



Ambient noise decreases detectability of songbird vocalizations in passive acoustic recordings in a consistent pattern across species, frequency, and analysis method

Chad A. Apol, Ethan C. Valentine & Darren S. Proppe

To cite this article: Chad A. Apol, Ethan C. Valentine & Darren S. Proppe (2020) Ambient noise decreases detectability of songbird vocalizations in passive acoustic recordings in a consistent pattern across species, frequency, and analysis method, *Bioacoustics*, 29:3, 322-336, DOI: [10.1080/09524622.2019.1605310](https://doi.org/10.1080/09524622.2019.1605310)

To link to this article: <https://doi.org/10.1080/09524622.2019.1605310>



Published online: 19 Apr 2019.



Submit your article to this journal [↗](#)



Article views: 86



View related articles [↗](#)



View Crossmark data [↗](#)



Citing articles: 1 View citing articles [↗](#)



Ambient noise decreases detectability of songbird vocalizations in passive acoustic recordings in a consistent pattern across species, frequency, and analysis method

Chad A. Apol^a, Ethan C. Valentine^a and Darren S. Proppe^{id a,b}

^aBiology Department, Calvin College, Grand Rapids, MI, USA; ^bAu Sable Institute, Mancelona, MI, USA

ABSTRACT

The presence of ambient noise is a potential constraint that can impact studies that rely on passive acoustic recording units to compare biotic signals across a range of ambient noise levels. To investigate the hypothesis that ambient noise will impact the detectability of recorded acoustic signals, we projected noise with different amplitudes and frequency distributions into one microphone on a passive acoustic recording unit, while recording simultaneously from a second unit free of noise stimuli. We compared detection rates for five frequently recorded bird species derived from three different analysis methods. As predicted, amplitude had a strongly negative impact on detectability. There were also absolute differences in detection rates between species and the analysis methods, but the pattern of change as amplitude increased did not differ across treatments. The frequency distribution of the noise stimuli had no impact on detectability. Based on the consistent impact of amplitude on signal detection, we formulated a single correction factor to estimate the proportion of detections being lost to background ambient noise. While this formula will benefit from additional testing across an array of species and conditions, it is clear that ambient noise alters detection rates in passive acoustic recordings.

ARTICLE HISTORY

Received 16 December 2018

Accepted 2 April 2019

KEYWORDS

Automated; spectrogram; anthropogenic; amplitude; detectability

Introduction

Acoustic signals are integral to the communication systems of many terrestrial and aquatic organisms (Bradbury and Vehrencamp 2011). In terrestrial systems, many mammals, insects, frogs, and birds rely on acoustic signals for mate selection, territory and predator defence, alarm, announcement of food, and even declaration of individual identity (Zelick et al. 1999; Gerhardt and Huber 2002; Altringham and Fenton 2003; Catchpole and Slater 2008). Acoustic signals are also integral to many fields of animal research where signal detection provides crucial data. One effective way of collecting acoustic data is through the use of passive acoustic recording units. For example, acoustic recordings obtained from microphones located on passive acoustic recorders have been used to compare biodiversity across habitats (e.g., Gasc et al. 2013) and to determine species richness in several taxa (Brandes et al. 2006; Wimmer et al. 2013;

Froidevaux et al. 2014). Surveys of animal communities have been conducted with both single-channel units and multi-channel microphone arrays (Alquezar and Machado 2015; Haselmayer and Quinn 2000; Celis-Murillo et al. 2009). Passive acoustic recording units can also be placed in remote areas that would be otherwise difficult to monitor. Fitzpatrick et al. (2005) used single-channel units to monitor over 40,000 ha of bottomland forest in Florida and Arkansas for acoustic evidence of the ivory-billed woodpecker. Passive acoustic recording units have also been used to study signal evolution (Apol et al. 2018), community signalling patterns (Hart et al. 2015), and signal information (Elie and Theunissen 2016). One crucial aspect, common to all bioacoustic research, is the necessity to detect biotic signals in the environment.

One environmental constraint that may limit the collection of accurate bioacoustic data is the presence of background ambient noise. Ambient noise can acoustically mask biotic signals and thus impair signal detection. For example, higher amplitudes of ambient noise decrease the signal-to-noise ratio of a vocalization (Klump 1996) and can reduce the distance over which a receiver can detect a signal (Lohr et al. 2003). In humans, the detection radius for avian point-counts is effectively reduced as ambient noise levels increase (Pacifici et al. 2008). Further, the impact of otherwise pertinent signals on the receiver is reduced as noise increases in many animal systems (e.g., Siemers and Schaub 2010; Leonard and Horn 2012). While vigilance and stress may also play a role in these altered behavioural responses, acoustic masking is a likely a predominant mechanism (Barber et al. 2010).

Both amplitude and frequency of an acoustic signal are related to the level of acoustic masking incurred. To reduce the effects of acoustic masking, some avian species will increase the amplitude of their acoustic signals when environmental noise levels are high (Manabe et al. 1998; Brumm 2004). Studies in birds have also shown that masking is most pronounced when the frequencies of ambient noise and vocal signals overlap (Goodwin and Podos 2013). For example, species with higher frequency songs are less impacted by low-frequency sounds (Francis et al. 2011; Proppe et al. 2013). Shifting to higher frequencies is another putative mechanism for reducing the impact of acoustic masking from low-frequency anthropogenic sources (Slabbekoorn and Peet 2003; Fernández-Juricic et al. 2005; Wood and Yezerinac 2006), although the ecological benefits of frequency-shifting are somewhat debated (Nemeth and Brumm 2010; Zollinger et al. 2017). Parris and McCarthy (2013) demonstrated that shifting an acoustic signal to higher frequencies in the presence of low-frequency urban noise can increase active space. Thus, it is reasonable to predict that the distribution of spectral power (i.e., amount of signal power (dB) at different frequencies (Hz)) of ambient noise could affect the level of acoustic masking on biotic signals (Wiley and Richards 1978). Further, particular vocalizations and species may be impacted by noise differently due to the frequency distribution of their signals.

