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Methodology, part of a Special Feature on Advancing bird population monitoring with acoustic recording technologies

Experimentally derived detection distances from audio recordings and human observers enable integrated analysis of point count data

Daniel A. Yip¹, Lionel Leston¹, Erin M. Bayne¹, Péter Sólomos^{1,2} and Alison Grover¹

¹Department of Biological Sciences, University of Alberta, ²Alberta Biodiversity Monitoring Institute

ABSTRACT. Point counts are one of the most commonly used methods for assessing bird abundance. Autonomous recording units (ARUs) are increasingly being used as a replacement for human-based point counts. Previous studies have compared the relative benefits of human versus ARU-based point count methods, primarily with the goal of understanding differences in species richness and the abundance of individuals over an unlimited distance. What has not been done is an evaluation of how to standardize these two types of data so that they can be compared in the same analysis, especially when there are differences in the area sampled. We compared detection distances between human observers in the field and four commercially available recording devices (Wildlife Acoustics SM2, SM3, RiverForks, and Zoom H1) by simulating vocalizations of various avian species at different distances and amplitudes. We also investigated the relationship between sound amplitude and detection to simplify ARU calibration. We used these data to calculate correction factors that can be used to standardize detection distances of ARUs relative to each other and human observers. In general, humans in the field could detect sounds at greater distances than an ARU although detectability varied depending on species song characteristics. We provide correction factors for four commonly used ARUs and propose methods for calibrating ARUs relative to each other and human observers.

Dérivation expérimentale de distances de détection d'enregistrements audio et d'observateurs humains permettant l'analyse intégrée de points d'écoute

RÉSUMÉ. Les points d'écoute sont une des méthodes les plus courantes pour évaluer l'abondance d'oiseaux. Les unités d'enregistrement autonomes (ARU, *pour autonomus recording units*) sont de plus en plus utilisées pour remplacer les points d'écoute réalisés par des observateurs. Les études antérieures ont comparé les avantages relatifs des dénombrements par point d'écoute faits par des observateurs comparativement à ceux réalisés au moyen d'ARU, principalement pour évaluer les différences de richesse spécifique et d'abondance sur une distance illimitée. Ce qui n'a pas été testé toutefois est comment standardiser ces deux types de données de façon à ce qu'elles soient comparables dans une même analyse, particulièrement lorsqu'il y a des différences d'aire échantillonnée. Nous avons comparé la distance de détection entre des observateurs sur le terrain et quatre enregistreurs commerciaux (Wildlife Acoustics SM2, SM3, RiverForks et Zoom H1), en simulant les vocalisations de diverses espèces aviaires à des distances et des amplitudes variées. Nous avons aussi exploré la relation entre l'amplitude du son et la détectabilité dans le but de simplifier la calibration d'ARU. Nous avons utilisé ces données afin de calculer des facteurs de correction servant à standardiser les distances de détection des ARU entre eux et avec les observateurs. En général, les observateurs sur le terrain pouvaient détecter des sons à des distances plus grandes que ne le faisaient les ARU, quoique la détectabilité variait selon les caractéristiques du chant des espèces. Nous fournissons des facteurs de correction pour quatre ARU couramment utilisés et proposons une méthode pour calibrer les ARU entre eux et avec les observateurs.

Key Words: *autonomous recording unit; bioacoustics; effective detection radius; maximum detection distance; survey bias*

INTRODUCTION

There is growing interest in combining data from multiple point count studies to draw inferences about environmental processes influencing birds at larger spatial and temporal scales than the original studies intended (Cumming et al. 2010). Traditionally, human observers have collected point count data (hereafter HPC) by identifying species using acoustic and visual cues while following standardized protocols (Ralph et al. 1995). However, many differences exist between HPC studies in the point count methods used, i.e., duration of count, fixed or unlimited distance counts (Matsuoka et al. 2014). As well, concerns about human observers not detecting species that are present during a single visit have led to calls for replicating effort at the same locations

(Royle and Nichols 2003, Kéry et al. 2005). The use of repeated point counts at the same location within a season to account for varying detection probability among visits has increased interest in the use of autonomous recording units (ARUs; Haselmayer and Quinn 2000, Hobson et al. 2002).

A major benefit of ARUs is that humans only visit each location twice and spend time only deploying and picking up the ARU. The ARU itself can record over an extended period and create an almost unlimited number of repeated surveys of virtually any duration (Haselmayer and Quinn 2000, Hobson et al. 2002). Human observers are more likely to detect some species visually, which can increase the odds of detection, although visual detection area is likely much smaller than aural detection area in

heavily vegetated environments (Haselmayer and Quinn 2000, Hutto and Stutzman 2009). Human observers can also estimate distances to individual birds to enable the use of a bounded point count radius and/or distance-based density estimation (Buckland et al. 1993). The relative importance of being able to cost-effectively conduct repeated visits via ARUs versus estimate distance via HPC is unclear in terms of accuracy and precision when assessing trend and status of birds. Regardless, to make the best use of point count data, ornithologists need to evaluate ways to standardize HPC and ARU data to use both data types in the same analyses.

To accurately use data from different point count datasets, ornithologists have converted counts to a common standard, which is typically density (Sólymos et al. 2013). Estimating density of birds using point counts requires the following: (1) accounting for individuals that are available to be detected but do not vocalize or are not seen (Farnsworth et al. 2002, Dawson and Efford 2009); and (2) accounting for declining detection of more distant individuals (Buckland et al. 1993). Removal sampling can address the problem of animal availability based on multiple time intervals that can exist for both HPC and ARU data. However, the second problem of correcting for the area sampled and the distance over which birds are counted is more fundamental. Sound travels different distances depending on the vegetation and atmospheric conditions occurring between the signaller and the receiver (Holland 2001, Padgham 2004, Simons et al. 2007, Pacifici et al. 2008, Tarrero et al. 2008). Detectability can also vary between observers depending on factors such as age, sex, and experience (Pearson et al. 1995, Helzner et al. 2005). To compare the observed number of bird detections between point counts in two separate studies or in two separate vegetation types within the same study, ornithologists should account for the distance travelled by bird song and effective area sampled (Yip et al. 2017). Otherwise, biases in our understanding of habitat selection, population status, and temporal trend may occur if environmental conditions influencing sound transmission significantly differ between sites and times.

There are three main approaches for calculating the area over which bird sounds are detected and thus converted to density: (1) fixed-distance point counts, hereafter FIXED (Hutto et al. 1986, Petit et al. 1995); (2) maximum detected distance (MDD) at which a given species can be detected (Emlen and DeJong 1981, Rosenberg and Blancher 2005); or (3) effective detection radius (EDR) based on distance-sampling methods (Buckland et al. 1993). The FIXED approach does not seem to be possible for ARU-based point counts because signal strength from a species, and hence accuracy of distance estimation will differ because of sound absorption and reflectance varying among environmental conditions (Petit et al. 1995, Padgham 2004, Pacifici et al. 2008). In addition, such approaches discard a lot of useful data on birds that are detected past the fixed distance. In contrast, ornithologists can calculate MDD and EDR for a species from ARU-based data if (1) there are known distances to recordings of birds, and (2) if there is some simultaneously collected distance data from HPC for which MDD or EDR and ARUs can be compared and calibrated. Partners in Flight has used MDD to estimate population sizes (Rosenberg and Blancher 2005), but the Partners in Flight approach to estimating MDD is coarse and does not consider vegetation or atmospheric effects that influence

MDD, leading to concerns about this approach when calculating density (Thogmartin et al. 2006). EDR accounts for the decline in detectability as the distance from an observer increases, but like the FIXED approach, EDR varies among species and environmental conditions, and reliable EDR estimates depend on well-trained field observers, accurate distance estimation, and point count methods meeting assumptions of distance sampling (Buckland et al. 1993).

Understanding how microphone and recording settings influence the area sampled for birds is crucial to ensuring that long-term monitoring and comparisons made between studies are valid using ARU techniques. Research programs and monitoring agencies have different preferences, goals, and budgets, which influences the type of ARU they decide to use and these must be calibrated to account for differences in area sampled if results are to be compared. Availability of different ARUs also changes over time as ARUs are continuously improved.

Our approach to comparing ARU models and how far they detect birds relative to human observers relies on using song broadcasts of known amplitude and distance. Distance-based broadcasts whereby a sound is played at varying distances from the observer or recorder are labor-intensive. A potential alternative could involve using a relatively limited number of distances when conducting broadcast trials but varying the volume (amplitude) of the broadcast speaker between ambient background levels and the upper range that birds are known to sing. Quantifying the relationship between amplitude and distance of different species for different ARUs could be a cost-effective way of ensuring that all ARUs are calibrated to a known and documented standard. Although the true relationship between amplitude and distance is unknown, this approach effectively identifies relative differences among ARUs.

We had three objectives. First, we developed and tested two field broadcast and modeling methods to evaluate how detection of birds is influenced by distance, ARU type, amplitude, and environmental variables relative to HPC. We did this by broadcasting sounds with varying frequencies and under different vegetation conditions over a range of distances. We then tested which sounds were detected by HPC in the field and when listening to ARU recordings in the lab. Second, we used known principles of sound physics to estimate EDR and MDD for various species. Third, we provided an approach for standardizing HPC and ARU data in the same analysis by creating generalized correction factors and a simple approach to calibration that can be used to standardize raw counts to density regardless of the method of sampling.

METHODS

Using known distance data to estimate effects of recorder technology, vegetation, weather, and species on detection radius

Study area

We collected data near Calling Lake (55°11' N, 113°12' W) and Lac la Biche, Alberta (54°38' N, 111°58' W) in August 2014. We conducted our surveys in August to reduce the chance of confusing broadcasted sounds (see below) with the songs of real

birds. Broadcasts took place between 07:00–20:00 MST. We recorded broadcasted sounds that we used in our study at a total of 20 sites using ARUs (10 road sites, 5 coniferous forests, and 5 deciduous forests). Coniferous sites consisted primarily of white spruce (*Picea glauca*) while deciduous sites consisted primarily of trembling aspen (*Populus tremuloides*). Road sites occurred on flat, low-use forestry roads composed of gravel and clay. At a subset of the 20 sites (8 road, 4 coniferous, and 4 deciduous), observers stood adjacent to the ARUs and indicated which broadcasted sounds they were able to detect.

Data collection

At each site, we broadcasted known sounds from varying distances (see below) and evaluated whether or not a human observer could detect them. At the same time and location, we also recorded the broadcast sounds on four types of ARUs. All recordings made by the ARUs used 2-channel stereo recordings at 44 kHz and 16-bit .wav format. The four ARUs were (1) Wildlife Acoustics' SongMeter SM2+ GPS-enabled recording units equipped with SMX-II weatherproof microphones (5 units); (2) Wildlife Acoustics' SM3 ARUs (5 units); (3) RiverForks CZM recorders (2 units); and (4) Zoom H1 handheld recorders (3 units). We broadcasted sounds with an Alpine® SPR-60, 6-1/2" car speaker/tweeter and an Alpine® UTE-42BT car stereo/audio player (Gentec Int'l, Markham, Ontario), both installed into an 11" (width) x 10" (depth) x 15" (height) plywood speaker box, along a transect from 12 to 1312m. We placed the speaker at 25-m intervals for the first 400 m, 50-m intervals between 400–800m, and 100-m intervals for broadcasts beyond 800 m. The same sequence of calls was broadcast at each distance. On forested transects where the ARU was not visible from the transmitting unit, we used a GPS and compass to properly align the speaker toward the ARU.

The broadcasted sequence began with a series of 7 pure tones (at frequencies of 1000Hz, 1414Hz, 2000Hz, 2828Hz, 4000Hz, 5656Hz, and 8000Hz) generated using Adobe Audition CS6. The song sequence following the tones consisted of 23 boreal bird species and 2 amphibian species broadcast in the following order: Clay-colored Sparrow (*Spizella pallida*; CCSP), Black-and-white Warbler (*Mniotilta varia*; BAWW), Lincoln's Sparrow (*Melospiza lincolni*; LISP), Brown-headed Cowbird (*Molothrus ater*; BHCO), Red-breasted Nuthatch (*Sitta canadensis*; RBNU), 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 (*Megaceryle 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*; YEAR), Western Toad (*Anaxyrus boreas*; WETO), Canadian Toad (*Anaxyrus hemiophys*; CATO), Northern Saw-whet Owl (*Aegolius acadicus*; NSWOW), Boreal Owl (*Aegolius funereus*; BOOW), Long-eared Owl (*Asio otus*; LEOW), Great Gray Owl (*Strix nebulosa*; GGOW), and Barred Owl (*Strix varia*; BADO). We selected these species for a variety of song characteristics that may affect probability of detection (pitch, song length). All sounds were normalized in Audition to bring peak amplitude to a standardized level. We broadcasted sounds at 90 dB, which we

measured 1 m from the speaker system (based on fast-time A-weighting) using a handheld sound meter (Sper Scientific 840018).

At each transect, we attached each of the 4 ARU types to a tree or post at a height of 1.5 m. This was the same height as the speaker broadcasting the recordings at the starting point of the transect and we chose transects with minimal elevational change. For each point along a transect, we recorded the time of the broadcast and distance of the broadcast speaker from the ARUs and human observer using a GPS (± 3 m). We also measured temperature, humidity, and wind speed during each broadcast using a Kestrel 3000 pocket weather meter. Following the end of the broadcasted sequence, the first observer moved the speaker an additional 25 m along the transect and the process was repeated.

We clipped recordings into individual files for each distance from each type of ARU. Observers in the lab listened to these files at standardized volume levels and noted which species and tones they could identify and detect for each distance and each type of ARU recording. For this experiment, observers in the lab listened to tones and songs in the recordings in the original sequence that the tones and songs were broadcast to make things directly comparable to the HPC. For pure tones, observers only had to identify that a tone was present, not what frequency was broadcast. Using this method, we generated a large dataset of detections or nondetections from sounds that were known to have occurred ($n = 96,502$). During the HPC, the observer in the field recorded whether they could hear and correctly identify each sound as it was broadcast in sequence.

