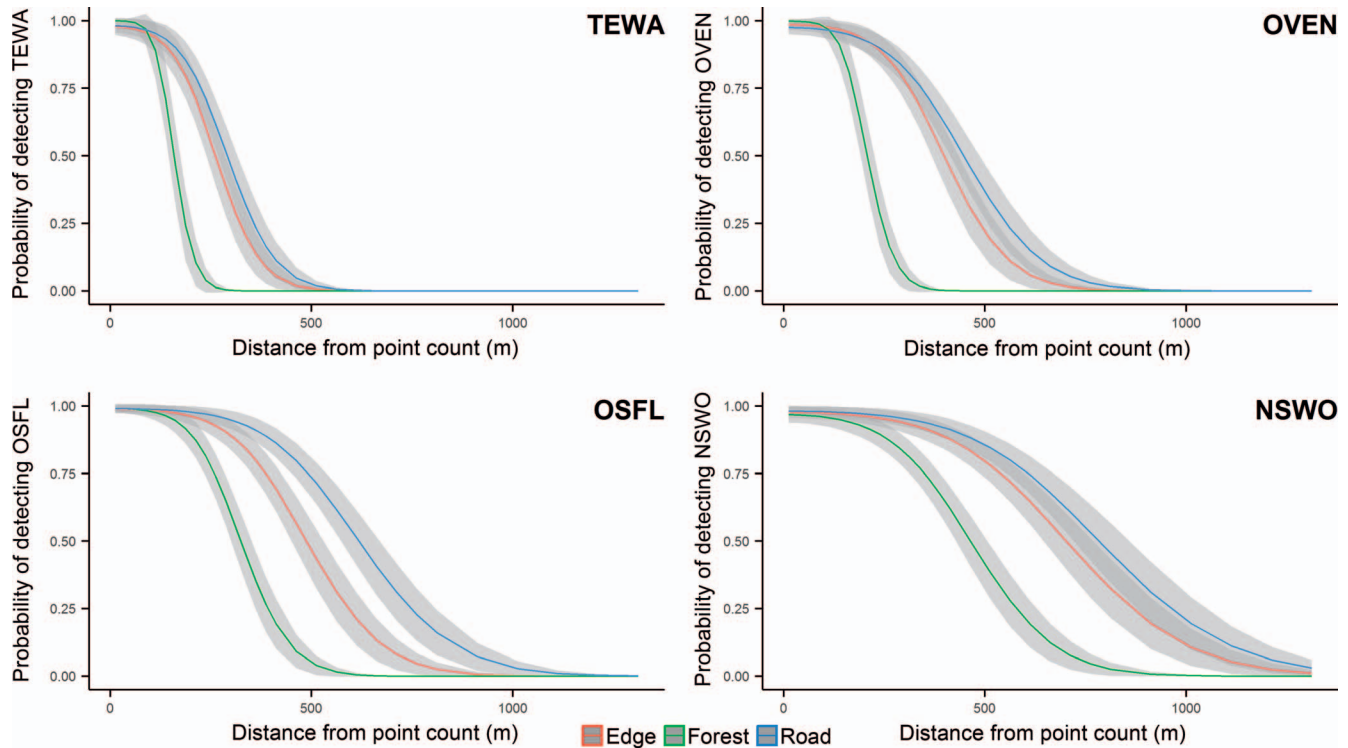


FIGURE 5. Probability of detecting Tennessee Warbler (TEWA), Ovenbird (OVEN), Olive-sided Flycatcher (OSFL), and Northern Sawwhet Owl (NSWO) with distance and transect type for the study area near Calling Lake, Alberta, Canada. Predictions are calculated from binomial detection data and plotted with 95% confidence intervals.

forest interior in comparison to road and forest edge. High-frequency songbirds generally had smaller EDR values than lower-frequency species like owls, and higher-frequency sounds had greater difference in EDR between the forest and road, indicating high attenuation along forest transects (Figure 3). Pure tones had some of the largest EDR values, but the correction varied by frequency. Correction factors for road–forest comparisons were the largest, followed by forest edge–forest and road–forest edge in descending order.

