


ORIGINAL RESEARCH

Sound level measurements from audio recordings provide objective distance estimates for distance sampling wildlife populations

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Abstract

Distance sampling is widely used to estimate animal population densities by accounting for imperfect detection of individuals with increasing distance from an observer. Distance sampling assumes that distances are measured without error; however, it is often applied to human estimated distances, which are known to be inconsistent, inaccurate, and biased. We present an objective technique for estimating distance to vocalizing individuals that relies on the relative sound level (RSL) of the vocalization extracted from autonomous recording unit (ARU) recordings and show the error is less than human estimated error extracted from a literature case study. RSL predicted distances can be obtained by manual measurement in sound viewing software, or automatically with automated signal recognition software. We built calibration datasets of Ovenbirds (*Seiurus aurocapilla*) and Common Nighthawks (*Chordeiles minor*) recorded at known distances and used regression of RSL from those recordings to predict distance. There was no error bias of RSL predicted distances when compared to known distances for Common Nighthawk, minimal error bias for Ovenbird, and error from all RSL predicted distances was less than human estimated error extracted from the literature. We then simulated ARU point count surveys with a known density and estimated that density with distance sampling to test whether RSL distance prediction does not violate the assumption that distances are measured without error. There was no difference in density estimates from known distance and density estimates obtained from RSL predicted distance, while density estimates contaminated with human estimated error were significantly lower than density estimates from known distance. We found that a calibration dataset of approximately 300 vocalizations was suitable to minimize error for both species, and so conclude that RSL distance prediction is an accessible method of improving distance estimates relative to human estimation. We provide general recommendations on how to collect calibration recordings for the application of RSL distance prediction to other species and areas.

Introduction

Estimating density is a fundamental objective of wildlife management. Distance sampling corrects for the decline in detection probability that occurs as distance from an animal to the observer increases (Buckland et al. 2001) and is among the most widely used approaches for

estimating animal density. Distance sampling has five key assumptions: (1) distance to individuals is measured independent of animal movement, (2) individuals are perfectly detected at zero distance, (3) distance is measured without error, (4) individuals are detected at their initial location, and (5) individuals are not double counted (Table 1). Distance sampling is commonly applied to

Table 1. Violations of distance sampling assumptions and solutions to violations for point surveys conducted by human surveyors and ARUs. Multiple violations to the same assumption and corresponding solutions are lettered.

Distance sampling assumption	Violation by human surveyor surveys	Solution for human surveyor surveys	Violation by ARU surveys	Solution for ARU surveys	Advantage of ARU surveys
1. Distance to individuals is measured independent of animal movement	Only if sampling design is not randomly selected (Buckland et al. 2015).	Correct for bias by separating availability and detection functions (Marques et al. 2010).	Only if sampling design is not randomly selected (Buckland et al. 2015).	Correct for bias by separating availability and detection functions (Marques et al. 2010).	None
2. Individuals are perfectly detected at zero distance*	a. Availability bias: if individuals at zero distance are not available for detection (e.g., does not vocalize). b. Perception bias: if observer fails to detect an individual.	a. Availability bias: Estimate proportion of available animals if availability is static, including any relevant covariates (Diefenbach et al. 2007; Thomson et al. 2012); incorporate intermittent availability pattern with hidden Markov models (Borchers et al. 2013; Langrock et al. 2013). b. Perception bias: Mark-recapture methods, double observer survey.	a. Availability bias: if individuals at zero distance are not available for detection (e.g., does not vocalize).	a. Availability bias: assume 100% availability by increasing sampling period to match vocalization availability (Barlow et al. 2013); other statistical methods used for human surveyors.	Permanent record from ARU recordings can be used to eliminate perception bias.
3. Distance is measured without error.	Significant error and bias in distance estimation by human surveyors.	Use a laser rangefinder to obtain estimates; integrate measurement error in distance sampling models (Borchers et al. 2010).	Often unknown for point count surveys (but see Darras et al. 2018b). Current methods rely on costly array designs and localization.	RSL distance prediction (this paper); integrate measurement error in distance sampling models (Borchers et al. 2010).	Error from RSL distance predictions small enough to not violate the assumption.
4. Individuals are detected at their initial location.	a. Individuals move around during survey. b. Individuals avoid the human surveyor.	a. Snapshot method (Buckland et al. 2006). b. Allow individuals to "settle" before starting survey; revise methods if double observer data indicates avoidance (Buckland et al. 2015).	a. Individuals move around during survey.	a. Initial location assumed to be first vocalization event	Individuals less likely to be influenced by presence of ARU than human surveyor.
5. Individuals are not double-counted.	a. Movement of individuals during count can result in an individual being counted twice.	a. Cue counting (Hiby 1985; Buckland et al. 2015).	a. Movement of individuals during count can result in an individual being counted twice. b. Individuals can be difficult to separate without directional cues (unavailable for mono recordings).	a. Cue counting (Hiby 1985; Buckland et al. 2015). b. Separation of individuals using multichannel recordings (Dawson and Efford 2009).	Permanent record from ARU recordings can provide a more accurate cue count.