Modeling sources of variation influencing detection of sounds

We divided data randomly into 70% training data ($n = 1898$ for each species or tone, without replacement) for model development and 30% test data ($n = 813$ for each species or tone) for model validation (sample function, R [R Core Team 2013]). We assessed the detection/nondetection of each species or tone using generalized linear models (glm function, R [R Core Team 2013]) with a binomial error family. All models included distance as a predictor of whether a tone or song was detected. We used a model where distance was the only predictor as a null model, where $p(d)$ declined with distance at the same rate in different habitats, in different weather conditions, and for human observers versus different ARU brands. We compared this null model to 11 candidate models (Table 1). For the weather models, we had considered temperature as well, but dropped that variable because it was positively correlated with humidity.

We used Akaike's Information Criterion to rank the relative fit of models (Burnham and Anderson 2002, Arnold 2010). To assess the absolute model fit or goodness-of-fit of the top AIC-ranked model, we used the area-under-the-curve (AUC) within receiver-operator curves for each species as a test statistic (roc function, *pROC* package, R [Robin et al. 2011]). AUC measures the proportion of actual detections and nondetections that were correctly predicted by the best model as opposed to false negatives or positives. We calculated AUC for the test data set excluded from model generation. We rated models with $AUC > 0.70$ as having sufficient ability to correctly predict if a song or tone was or was not detected (Vanagas 2004).

Table 1. Candidate models to be compared against a null distance model for the autonomous recording units (ARUs) experiment.

Model	Parameters
D*V+A*V+H	Distance * Vegetation + ARU Type * Vegetation + Humidity
D*V+A*V+W+H	Distance * Vegetation + ARU Type * Vegetation + Wind + Humidity
D*V+A*V+W	Distance * Vegetation + ARU Type * Vegetation + Wind
D*V+A*V	Distance * Vegetation + ARU Type * Vegetation
D*V+A+H	Distance * Vegetation + ARU Type + Humidity
D*V+A+W+H	Distance * Vegetation + ARU Type + Wind + Humidity
D*V+A+W	Distance * Vegetation + ARU Type + Wind
D+V*A	Distance + Vegetation * ARU Type
D*V+A	Distance * Vegetation + ARU Type
D+V+A	Distance + Vegetation + ARU Type
null	Distance

Estimating effective detection radius for different sounds

EDR gives the radius of the circle where the expected number of available individuals not detected within the distance equals the expected number of the detected individuals outside of that distance (Buckland et al. 1993). We estimated EDR for our Calling Lake dataset with a separate set of models rather than the set used for modeling detectability. The shape of the distance function describes how detection probability attenuates as a function of broadcast speaker distance (d) from the ARUs and human observer. The distance function is a strictly monotonic decreasing function with increasing distance. There are many different mathematical formulations to describe this shape, however we chose the half-normal distance function because of its simplicity, as well as the fact that its standard deviation parameter (τ) is directly interpretable as effective detection radius (EDR) for unlimited, i.e., not truncated, point counts in bird surveys (Sólymos et al. 2013). In the half-normal distance function, detection at a given distance can be modeled as $p(d) = \exp(-d^2/\tau^2)$ in which detection declines as object distance (d) from the observer increases, but declines at a slower rate as τ increases. We transformed distance in metres to $-d^2$ prior to modeling to linearize the relationship. We used the coefficients for different predictors in the best model to calculate EDR for each species or tone for different vegetation types, human observers, and ARU types. In all models, we set the intercept to zero so that $p(d) = 1$ at $d = 0$, and used a complementary log-log link function instead of the usual logit link function for GLMs with a binomial dependent variable, to simplify the estimation of EDR and approximate a log-linear model (Yip et al. 2017). EDR was estimated as $\tau = (1/\beta)^{0.5}$, where β is the sum of coefficients for the main effect of distance (transformed as $-d^2$) and any interaction effects with $-d^2$ (for example: $\beta_{\text{ARU[relative to human observer]}} + \beta_{-d^2} + \beta_{\text{Habitat[relative to coniferous forest]}}$). After calculating EDR for the human observer and each ARU type, we then calculated a correction factor for the effective area sampled by each ARU type relative to human observers ($A/A = \text{EDR}_{\text{ARU}}^2 / \text{EDR}_{\text{human}}^2$) in each vegetation type. This correction factor can be used to standardize the area parameter for animal density when comparing data from ARUs and human observers.

We performed Monte Carlo simulations to (1) estimate uncertainty in EDR point estimates for each sound, and (2) test for statistical differences between different vegetation types. We generated coefficients ($n = 1000$) using maximum-likelihood estimates and variance-covariance matrices from the original models to calculate 90% confidence intervals from the predicted values (Appendix 1; Yip et al. 2017). We omitted EDR estimates that (1) failed to solve because of a lack of nondetections in the raw data, or (2) failed to generate confidence intervals because of high uncertainty when predicting from the original model.

We estimated MDD for the same data by selecting the largest distance with a correctly identified detection based on the 95% quantile of positive detections for each species. We estimated MDD separately for ARUs and human observers using the same data for our EDR calculations to compare results from both approaches. After estimating MDD, we calculated the maximum area sampled and correction factors for each ARU type relative to human observers ($A/A = \text{MDD}_{\text{ARU}}^2 / \text{MDD}_{\text{human}}^2$) in each vegetation type, using the same method as for calculating correction factors for EDR.

Using known distance data to estimate effects of sound amplitude on detection

Study area

We used known distance data and broadcasts of the same species and tones to explore effects of sound amplitude on detection by ARUs. We conducted the amplitude study from September–October 2014 in the Blackfoot-Cooking Lake Natural Area (53° 25' N, 112° 49' W) near Edmonton, Alberta from 09:00–16:00 MST. We placed 10 transects in open vegetation (> 75% grass cover, < 5% shrub cover, 0% tree cover) and 10 in denser vegetation (mature deciduous stands composed primarily of trembling aspen with small amounts of balsam poplar [*Populus balsamifera*] and white spruce).

Data collection

At each transect we placed a SM2+ ARU in the same setup as the previous experiment and broadcasted songs and tones from a distance of 50, 100, and 150 m away. We broadcast each song or tone at 11 sound pressure levels (a-weighted SPL, a measure of sound pressure relative to the threshold for human hearing) from 40 to 90 dB at 5 dB increments (= 23 songs*11 amplitudes = 253 sounds played at each of the three distances). Each sequence of sounds at each amplitude lasted 1:43 and the full broadcast for all amplitudes was 18:53. For each distance within a transect, we noted temperature, humidity, and wind speed values averaged over the duration of the broadcast using a handheld Kestrel 3000 handheld weather metre (Nielsen-Kellerman Co., Boothwyn, Pennsylvania).

Following field data collection, we used the programs PRAAT © version 5.4 and Adobe Audition © version 5.0 to cut all recordings into separate clips for each call on the recording and labelled calls according to site type (open or closed), site number (1–10), species call/tone, and amplitude. We randomized the clipped files by shuffling them with generic empty clips (containing only ambient background noise). Without knowing the file contents, 4 volunteers trained in avian call detection and recognition listened to and labelled each sound clip by whether or not a call was heard, and if so, of what species.

Modelling sources of variation influencing detection of sounds

As in the HPC/ARU study, we used GLMs with intercept set to 0, distance transformed to $-d^2$, and a complimentary log-log link function to model whether or not a given song or tone was detected by observers listening to the ARU recordings. For each species or tone, we used a model where additive effects of distance and SPL were the only predictors of detection as a null model, where $p(d)$ declined with distance at the same rate in different habitats and weather conditions, and varied with broadcast amplitude. We compared this null model to five candidate models (Table 2). We followed the same procedure for assessing the relative fit of the above GLMs using AIC, and assessed the goodness-of-fit of the highest ranked or most parsimonious model for each species, using AUC statistics and receiver operating curves as in the HPC/ARU experiment (Table 3).

Table 2. Candidate models to be compared against a null distance model for the SPL experiment.

Model	Parameters
D*V+S+W+H	Distance * Vegetation + SPL + Wind + Humidity
D*V+S+H	Distance * Vegetation + SPL + Humidity
D*V+S+W	Distance * Vegetation + SPL + Wind
D*V+S	Distance * Vegetation + SPL
D+S+V	Distance + SPL + Vegetation
null	Distance

Estimating effective detection radius for different sounds

We used the coefficients for different predictors in the best model to calculate EDR for each species or tone for different vegetation types and SPLs as with the previous experiment. EDR was estimated as $\tau = (1/\beta)^{0.5}$, where β is the sum of coefficients for the main effect of distance (transformed as $-d^2$) and any interaction effects with $-d^2$ (for example: $\beta_{\text{SPL}[45-90 \text{ dB in } 5\text{-dB increments}]} + \beta_{-d^2} + \beta_{\text{Open habitat[relative to closed habitat]}}$). We estimated uncertainty using the same Monte Carlo method to calculate 90% confidence intervals for our EDR estimates. We did not estimate MDD for our second experiment because of a lack of precision with our distance variables (only three were used).

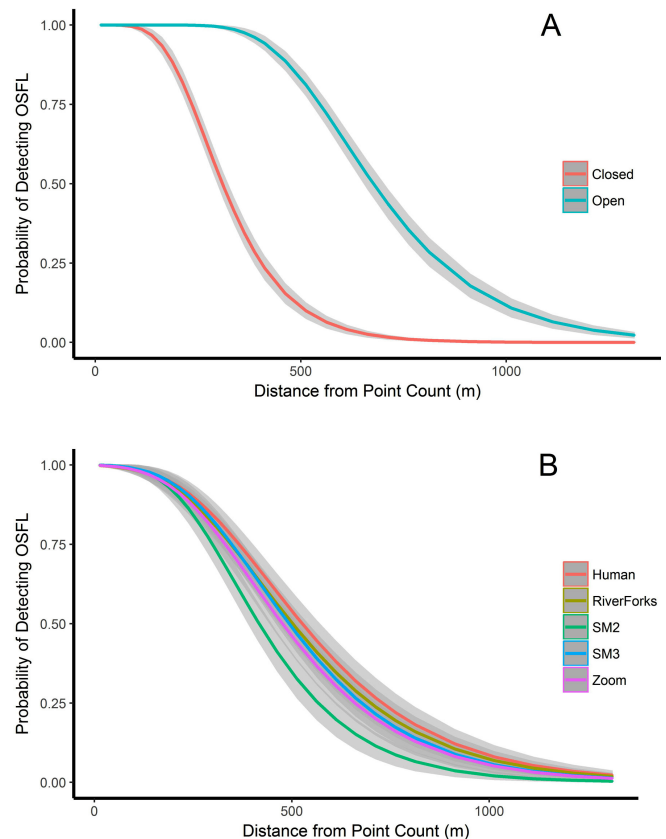
RESULTS

Using known distance data to estimate effects of recorder technology, vegetation type, weather, and species detection

Effective detection radii for humans and ARUs in different vegetation types with known-distance data

Detectability declined as distance to sound increased for all species and tones (mean \pm SD across all models $\beta_x = 1.312 \times 10^{-5} \pm 1.399 \times 10^{-5}$; Table 4). Declines in detection rate were greater in both coniferous (mean $\beta_{\text{coniferous}} = -0.165 \pm 1.066$ relative to road) and deciduous (mean $\beta_{\text{deciduous}} = -1.482 \pm 1.456$ relative to road) vegetation types in comparison to open roadside transects (Fig. 1). Ninety percent confidence intervals for our estimates of EDR from human detection data showed significant differences

Fig. 1. Probability of detecting OSFL with distance from ARU in (A) open (roadside) and closed (forested) habitat, and (B) with human observers, RiverForks, SM2, SM3, and Zoom recorders. Predictions are calculated from binomial detection data and plotted with 95% confidence intervals.



between roadside and forested detection distance for 18 of 32 sounds (5656Hz, 8000Hz, BAWW, BEKI, BHCO, BLWA, CCSP, DEJU, LISP, OSFL, OVEN, PISI, RBGR, RBNU, TEWA, WAVI, WTSP, YERA; Table 5). We were unable to assess roadside confidence intervals for five sounds (1414Hz, 2828Hz, CMWA, BOOW, NSW0) because of undefined EDR estimates. We found no significant difference in detection distance between coniferous or deciduous vegetation types. ARU type also influenced detectability although this varied depending on the species or tone present. However, detectability was generally higher for human observers relative to ARUs (mean relative to human: $\beta_{\text{SM2}} = -2.108 \pm 1.312$, $\beta_{\text{SM3}} = -0.963 \pm 1.086$, $\beta_{\text{RiverForks}} = -1.181 \pm 1.353$, $\beta_{\text{Zoom}} = -1.643 \pm 1.407$; Fig. 1). All top performing models included distance, transect type, and ARU type as important predictors (Table 5). The top performing model for 16 species and tones (1000Hz, 1414Hz, 2000Hz, BADO, CMWA, BOOW, CATO, CORA, GGOW, LEOW, NSW0, OSFL, RBGR, RBNU, WETO, WTSP) included humidity which positively influenced detectability for all sounds with the exception of CMWA (mean $\beta_{\text{humidity}} = 0.020 \pm 0.013$). Three species (CATO, WETO, YERA) had wind in their top performing model which also had a positive influence (mean $\beta_{\text{wind}} = 0.191 \pm 0.046$). Interaction effects between ARU and transect type were part of the top performing model

Table 3. Model selection for factors influencing detection probability of different sounds for the SPL experiment and AUC statistics on test data for the top AIC-ranked model testing differences in detection with varying SPL. All sounds used the same models for selection. We selected top models using lowest AICc value and Δ AICc. For multiple models with Δ AICc < 2, we selected the simplest model with fewest parameters (Arnold 2010). “df” is the degrees of freedom and “logLik” is the log likelihood value for that particular model. “**” indicates variable interactions.