Brown, pink, and white noise are mathematically derived noise types that differ in their spectral power densities in ways that can be used to simulate different sources of real-world ambient noise (Figure 1). The power density of white noise is equal across all frequencies, the power density of pink noise is inversely proportional to the frequency, and the power density of brown noise is inversely proportional to the square of the frequency. In other words, white noise has equal power across all frequencies, whereas

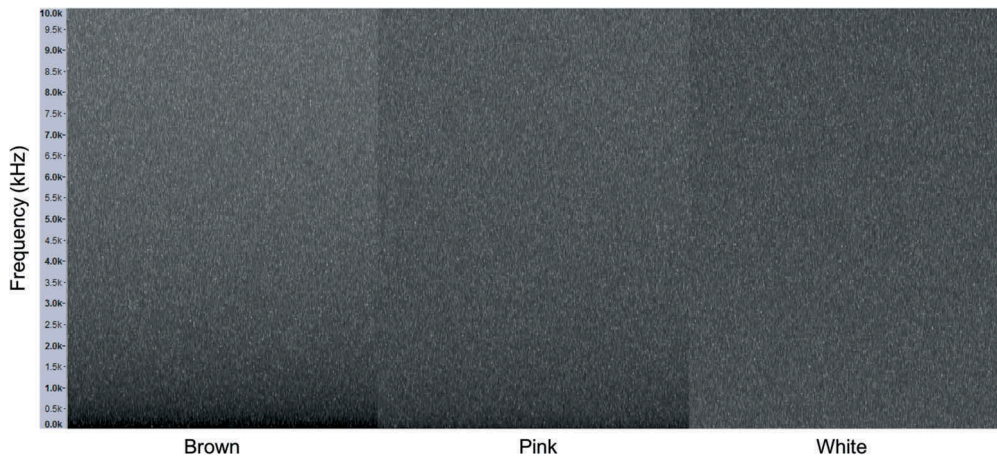


Figure 1. Spectrogram displaying the spectral power distribution of the three different noise types (Brown, Pink, White) utilized in our field recordings at an amplitude of 70 dB.

the power of pink and brown noise decreases with increasing frequency, being most strongly skewed in brown noise. White noise has been used to simulate the sound of high winds because wind impacts a broad range of frequencies (Turgeon et al. 2017). Pink noise has been used to simulate the generally low-frequency distribution of sound in anthropogenic noise (Potvin et al. 2016) and brown noise has been used to simulate sounds heavily skewed towards low-frequencies, such as waterfalls and thunder (Pacifiçi et al. 2008). Because animal signals are produced at particular frequencies (Catchpole and Slater 2008), these three types of synthetic noise could impact detectability differently among, and even within, species.

The presence of ambient noise potentially confounds research that relies on passive acoustic recordings units to compare biotic signals across a range of ambient noise levels. However, the impact of ambient noise level and the differential effects of noise type on signal detectability in passive acoustic recording units is poorly understood. We hypothesized that the amplitude and frequency distribution of ambient noise would impact signal detection rate, and that it may impact particular species differentially based on the frequency spectra of their species-specific vocalizations. We tested the effects of increasing amplitude in the three aforementioned noise types on signal detectability in five bird species. To test this, we recorded bird song simultaneously on two passive acoustic recording units placed adjacent to each other in multiple field locations, and projected different noise types at different amplitudes into one microphone of a multi-channel recording unit while leaving the other unit free of noise stimuli. Further, because there may be differences in detectability between humans and machine-based algorithms (Swiston and Mennill 2009), we compared rates of signal detection across treatments from 1) a trained observer who detected vocalizations aurally (auditory hereafter), 2) a trained observer who visually inspected spectrograms and detected vocalizations aurally (spectrogram hereafter), and 3) a machine-based automated algorithm. We predicted that increasing the amplitude of ambient noise would impact detectability regardless of noise type, but that white noise would have the largest masking effect because it has a constant power density across all frequencies,

thus equally masking all biotic signals. We predicted that the highest number of detections would result from spectrogram analysis because of the multi-sensory information available to the observer. Finally, if noise impacts on detection rates were relatively consistent across noise types and species, we aimed to develop a correction factor to account for noise-associated changes in detectability in passive acoustic recording units.

Materials and methods

Site selection and setup

We recorded the avian community in 20 remote northern hardwood forest sites in Kalkaska County, Michigan, which were dominated by American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) trees. To reduce the potential confound of elevated anthropogenic noise, all recording sites were isolated from human development, and >200 m away from any forest road or trail. We analysed vocalizations from the five avian species recorded most frequently in our beech-maple hardwood forests: blue jays (BLJA; *Cyanocitta cristata*), ovenbirds (OVEN; *Seiurus aurocapilla*), red-eyed vireos (REVI; *Vireo olivaceus*), black-throated green warblers (BTNW; *Setophaga virens*) and eastern wood-pewees (EAWP; *Contopus virens*). Vocal frequencies produced by each species vary, but all fall within 2–10 kHz (Craig 1943; Cohen 1977; Borror 1981; Lein 1981; Morse and Poole 2005). We collected all acoustic data between sunrise and 1130 h to maximize the number of recorded vocalizations.