DISCUSSION

Sound attenuation in forests often differs from that in open environments because of differences in microclimate, vegetation density, and forest structure, which can cause variable scattering and absorption of sound waves (Wiener and Keast 1959, Richards and Wiley 1980). We compared sound attenuation and detection distances in roadside and forest transects. Attenuation of pure tones increased (1) at a greater rate in forests than on roads or forest edges and (2) as frequency increased, which suggests that scattering or absorption by vegetation plays an important role in sound transmission. This trend in frequency is supported by past findings that higher frequencies attenuate faster for this reason (Piercy et al. 1977). Similarly, excess attenua-

tion was higher in forests than along roads, though we found no clear pattern in frequency. Sound attenuated less than expected from the inverse distance law when transmitted along roads at distances close to the source, possibly because the road's surface and corridor reflect sound, resulting in less attenuation (Bullen and Fricke 1976).

Detection was mainly influenced by distance and transect type. The magnitude of this effect was much larger for forest interior transects than for forest edge or road transects, and most sounds had greater detection distances on roads than in forests. Monte Carlo analysis in all owl species and the 4 lowest-frequency tones did not show a significant effect of transect type ([Supplemental Material Table S10](#)), but during AIC model selection all species and sounds included transect as an important parameter. This suggests that the overlapping confidence intervals found during Monte Carlo simulation result from a large degree of uncertainty and variance in detection for those species and sounds, instead of small differences in point predictions. We also found these low-frequency species to have the lowest AUC values during model validation. All sounds with $AUC < 0.90$ also had overlapping confidence intervals for all transects during Monte Carlo simulations. Due to the nature of our study design, sounds with larger detection distances had more

detections and fewer nondetections, which increases uncertainty in slope estimation for our models. We suggest that lower-frequency sounds are more prone to variability in detection and statistical uncertainty, resulting in larger confidence intervals and decreasing model fit during validation.

We found that higher-frequency sounds had lower detection probability and detection distance when calculating EDR (Figure 3). When ranking species and tones in descending order of correction value required us to standardize counts, we found that passerines and high-frequency tones required larger corrections than owls and lower-frequency tones. This suggests that low-frequency sounds are less prone to attenuation in forests, which is in line with previous literature (Fricke 1984). Detection probability of high-frequency sounds declined faster, but EDR for some of these species was over twice the distance on road compared to forest (Supplemental Material Table S9). We propose that when surveying songbirds, the effective area sampled is almost always larger when sampling from a road, resulting in inflated counts of species when surveys are done from roads, compared to the actual abundance in the forest interior. For the 8,000 Hz tone, we found observer to be an important parameter, a result we attribute to human hearing ability, given that this frequency approaches the upper threshold of the human hearing range. Some observers were able to identify these tones while others were unable to detect them consistently, regardless of distance. Observer hearing ability can be influenced by a variety of factors such as age or sex (Pearson et al. 1995, Helzner et al. 2005). Our observers consisted of a combination of men and women between the ages of 18 and 25, in order to reduce any observer-related hearing differences. Furthermore, the randomized nature of our study design means that observer bias toward any specific transect or distance should not be an issue.

We found mixed results for differences in attenuation between road and forest edge. Four tones (1,414, 2,000, 2,828, and 8,000 Hz) had no difference in relative attenuation between the 2 transect types, whereas the road transect for 3 tones (1,000, 4,000, and 5,656 Hz) had slightly higher attenuation than the forest edge. This contrasts with the patterns we see in our EDR estimates. We speculate that this resulted from our broadcasts at shorter distances having to travel slightly longer to the road ARU than to the edge ARU, due to how we set up the study design (Figure 1). This can influence our reference values and our measures of relative SPL. At greater distances, this difference decreases and becomes less important as it becomes less than the error of the GPS units we used to measure distance. Ultimately, this should not affect our estimates of EDR because they were based on binary detection data and all sounds were detected at smaller distances.