Sound	Model	df	logLik	AICc	Δ AIC	AICw	AUC
1000Hz	D+S+V	4	-174.77	357.624	1.02958	0.23285	0.8989
	null	3	-204.68	415.407	58.8134	0	
1414Hz	D*V+S+W	6	-157	326.164	0	0.70592	0.9337
	null	3	-212.93	431.9	105.736	0	
2000Hz	D*V+S	5	-130.41	270.956	0	0.47529	0.9376
	null	3	-196.99	400.037	129.08	0	
2828Hz	D+S+V	4	-128.21	264.511	1.05645	0.18359	0.9530
	null	3	-183.54	373.134	109.679	0	
4000Hz	D*V+S+H	6	-137.36	286.892	0	0.65231	0.9286
	null	3	-200.76	407.57	120.678	0	
5656Hz	D*V+S	5	-134.05	278.227	0	0.47408	0.9468
	null	3	-219.32	444.684	166.457	0	
8000Hz	D+S+V	4	-145.2	298.489	0	0.4728	0.8732
	null	3	-154.28	314.617	16.1271	0.00015	
BADO	D*V+S	5	-174.47	359.069	0.04153	0.29076	0.9026
	null	3	-184.18	374.401	15.3734	0.00014	
BAWW	D*V+S	5	-121.15	252.422	0.17268	0.34988	0.9484
	null	3	-188.9	383.846	131.597	0	
BEKI	D*V+S	5	-94.142	198.408	0	0.43996	0.9669
	null	3	-179.37	364.798	166.39	0	
BHCO	D*V+S	5	-138.66	287.446	0	0.51571	0.9150
	null	3	-231.26	468.563	181.116	0	
BLWA	D*V+S	5	-122.69	255.513	0	0.41554	0.9556
	null	3	-185.04	376.137	120.623	0	
BOOW	D*V+S	5	-141.16	292.459	0	0.44656	0.9473
	null	3	-168.2	342.459	50.0003	0	
CATO	D+S+V	4	-125.29	258.672	0.65638	0.26736	0.9612
	null	3	-173.07	352.203	94.1878	0	
CCSP	D*V+S	5	-110.37	230.876	0	0.34889	0.9627
	null	3	-212.21	430.469	199.593	0	
CMWA	D*V+S+W+H	7	-115.55	245.34	0	0.57437	0.8705
	null	3	-140.1	286.247	40.907	0	
CORA	D*V+S	5	-131.11	272.361	1.91579	0.20263	0.9286
	null	3	-190.52	387.094	116.648	0	
DEJU	D*V+S	5	-121.69	253.499	0	0.50504	0.9476
	null	3	-221.87	449.795	196.296	0	
GGOW	D+S+V	4	-154.01	316.097	1.41848	0.19217	0.9205
	null	3	-177.89	361.824	47.1454	0	
LEOW	D*V+S+W	6	-167.41	347.01	0	0.58855	0.9505
	null	3	-173.06	352.173	5.16266	0.04454	
LISP	D*V+S	5	-107.61	225.361	0	0.53271	0.9808
	null	3	-197.36	400.777	175.416	0	
NSWO	D*V+S	5	-152.5	315.116	0	0.4052	0.9113
	null	3	-209.02	424.082	108.967	0	
OSFL	D*V+S	5	-126.27	262.68	0	0.44356	0.9836
	null	3	-193.46	392.968	130.289	0	
OVEN	D*V+S	5	-99.705	209.536	0	0.53143	0.9649
	null	3	-213.27	432.587	223.051	0	
PISI	D*V+S	5	-103.87	217.868	0.38708	0.32376	0.9721
	null	3	-216.71	439.46	221.979	0	
RBGR	D*V+S	5	-149.31	308.756	0.53372	0.2544	0.9569
	null	3	-208.46	422.974	114.752	0	
RBNU	D*V+S	5	-95.736	201.6	0	0.40291	0.9823
	null	3	-187.34	380.727	179.127	0	
TEWA	D*V+S	5	-94.862	199.85	0	0.51786	0.9828
	null	3	-155.97	317.992	118.142	0	
WAVI	D*V+S	5	-110.61	231.344	0	0.32514	0.9561
	null	3	-187.42	380.898	149.554	0	
WETO	D*V+S+H	6	-134.66	281.524	0	0.68689	0.9363
	null	3	-180.56	367.18	85.656	0	
WTSP	D*V+S	5	-97.034	204.205	0	0.40879	0.9708
	null	3	-190.93	387.906	183.701	0	
YERA	D*V+S+W	6	-96.075	204.342	0	0.43954	0.9650
	null	3	-134.19	274.437	70.0948	0	

Table 5. Model selection for factors influencing detection probability of different sounds for the ARU experiment and AUC statistics on test data for the top AIC-ranked model testing differences in detection distance between multiple models of ARU. All sounds used the same models for selection. We selected top models using lowest AICc value and Δ AICc. For multiple models with Δ AICc < 2, we selected the simplest model with fewest parameters (Arnold 2010). “df” is the degrees of freedom and “logLik” is the log likelihood value for that particular model. “*” indicates variable interactions.

Sound	Model	df	logLik	AICc	Δ AIC	AICw	AUC
1000Hz	D*V+A+H	11	-678.06	1378.21	0	0.51881	0.9441
	null	2	-916.19	1836.39	458.183	0	
1414Hz	D*V+A+H	11	-689.35	1400.8	0	0.49834	0.9360
	null	2	-936.46	1876.91	476.112	0	
2000Hz	D*V+A+H	11	-623.6	1269.31	0	0.6919	0.9672
	null	2	-942.84	1889.69	620.382	0	
2828Hz	D*V+A	10	-659.49	1339.06	1.21257	0.21324	0.9636
	null	2	-1036.5	2077.1	739.249	0	
4000Hz	D*V+A	10	-618.16	1256.4	0.44416	0.28574	0.9648
	null	2	-1047.1	2098.23	842.276	0	
5656Hz	D*V+A	10	-534.65	1089.37	0.49016	0.29669	0.9752
	null	2	-914.53	1833.06	744.179	0	
8000Hz	D*V+A	10	-391.46	802.998	1.89928	0.13075	0.9856
	null	2	-647.63	1299.26	498.162	0	
BADO	D*V+A*V+H	19	-965.55	1969.38	0	0.70662	0.9203
	null	2	-1215	2434.02	464.639	0	
BAWW	D*V+A*V	18	-379.28	794.816	1.30815	0.18797	0.9862
	null	2	-646.36	1296.73	503.219	0	
BEKI	D*V+A	10	-556.69	1133.46	0.08014	0.24845	0.9758
	null	2	-924.58	1853.17	719.793	0	
BHCO	D*V+A	10	-622.73	1265.54	1.04612	0.14687	0.9662
	null	2	-1006.3	2016.59	752.104	0	
BLWA	D*V+A	10	-444.07	908.223	0.75359	0.29277	0.9858
	null	2	-763.45	1530.91	623.443	0	
BOOW	D*V+A*V+H	19	-827.59	1693.47	0	0.54341	0.9436
	null	2	-1074.3	2152.68	459.214	0	
CATO	D*V+A+W+H	12	-733.55	1491.24	0.23228	0.46589	0.9416
	null	2	-1007.2	2018.32	527.319	0	
CCSP	D*V+A	10	-468.75	957.582	0	0.35225	0.9859
	null	2	-897.44	1798.89	841.306	0	
CMWA	D*V+A*V+H	19	-368.18	774.646	0	0.65587	0.9865
	null	2	-641	1286.01	511.363	0	
CORA	D*V+A+H	11	-735.12	1492.33	0.92028	0.28789	0.9490
	null	2	-1172.7	2349.34	857.927	0	
DEJU	D*V+A	10	-590.54	1201.15	1.62045	0.11057	0.9765
	null	2	-1026.7	2057.33	857.799	0	
GGOW	D*V+A*V+H	19	-855.99	1750.26	0	0.73321	0.9483
	null	2	-1142	2288.09	537.832	0	
LEOW	D*V+A*V+H	19	-892.55	1823.39	0.08974	0.48878	0.9180
	null	2	-1258.4	2520.75	697.458	0	
LISP	D*V+A	10	-628.42	1276.92	0	0.29553	0.9655
	null	2	-1062.2	2128.4	851.48	0	
NSWO	D*V+A+H	11	-852.58	1727.25	0	0.47978	0.9359
	null	2	-1115.4	2234.75	507.495	0	
OSFL	D*V+A+H	11	-688.72	1399.54	0	0.58399	0.9564
	null	2	-1097.5	2198.97	799.422	0	
OVEN	D*V+A	10	-575.18	1170.44	0	0.27342	0.9789
	null	2	-1010.3	2024.55	854.107	0	
PISI	D*V+A	10	-508.41	1036.89	0	0.37464	0.9829
	null	2	-900.73	1805.46	768.572	0	
RBGR	D*V+A+H	11	-737.08	1496.26	0	0.64593	0.9634
	null	2	-1171.1	2346.27	850.011	0	
RBNU	D*V+A+H	11	-671.8	1365.71	0	0.42648	0.9602
	null	2	-1107.2	2218.38	852.67	0	
TEWA	D*V+A*V	18	-508.71	1053.67	1.96814	0.17829	0.9786
	null	2	-910.98	1825.97	774.272	0	
WAVI	D*V+A	10	-588.4	1196.88	0	0.38132	0.9740
	null	2	-1014.6	2033.14	836.257	0	
WETO	D*V+A+W+H	12	-825.33	1674.79	0	0.63449	0.9302
	null	2	-1085.2	2174.5	499.706	0	
WTSP	D*V+A+H	11	-661.53	1345.16	0	0.61309	0.9711
	null	2	-1065.4	2134.85	789.682	0	
YERA	D*V+A+W	11	-447.41	916.932	0	0.54501	0.9776
	null	2	-699.65	1403.31	486.381	0	

for seven sounds (BADO, BAWW, CMWA, BOOW, GGOW, LEOW, TEWA) indicating that detectability varied with both the type of ARU and the transect the sounds were broadcast through. For these sounds, detectability declines suddenly relative to ARUs as distance increases, particularly in coniferous vegetation types. Mean (\pm SD) wind speed averaged over the duration of the broadcast sequence at each distance along a transect was 1.1 ± 1.4 km/h. Mean temperatures during each broadcast was 23.7 ± 6.5 °C. Relative humidity was $59.0 \pm 18.9\%$. Performance for all models was excellent (AUC: min = 0.9180, max = 0.9659, median = 0.9647; Table 5).

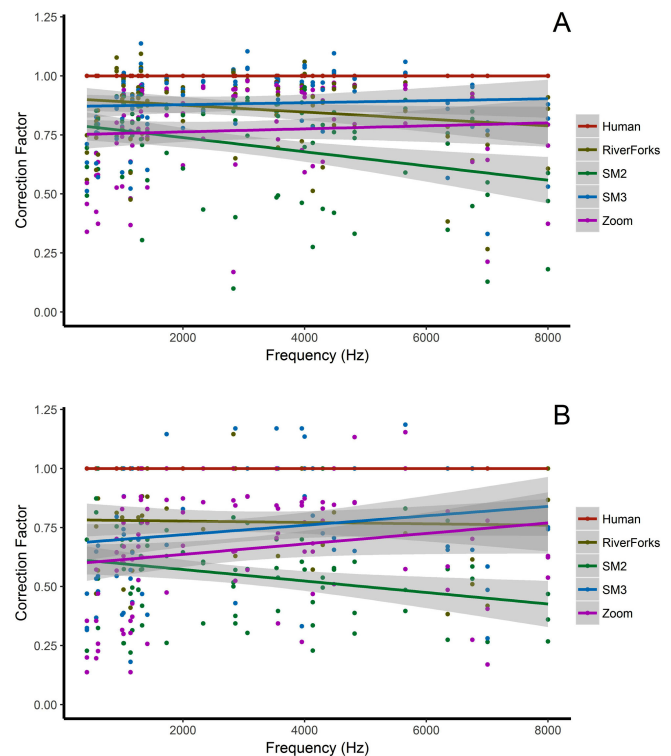
EDR and MDD values showed consistent differences between humans and different ARUs (Mean \pm SD EDR for all sounds: Human = 494 ± 233 m, SM2 = 421 ± 188 m, SM3 = 461 ± 198 m, RiverForks = 470 ± 222 m, Zoom = 431 ± 183 m; MDD: Human = 567 ± 266 m, SM2 = 427 ± 235 m, SM3 = 485 ± 231 m, RiverForks = 516 ± 250 m, Zoom = 442 ± 208 m; Fig. 2; Appendix 1, 2). Species and tones with lower detection probability (e.g., higher frequency tones, CMWA, BAWW, BLWA, YERA) had smaller EDR values than species with higher detection probability (e.g., lower-frequency tones, RBGR, toads, owls). EDR and MDD values were generally higher along roadsides than in forests (Mean EDR: Roadside = 612 ± 182 m, Coniferous = 365 ± 114 m, Deciduous = 378 ± 163 m; Mean MDD: Roadside = 674 ± 227 m, Coniferous = 364 ± 155 m, Deciduous = 425 ± 221 m). Human observers were consistently able to hear farther than the ARUs and had higher EDR and MDD values. SM2s had the lowest EDR and MDD values (mean ratios across all sounds: $EDR_{SM2}/EDR_{Human} = 0.789 \pm 0.624$; $MDD_{SM2}/MDD_{Human} = 0.558 \pm 0.212$; Figure 2). RiverForks ($EDR_{RiverForks}/EDR_{Human} = 0.940 \pm 0.680$; $MDD_{RiverForks}/MDD_{Human} = 0.861 \pm 0.354$) and SM3 ($EDR_{SM3}/EDR_{Human} = 0.897 \pm 0.137$; $MDD_{SM3}/MDD_{Human} = 0.770 \pm 0.259$) had the most similar detection distance relative to humans. These ratios increased at higher sound frequencies for the SM2 and RiverForks but decreased with Zoom recorders (Fig. 2; Appendix 1, 2). Thus, SM2s require larger correction factors ($= [EDR_{SM2}/EDR_{Human}]^{-1}$) than other types of ARUs relative to humans.