At each site, two passive acoustic recording units with dual omnidirectional microphones (Song Meter SM4; 44,100 Hz sampling rate, WAV, 16-bit format; Wildlife Acoustics 2017, firmware 1.2.2) were placed 2 m above the ground and attached to two trees separated by 2–3 m. The two recording units were oriented such that the microphones on each unit were parallel, thus recording nearly identical acoustic space. Different noise amplitudes and types of ambient noise were projected into one microphone of the experimental recording unit via a pair of headphones (Apple Earbud; MD827LLA-AP). Headphones were fastened directly to the surface of the microphone windshield and connected to a playback unit equipped with an external speaker and headphone jack (Sound Oasis Bluetooth Speaker; BST-100) that housed all noise tracks. To test whether the small spatial difference between unit location or the placement of headphones impacted detectability, the headphones were attached to the experimental microphone while recording the avian chorus prior to noise playback, and detections were compared to the adjacent control microphone with no headphones. All recordings occurred on mornings without precipitation or wind over two on the Beaufort scale.

Sound files and playback

All noise playback files were housed within a single 90-min wav file that consisted of 13 individual tracks: a 6 min 70 dBA test track used only to ensure that equipment was operational, and twelve, seven-minute tracks that represented brown (B), pink (P), and white (W) ambient noise played at 40, 50, 60, and 70 dBA. The track progressed from 40 to 70 dBA, such that higher amplitudes occurred at a later time of day in each

recording (i.e., B40, P40, W40, B50, P50, W50, B60, P60, W60, B70, P70, W70). All noise tracks were created in Audacity V2.1.2 (Function = Generate: Noise) and amplified or attenuated until target dBA levels were produced (measured initially via the Average Power (dB) function in Raven Pro V 1.5, Ithaca, NY). All decibel levels were measured using A-weighting because it is common in the literature and recognizable across acoustic sub-disciplines.

To ensure that all acoustic tracks produced full spectra sounds at the target intensities (± 2 dB), each track was first tested in a silent room by placing a sound level meter (Casella CEL-620.A2/K1) 1 m from the external speaker built into the playback unit and assessing the time-averaged decibel level over 30 s of continuous playback. Playback was simultaneously recorded with a digital recorder (Marantz PMD 670; 44,100 Hz sampling rate, gain 2.5/10, PCM, 16-bit format; New York, USA) and directional microphone (Sennheiser ME66; Wedemark, Germany), which was used to produce a spectrogram for amplitude measurement in Raven Pro V 1.5 (Average Power (dB)). Second, noise files were also played through headphones plugged into the playback unit, mimicking the setup to be used in the field. Sound levels and spectrograms were produced in a manner similar to the procedure described above, except that the headphones were placed in direct contact with the sound level meter and omnidirectional microphone. Amplitude readings from the sound level meter and spectrograms both indicated that decibel levels from the headphones were within ± 2 dB of the external speaker. Spectrogram measurements (in 1 kHz bins) indicated that sound was similarly distributed across the frequencies of interest (1–10 kHz). Headphones produced slightly less energy in the 0–1 kHz spectral range, but this is below the frequencies used by our target species.

To record ambient noise conditions in each field location, both passive acoustic recording units recorded in unison for 5 min prior to the addition of any noise stimulus. With both recorders off, the 70 dBA test track and our sound level meter were used to ensure that output amplitude levels were correct. The playback unit was then connected to the headphones, which were already in place on the microphone of the passive acoustic recorder. Playback and recording were both programmed to initiate 5 min after activation to allow researchers time to clear the area. Upon activation, both passive acoustic recorders continued to operate on a 5 min on, 2 min off routine for the duration of the experiment. The first noise playback (Brown 40 dB) began 1 min prior to the first 5-min recording. This ensured that every 7-min ambient noise track covered one full 5-min recording cycle of the passive acoustic recording units. The setup was undisturbed for the duration of the full noise playback file.

Acoustic analysis

Thirteen sound files were collected from the control and experimental microphones for each trial. The ambient noise level prior to noise playback at each site was calculated in Raven Pro by measuring the Average Power (dB, 1–13 kHz) in a 1-s sample free from biotic sounds during playback of 40 dB white noise and a corresponding 1-s measurement from the 5-min ambient recording. The amplitude difference (Δ dB) between the two files was then subtracted from 40 dB to derive the ambient noise level.

To facilitate machine-based classification, we pretrained the cluster analysis function in Kaleidoscope Pro to automatically detect vocalizations from our five-target species (Wildlife Acoustics 2017, version 4.3.2). Between 6 and 13 foreign acoustic recording files (downloaded from <https://www.xeno-canto.org> and <https://www.macaulylibrary.org>) of each of our five species and 205 local files containing all of our species were used to train the cluster analysis program. Each file was inspected visually, and correct vocalizations for each species were identified and saved. We used multiple vocalization types to train Kaleidoscope for each species, although chips and non-distinct calls were excluded. Compiled training results were added to the cluster analysis program so that pairwise classifiers could be created to automatically detect vocalizations from our five species in acoustic recordings. For each file, we visually evaluated detection results from the automated process and removed false detections since these do not represent accurate identification of the species of interest. The total number of correct detections from each file was used for statistical analysis. Cluster analysis was conducted on all acoustic files from all 20 field sites.

To facilitate blind spectrogram (visual) and auditory review of acoustic recordings, all sites were given a randomly generated number (1–20). Sites 1–10 were assigned for spectrogram analysis, and sites 11–20 were assigned for auditory analysis. Spectrogram analysis was conducted visually and audibly in Kaleidoscope Pro. A single observer detected every vocalization of our five-target species within each track. Sites 11–20 were analysed by listening to each recorded file on a continuous stream – much like a point-count where the vast majority of detections are aural (e.g., Bibby et al. 1992; Cooper and Blaha 2002). Every vocalization from a target species was recorded. Total detections were calculated for each species, and from each method in every file.