*Availability bias and perception bias can be hard to separate.

acoustic surveys (Buckland et al. 2001), where a human surveyor estimates the distance of a sound signal. However, the assumptions of distance sampling are often violated when distances are estimated by human surveyors (Table 1; Scott et al. 1981; Alldredge et al. 2007; Nadeau and Conway 2012).

We focus on the assumption that distance is measured without error (hereafter “distance estimation assumption”; Table 1). Field evaluations of point count surveys by human surveyors have found distance estimates are generally inaccurate and often biased, and as a result, often binned into distance intervals (e.g., 0–50, 50–100, >100 m). Estimates of distance by humans can range from 0.25 to almost 30 times the true distance (Scott et al. 1981; Nadeau and Conway 2012), and error often increases with distance (Nadeau and Conway 2012). After comparing human distance estimates to true distances, Alldredge et al. (2007) concluded that humans cannot accurately estimate distances over 65 m. A human’s ability to determine distance from aural cues can be hindered by environmental effects on sound attenuation and degradation (Wiley and Richards 1982; Pacifici et al. 2008; Yip et al. 2017b), as well as interference from background noise (Simons et al. 2007). Estimates by people can also be biased and are often clumped because training and experience create bias and variation in distance estimates (Scott et al. 1981; Alldredge et al. 2007; Simons et al. 2007).

Audio recordings present an opportunity to remove the subjectivity from distance estimation and potentially reduce estimation error. The relative sound level (RSL) of an acoustic signal in audio recordings has a predictable logarithmic relationship with distance and has the potential to be used as a proxy for estimating density in a distance sampling framework (Yip et al. 2017a). RSL is a relative measure of the energy of a sound signal at the point when sound waves reach a microphone and can be measured using acoustic software programs. RSL is generally measured in decibels (dB) that are relative to the maximum output of the microphone. In the absence of environmental factors that affect sound propagation, every doubling of distance results in a decrease in RSL of 6 dB due to spherical spreading (Wiley and Richards 1982). The potential for RSL to predict distance is not well understood and may be influenced by environmental factors, such as vegetation density, that affect spherical spreading via changes in attenuation (Darras et al. 2016). Distance prediction with RSL may also vary between species depending on the degree of directionality of each species’ vocalizations (Catchpole and Slater 2008).

RSL distance prediction could be applied to audio recordings from autonomous recording units (ARUs), which are increasingly used to conduct ecological surveys (Shonfield and Bayne 2017) and have several advantages

over human surveys that are consistent with the assumptions of distance sampling (Table 1). Previously, distance sampling with ARUs has been hindered by an assumed inability to estimate distance to a signal in a recording (Dawson and Efford 2009), and so has only been applied to ARU array datasets with localized individuals (Cato 1998; McDonald and Fox 1999), which are laborious to collect (Mellinger et al. 2007). More recently, distance sampling has been applied to point count ARU datasets via human estimation of distance on recordings (Darras et al. 2018b) and via distance prediction from RSL (Sebastián-González et al. 2018). We propose that distance can be automatically estimated from sound recordings with a four-step process: (1) Build a calibration dataset of a focal species recorded at known distance; (2) train a recognizer with signal recognition technology (Knight et al. 2017; Priyadarshani et al. 2018) to detect the focal species and measure RSL of each detection; (3) determine the source level (i.e., intercept) and attenuation rate (i.e., slope) of RSL relative to distance with a regression model; and (4) use the recognizer to automatically extract RSL of species detections from recordings of unknown distance and predict distance with the estimated regression equation.