Using known distance data to estimate effects of sound amplitude on detection

Effective detection radii for sounds at different amplitudes in different vegetation types

For all species and tones in the sound amplitude study, detection probability declined with increasing distance (mean \pm SD across all models $\beta_x = 2.913 \times 10^{-4} \pm 1.476 \times 10^{-4}$; Table 6) and decreasing sound amplitude (mean $\beta_{SPL} = 0.183 \pm 0.037$). Probability of detection at a given distance was higher in open vegetation than in closed vegetation (mean $\beta_{OpenHabitat} = 1.983 \pm 0.899$, relative to closed habitat). The best model predicting detection of each species or tone generally included distance, vegetation type, and amplitude (Table 3). Three sounds (1414 Hz, LEOW, YERA) included wind in their top performing model, two sounds (4000 Hz, WETO) included humidity, and one sound (CMWA) included both wind and humidity. Wind negatively influenced detectability (mean $\beta_{Wind} = -0.168 \pm 0.076$) for all four sounds while humidity had a positive effect for CMWA ($\beta_{Humidity} = 0.023$) and WETO ($\beta_{Humidity} = 0.042$) but negative for 4000 Hz ($\beta_{Humidity} = -0.036$). Mean wind speed averaged over the duration of the broadcast sequence at each distance along a transect was 4.0 ± 2.8 km/h. Mean temperatures during each broadcast was

Fig. 2. Correction factors for (A) EDR and (B) MDD of various ARU types at different frequencies. ARUs are in comparison to human detection as a reference. Correction factors are calculated using a ratio of detection area of ARU to detection area of a field observer (Appendix 1, 2). Correction factors less than 1 mean smaller detection distances than human observers in the field and can be applied to ARU data to standardize it with data from HPC.



15.2 ± 6.4 °C. Relative humidity was $50.5 \pm 14.2\%$. Performance for all models was excellent (AUC: min = 0.8705, max = 0.9836, median = 0.9495; Table 3).

As in the human-ARU comparison study, species with relatively low detection probability (e.g., BAWW, CMWA) had smaller EDR values than species with relatively high detection probability (e.g., owls; Appendix 3). EDR values were generally higher in open vegetation than closed vegetation and increased as sound amplitude increased. When sounds were pooled into one general model, we found no significant interaction effects between SPL and the type of sound (i.e., species or tone) indicating a consistent positive relationship between EDR and SPL for all sounds broadcasted (Fig. 3). Many EDR values were undefined at higher broadcast SPL in open vegetation because of an inadequate number of nondetections. For EDR to be defined, nondetections must occur at the furthest distances, which did not occur at higher sound amplitudes.

DISCUSSION

Detectability of avian vocalizations can be influenced by the surrounding environment (Darras et al. 2016, Yip et al. 2017) and by the methods used to record and identify observations (Haselmayer and Quinn 2000). We compared detection distances of different ARUs as well as human observers in the field and

Table 6. Model coefficients (amplitude, distance, habitat type, interactions between habitat type and distance, wind, humidity) for the top AIC-ranked model predicting probability of detecting each species and tone, in listening trials conducted along 20 transects in the Blackfoot-Cooking Lake Natural Area near Edmonton, Alberta, Canada in 2014. “x” is equal to $-(\text{Distance})^2$. SPL = amplitude (dB). The reference level for open habitat is closed habitat. “NA” means that variable was not included in the top model for that sound.

Sound	Intercept	x	HabitatOPEN	SPL	Wind	Humidity	x*HabitatOPEN
1000Hz	-5.522 ± 0.8325	1.05E-04 ± 2.09E-05	2.151 ± 0.3579	0.1075 ± 0.01356	NA	NA	NA
1414Hz	-9.444 ± 1.16	1.74E-04 ± 3.29E-05	2.505 ± 0.6005	0.181 ± 0.02048	-0.1651 ± 0.06309	NA	-4.16E-05 ± 4.16E-05
2000Hz	-8.87 ± 1.232	2.05E-04 ± 3.60E-05	1.999 ± 0.6706	0.1708 ± 0.02141	NA	NA	-1.39E-04 ± 4.89E-05
2828Hz	-9.332 ± 1.204	1.55E-04 ± 2.55E-05	3.335 ± 0.4805	0.1725 ± 0.0205	NA	NA	NA
4000Hz	-8.304 ± 1.295	2.06E-04 ± 3.96E-05	3.444 ± 0.7512	0.1861 ± 0.02251	NA	-0.0356 ± 0.01425	6.09E-05 ± 4.81E-05
5656Hz	-8.75 ± 1.184	2.91E-04 ± 4.59E-05	2.197 ± 0.6653	0.1569 ± 0.01883	NA	NA	-1.68E-04 ± 5.14E-05
8000Hz	-8.673 ± 1.214	1.52E-04 ± 2.90E-05	1.334 ± 0.3882	0.1071 ± 0.01543	NA	NA	NA
BADO	-8.549 ± 1.046	1.73E-04 ± 3.29E-05	0.5262 ± 0.544	0.1614 ± 0.01756	NA	NA	-6.68E-05 ± 4.02E-05
BAWW	-11.46 ± 1.605	4.53E-04 ± 9.51E-05	2.023 ± 0.778	0.1832 ± 0.02288	NA	NA	-2.77E-04 ± 9.32E-05
BEKI	-15.62 ± 2.215	5.49E-04 ± 1.21E-04	2.134 ± 0.8948	0.2316 ± 0.03046	NA	NA	-4.11E-04 ± 1.19E-04
BHCO	-11.11 ± 1.447	3.37E-04 ± 5.96E-05	2.265 ± 0.6906	0.1859 ± 0.02231	NA	NA	-2.31E-04 ± 6.24E-05
BLWA	-10.33 ± 1.472	4.09E-04 ± 9.06E-05	1.271 ± 0.7414	0.1591 ± 0.01998	NA	NA	-2.95E-04 ± 9.21E-05
BOOW	-7.506 ± 1.05	1.85E-04 ± 3.42E-05	0.9213 ± 0.6025	0.1457 ± 0.01773	NA	NA	-8.26E-05 ± 4.37E-05
CATO	-12.3 ± 1.453	1.38E-04 ± 2.60E-05	2.844 ± 0.4705	0.1898 ± 0.02177	NA	NA	NA
CCSP	-13.21 ± 1.783	5.16E-04 ± 9.73E-05	2.498 ± 0.794	0.221 ± 0.02743	NA	NA	-3.60E-04 ± 9.33E-05
CMWA	-12.48 ± 2.066	2.82E-04 ± 9.71E-05	1.866 ± 0.7697	0.1466 ± 0.0229	-0.05099 ± 0.1022	0.02312 ± 0.016	-8.02E-05 ± 1.01E-04
CORA	-12.54 ± 1.567	2.33E-04 ± 4.63E-05	1.486 ± 0.6848	0.2076 ± 0.02417	NA	NA	-1.50E-04 ± 5.13E-05
DEJU	-11.94 ± 1.577	3.22E-04 ± 5.93E-05	2.774 ± 0.7522	0.1919 ± 0.02333	NA	NA	-1.96E-04 ± 6.31E-05
GGOW	-9.475 ± 1.07	1.31E-04 ± 2.39E-05	2.06 ± 0.3742	0.1564 ± 0.0168	NA	NA	NA
LEOW	-7.861 ± 0.9351	1.02E-04 ± 2.97E-05	0.5742 ± 0.527	0.1354 ± 0.01439	-0.09756 ± 0.05937	NA	6.13E-06 ± 3.86E-05
LISP	-11.07 ± 1.461	3.68E-04 ± 7.15E-05	1.741 ± 0.6862	0.1805 ± 0.02161	NA	NA	-2.49E-04 ± 7.50E-05
NSWO	-10.13 ± 1.253	2.57E-04 ± 3.77E-05	0.8892 ± 0.6186	0.184 ± 0.02056	NA	NA	-1.91E-04 ± 4.64E-05
OSFL	-8.271 ± 1.1	2.19E-04 ± 3.94E-05	2.247 ± 0.6157	0.145 ± 0.01765	NA	NA	-9.70E-05 ± 4.50E-05
OVEN	-14.44 ± 2.058	4.93E-04 ± 1.03E-04	3.408 ± 0.959	0.2366 ± 0.03041	NA	NA	-2.80E-04 ± 9.77E-05
PISI	-13.97 ± 1.972	5.63E-04 ± 1.13E-04	2.798 ± 0.9211	0.2329 ± 0.0294	NA	NA	-4.07E-04 ± 1.09E-04
RBGR	-9.132 ± 1.157	2.59E-04 ± 4.40E-05	0.6957 ± 0.598	0.1522 ± 0.01721	NA	NA	-1.92E-04 ± 4.89E-05
RBNV	-12.5 ± 1.646	3.32E-04 ± 5.34E-05	2.046 ± 0.777	0.2222 ± 0.02729	NA	NA	-2.24E-04 ± 5.73E-05
TEWA	-15.43 ± 2.033	4.40E-04 ± 1.11E-04	2.095 ± 0.8189	0.2191 ± 0.02727	NA	NA	-2.87E-04 ± 1.11E-04
WAVI	-12.28 ± 1.496	4.03E-04 ± 7.74E-05	1.22 ± 0.71	0.2048 ± 0.02313	NA	NA	-2.99E-04 ± 8.00E-05
WETO	-13.72 ± 1.78	2.04E-04 ± 3.84E-05	1.527 ± 0.649	0.19 ± 0.02214	NA	0.04153 ± 0.01314	-1.18E-04 ± 4.55E-05
WTSP	-11.42 ± 1.575	2.44E-04 ± 4.56E-05	3.909 ± 0.858	0.2021 ± 0.02622	NA	NA	-1.01E-04 ± 5.44E-05
YERA	-14.08 ± 2.14	3.79E-04 ± 1.21E-04	1.593 ± 0.8316	0.1949 ± 0.02761	-0.1427 ± 0.09392	NA	-2.44E-04 ± 1.22E-04

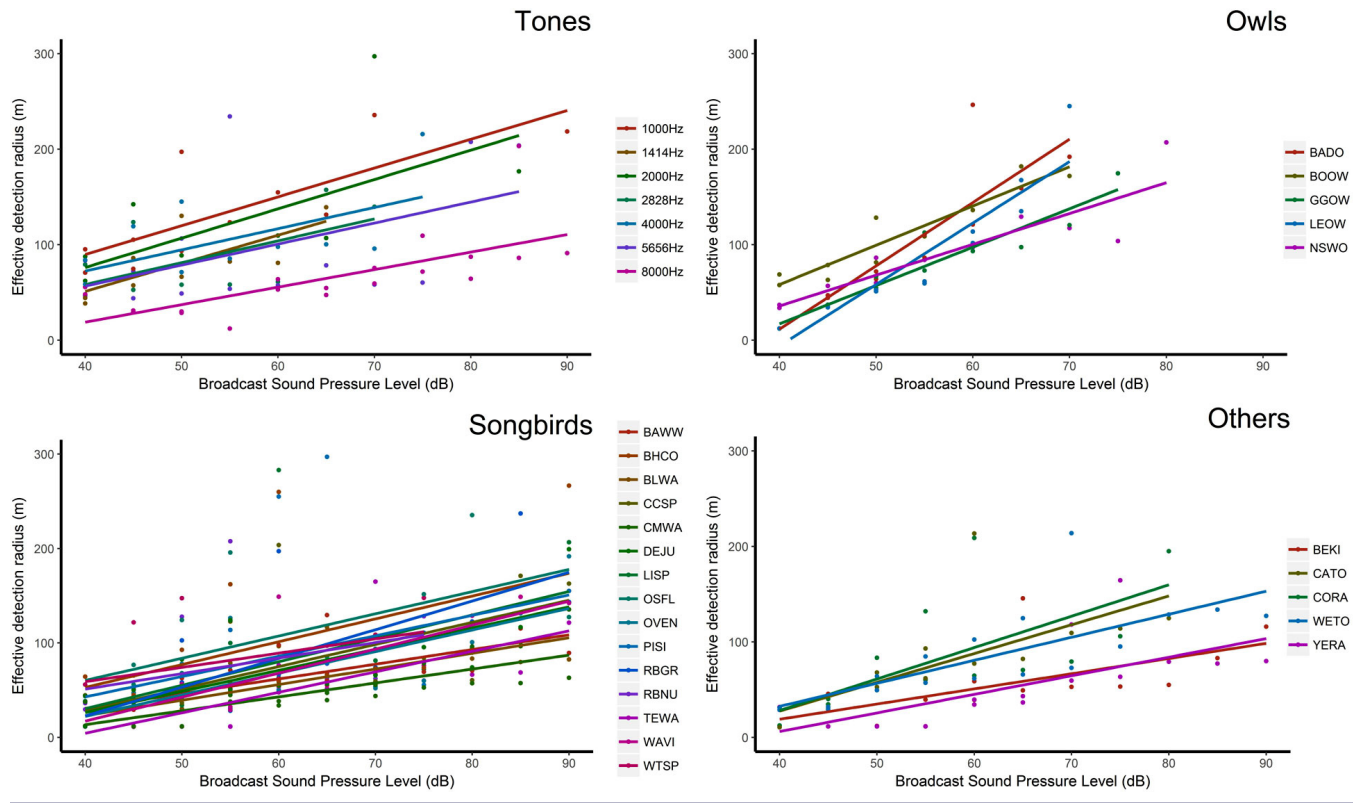
found differences in detectability depending on which method was used. Using the ARU-human comparison calculated here, we conclude that ARU data can be integrated with HPC datasets into larger analyses to increase the scope of inferences made about birds (Cumming et al. 2010). For example, EDR has been estimated for over 100 species by the Boreal Avian Modelling Project (hereafter BAM; <http://www.borealbirds.ca/>) using human-based distance estimation. Similarly, MDD for all North American species have been agreed upon by Partners in Flight (hereafter PIF; Rosenberg and Blancher 2005). For example, BAM estimates EDR for BAWW to be 50.1 m and PIF uses a MDD value of 100 m (PIF Science Committee 2013). Thus, for surveys in deciduous forest using an SM2 wildlife recorder, the EDR correction factor calculated from our study would be 0.757 and the MDD correction factor 0.779 (Appendix 1, 2). The corrected EDR would then be 37.9 m and corrected MDD would be 77.9 m for counts done using an SM2 in similar habitat. Ornithologists can directly compare density estimates from HPC and ARU data after standardizing both data types using this technique, enabling organizations like BAM or PIF to augment their existing HPC data with ARU data.