The 4,000 Hz tone and some species with a minimum frequency of $\sim 4,000$ Hz (WTSP, WAVI, and PISI) had higher-than-normal EDRs for what our models predicted. We have 2 possible explanations for this. First, the frequency sensitivity of the human ear peaks at $\sim 4,000$ Hz, which means that human observers should be able to better detect these frequencies. Second, the frequency response of our playback speaker was slightly higher when measuring SPL for the 4,000 Hz tone. We consider the pattern seen for observer detection of sounds at $\sim 4,000$ Hz to have resulted from a combination of these 2 factors. However, because we use the relative difference for EDR between roadside and off-road transects, this does not influence the calculation of correction factors.

Our models for lower-frequency species generally include weather parameters in the top model for predicting detectability. We found that models for 15 species included weather variables; only 3 of these species were high-frequency passerines (BAWW, OVEN, and CCSP). The rest, including CORA, RBNU, and all owl species (and pure tones from 2,000 to 2,828 Hz) are generally lower frequency and have higher EDRs. However, our pure-tone attenuation models did not include any weather variables with the exception of 8,000 Hz. We propose 2 possible explanations for this observation. First, wind and associated abiotic noise from vegetation usually occupy lower-frequency bands and could influence detection by masking signals more than high-frequency sounds. This affects an observer's ability to identify a sound but does not decrease SPL. Second, the larger EDR estimates associated with many of these species and sounds mean that there is greater distance between signal and receiver over which weather can influence sound transmission.

Local atmospheric conditions also influenced detection probability, although this effect was much weaker than distance or transect type. Patterns seen in the effect of wind on detection probability suggest that a decrease in detection probability is influenced primarily by the interaction of wind and vegetation. We found no negative effect of wind when playback was done on roads, but a significant effect on forest edges where vegetation was present for species models containing weather. This suggests that increasing wind causes vegetation noise that reduces detection probability at the lower-frequency range, due to signal overlap with sounds like rustling vegetation. Detection modeling associated wind with an increased detection probability for 4 species (BAWW, CCSP, OVEN, and BHCO). We can think of no logical reason for this result, and it may have resulted from some error in our measurements of wind speed. We did not find any effect of wind in the interior forest, but the overall level of wind was lower than on the road or forest edge. However, we measured wind speed at ground level, which is not necessarily representative of wind speed at canopy height,

where birds may call from. Future studies should consider measuring wind using the Beaufort scale, which is related to canopy wind speed and is used during point counts to account for wind-related noise. Our study design also minimizes effects of wind by deliberately sampling during periods of low wind velocity. Therefore, our study may not be informative regarding the effect of wind. Relative humidity had a negative relationship with detection probability but, given that we found strong correlation with temperature, further studies are needed to separate the importance of each of these variables.

Our conclusion about how to correct EDR between road-based and forest surveys assumes that playback experiments adequately represent how real bird sounds propagate through forests and along roads, and how observers detect them. Our choice of recordings, broadcast and recording equipment, and volume settings don't necessarily reflect the conditions of a standard BBS point count, although 90 dB is within the range of what is considered natural amplitude in many species (Brumm 2004, Patricelli et al. 2007). However, several of our EDR values are many times higher than published EDRs for real birds such as those from the Boreal Avian Modelling Project (BAM; <http://www.borealbirds.ca>), which suggests that our broadcasts could be much louder than the singing volume of some species. The relationship between height from which a signal is broadcast and height at which it is received is known to influence sound attenuation (Padgham 2004, Brumm and Naguib 2009). However, we always broadcast sounds from the same height for roads (from the forest edge), forest edges, and interior forest. Improved roads with pavement or gravel are often elevated above the surrounding landscape, which means that the observer may be elevated as well for roadside surveys, possibly increasing detection distance even further. We strongly emphasize the importance of using our EDR measurements as a relative comparison between treatments. The value in these results lies not with the raw EDR measures, which may be unrealistically high (i.e. we estimate Ovenbird EDR to be 204 m, compared to published data suggesting an EDR of 84 m; Cumming et al. 2010). However, the correction factors that are calculated from our approach represent percentages that will remain the same regardless of the actual EDR. We presented correction factors based on 2 different shapes, a simple ellipse and a shape that factors the angle of detection to the road and the proportion of the signal that travels through the road compared to the forest. We believe the ellipse to be at the upper bound of the effective area surveyed and the other shape to be at the lower end. Realistically, detection area and correction values are likely somewhere between these 2 values because the road corridor may act to propagate sound (i.e. less attenuation