Statistics

All statistical analyses were conducted in R version 3.5.1. To test whether the slight spatial separation or placing headphones on the experimental recording unit altered detectability, we ran a paired *t*-test to determine whether mean detections differed between the experimental and control microphones without any noise stimulus ($\alpha = 0.05$). Zero-inflated negative binomial models (package *pscl*; Zeileis et al. 2008) were built to test the effects of treatment (control, noise), species (BLJA, REVI, OVEN, BTNW, EAWP), noise type (B, P, W), analysis (spectrogram, auditory, automated), and amplitude (ambient, 40, 50, 60, 70 dB) on detections. Our data set included a high number of zeros ($n = 3,491$). Zeros resulted from two separate phenomena; a) no detections made because a species was not present at a site (false zero), or b) no detections made because of the masking effects of the noise treatment (true zero). To account for this, we modelled our data using a zero-inflated negative binomial distribution (ZINB). A ZINB model is composed of a logistic regression component that models the probability of a false zero, and a component that models count data as a negative binomial distribution. While the results from both models are reported (Table 1), only the negative binomial model components are interpreted because our research question focuses on the count of detections rather than the probability of false zeros. Parameter estimates from our top ZINB model were exponentiated to represent odds ratios (e.g., Sheu et al. 2004).

Table 1. Zero-inflated negative binomial (NB) and logit model results.

Parameter	NB			Logit		
	Estimate	e^(Estimate)	z-value	Estimate	e^(Estimate)	z-value
Intercept	3.518	33.73	30.29 ***	-.4093	.6641	-2.079 *
Amplitude	-0.0075	.9926	-3.969 ***	0.0071	1.007	2.098 *
Treatment:Noise	0.9877	2.685	5.364 ***	-3.163	.0423	-11.26 ***
Species:BTNW	0.2736	1.315	3.333 ***	0.0653	1.068	0.630
Species:OVEN	-0.7543	.4704	-10.39 ***	-1.941	.1435	-14.17 ***
Species:REVI	1.794	6.011	26.17 ***	-2.193	.1116	-19.27 ***
Species:EAWP	0.1627	1.177	1.956	0.1548	1.167	1.483
Analysis:Spectrogram	1.123	3.075	21.20 ***	-0.1131	.8930	-1.174
Analysis:Auditory	.8050	2.237	15.62 ***	0.7322	2.080	8.589 ***
Amplitude*Treatment:Noise	-0.0293	.9711	-7.039 ***	0.0950	1.100	16.31 ***

*** = $p < .00001$

** = $p < .001$

* = $p < .01$

A hierarchical variable selection process was used for model development. We first fit the null (detection ~ 1) and amplitude only models (detection $\sim$ amplitude), retaining only the model with the lowest BIC for additional analysis. BIC was used for model selection because our sample size was large ($n = 6,000$) and AIC is prone to favour model complexity (Aho et al. 2014). Additional parameters (treatment, species, analysis, noise type) were then added iteratively, retaining the lowest BIC model. Finally, interaction terms between retained parameters were added, again selecting the model producing the lowest BIC. Predictions and confidence intervals from our top model were generated using emmeans (package emmeans; Lenth 2018). A correction factor was derived based upon the predicted proportion of detections lost due to noise (i.e., noise detection rate/control detection rate for each decibel from 30 to 70 dB). Results are presented as means $\pm$ 95% confidence intervals (CI).

Results

One 5-min recording of each noise condition, including no playback, was collected from each recorder and site for a total of 20 paired observations per treatment. Our paired t -test indicated that there was no significant difference in the mean detection rates between the control ($25.4 \pm 7.9/\text{track}$) and experimental microphones (25.1 ± 7.7 ; $t = 0.05$, $df = 398$, $p = 0.961$) when no noise stimuli was projected (average amplitude: 31.8 ± 0.3). Our final zero-inflated negative binomial model retained amplitude, treatment, species, analysis, and a single interaction term: amplitude*treatment. This model represented a $\Delta 3,745.61$ BIC improvement over the null model and was 28.63 BIC units lower than the next lowest model. Red-eyed vireos had the highest number of average detections (63.8 ± 4.7 , $n = 20$ sites), followed by black-throated green warblers (5.0 ± 0.6 , $n = 16$), blue jays (4.5 ± 0.7 , $n = 17$), Eastern wood-pewees (4.5 ± 0.6 , $n = 14$), and ovenbirds (4.4 ± 0.4 , $n = 20$; Figure 2). For analysis type, the spectrogram method had the highest number of average detections (31.3 ± 3.5), followed by the auditory (21.3 ± 2.4), and automated analysis (6.6 ± 0.6 ; Figure 3). It is important to note that while the trends between the spectrogram and auditory methods are reflected in our results, each method analysed different subsets of data and thus they are not directly comparable.

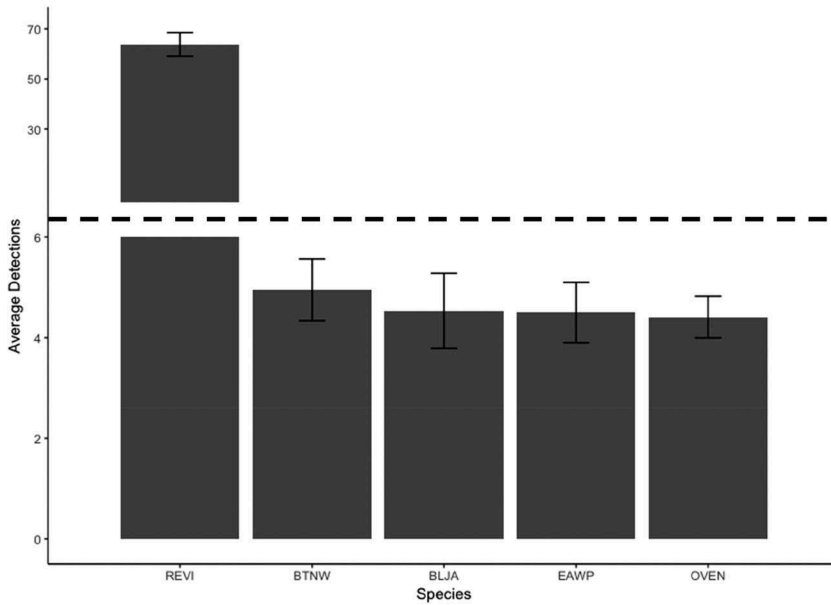


Figure 2. Average number of vocal detections per track for each of the five-target species. The horizontal broken line represents a gap added to the y axis to enhance side by side comparisons of species. Four letter codes stand for the red-eyed vireo (REVI), black-throated green warbler (BTNW), blue jay (BLJA), Eastern wood-pewee (EAWP), and ovenbird (OVEN). Error bars represent 95% confidence intervals.