Human field observers had the highest detectability and detection distances in comparison to recordings from the SM2s, SM3s, RiverForks, and Zoom recorders. SM2s had the lowest detectability and detection distances followed by Zoom recorders,

RiverForks, and SM3s. The use of ARUs to record animals introduces additional static, white noise, and electronic interference during the detection process of avian vocalizations, likely contributing to the patterns of decreasing detectability from recordings. However, we presented observers with a limited variety of species and sounds and in the first experiment, observers knew the order that the sounds would be occurring. When sounds are unpredictable and there is uncertainty about what species may be present, detections from recordings will likely increase relative to field surveys from humans because of the opportunity to double check observations in a lab-based environment.

Probability of detecting species declined more rapidly with increasing distance in closed vegetation than in open vegetation in both of our experiments (first experiment: roadside vs forest, second experiment: open grassland vs closed forest). These results are consistent with previously documented differences in detection between vegetation types (Schieck 1997, Pacifici et al. 2008). However, we observed differences in the effect of weather variables between experiments, which may have been due to the distance over which the experiments occurred. Weather effects were influential for sounds with larger EDR values (17/32 sounds; Table 5) in our first experiment as in Holland (2001) and Simons et al. (2007), but were not as prevalent in our second experiment (6/32 sounds; Table 3). In our second experiment, broadcasts only

Fig. 3. Influence of the sound pressure level (dB) of our song broadcasts on EDR for tones, owls, songbirds, and all other species, plotted separately. We found no statistically significant interaction between different species/tones although EDR for two species of owl (GGOW and LEOW) appear to increase at a greater rate with distance than other sounds.



occurred to a maximum of 150 m, meaning weather variables may not have as much distance over which to act on broadcasted signals, suggesting there may be an interaction between weather conditions, distance, and sound transmission. Humidity had a consistently positive effect on detectability except for one species (CMWA) in our first experiment and one tone (4000Hz) in our second. However, the relationship between wind and detectability differed between the first (positive relationship) and second (negative relationship) experiment although wind was not included in many of our top performing models. We did not record the direction of the wind relative to the direction of our broadcasts, which may have contributed to this pattern. We also recorded higher but more consistent wind speeds in our second experiment relative to the first. A more limited range of wind speeds in the second experiment may be the reason wind was not included in those models as often. Knowing how factors like weather influences the area sampled is crucial to converting counts from ARUs and humans to accurate density estimates and is an area that we argue needs more work.

We found that EDR was consistently, positively correlated with broadcast SPL regardless of species (Fig. 3). This is important for two reasons. First, we broadcast sounds at 90 dB, which we believe to be the upper range of amplitudes that birds might vocalize at (Brumm 2004, Patricelli et al. 2007). We also had our speaker oriented directly at the receiver, which may result in unrealistic and overestimated EDRs. However, the importance of

this study lies in the relative difference in EDR between treatments, which should remain the same regardless of SPL. Given that EDR increased consistently with SPL for all species (Fig. 3), we believe singing volume could be estimated for real birds using predictions from our EDR models, corrections factors, and applying our model predictions to EDRs from BAM's human based estimates of EDR, albeit with varying degrees of uncertainty depending on model performance. This would also be under the assumption that EDRs estimated from BAM were calculated under similar conditions and that human observers estimate EDR accurately. It is not clear how accurate EDR measurements are by humans and our results show the importance of environmental variables such as the openness of the surrounding environment. Although our best performing models suggest that EDR increases consistently with SPL for most sounds, there were outlier sounds (BADO, LEOW) where EDR increased differently relative to the general trend (Fig. 3), possibly because of uncertainty in our EDR estimates.

The second reason that the consistent response of EDR to SPL is important is that it may provide a simpler way to calibrate ARUs to humans and each other. More recorder models are becoming available and the ones currently in use are routinely being updated with newer models, which have different gain settings, sensitivities, and residual electronic noise. All of these factors influence the area sampled for birds relative to humans and other ARUs (Rempel et al. 2005). Sound frequency acted differently on each

recorder suggesting that microphone frequency response plays a role in detectability. Detectability decreased and differences in EDR and resulting correction factors increased with frequency for SM2s while the opposite was observed with SM3s and Zoom recorders (Fig. 2). The method we used to compare EDR between various recorders and human observers in our first experiment provided high resolution information on relative differences in detection distance, but was time consuming to carry out. We argue that, in the future, we could calibrate EDR at different amplitudes for multiple brands of ARUs using relatively few distances as in our second experiment because EDR decreased consistently for most sounds as SPL declines and would be comparable to the relative difference in EDR at 90 dB. This would allow researchers to calculate a correction factor more quickly based on the relative difference.

Our results provide further evidence supporting conclusions of previous researchers (Haselmayer and Quinn 2000, Hobson et al. 2002, Celis-Murillo et al. 2009) that the counts derived from both ARUs and human observers are relatively comparable. However, our study tested detectability under relatively controlled conditions through broadcasts and with a limited variety of species and sounds. The results found in this study may differ when field observers must identify overlapping vocalizations, unfamiliar species, or sounds in acoustically busy sampling periods that would likely have a larger influence on detectability than with ARUs. Although human observers appeared to generally detect more of the broadcasted sounds than different ARUs (particularly the SM2+), EDR and effective area sampled by some ARUs was comparable to that for human observers for some species. Furthermore, differences between recorders should be irrelevant if we can standardize data from different sources by offsetting varying detection distances and areas of ARUs. Influences of weather on EDR can be controlled to an extent by survey protocol (e.g., survey only when wind is < 2 on the Beaufort scale, when there is no rain, etc.) and corrections for variables such as vegetation/habitat type can be calculated separately (Yip et al. 2017) and applied in conjunction with corrections calculated in this study.

Although we demonstrate that simultaneous comparisons of HPC and ARU data potentially enable the calculation of EDR and densities of birds from ARU recordings, this approach still relies on accurate distance estimation during HPCs, an assumption that is frequently violated during avian surveys (Alldredge et al. 2007, Nadeau and Conway 2012). Errors in distance estimation can bias EDR and bird density calculations and will persist when using our correction approach for ARU data. There are also factors unrelated to distance estimation that should also be considered before collating these two types of point counts for the same analysis. First, some detections in HPC may be only visual, particularly of rare or of quiet species that are unavailable to ARUs, or rarely vocalizing species that are unlikely to be detected in short-duration recordings (Haselmayer and Quinn 2000, Hutto and Stutzman 2009). Second, because ARUs provide a permanent record for review, there may be a negative bias associated with species detection in HPC relative to ARU recordings because people listening to ARU data can relisten to a sound (Tegeler et al. 2012). This bias could be modeled as observer effects. Calibration of ARUs should also be an important part of the permanent record. Microphone sensitivity

can decrease with use (Turgeon et al. 2017) and influence the area surveyed. Microphone quality should be checked regularly to ensure minimal variation in detection distance within recorder models. Variation in detectability between observers can be large and influence results in both HPC and from ARU recordings in part because of differences in hearing ability and experience identifying species (Sauer et al. 1994). Observer variation within ARU point counts is likely lower than HPC as a permanent record allows multiple observers to process recordings and double check unknown species. Our study should minimize interobserver variability because observers were presented with a limited number of sounds that they could review prior to the experiment. Observers were also composed of males and females between the ages of 18 and 28 who are more likely to have similar hearing levels (Emlen and DeJong 1992).

Our objectives were to investigate relative differences between ARUs and HPC. We provide methods for standardizing and correcting detection distances to derive avian densities from ARUs by accounting for differences in the area surveyed through each method. We used the ecosystems presented in this study as a case study to demonstrate application of this method, however these methods can be applied to other habitat types to broaden their use. This approach to density estimation would be more logistically feasible and affordable than studies using microphone arrays to obtain density (Efford et al. 2009). Integration of data from ARUs and HPCs could allow for larger meta-analyses to make environmental inferences about interactions between birds and the environment at larger spatial scales (Cumming et al. 2010).

Responses to this article can be read online at:
<http://www.ace-eco.org/issues/responses.php/997>

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Appendix 1. Detection radius, detection area, and correction factors calculated for EDR for different songs and tones detected by four brands of autonomous recording units (ARUs), from listening trials conducted at 20 transects near Calling Lake and Lac La Biche, Alberta, Canada in 2014. Correction factors are relative to human observers in the field and are calculated using a ratio of ARU to Field Observer detection areas. Values less than 1 indicate a smaller detection area relative to human observers and values greater than 1 indicate greater detection area relative to human observers. Correction factors can be applied to ARU data to standardize survey areas with those of observers in the field. “NA” indicates EDR values that could not be solved by our models due to uncertainty caused by insufficient non-detections.

Sound	Habitat	Effective Detection Radius (m) \pm 90% CI					Effective Detection Area (m ²)					EDR Correction Factor				
		Human	RiverForks	SM2	SM3	Zoom	Human	RiverForks	SM2	SM3	Zoom	Human	RiverForks	SM2	SM3	Zoom
1000Hz	Conifer	612 \pm 118	586 \pm 106	549 \pm 91	553 \pm 87	540 \pm 84	1175276	1077627	946839	961247	915295	1.0000	0.9169	0.8056	0.8179	0.7788
1000Hz	Deciduous	676 \pm 141	642 \pm 119	594 \pm 105	600 \pm 105	583 \pm 98	1436767	1293480	1109522	1129359	1066455	1.0000	0.9003	0.7722	0.7860	0.7423
1000Hz	Road	1078 \pm 611	952 \pm 376	815 \pm 254	829 \pm 245	786 \pm 223	3650033	2848426	2086584	2157865	1939301	1.0000	0.7804	0.5717	0.5912	0.5313
1414Hz	Conifer	601 \pm 110	568 \pm 94	536 \pm 86	545 \pm 85	529 \pm 82	1135418	1014684	902944	934322	879387	1.0000	0.8937	0.7953	0.8229	0.7745
1414Hz	Deciduous	658 \pm 127	615 \pm 113	575 \pm 93	587 \pm 100	566 \pm 91	1359334	1189839	1039059	1080828	1007986	1.0000	0.8753	0.7644	0.7951	0.7415
1414Hz	Road	NA	903 \pm 323	788 \pm 224	818 \pm 237	766 \pm 200	NA	2560424	1951144	2103814	1844379	NA	NA	NA	NA	NA
2000Hz	Conifer	567 \pm 105	553 \pm 92	531 \pm 86	551 \pm 92	533 \pm 85	1010637	961422	887345	952392	893324	1.0000	0.9513	0.8780	0.9424	0.8839
2000Hz	Deciduous	680 \pm 142	656 \pm 128	621 \pm 115	652 \pm 126	624 \pm 115	1452730	1353163	1210887	1335343	1222048	1.0000	0.9315	0.8335	0.9192	0.8412
2000Hz	Road	1223 \pm 0	1099 \pm 610	953 \pm 396	1079 \pm 537	964 \pm 406	4698534	3795315	2854582	3658388	2917393	1.0000	0.8078	0.6075	0.7786	0.6209
2828Hz	Conifer	566 \pm 98	570 \pm 96	536 \pm 85	571 \pm 96	549 \pm 89	1005770	1019704	903720	1022910	948115	1.0000	1.0139	0.8985	1.0170	0.9427
2828Hz	Deciduous	707 \pm 150	715 \pm 146	652 \pm 121	717 \pm 150	676 \pm 130	1570691	1604941	1335227	1612896	1434465	1.0000	1.0218	0.8501	1.0269	0.9133
2828Hz	Road	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4000Hz	Conifer	450 \pm 74	451 \pm 74	439 \pm 72	458 \pm 76	432 \pm 68	635063	639295	604230	658029	587147	1.0000	1.0067	0.9514	1.0362	0.9245
4000Hz	Deciduous	495 \pm 85	497 \pm 84	481 \pm 81	506 \pm 93	473 \pm 73	771104	777352	726114	805228	701584	1.0000	1.0081	0.9417	1.0443	0.9098
4000Hz	Road	1308 \pm 783	1346 \pm 679	1093 \pm 465	NA	1006 \pm 326	5370930	5689426	3751783	NA	3177717	1.0000	1.0593	0.6985	NA	0.5917
5656Hz	Conifer	358 \pm 62	351 \pm 60	333 \pm 52	361 \pm 63	348 \pm 57	403523	387750	347486	408884	381134	1.0000	0.9609	0.8611	1.0133	0.9445
5656Hz	Deciduous	301 \pm 52	297 \pm 49	285 \pm 45	302 \pm 52	295 \pm 47	284257	276339	255260	286907	272962	1.0000	0.9721	0.8980	1.0093	0.9603
5656Hz	Road	743 \pm 210	686 \pm 168	571 \pm 135	765 \pm 207	664 \pm 161	1734810	1476581	1024515	1838439	1385027	1.0000	0.8511	0.5906	1.0597	0.7984
8000Hz	Conifer	219 \pm 46	203 \pm 37	150 \pm 26	198 \pm 34	184 \pm 30	150853	129882	70873	123612	106319	1.0000	0.8610	0.4698	0.8194	0.7048
8000Hz	Deciduous	173 \pm 41	165 \pm 35	132 \pm 24	162 \pm 33	154 \pm 29	93671	85135	55077	82396	74337	1.0000	0.9089	0.5880	0.8796	0.7936
8000Hz	Road	439 \pm 111	342 \pm 77	187 \pm 45	320 \pm 74	268 \pm 61	605363	367344	109498	321258	225806	1.0000	0.6068	0.1809	0.5307	0.3730
BADO	Conifer	550 \pm 117	476 \pm 81	459 \pm 77	464 \pm 74	407 \pm 56	951248	711751	660835	676513	519872	1.0000	0.7482	0.6947	0.7112	0.5465
BADO	Deciduous	658 \pm 166	541 \pm 100	516 \pm 88	524 \pm 90	445 \pm 64	1362132	919221	836029	861281	622494	1.0000	0.6748	0.6138	0.6323	0.4570
BADO	Road	842 \pm 360	630 \pm 155	591 \pm 134	603 \pm 133	491 \pm 88	2229825	1246571	1098354	1142356	757137	1.0000	0.5590	0.4926	0.5123	0.3396
BAWW	Conifer	238 \pm 50	206 \pm 35	201 \pm 33	221 \pm 42	201 \pm 35	178608	132841	127386	153547	127431	1.0000	0.7438	0.7132	0.8597	0.7135
BAWW	Deciduous	213 \pm 43	189 \pm 33	185 \pm 31	200 \pm 36	185 \pm 32	142657	111873	107979	126205	108011	1.0000	0.7842	0.7569	0.8847	0.7571
BAWW	Road	515 \pm 126	319 \pm 71	304 \pm 67	388 \pm 89	304 \pm 70	834320	319744	289867	473396	290097	1.0000	0.3832	0.3474	0.5674	0.3477
BEKI	Conifer	294 \pm 50	286 \pm 46	257 \pm 39	297 \pm 51	287 \pm 46	272203	256849	207309	277682	258925	1.0000	0.9436	0.7616	1.0201	0.9512
BEKI	Deciduous	224 \pm 39	221 \pm 38	206 \pm 31	226 \pm 42	221 \pm 37	158083	152779	133765	159915	153511	1.0000	0.9664	0.8462	1.0116	0.9711
BEKI	Road	619 \pm 160	550 \pm 123	401 \pm 84	647 \pm 156	559 \pm 125	1202325	951184	504616	1317122	980290	1.0000	0.7911	0.4197	1.0955	0.8153
BHCO	Conifer	341 \pm 58	333 \pm 54	293 \pm 42	339 \pm 58	334 \pm 55	366090	348880	269548	361559	350184	1.0000	0.9530	0.7363	0.9876	0.9566
BHCO	Deciduous	318 \pm 54	312 \pm 50	278 \pm 41	317 \pm 52	312 \pm 51	318681	305559	242938	315242	306559	1.0000	0.9588	0.7623	0.9892	0.9620
BHCO	Road	811 \pm 241	717 \pm 178	467 \pm 102	784 \pm 209	724 \pm 180	2067520	1617024	683986	1930874	1645432	1.0000	0.7821	0.3308	0.9339	0.7958
BLWA	Conifer	220 \pm 40	209 \pm 36	199 \pm 32	214 \pm 37	209 \pm 36	151680	137797	124066	144512	137427	1.0000	0.9085	0.8179	0.9527	0.9060