than expected at close distances), which suggests that while sound traveling directly through the forest may attenuate at a given rate, we can't discount a proximity effect of the road. Instead, we believe that some sort of gradient effect is more realistic as sound travels spherically from the source and could still be carried by the road corridor. Sound attenuation through the road-forest interface is complicated and not fully understood, and our models are our best approximation of the processes that occurred.

The narrow gravel or dirt roads that we studied may also have differed from some of the wider roads on which many BBS routes are located. Narrow roads likely have less influence on sound attenuation than wider roads because the total volume of the hemisphere around the sound source is lower. In addition, more improved roads tend to have wider ditch widths that are often maintained by haying or mowing activities. The low-use forestry roads that we studied generally had sharp shoulders and narrow ditches that terminated sharply at the forest edge. Furthermore, our classification of deciduous and conifer forests along roadways may not be as accurate within interior forests, given that some form of early-stage vegetation was usually present on forest edges, generally fast-growing aspen that were quite dense. Finally, our comparison of EDR between roads and interior forest may represent a more extreme outcome than is realistic. During roadside point counts, most bird detections are from within the forest itself, and the distribution of vocalizing individuals within the area of detection may not be homogeneous. Thus, while some birds will call from at or near the forest edge and be detected at greater distances, most birds will vocalize from within the forest interior.

Nevertheless, our results demonstrate that differential transmission along open road corridors may significantly alter observer bird counts, a situation particularly relevant when comparing roadside data such as the BBS to off-road surveys. Detection radius of birds in a homogeneous forest habitat is assumed to be circular. With roadside surveys, this detection radius becomes elliptical. Our results suggest that, for some species, area surveyed can more than double when surveying from a road rather than within the interior forest. This yields avian estimates that can be twice as large if we assume that the area surveyed is constant between those 2 environments. Having this type of information is fundamental for interpreting results from any type of avian point count, given that different species can be detected at different maximum distances in different environments (Schieck 1997). When making relative comparisons of bird counts between environmental factors (i.e. on-road vs. off-road, different forest types, etc.), we suggest using statistical methods, such as distance sampling, to correct for inequalities in detectability

(Marques et al. 2010). However, roads present a directionally dependent effect on sound attenuation that cannot be solved using conventional distance sampling. Our results allow us to quantify this pattern to estimate the effect on survey area and help address this challenge with first approximations. As we strive to understand how avian populations are changing across landscapes, it is important to ensure that we do not make incorrect assessments because we have failed to meet the underlying assumptions of our survey methods.

ACKNOWLEDGMENTS

The hard work of L. McLeod, C. Hardie, N. Annich, E. Beck, and R. Kong in the field is greatly appreciated. The ideas and insights of the technical committee and research team from the Boreal Avian Modelling project (<http://www.borealbirds.ca>) were invaluable. We particularly thank J. Ng, J. Schieck, S. Song, D. Stralberg, and S. Matsuoka, who provided an important sounding board for many stages of the project.