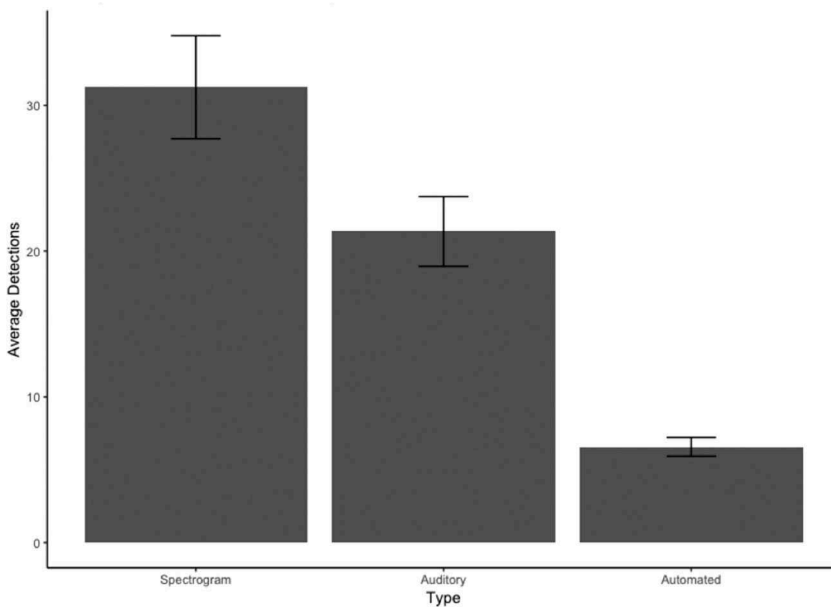


Figure 3. Average number of vocal detections per track by analysis type. Spectrogram analysis included visual and aural inspection of acoustic recordings, Auditory analysis involved only aural inspection, and Automated analysis was a result from a pre-trained cluster analysis conducted in Kaleidoscope Pro acoustic software. Error bars represent 95% confidence intervals.

Because the amplitude*treatment interaction was retained in our final model, amplitude and treatment alone become conditional effects, rather than main effects (Cleary and Kessler 1982). Our results indicate that when amplitude is 0, the number of detections in the noise treatment will be greater than in the control, by a factor of 2.7. But, because field recording conditions never occur at 0 dB of ambient noise, the conditional effect of the noise treatment is not a meaningful predictor (Aiken et al. 1991). The biologically relevant interaction term indicates that a one-decibel increase in amplitude decreases the number of detections in noise-impacted recordings by a factor of .971 relative to the control treatment (Table 1).

The predicted decreases in the number of vocal detections due to noise masking were 28% at 40 dB, 61% at 50 dB, 83% at 60 dB, and 94% at 70 dB (Figure 4). Since noise-related trends did not differ between species, noise type, or analysis method, we develop a single equation to adjust detection rates in noise-masked recordings. To do this, we divided the predicted noise-impacted detection rate by the predicted control detection rate for each decibel from 30 to 70 dB, the amplitude range covered by our experiment. Predicted proportion values were represented by the polynomial equation:

$$y = .0006x^2 - .0851x + 3.2056,$$

where x was the measured noise level (in dB), and y was the percent change in detection rate between the observed decibel level (x) and the amplitude at which no noise impact was observed. To calculate the amplitude at which noise had no impact on detectability,

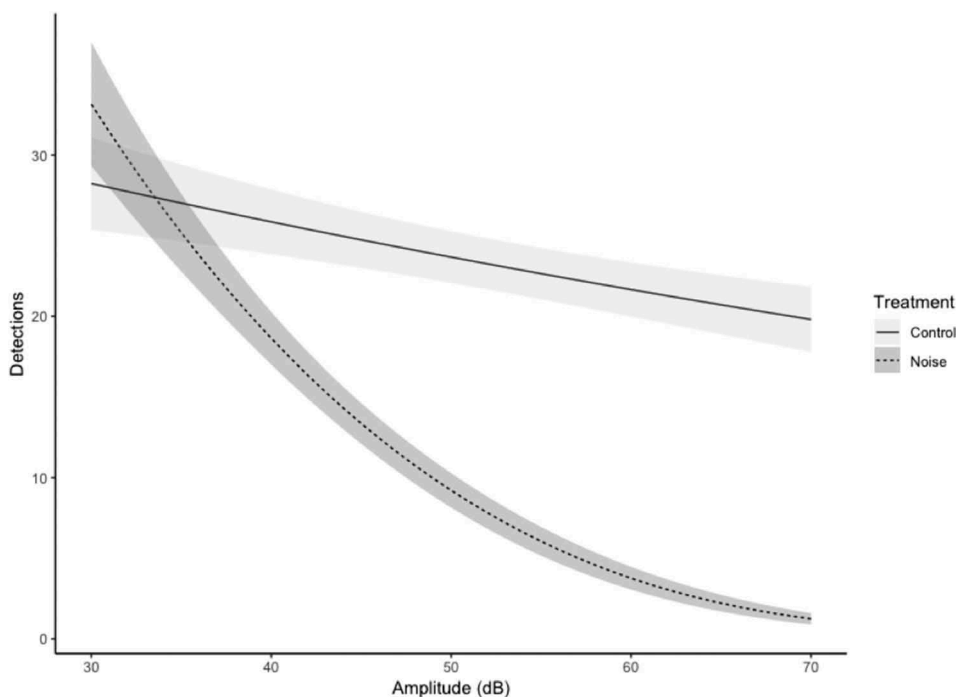


Figure 4. Predicted vocal detections by treatment (noise/control) with increasing amplitude (dB) of noise playback. Due to the lack of a treatment interaction with species, analysis method, or noise types, the predictions have been averaged across these parameters. Shaded ribbons represent 95% confidence intervals.