BLWA	Deciduous	197 ± 36	189 ± 33	181 ± 29	193 ± 33	189 ± 32	121478	112408	103100	116837	112162	1.0000	0.9253	0.8487	0.9618	0.9233
BLWA	Road	517 ± 136	414 ± 94	346 ± 80	458 ± 108	412 ± 93	838861	538708	376011	658290	533089	1.0000	0.6422	0.4482	0.7847	0.6355
BOOW	Conifer	593 ± 127	548 ± 105	536 ± 99	529 ± 90	473 ± 74	1106172	944125	903878	879743	702424	1.0000	0.8535	0.8171	0.7953	0.6350
BOOW	Deciduous	665 ± 156	603 ± 117	588 ± 115	578 ± 106	507 ± 76	1389224	1142871	1084420	1049866	806810	1.0000	0.8227	0.7806	0.7557	0.5808
BOOW	Road	NA	827 ± 287	788 ± 259	766 ± 220	620 ± 133	NA	2150999	1952887	1843612	1205750	NA	NA	NA	NA	NA
CATO	Conifer	369 ± 54	360 ± 52	345 ± 47	358 ± 52	346 ± 48	428512	407623	372931	402582	375217	1.0000	0.9513	0.8703	0.9395	0.8756
CATO	Deciduous	453 ± 79	437 ± 70	409 ± 61	433 ± 70	411 ± 60	644911	598735	526759	587920	531331	1.0000	0.9284	0.8168	0.9116	0.8239
CATO	Road	527 ± 110	501 ± 100	461 ± 82	495 ± 99	464 ± 86	871521	789262	668798	770577	676186	1.0000	0.9056	0.7674	0.8842	0.7759
CCSP	Conifer	323 ± 56	304 ± 50	288 ± 45	313 ± 56	306 ± 49	327909	290576	259790	308570	293834	1.0000	0.8861	0.7923	0.9410	0.8961
CCSP	Deciduous	221 ± 38	215 ± 35	208 ± 33	218 ± 37	215 ± 36	153281	144597	136545	148918	145399	1.0000	0.9433	0.8908	0.9715	0.9486
CCSP	Road	717 ± 192	561 ± 129	474 ± 104	627 ± 153	572 ± 135	1615921	989455	704981	1234604	1028273	1.0000	0.6123	0.4363	0.7640	0.6363
CMWA	Conifer	204 ± 58	171 ± 37	143 ± 29	178 ± 42	163 ± 35	130129	92195	64544	99939	83796	1.0000	0.7085	0.4960	0.7680	0.6439
CMWA	Deciduous	183 ± 50	159 ± 34	136 ± 25	164 ± 36	152 ± 31	105434	79073	57826	84702	72813	1.0000	0.7500	0.5485	0.8034	0.6906
CMWA	Road	NA	272 ± 101	189 ± 53	303 ± 128	243 ± 80	NA	232105	111667	288352	185335	NA	NA	NA	NA	NA
CORA	Conifer	339 ± 52	336 ± 51	324 ± 45	335 ± 49	324 ± 46	360271	355630	329144	351526	328965	1.0000	0.9871	0.9136	0.9757	0.9131
CORA	Deciduous	402 ± 64	398 ± 62	377 ± 55	395 ± 61	377 ± 54	506688	497556	447208	489560	446878	1.0000	0.9820	0.8826	0.9662	0.8820
CORA	Road	617 ± 162	604 ± 149	538 ± 117	593 ± 141	538 ± 112	1195481	1145859	909937	1104322	908571	1.0000	0.9585	0.7611	0.9237	0.7600
DEJU	Conifer	338 ± 58	325 ± 53	305 ± 47	332 ± 56	323 ± 51	359372	331614	291619	345693	328565	1.0000	0.9228	0.8115	0.9619	0.9143
DEJU	Deciduous	272 ± 48	265 ± 44	253 ± 39	268 ± 47	264 ± 44	231936	220049	201693	226161	218702	1.0000	0.9487	0.8696	0.9751	0.9429
DEJU	Road	857 ± 266	691 ± 166	543 ± 124	765 ± 205	677 ± 168	2306824	1500568	925935	1839584	1440084	1.0000	0.6505	0.4014	0.7975	0.6243
GGOW	Conifer	451 ± 81	406 ± 62	417 ± 68	410 ± 61	370 ± 48	640105	517272	545437	528611	430366	1.0000	0.8081	0.8521	0.8258	0.6723
GGOW	Deciduous	552 ± 113	474 ± 76	492 ± 86	482 ± 78	420 ± 59	958741	707208	760929	728575	554202	1.0000	0.7376	0.7937	0.7599	0.5781
GGOW	Road	754 ± 288	585 ± 131	619 ± 163	598 ± 144	491 ± 88	1787139	1074656	1203800	1124781	757050	1.0000	0.6013	0.6736	0.6294	0.4236
LEOW	Conifer	439 ± 79	375 ± 52	376 ± 53	384 ± 56	350 ± 46	604238	442240	444761	463471	384757	1.0000	0.7319	0.7361	0.7670	0.6368
LEOW	Deciduous	604 ± 142	464 ± 78	466 ± 76	481 ± 81	419 ± 61	1147801	676832	682755	727862	550874	1.0000	0.5897	0.5948	0.6341	0.4799
LEOW	Road	761 ± 298	525 ± 110	528 ± 109	550 ± 121	462 ± 81	1818378	864916	874612	950033	669342	1.0000	0.4757	0.4810	0.5225	0.3681
LISP	Conifer	340 ± 56	335 ± 55	311 ± 46	335 ± 54	331 ± 53	362661	353478	303974	353358	344209	1.0000	0.9747	0.8382	0.9743	0.9491
LISP	Deciduous	315 ± 55	312 ± 51	292 ± 44	312 ± 51	308 ± 51	312364	305527	267827	305438	298578	1.0000	0.9781	0.8574	0.9778	0.9559
LISP	Road	883 ± 291	815 ± 222	582 ± 133	814 ± 227	757 ± 199	2450595	2084615	1063347	2080457	1798947	1.0000	0.8507	0.4339	0.8490	0.7341
NSWO	Conifer	514 ± 101	520 ± 101	492 ± 86	490 ± 85	461 ± 75	831479	848211	759484	755817	666715	1.0000	1.0201	0.9134	0.9090	0.8018
NSWO	Deciduous	654 ± 150	664 ± 155	609 ± 125	606 ± 120	553 ± 98	1342154	1386295	1164038	1155446	959430	1.0000	1.0329	0.8673	0.8609	0.7148
NSWO	Road	NA	1019 ± 570	846 ± 344	840 ± 304	712 ± 200	NA	3261993	2250769	2218867	1593628	NA	NA	NA	NA	NA
OSFL	Conifer	360 ± 57	356 ± 56	337 ± 49	359 ± 57	350 ± 54	407639	399089	357836	403974	385462	1.0000	0.9790	0.8778	0.9910	0.9456
OSFL	Deciduous	385 ± 66	381 ± 63	358 ± 55	383 ± 65	373 ± 62	466053	454911	402075	461269	437290	1.0000	0.9761	0.8627	0.9897	0.9383
OSFL	Road	672 ± 237	649 ± 204	552 ± 139	662 ± 216	614 ± 182	1419791	1321209	956249	1376306	1182781	1.0000	0.9306	0.6735	0.9694	0.8331
OVEN	Conifer	325 ± 52	315 ± 47	298 ± 43	319 ± 49	313 ± 46	331061	311820	278854	319042	308335	1.0000	0.9419	0.8423	0.9637	0.9314
OVEN	Deciduous	268 ± 46	262 ± 43	252 ± 39	264 ± 43	261 ± 41	225414	216326	199929	219777	214643	1.0000	0.9597	0.8869	0.9750	0.9522
OVEN	Road	810 ± 241	688 ± 167	550 ± 131	729 ± 201	670 ± 165	2059789	1488393	951477	1668686	1412204	1.0000	0.7226	0.4619	0.8101	0.6856
PISI	Conifer	309 ± 54	296 ± 48	281 ± 44	305 ± 52	298 ± 48	299449	275404	248338	292895	278887	1.0000	0.9197	0.8293	0.9781	0.9313
PISI	Deciduous	251 ± 44	244 ± 41	236 ± 36	249 ± 43	245 ± 43	198113	187294	174370	195222	188899	1.0000	0.9454	0.8802	0.9854	0.9535
PISI	Road	690 ± 184	576 ± 134	484 ± 105	654 ± 157	590 ± 138	1494823	1041080	737311	1344611	1092670	1.0000	0.6965	0.4932	0.8995	0.7310
RBGR	Conifer	352 ± 54	355 ± 53	337 ± 48	357 ± 55	345 ± 49	388454	396463	357506	399853	372913	1.0000	1.0206	0.9203	1.0293	0.9600
RBGR	Deciduous	460 ± 82	468 ± 82	429 ± 67	472 ± 80	445 ± 72	665431	689281	579496	699595	621090	1.0000	1.0358	0.8709	1.0513	0.9334
RBGR	Road	724 ± 246	757 ± 265	619 ± 161	772 ± 271	667 ± 191	1646605	1800795	1204587	1872936	1399394	1.0000	1.0936	0.7316	1.1375	0.8499
RBNU	Conifer	384 ± 54	383 ± 53	367 ± 49	385 ± 55	372 ± 52	462807	462006	422414	464594	435349	1.0000	0.9983	0.9127	1.0039	0.9407
RBNU	Deciduous	457 ± 71	457 ± 71	429 ± 62	459 ± 70	438 ± 63	657096	655483	578549	660704	603090	1.0000	0.9975	0.8805	1.0055	0.9178
RBNU	Road	686 ± 200	685 ± 189	601 ± 143	691 ± 189	626 ± 146	1480552	1472391	1133737	1498995	1231977	1.0000	0.9945	0.7658	1.0125	0.8321
TEWA	Conifer	242 ± 44	227 ± 36	205 ± 30	237 ± 41	232 ± 37	184312	161263	131965	176926	168614	1.0000	0.8749	0.7160	0.9599	0.9148
TEWA	Deciduous	200 ± 39	191 ± 34	177 ± 28	197 ± 37	194 ± 36	125623	114471	98887	122147	118127	1.0000	0.9112	0.7872	0.9723	0.9403
TEWA	Road	625 ± 159	447 ± 98	328 ± 71	553 ± 138	491 ± 115	1227152	628779	337030	960241	757566	1.0000	0.5124	0.2746	0.7825	0.6173
WAVI	Conifer	325 ± 54	319 ± 52	299 ± 44	324 ± 51	318 ± 50	330968	320161	280277	329029	317975	1.0000	0.9673	0.8468	0.9941	0.9607
WAVI	Deciduous	283 ± 48	280 ± 48	266 ± 42	283 ± 47	279 ± 47	252295	245966	221726	251166	244673	1.0000	0.9749	0.8788	0.9955	0.9698
WAVI	Road	787 ± 239	719 ± 181	548 ± 125	774 ± 219	707 ± 172	1946153	1623847	943138	1880981	1569126	1.0000	0.8344	0.4846	0.9665	0.8063
WETO	Conifer	340 ± 47	327 ± 44	312 ± 40	326 ± 43	306 ± 37	364208	335585	305270	333213	293587	1.0000	0.9214	0.8382	0.9149	0.8061