Funding statement: We acknowledge the financial support of the Alberta Biodiversity Monitoring Institute, Alberta Conservation Association, Northern Scientific Training Program, Canadian Circumpolar Institute, Oilsands Monitoring Program, and the Ecological Monitoring Committee for the Lower Athabasca. D.A.Y. was supported by an Industrial Postgraduate Scholarship from the Natural Sciences and Engineering Research Council of Canada and Suncor Energy. None of the funders had any input into the manuscript, and approval was not required prior to submission or publication.

Ethics statement: This study complies with all ethics and permitting requirements associated with the University of Alberta and the Province of Alberta, Canada (permit no. GP-54843).

Author contributions: D.A.Y., E.M.B., J.C., and D.P. conceived the idea, design, and experiment. D.A.Y. performed the experiments. D.A.Y., E.M.B., J.C., and D.P. wrote or substantially edited the paper. D.A.Y., E.M.B., P.S., J.C., and D.P. developed or designed the methods. D.A.Y. and P.S. analyzed the data.

LITERATURE CITED

- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- Aylor, D. (1972). Noise reduction by vegetation and ground. *The Journal of the Acoustical Society of America* 51:197.
- Bart, J., M. Hofschien, and B. G. Peterjohn (1995). Reliability of the Breeding Bird Survey: Effects of restricting surveys to roads. *The Auk* 112:758–761.
- Bartoń, K. (2015). MuMIn: Multi-model inference. R package 1.15.1. <http://CRAN.R-project.org/package=MumIn>
- Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Berg, R. E., and D. G. Stork (2004). *The Physics of Sound*, third edition. Addison-Wesley, Boston, MA, USA.
- Boersma, P., and D. Weenink (2015). *Praat: Doing Phonetics by Computer*. University of Amsterdam, Amsterdam, The Netherlands. <http://www.fon.hum.uva.nl/praat/>
- Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology* 73: 434–440.
- Brumm, H., and M. Naguib (2009). Environmental acoustics and the evolution of bird song. *Advances in the Study of Behavior* 40:1–33.
- Bullen, R., and F. Fricke (1976). Sound propagation in a street. *Journal of Sound and Vibration* 46:33–42.
- Burnham, K. P., and D. R. Anderson (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second edition. Springer-Verlag, New York, NY, USA.
- Charif, R. A., A. M. Waack, and L. M. Strickman (2010). *Raven Pro 1.4 User's Manual*. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Cumming, S. G., K. L. Lefevre, E. Bayne, T. Fontaine, F. K. A. Schmiegelow, and S. J. Song (2010). Toward conservation of Canada's boreal forest avifauna: Design and application of ecological models at continental extents. *Avian Conservation and Ecology* 5:8.
- Droege, S. (1990). The North American Breeding Bird Survey. In *Survey Designs and Statistical Methods for the Estimation of Avian Population Trends* (J. R. Sauer and S. Droege, Editors). Biological Report 90(1). U.S. Fish and Wildlife Service, Washington, DC, USA. pp. 1–4.
- Fricke, F. (1984). Sound attenuation in forests. *Journal of Sound and Vibration* 92:149–158.
- Harris, C. M. (1966). Absorption of sound in air versus humidity and temperature. *Journal of the Acoustical Society of America* 40:148–159.
- Helzner, E. P., J. A. Cauley, S. R. Pratt, S. R. Wisniewski, J. M. Zmuda, E. O. Talbott, N. de Rekeneire, T. B. Harris, S. M. Rubin, E. M. Simonsick, F. A. Tyllavsky, and A. B. Newman (2005). Race and sex differences in age-related hearing loss: The Health, Aging and Body Composition Study. *Journal of the American Geriatrics Society* 53:2119–2127.
- Keller, C. M. E., and J. T. Scallan (1999). Potential roadside biases due to habitat changes along Breeding Bird Survey routes. *The Condor* 101:50–57.
- Koloff, J., and D. J. Mennill (2013). The responses of duetting antbirds to stereo duet playback provide support for the joint territory defence hypothesis. *Ethology* 119:462–471.
- Lawler, J. J., and R. J. O'Connor (2004). How well do consistently monitored Breeding Bird Survey routes represent the environments of the conterminous United States? *The Condor* 106:801–814.
- Marques, T. A., S. T. Buckland, D. L. Borchers, D. Tosh, and R. A. McDonald (2010). Point transect sampling along linear features. *Biometrics* 66:1247–1255.
- Maynard, D. F., K.-A. A. Ward, S. M. Doucet, and D. J. Mennill (2012). Calling in an acoustically competitive environment: Duetting male Long-tailed Manakins avoid overlapping neighbours but not playback-simulated rivals. *Animal Behaviour* 84:563–573.
- Morton, E. S. (1975). Ecological sources of selection on avian sounds. *The American Naturalist* 109:17–34.