we solved x for the value $y = 1$. At this value, $x = 34.13$ dB, indicating that our equation is applicable for passive acoustic recordings with noise levels that fall within 35–70 dB.

Utilizing the proportion of detections (i.e., control/experiment microphone) rather than total detections in different noise conditions to create our polynomial equation was critical because detection rates for each amplitude treatment were assessed on a unique set of acoustic recordings. Total detections are reflective of the rate of vocalizations produced and the number of vocalizations detected. Differences in production rates are exhibited in our control recordings where total detections decreased as amplitude increased, although noise playback never occurred (Figure 4). The observed pattern is most likely a result of playback timing. The amplitude of noise playback (in name only for controls) always increased as time progressed, which correlates with decreased singing rates during the dawn chorus (Henwood and Fabrick 1979; Kacelnik and Krebs 1982; Brown and Handford 2003). A similar pattern could also result if noise spillover from the headphones was impacting the control microphone, but spatial separation between the recording made this scenario unlikely. Further, visual inspection of control spectrograms during the time when noise playback occurred in the experimental unit confirmed that background noise was not detectable.

Discussion

Our prediction that neither the slight spatial separation between units nor the presence of headphones on the microphone of a passive acoustic recording unit would have a significant impact on the detection of biotic vocalizations was supported. Results from our negative binomial model revealed that increasing amplitude significantly reduced detection rates. The absence of interaction terms between amplitude and factors other than treatment indicated that masking patterns were similar regardless of the species, noise type, or analysis method. Despite the lack of unique noise-related trends, absolute detections differed dramatically between species and by analysis method. Counter to our prediction, noise type had no impact on detectability.

Because noise-associated detectability trends did not differ significantly between species, noise type, or analysis method, we derived a single formula to correct for noise masking in passive acoustic recordings. It is unlikely that these factors have no impact on detectability rates, but rather, that increasing amplitude has a far greater effect. As a result, our single formula may sufficiently estimate the proportion of signals in birds, and potentially other organisms, that are being lost due to ambient noise levels by simply measuring background noise in acoustic recordings. We emphasize that this correction factor only *estimates* the proportion of masked detections, although similarly, point counts are also only estimates of abundance (Simons et al. 2007). Currently, our polynomial function should only be applied to acoustic recordings with ambient noise levels within 35–70 dB. Although our results were robust across a number of factors, we recommend that our correction factor be applied with caution, and we invite others to test and refine our results. While the vocalizations from our five-target species varied naturally in amplitude and pitch, further testing of additional species is important to test the tractability of this formula more generally. Nonetheless, we present the first empirically-derived correction factor for noise-masking in passive acoustic recordings, which is a substantial improvement over disregarding that detectability differences are occurring across varying levels of noise.

Although noise-related trends were not evident between species and noise types, several absolute differences were notable. Red-eyed vireos were detected at far greater rates than other species. This is likely related to their persistent singing behaviour (Hartshorne 1956; Buskirk and McDonald 1995) and the way their vocalizations were counted. Because red-eyed vireos have a non-consistent song pattern (Hartshorne 1956), each element was treated as an individual detection. In comparison to blue jays, black-throated green warblers vocalized more often, and ovenbirds vocalized less. Despite its lower vocalization rate, the ovenbird was the second most regularly recorded species, which correlates with its known prevalence in our study region (Kendeigh 1948).

As predicted, spectrogram analysis had the highest average number of detections, followed by the auditory and automated analyses. Direct comparisons between the spectrogram and auditory analyses cannot be made because each method was used to analyse acoustic recordings from 10 unique sites. Site-dependent variables (i.e., time of day, different number of vocalizing species/individuals) could have played a role in the difference between the results for these two analyses methods. Nonetheless, since spectrogram analyses included both visual and aural components, it is likely that this method would result in more detections than auditory assessments regardless of site-dependent variables. However, both techniques could be compared directly to our automated analysis, and both resulted in higher detection rates. While machine learning has advanced significantly in recent years, and is much more efficient than other analysis techniques, the variability within species-specific acoustic signatures still limits the accuracy of automated programs. However, the lack of an interaction between noise and analysis method in our model indicates that masking from noise impacts detectability in humans and automated recorders similarly. These results indicate that differences in the absolute number of detections between methods more likely arises from inaccurate classification rather than inherent differences in the ability to detect acoustic signals. In cases where rates of change are of interest rather than absolute detections, noise impacted acoustic recordings may be comparable across methods.

It was somewhat surprising that the only term completely absent from our final model was noise type. While vocal frequencies varied by species, all occurred between 2 and 10 kHz. We predicted that white noise would have the largest masking effect because it has equal power densities across all frequencies, and thus, higher densities in the higher pitches. However, the idea that spectral separation offers minimal release from acoustic masking aligns with a handful of studies showing that songbird vocalizations shifted to higher frequencies provide only marginal increases in detectability in the presence of low-frequency ambient noise (Nemeth and Brumm 2010; Zollinger et al. 2017). Specifically, Parris and McCarthy (2013) reported a < 4% increase in a signal's active space when frequencies were >2 kHz. Taken together, this evidence suggests that the spectral power density of ambient noise has less impact on acoustic masking than its amplitude. Thus, quantifying amplitude may be of primary importance for understanding the impact of ambient noise on both passive acoustic recorders and biological receivers (e.g., Potvin et al. 2016; Lohr et al. 2003).