WETO	Deciduous	386 ± 57	367 ± 53	346 ± 47	365 ± 51	337 ± 44	468266	421989	375143	418246	357653	1.0000	0.9012	0.8011	0.8932	0.7638
WETO	Road	449 ± 84	419 ± 75	388 ± 61	417 ± 73	377 ± 59	633332	551529	474144	545152	446545	1.0000	0.8708	0.7487	0.8608	0.7051
WTSP	Conifer	398 ± 65	394 ± 64	379 ± 57	404 ± 70	394 ± 64	497421	488406	450744	512106	487937	1.0000	0.9819	0.9062	1.0295	0.9809
WTSP	Deciduous	427 ± 67	423 ± 66	404 ± 61	434 ± 70	422 ± 66	572980	561051	511915	592552	560432	1.0000	0.9792	0.8934	1.0342	0.9781
WTSP	Road	721 ± 239	700 ± 218	623 ± 169	758 ± 289	699 ± 214	1634891	1541379	1219736	1805002	1536714	1.0000	0.9428	0.7461	1.1041	0.9399
YERA	Conifer	212 ± 44	568 ± 41	536 ± 28	207 ± 43	203 ± 39	140596	1014684	902944	134210	129845	1.0000	7.2170	6.4223	0.9546	0.9235
YERA	Deciduous	188 ± 39	183 ± 37	158 ± 27	185 ± 37	182 ± 35	111247	105054	78683	107211	104407	1.0000	0.9443	0.7073	0.9637	0.9385
YERA	Road	442 ± 119	384 ± 92	244 ± 55	402 ± 108	379 ± 98	614773	463702	187026	508896	451357	1.0000	0.7543	0.3042	0.8278	0.7342

Appendix 2. Detection radius, detection area, and correction factors calculated for MDD of different songs and tones detected by four brands of autonomous recording units (ARUs), from listening trials conducted at 20 transects near Calling Lake and Lac La Biche, Alberta, Canada in 2014.

Correction factors are relative to human observers in the field and are calculated using a ratio of ARU to Field Observer detection areas. Values less than 1 indicate a smaller detection area relative to human observers and values greater than 1 indicate greater detection area relative to human observers. Correction factors can be applied to ARU data to standardize survey areas with those of observers in the field.

Sound	Habitat	Maximum Detection Distance (m)					Maximum Detection Area (m ²)					MDD Correction Factor				
		Human	RiverForks	SM2	SM3	Zoom	Human	RiverForks	SM2	SM3	Zoom	Human	RiverForks	SM2	SM3	Zoom
1000Hz	Conifer	913	813	763	563	513	2615867	2073942	1826542	994020	825159	1.0000	0.7928	0.6983	0.3800	0.3154
1000Hz	Deciduous	913	763	763	713	713	2615867	1826542	1826542	1594849	1594849	1.0000	0.6983	0.6983	0.6097	0.6097
1000Hz	Road	1113	1113	913	1013	1013	3888212	3888212	2615867	3220623	3220623	1.0000	1.0000	0.6728	0.8283	0.8283
1414Hz	Conifer	913	763	763	563	463	2615867	1826542	1826542	994020	672006	1.0000	0.6983	0.6983	0.3800	0.2569
1414Hz	Deciduous	813	763	713	713	713	2073942	1826542	1594849	1594849	1594849	1.0000	0.8807	0.7690	0.7690	0.7690
1414Hz	Road	1113	1113	913	1013	1013	3888212	3888212	2615867	3220623	3220623	1.0000	1.0000	0.6728	0.8283	0.8283
2000Hz	Conifer	513	663	613	563	463	825159	1378865	1178588	994020	672006	1.0000	1.6710	1.4283	1.2046	0.8144
2000Hz	Deciduous	763	713	613	713	713	1826542	1594849	1178588	1594849	1594849	1.0000	0.8732	0.6453	0.8732	0.8732
2000Hz	Road	1113	1013	913	1013	913	3888212	3220623	2615867	3220623	2615867	1.0000	0.8283	0.6728	0.8283	0.6728
2828Hz	Conifer	513	613	363	513	413	825159	1178588	412825	825159	534562	1.0000	1.4283	0.5003	1.0000	0.6478
2828Hz	Deciduous	713	763	513	663	663	1594849	1826542	825159	1378865	1378865	1.0000	1.1453	0.5174	0.8646	0.8646
2828Hz	Road	913	1013	813	1013	913	2615867	3220623	2073942	3220623	2615867	1.0000	1.2312	0.7928	1.2312	1.0000
4000Hz	Conifer	413	388	363	388	363	534562	471730	412825	471730	412825	1.0000	0.8825	0.7723	0.8825	0.7723
4000Hz	Deciduous	513	513	388	513	413	825159	825159	471730	825159	534562	1.0000	1.0000	0.5717	1.0000	0.6478
4000Hz	Road	763	813	763	813	713	1826542	2073942	1826542	2073942	1594849	1.0000	1.1354	1.0000	1.1354	0.8732
5656Hz	Conifer	413	313	288	313	313	534562	306796	259672	306796	306796	1.0000	0.5739	0.4858	0.5739	0.5739
5656Hz	Deciduous	338	288	213	363	363	357847	259672	141863	412825	412825	1.0000	0.7257	0.3964	1.1536	1.1536
5656Hz	Road	563	563	513	613	563	994020	994020	825159	1178588	994020	1.0000	1.0000	0.8301	1.1857	1.0000
8000Hz	Conifer	238	188	163	188	188	177205	110447	82958	110447	110447	1.0000	0.6233	0.4681	0.6233	0.6233
8000Hz	Deciduous	188	188	113	163	138	110447	110447	39761	82958	59396	1.0000	1.0000	0.3600	0.7511	0.5378
8000Hz	Road	363	338	188	313	288	412825	357847	110447	306796	259672	1.0000	0.8668	0.2675	0.7432	0.6290
BADO	Conifer	813	463	388	463	363	2073942	672006	471730	672006	412825	1.0000	0.3240	0.2275	0.3240	0.1991
BADO	Deciduous	913	1013	763	513	338	2615867	3220623	1826542	825159	357847	1.0000	1.2312	0.6983	0.3154	0.1368
BADO	Road	1113	763	763	763	663	3888212	1826542	1826542	1826542	1378865	1.0000	0.4698	0.4698	0.4698	0.3546
BAWW	Conifer	263	163	138	213	238	216475	82958	59396	141863	177205	1.0000	0.3832	0.2744	0.6553	0.8186
BAWW	Deciduous	213	213	188	213	163	141863	141863	110447	141863	82958	1.0000	1.0000	0.7785	1.0000	0.5848
BAWW	Road	413	313	313	338	288	534562	306796	306796	357847	259672	1.0000	0.5739	0.5739	0.6694	0.4858
BEKI	Conifer	313	288	238	263	288	306796	259672	177205	216475	259672	1.0000	0.8464	0.5776	0.7056	0.8464
BEKI	Deciduous	263	263	213	213	188	216475	216475	141863	141863	110447	1.0000	1.0000	0.6553	0.6553	0.5102
BEKI	Road	513	463	388	563	513	825159	672006	471730	994020	825159	1.0000	0.8144	0.5717	1.2046	1.0000
BHCO	Conifer	338	313	263	313	313	357847	306796	216475	306796	306796	1.0000	0.8573	0.6049	0.8573	0.8573
BHCO	Deciduous	388	313	213	313	413	471730	306796	141863	306796	534562	1.0000	0.6504	0.3007	0.6504	1.1332
BHCO	Road	663	613	413	663	613	1378865	1178588	534562	1378865	1178588	1.0000	0.8548	0.3877	1.0000	0.8548
BLWA	Conifer	213	238	163	213	238	141863	177205	82958	141863	177205	1.0000	1.2491	0.5848	1.0000	1.2491
BLWA	Deciduous	263	188	138	213	138	216475	110447	59396	141863	59396	1.0000	0.5102	0.2744	0.6553	0.2744
BLWA	Road	463	363	338	388	388	672006	412825	357847	471730	471730	1.0000	0.6143	0.5325	0.7020	0.7020
BOOW	Conifer	813	613	463	563	413	2073942	1178588	672006	994020	534562	1.0000	0.5683	0.3240	0.4793	0.2578

BOOW	Deciduous	763	713	763	563	363	1826542	1594849	1826542	994020	412825	1.0000	0.8732	1.0000	0.5442	0.2260
BOOW	Road	1113	913	813	913	763	3888212	2615867	2073942	2615867	1826542	1.0000	0.6728	0.5334	0.6728	0.4698
CATO	Conifer	413	463	288	338	338	534562	672006	259672	357847	357847	1.0000	1.2571	0.4858	0.6694	0.6694
CATO	Deciduous	663	563	463	563	563	1378865	994020	672006	994020	994020	1.0000	0.7209	0.4874	0.7209	0.7209
CATO	Road	913	813	763	763	663	2615867	2073942	1826542	1826542	1378865	1.0000	0.7928	0.6983	0.6983	0.5271
CCSP	Conifer	338	313	238	288	313	357847	306796	177205	259672	306796	1.0000	0.8573	0.4952	0.7257	0.8573
CCSP	Deciduous	213	213	213	238	188	141863	141863	141863	177205	110447	1.0000	1.0000	1.0000	1.2491	0.7785
CCSP	Road	563	463	413	513	513	994020	672006	534562	825159	825159	1.0000	0.6760	0.5378	0.8301	0.8301
CMWA	Conifer	213	138	113	163	188	141863	59396	39761	82958	110447	1.0000	0.4187	0.2803	0.5848	0.7785
CMWA	Deciduous	213	188	113	113	88	141863	110447	39761	39761	24053	1.0000	0.7785	0.2803	0.2803	0.1696
CMWA	Road	413	263	213	288	263	534562	216475	141863	259672	216475	1.0000	0.4050	0.2654	0.4858	0.4050
CORA	Conifer	363	363	288	313	288	412825	412825	259672	306796	259672	1.0000	1.0000	0.6290	0.7432	0.6290
CORA	Deciduous	663	463	338	413	363	1378865	672006	357847	534562	412825	1.0000	0.4874	0.2595	0.3877	0.2994
CORA	Road	813	813	713	813	713	2073942	2073942	1594849	2073942	1594849	1.0000	1.0000	0.7690	1.0000	0.7690
DEJU	Conifer	388	313	238	313	313	471730	306796	177205	306796	306796	1.0000	0.6504	0.3757	0.6504	0.6504
DEJU	Deciduous	363	288	213	238	263	412825	259672	141863	177205	216475	1.0000	0.6290	0.3436	0.4293	0.5244
DEJU	Road	613	613	463	663	563	1178588	1178588	672006	1378865	994020	1.0000	1.0000	0.5702	1.1699	0.8434
GGOW	Conifer	513	463	463	413	388	825159	672006	672006	534562	471730	1.0000	0.8144	0.8144	0.6478	0.5717
GGOW	Deciduous	763	663	713	463	338	1826542	1378865	1594849	672006	357847	1.0000	0.7549	0.8732	0.3679	0.1959
GGOW	Road	1113	763	813	813	663	3888212	1826542	2073942	2073942	1378865	1.0000	0.4698	0.5334	0.5334	0.3546
LEOW	Conifer	613	338	288	463	338	1178588	357847	259672	672006	357847	1.0000	0.3036	0.2203	0.5702	0.3036
LEOW	Deciduous	913	763	763	388	338	2615867	1826542	1826542	471730	357847	1.0000	0.6983	0.6983	0.1803	0.1368
LEOW	Road	1113	713	763	813	663	3888212	1594849	1826542	2073942	1378865	1.0000	0.4102	0.4698	0.5334	0.3546
LISP	Conifer	338	313	263	313	313	357847	306796	216475	306796	306796	1.0000	0.8573	0.6049	0.8573	0.8573
LISP	Deciduous	363	313	213	363	413	412825	306796	141863	412825	534562	1.0000	0.7432	0.3436	1.0000	1.2949
LISP	Road	663	663	513	663	663	1378865	1378865	825159	1378865	1378865	1.0000	1.0000	0.5984	1.0000	1.0000
NSWO	Conifer	463	813	388	413	388	672006	2073942	471730	534562	471730	1.0000	3.0862	0.7020	0.7955	0.7020
NSWO	Deciduous	763	913	663	563	613	1826542	2615867	1378865	994020	1178588	1.0000	1.4321	0.7549	0.5442	0.6453
NSWO	Road	1013	913	813	813	763	3220623	2615867	2073942	2073942	1826542	1.0000	0.8122	0.6440	0.6440	0.5671
OSFL	Conifer	363	338	288	338	338	412825	357847	259672	357847	357847	1.0000	0.8668	0.6290	0.8668	0.8668
OSFL	Deciduous	563	513	288	463	388	994020	825159	259672	672006	471730	1.0000	0.8301	0.2612	0.6760	0.4746
OSFL	Road	713	713	613	763	713	1594849	1594849	1178588	1826542	1594849	1.0000	1.0000	0.7390	1.1453	1.0000
OVEN	Conifer	338	313	263	313	313	357847	306796	216475	306796	306796	1.0000	0.8573	0.6049	0.8573	0.8573
OVEN	Deciduous	413	238	213	238	213	534562	177205	141863	177205	141863	1.0000	0.3315	0.2654	0.3315	0.2654
OVEN	Road	613	613	513	663	563	1178588	1178588	825159	1378865	994020	1.0000	1.0000	0.7001	1.1699	0.8434
PISI	Conifer	338	288	213	288	288	357847	259672	141863	259672	259672	1.0000	0.7257	0.3964	0.7257	0.7257
PISI	Deciduous	363	288	213	213	213	412825	259672	141863	141863	141863	1.0000	0.6290	0.3436	0.3436	0.3436
PISI	Road	563	513	413	563	513	994020	825159	534562	994020	825159	1.0000	0.8301	0.5378	1.0000	0.8301
RBGR	Conifer	363	363	288	338	338	412825	412825	259672	357847	357847	1.0000	1.0000	0.6290	0.8668	0.8668
RBGR	Deciduous	513	613	388	563	513	825159	1178588	471730	994020	825159	1.0000	1.4283	0.5717	1.2046	1.0000
RBGR	Road	813	813	713	913	763	2073942	2073942	1594849	2615867	1826542	1.0000	1.0000	0.7690	1.2613	0.8807
RBNU	Conifer	413	388	313	388	338	534562	471730	306796	471730	357847	1.0000	0.8825	0.5739	0.8825	0.6694
RBNU	Deciduous	663	563	338	563	513	1378865	994020	357847	994020	825159	1.0000	0.7209	0.2595	0.7209	0.5984
RBNU	Road	813	813	763	813	763	2073942	2073942	1826542	2073942	1826542	1.0000	1.0000	0.8807	1.0000	0.8807
TEWA	Conifer	288	238	138	238	238	259672	177205	59396	177205	177205	1.0000	0.6824	0.2287	0.6824	0.6824
TEWA	Deciduous	238	213	138	213	163	177205	141863	59396	141863	82958	1.0000	0.8006	0.3352	0.8006	0.4681
TEWA	Road	513	388	338	513	413	825159	471730	357847	825159	534562	1.0000	0.5717	0.4337	1.0000	0.6478
WAVI	Conifer	313	313	263	313	313	306796	306796	216475	306796	306796	1.0000	1.0000	0.7056	1.0000	1.0000
WAVI	Deciduous	313	363	238	263	263	306796	412825	177205	216475	216475	1.0000	1.3456	0.5776	0.7056	0.7056
WAVI	Road	613	613	513	663	563	1178588	1178588	825159	1378865	994020	1.0000	1.0000	0.7001	1.1699	0.8434
WETO	Conifer	513	413	288	338	313	825159	534562	259672	357847	306796	1.0000	0.6478	0.3147	0.4337	0.3718
WETO	Deciduous	463	563	363	463	363	672006	994020	412825	672006	412825	1.0000	1.4792	0.6143	1.0000	0.6143
WETO	Road	1013	763	713	813	663	3220623	1826542	1594849	2073942	1378865	1.0000	0.5671	0.4952	0.6440	0.4281
WTSP	Conifer	413	388	313	388	388	534562	471730	306796	471730	471730	1.0000	0.8825	0.5739	0.8825	0.8825