- Nakagawa, S., and H. Schielzeth (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Padgham, M. (2004). Reverberation and frequency attenuation in forests—implications for communication in animals. *The Journal of the Acoustical Society of America* 115:402–410.
- Parris, K. M., and A. Schneider (2008). Impacts of traffic noise and traffic volume on birds of roadside habitats. *Ecology and Society* 14:29.
- Patricelli, G. L., M. S. Dantzker, and J. W. Bradbury (2007). Differences in acoustic directionality among vocalizations of the male Red-winged Blackbird (*Agelaius phoeniceus*) are related to function in communication. *Behavioral Ecology and Sociobiology* 61:1099–1110.
- Pearson, J. D., C. H. Morrell, S. Gordon-Salant, L. J. Brant, E. J. Metter, L. L. Klein, and J. L. Fozard (1995). Gender differences in a longitudinal study of age-associated hearing loss. *The Journal of the Acoustical Society of America* 97:1196–1205.
- Piercy, J. E., T. F. W. Embleton, and L. C. Sutherland (1977). Review of noise propagation in the atmosphere. *The Journal of the Acoustical Society of America* 61:1403–1418.
- R Development Core Team (2015). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Richards, D. G., and R. H. Wiley (1980). Reverberations and amplitude fluctuations in the propagation of sound in a forest: Implications for animal communication. *The American Naturalist* 115:381–399.
- Robin, X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, J.-C. Sanchez, and M. Müller (2011). pROC: An open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics* 12:77.
- Sandoval, L., T. Dabelsteen, and D. J. Mennill (2015). Transmission characteristics of solo songs and duets in a Neotropical thicket habitat specialist bird. *Bioacoustics* 24:289–306.
- Schieck, J. (1997). Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. *The Condor* 99:179–190.
- Sólymos, P., S. M. Matsuoka, E. M. Bayne, S. R. Lele, P. Fontaine, S. G. Cumming, D. Stralberg, F. K. A. Schmiegelow, and S. J. Song (2013). Calibrating indices of avian density from non-standardized survey data: Making the most of a messy situation. *Methods in Ecology and Evolution* 4:1047–1058.
- Trombulak, S. C., and C. A. Frissell (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- U.S. Geological Survey (2009). North American Breeding Bird Survey bibliography. <https://www.pwrc.usgs.gov/bbs/about/bbsbib.pdf>
- Wiener, F. M., and D. N. Keast (1959). Experimental study of the propagation of sound over ground. *The Journal of the Acoustical Society of America* 31:724–733.
- Wiley, R. H., and D. G. Richards (1982). Adaptations for acoustic communication in birds: Sound transmission and signal detection. In *Acoustic Communication in Birds* (D. E. Kroodsma, E. H. Miller, and H. Ouellet, Editors). Academic Press, Waltham, MA, USA. pp. 131–181.
- Yang, H.-S., J. Kang, and C. Cheal (2013). Random-incidence absorption and scattering coefficients of vegetation. *Acta Acustica united with Acustica* 99:379–388.