In summary, the presence of ambient noise significantly altered the detectability of songbird vocalizations in acoustic data derived from passive acoustic recording units, and presents a potential confound for comparisons between recordings made in

different ambient conditions. We present the first empirically derived correction factor to account for the proportion of detections lost due to ambient noise in the recording soundscape. Because amplitude impacted detection similarly across our five species, three noise types, and three analysis methods, a single correction factor was sufficient for estimating noise-associated decreases in detectability in all conditions. We encourage others to investigate the tractability of our correction factor for other avian and non-avian species, and in different recording conditions. Regardless of the method, our results make it clear that ambient noise must be accounted for in order to accurately compare detection rates in acoustic recordings across ambient conditions.

Acknowledgements

We thank Wildlife Acoustics for their generous equipment grant which provided the technology needed to make this research possible. We are also grateful to the Au Sable Institute for providing housing and the Calvin College Science Division for supplying research stipends. Finally, we are thankful to A Horn and two anonymous reviewers for their suggestions that greatly improved the manuscript.

Disclosure statement

The authors received an equipment grant from Wildlife Acoustics, but there were no stipulations or pressure to report anything other than what was observed in the resulting data set. Thus, the authors have no conflict of interests to report.

Funding

This work was supported by Calvin College; Wildlife Acoustics; Scientific Product Grant.

ORCID

Darren S. Proppe  <http://orcid.org/0000-0001-7741-6504>

References

- Aho K, Derryberry D, Peterson T. 2014. Model selection for ecologists: the worldviews of AIC and BIC. *Ecology*. 95(3):631–636.
- Aiken LS, West SG, Reno RR. 1991. Multiple regression: testing and interpreting interactions. In: *Interactions between continuous predictors in multiple regression*. Thousand Oaks (CA): Sage Publications, Inc.
- Alquezar RD, Machado RB. 2015. Comparisons between autonomous acoustic recordings and avian point counts in open woodland savanna. *Wilson J Ornithol*. 127(4):712–723.
- Altringham JD, Fenton MB. 2003. Sensory ecology and communication in the Chiroptera. In: Kunz T, Fenton B, editors. *Bat Ecology*. Chicago (IL): University of Chicago Press.
- Apol CA, Sturdy C, Proppe DS. 2018. Seasonal variability in habitat structure may have shaped acoustic signals and repertoires in the black-capped and boreal chickadees. *Evol Ecol*. 32(1):57–74.
- Barber JR, Crooks KR, Fristrup KM. 2010. The costs of chronic noise exposure for terrestrial organisms. *Trends Ecol Evol*. 25(3):180–189.

- Bibby C, Burgess ND, Hill DA. 1992. Bird census techniques. Cambridge (MA): Academic Press.
- Borror DJ. 1981. The songs and singing behavior of the Red-eyed Vireo. *Condor*. 83:217–228.
- Bradbury JW, Vehrencamp SL. 2011. Principles of animal communication. 2nd. Sunderland (MA): Sinauer Associates.
- Brandes TS, Naskrecki P, Figueroa HK. 2006. Using image processing to detect and classify narrow-band cricket and frog calls. *J Acoust Soc Am*. 120(5):2950–2957.
- Brown TJ, Handford P. 2003. Why birds sing at dawn: the role of consistent song transmission. *Ibis*. 145(1):120–129.
- Brumm H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *J Anim Ecol*. 73(3):434–440.
- Buskirk WH, McDonald JL. 1995. Comparison of point count sampling regimes for monitoring forest birds. In: Ralph JC, Sauer JR, Droege S, editors. *Monitoring bird populations by point counts*. Albany (CA): U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station; p. 25–34.
- Catchpole CK, Slater PJB. 2008. Bird song: biological themes and variations. Cambridge (UK): Cambridge University Press.
- Celis-Murillo A, Deppe JL, Allen MF. 2009. Using soundscape recordings to estimate bird species abundance, richness, and composition. *J Field Ornithol*. 80(1):64–78.
- Cleary PD, Kessler RC. 1982. The estimation and interpretation of modifier effects. *J Health Soc Behav*. 23(2):159–169.
- Cohen SM. 1977. Blue Jay vocal behavior. Phd Thesis, Univ. of Michigan, Ann Arbor.
- Cooper BA, Blaha RJ. 2002. Comparisons of radar and audio-visual counts of marbled murrelets during inland forest surveys. *Wildl Soc Bull*. 30(4):1182–1194.
- Craig W. 1943. The song of the wood pewee *Myiochanes virens* Linnaeus: a study of bird music. N.Y. State Mus. Bull. no. 334.
- Elie JE, Theunissen FE. 2016. The vocal repertoire of the domesticated zebra finch: a data-driven approach to decipher the information-bearing acoustic features of communication signals. *Anim Cogn*. 19(2):285–315.
- Fernández-Juricic E, Poston R, Collibus KD, Morgan T, Bastain B, Martin C, Jones K, Treminio R. 2005. Microhabitat selection and singing behavior patterns of male house finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the western U.S. *Urban Habitats*. 3:49–69.
- Fitzpatrick JW, Lammertink M, Luneau MDJ, Gallagher TW, Harrison BR, Sparling GM, Rosenberg KV, Rohrbaugh RW, Swarthout ECH, Wrege PH, et al. 2005. Ivory-billed Woodpecker (*Campephilus principalis*) persists in continental North America. *Science*. 308(5727):1460–1462.
- Francis CD, Ortega CP, Cruz A. 2011. Noise pollution filters bird communities based on vocal frequency. *PLoS One*. 6(11):e27052.
- Froidevaux JS, Zellweger F, Bollmann K, Obrist MK. 2014. Optimizing passive acoustic sampling of bats in forests. *Ecol Evol*. 4(24):4690–4700.
- Gasc A, Sueur J, Pavoine S, Pellens R, Grandcolas P. 2013. Biodiversity sampling using a global acoustic approach: contrasting sites with microendemics in New Caledonia. *PLoS One*. 8(5):e65311.
- Gerhardt HC, Huber F. 2002. Acoustic communication in insects and anurans: common problems and diverse solutions. Chicago (IL): University of Chicago Press.
- Goodwin SE, Podos J. 2013. Shift of song frequencies in response to masking tones. *Anim Behav*. 85(2):435–440.
- Hart PJ, Hall R, Ray W, Beck A, Zook J. 2015. Cicadas impact bird communication in a noisy tropical rainforest. *Behav Ecol*. 26(3):839–842.
- Hartshorne C. 1956. The monotony-threshold in singing birds. *Auk*. 73(2):176–192.
- Haselmayer J, Quinn JS. 2000. A comparison of point counts and sound recording as bird survey methods in Amazonian southeast Peru. *Condor*. 102(4):887–893.