WTSP	Deciduous	613	613	338	463	463	1178588	1178588	357847	672006	672006	1.0000	1.0000	0.3036	0.5702	0.5702
WTSP	Road	813	763	713	813	763	2073942	1826542	1594849	2073942	1826542	1.0000	0.8807	0.7690	1.0000	0.8807
YERA	Conifer	238	213	138	163	188	177205	141863	59396	82958	110447	1.0000	0.8006	0.3352	0.4681	0.6233
YERA	Deciduous	213	138	138	188	213	141863	59396	59396	110447	141863	1.0000	0.4187	0.4187	0.7785	1.0000
YERA	Road	413	388	313	413	363	534562	471730	306796	534562	412825	1.0000	0.8825	0.5739	1.0000	0.7723

Appendix 3. Effective detection radius (EDR) for SM2 recorders at different sound pressure levels (SPL) in open and closed habitat for different songs and tones. Data were collected from listening trials conducted along 20 transects in the Blackfoot-Cooking Lake Natural Area near Edmonton, Alberta, Canada in 2014. “NA” values indicate undefined EDR due to an insufficient number of non-detections at that SPL for that species.

Sound	Closed Habitat											Open Habitat											
	40dB	45dB	50dB	55dB	60dB	65dB	70dB	75dB	80dB	85dB	90dB	40dB	45dB	50dB	55dB	60dB	65dB	70dB	75dB	80dB	85dB	90dB	
1000Hz	71 ± 25	75 ± 26	93 ± 35	123 ± 62	NA	NA	NA	NA	NA	NA	NA	95 ± 61	105 ± 76	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1414Hz	38 ± 17	57 ± 22	66 ± 19	82 ± 29	81 ± 28	NA	NA	NA	NA	NA	NA	44 ± 26	86 ± 73	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2000Hz	62 ± 19	75 ± 22	89 ± 31	92 ± 32	110 ± 62	107 ± 56	NA	NA	NA	NA	NA	87 ± 53	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2828Hz	47 ± 14	53 ± 15	58 ± 18	58 ± 18	61 ± 22	NA	NA	NA	NA	NA	NA	79 ± 49	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
4000Hz	58 ± 22	67 ± 20	71 ± 23	85 ± 41	NA	NA	96 ± 60	NA	NA	NA	NA	84 ± 70	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5656Hz	46 ± 11	44 ± 12	49 ± 12	54 ± 12	57 ± 17	78 ± 43	58 ± 19	60 ± 20	NA	NA	NA	83 ± 48	72 ± 42	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8000Hz	48 ± 20	29 ± 26	29 ± 25	12 ± 1	53 ± 24	47 ± 22	59 ± 23	72 ± 26	64 ± 24	86 ± 36	91 ± 40	56 ± 31	31 ± 29	30 ± 27	12 ± 1	64 ± 38	54 ± 33	76 ± 45	109 ± 76	87 ± 48	NA	NA	NA
BADO	12 ± 1	44 ± 21	64 ± 27	86 ± 37	121 ± 68	NA	NA	NA	NA	NA	NA	12 ± 1	47 ± 25	72 ± 39	110 ± 79	NA	NA	NA	NA	NA	NA	NA	NA
BAWW	12 ± 1	29 ± 25	46 ± 16	49 ± 18	56 ± 15	60 ± 16	67 ± 19	69 ± 21	71 ± 22	NA	89 ± 44	12 ± 1	32 ± 33	63 ± 38	71 ± 49	98 ± 63	NA	NA	NA	NA	NA	NA	NA
BEKI	12 ± 1	34 ± 14	12 ± 1	39 ± 13	39 ± 13	49 ± 13	53 ± 17	53 ± 16	55 ± 19	83 ± 59	NA	12 ± 1	45 ± 30	12 ± 1	60 ± 40	59 ± 38	NA	NA	NA	NA	NA	NA	NA
BHCO	45 ± 13	45 ± 15	51 ± 14	58 ± 13	60 ± 15	66 ± 23	73 ± 30	74 ± 28	90 ± 50	NA	NA	64 ± 36	66 ± 41	93 ± 69	NA	NA	NA	NA	NA	NA	NA	NA	NA
BLWA	12 ± 1	12 ± 1	28 ± 23	54 ± 15	59 ± 18	63 ± 16	74 ± 22	76 ± 26	83 ± 33	80 ± 31	83 ± 34	12 ± 1	12 ± 1	30 ± 28	79 ± 43	97 ± 72	117 ± 90	NA	NA	NA	NA	NA	NA
BOOW	58 ± 24	63 ± 23	81 ± 29	109 ± 48	NA	NA	NA	NA	NA	NA	NA	69 ± 41	79 ± 45	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
CATO	10 ± 1	30 ± 26	52 ± 22	62 ± 19	77 ± 23	82 ± 27	109 ± 57	114 ± 72	NA	NA	NA	11 ± 1	32 ± 31	68 ± 46	93 ± 58	NA	NA	NA	NA	NA	NA	NA	NA
CCSP	12 ± 1	33 ± 28	37 ± 14	51 ± 13	55 ± 14	60 ± 19	59 ± 18	84 ± 47	61 ± 19	NA	NA	12 ± 1	41 ± 42	48 ± 32	NA	NA	NA	NA	NA	NA	NA	NA	NA
CMWA	38 ± 16	12 ± 1	12 ± 1	38 ± 17	34 ± 14	39 ± 16	44 ± 17	53 ± 18	57 ± 21	57 ± 23	63 ± 28	44 ± 26	12 ± 1	12 ± 1	45 ± 28	38 ± 21	47 ± 27	56 ± 33	79 ± 57	NA	NA	NA	NA
CORA	12 ± 1	35 ± 30	53 ± 15	60 ± 16	65 ± 17	70 ± 21	79 ± 31	106 ± 74	NA	NA	NA	12 ± 1	40 ± 42	83 ± 53	NA	NA	NA	NA	NA	NA	NA	NA	NA
DEJU	12 ± 1	37 ± 14	46 ± 11	51 ± 11	55 ± 14	57 ± 16	66 ± 26	96 ± 56	74 ± 44	NA	NA	12 ± 1	50 ± 35	83 ± 49	NA	NA	NA	NA	NA	NA	NA	NA	NA
GGOW	12 ± 1	34 ± 31	55 ± 24	73 ± 23	93 ± 39	97 ± 38	120 ± 76	NA	NA	NA	NA	12 ± 1	37 ± 36	66 ± 42	113 ± 83	NA	NA	NA	NA	NA	NA	NA	NA
LEOW	12 ± 1	34 ± 31	51 ± 26	59 ± 34	102 ± 60	NA	NA	NA	NA	NA	NA	12 ± 1	35 ± 32	52 ± 28	61 ± 40	114 ± 93	NA	NA	NA	NA	NA	NA	NA
LISP	12 ± 1	33 ± 28	34 ± 30	54 ± 13	63 ± 18	68 ± 21	81 ± 44	72 ± 25	94 ± 57	101 ± 80	NA	12 ± 1	39 ± 40	40 ± 43	100 ± 66	NA	NA	NA	NA	NA	NA	NA	NA
NSWO	34 ± 29	47 ± 20	60 ± 19	84 ± 26	97 ± 39	NA	117 ± 79	104 ± 45	NA	NA	NA	37 ± 35	57 ± 34	86 ± 54	NA	NA	NA	NA	NA	NA	NA	NA	NA
OSFL	39 ± 18	56 ± 18	68 ± 19	75 ± 20	85 ± 31	85 ± 26	94 ± 43	NA	NA	NA	NA	44 ± 27	77 ± 45	124 ± 118	NA	NA	NA	NA	NA	NA	NA	NA	NA
OVEN	12 ± 1	34 ± 12	42 ± 12	46 ± 11	49 ± 14	49 ± 13	52 ± 16	60 ± 27	NA	NA	NA	12 ± 1	47 ± 29	78 ± 57	NA	NA	NA	NA	NA	NA	NA	NA	NA
PISI	12 ± 1	32 ± 12	40 ± 11	47 ± 12	51 ± 14	51 ± 13	54 ± 16	56 ± 19	91 ± 63	NA	NA	12 ± 1	40 ± 24	64 ± 38	114 ± 104	NA	NA	NA	NA	NA	NA	NA	NA
RBGR	12 ± 1	37 ± 15	58 ± 17	28 ± 23	67 ± 19	78 ± 27	74 ± 25	111 ± 81	NA	NA	NA	12 ± 1	43 ± 24	103 ± 88	31 ± 29	NA	NA	NA	NA	NA	NA	NA	NA
RBNU	30 ± 23	37 ± 14	48 ± 12	50 ± 12	53 ± 16	61 ± 32	62 ± 27	NA	NA	NA	NA	36 ± 36	52 ± 40	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
TEWA	11 ± 1	11 ± 1	11 ± 1	11 ± 1	48 ± 16	52 ± 15	57 ± 17	60 ± 19	67 ± 29	69 ± 30	NA	12 ± 1	11 ± 1	12 ± 1	12 ± 1	76 ± 51	97 ± 68	NA	NA	NA	NA	NA	NA
WAVI	12 ± 1	33 ± 28	44 ± 18	29 ± 25	62 ± 17	68 ± 19	72 ± 22	76 ± 28	NA	NA	NA	12 ± 1	37 ± 39	56 ± 41	32 ± 32	NA	NA	NA	NA	NA	NA	NA	NA
WETO	29 ± 24	29 ± 25	49 ± 17	57 ± 18	62 ± 20	66 ± 23	73 ± 29	NA	NA	NA	NA	31 ± 30	32 ± 30	64 ± 34	85 ± 55	NA	NA	NA	NA	NA	NA	NA	NA
WTSP	38 ± 14	47 ± 12	48 ± 12	52 ± 15	62 ± 27	55 ± 19	NA	NA	NA	NA	NA	56 ± 41	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
YERA	29 ± 25	11 ± 1	11 ± 1	11 ± 1	34 ± 31	37 ± 16	59 ± 21	63 ± 20	79 ± 42	77 ± 37	80 ± 40	32 ± 31	11 ± 1	12 ± 1	12 ± 1	40 ± 44	43 ± 28	NA	NA	NA	NA	NA	NA