- Henwood K, Fabrick A. 1979. A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. *Am Nat.* 114(2):260–274.
- Kacelnik A, Krebs JR. 1982. The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour.* 83(3/4):287–309.
- Kendeigh SC. 1948. Bird populations and biotic communities in northern lower Michigan. *Ecology.* 29:101–114.
- Klump GM. 1996. Bird communication in the noisy world. In: Kroodsmas DE, Miller EH, editors. *Ecology and evolution of acoustic communication in birds.* Ithica (NY): Cornell University Press; p. 321–338.
- Lein MR. 1981. Display behavior of Ovenbirds (*Seiurus aurocapillus*) II. Song variation and singing behavior. *Wilson Bull.* 93:21–41.
- Lenth R. 2018. emmeans: estimated marginal means, aka least-squares means. R package version 1.2.4.
- Leonard ML, Horn AG. 2012. Ambient noise increases missed detections in nestling birds. *Biol Lett.* 8(4):530–532.
- Lohr B, Wright TF, Dooling RJ. 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of signal. *Anim Behav.* 65(4):763–777.
- Manabe K, Sadr EI, Dooling RJ. 1998. Control of vocal intensity in budgerigars (*Melopsittacus undulatus*): differential reinforcement of vocal intensity and the Lombard effect. *J Acoust Soc Am.* 103(2):1190–1198.
- Morse DH, Poole AF. 2005. Black-throated Green Warbler (*Setophaga virens*), version 2.0. In: Poole AF, editor. *The Birds of North America.* Ithaca (NY, USA): Cornell Lab of Ornithology. doi:10.2173/bna.55
- Nemeth E, Brumm H. 2010. Birds and anthropogenic noise: are urban songs adaptive? *Am Nat.* 176(4):465–475.
- Pacifici K, Simons TR, Pollock KH. 2008. Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. *Auk.* 125(3):600–607.
- Parris KM, McCarthy MA. 2013. Predicting the effect of urban noise on the active space of avian vocal signals. *Am Nat.* 182(4):452–464.
- Potvin DA, Curcio MT, Swaddle JP, MacDougall-Shackleton SA. 2016. Experimental exposure to urban and pink noise affects brain development and song learning in zebra finches (*Taenopygia guttata*). *Peer J.* 4:e2287.
- Proppe DS, Sturdy CB, St. Clair CC. 2013. Anthropogenic noise decreases urban songbird diversity and may contribute to homogenization. *Glob Change Biol.* 19(4):1075–1084.
- Sheu ML, Hu TW, Keeler TE, Ong M, Sung HY. 2004. The effect of a major cigarette price change on smoking behavior in California: a zero-inflated negative binomial model. *Health Econ.* 13(8):781–791.
- Siemers BM, Schaub A. 2010. Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *P Roy Soc B-Biol Sci.* 278(1712):1646–1652.
- Simons TR, Alldredge MW, Pollock KH, Wettroth JM. 2007. Experimental analysis of the auditory detection process on avian point counts. *Auk.* 124(3):986–999.
- Slabbekoorn H, Peet M. 2003. Birds sing at a higher pitch in urban noise. *Nature.* 424(6946):267.
- Swiston KA, Mennill DJ. 2009. Comparison of manual and automated methods for identifying target sounds in audio recordings of Pileated, Pale billed, and putative Ivory-billed woodpeckers. *J Field Ornithol.* 80(1):42–50.
- Turgeon PJ, Van Wilgenburg SL, Drake KL. 2017. Microphone variability and degradation: implications for monitoring programs employing autonomous recording units. *Avian Conserv Ecol.* 12(1):9.
- Wiley RH, Richards DG. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav Ecol Sociobiol.* 3(1):69–94.
- Wimmer J, Towsey M, Roe P, Williamson I. 2013. Sampling environmental acoustic recordings to determine bird species richness. *Ecol Appl.* 23(6):1419–1428.

- Wood WE, Yezerinac SM. 2006. Song sparrow (*Melospiza melodia*) song varies with urban noise. *Auk*. 123(3):650–659.
- Zeileis A, Kleiber C, Jackman S. 2008. Regression models for count data in R. *J Stat Softw*. 27(8).
- Zelick R, Mann DA, Popper AN. 1999. Acoustic communication in fishes and frogs. In: *Comparative hearing: fish and amphibians*. New York (NY): Springer..
- Zollinger SA, Slater PJB, Nemeth E, Brumm H. 2017. Higher songs of city birds may not be an individual response to noise. *Proc Biol Sci*. 284(1860):20170602.