We present a rigorous test of whether RSL distance prediction removes subjectivity and reduces error compared to human estimated distances. First, we tested whether RSL can be used to estimate distance by manually and automatically measuring RSL from calibration recordings of wild, free-ranging birds, predicting distance with the RSL measurements, and comparing to known distances of those recordings. We then compared the error in RSL predicted distances to human estimated error extracted from a literature case study to demonstrate that RSL distance prediction can reduce distance estimation bias and error. We also determined the sample size for calibration recordings that were required to reach an a priori threshold of variation in distance estimation error to help users determine the best approach for calibration recording collection. To examine whether RSL distance prediction violated the distance sampling assumption that distances are measured without error, we simulated ARU point count surveys and compared the true simulated estimate to density estimates from known distance, to those from RSL predicted distance, and to those contaminated with the human estimated error extracted from the literature.

Materials and Methods

Calibration data collection

We collected acoustic recordings of live birds recorded at known horizontal distance (hereafter “known distance”)

for two bird species with contrasting acoustic characteristics, the Common Nighthawk (*Chordeiles minor*, CONI) and Ovenbird (*Seiurus aurocapilla*, OVEN). The two species differ in acoustic signal complexity that could affect the error rate of RSL distance prediction. OVEN has a complex multi-phrased song that is 2.5–4.0 s in length (Porneluzi et al. 2011; Fig. 1), whereas CONI produces a simple single-note vocalization that is ~0.3 s in length (Fig. 1). The two species also differ in acoustic behavior that could lead to differences in sound transmission, affecting RSL distance prediction. OVEN sing from an above-ground perch at a mean height of 8.8 m (Lein 1981), while CONI call from the wing above the forest canopy (Brigham et al. 2011).

We determined OVEN singing locations using an acoustic location system (ALS) placed at seven mixed-wood sites in Alberta, Canada during June 2016 (see Wilson and Bayne 2018 for detailed methods). The ALS used 30 GPS-enabled SM3 ARUs equipped with external SMM-A1 microphones (Wildlife Acoustics, Concord, MA, USA) placed an average of 33.9 m (± 0.52 m SE) apart in a 5×5 grid, with a transect of five microphones extended from the center of each grid (Fig. 2). OVEN vocalizations ($n = 160$) were localized with the microphone grids using time to arrival methods. Accuracy of localization determined through playback experiments was 2.03 m (± 0.55 m SE). We determined the horizontal distance of each vocalization to each of the ten microphones in the center of the array to create a dataset of 1600 known distance clips (Fig. 2). We then clipped each vocalization using the *tuneR* R package (Ligges et al. 2016; R Core Team 2017), adding a buffer of 2 s to the

beginning and end of the vocalization for further RSL measurement.

We collected acoustic recordings of CONI with known locations by attracting males to a transect of SM4 ARUs (Wildlife Acoustics, Concord, MA, USA) using conspecific broadcast calls (Appendix S1; Fig. 2). The transect approach is an efficient method of collecting calibration recordings because it simultaneously records the calls of the same individual at multiple distances. We used an 800 m long transect that consisted of 15 ARUs placed at standardized distances along a linear feature. An observer stood at the beginning of the transect and recorded the time in milliseconds, height, horizontal distance, and bearing of every CONI vocalization. We minimized distance estimation error by using the same observer for all observations, by the observer calibrating their horizontal and vertical distance estimates with a laser range finder prior to every observation period, and by limiting observations to those within 20 m horizontal distance of the observer, because human surveyor distance estimation error is minimized at short distances (Nadeau and Conway 2012). We note that there is likely 5–10 m of error in our known distance estimates due to this method. We collected recordings an hour before sunset at eight transects in July 2016. We measured temperature, wind speed, and humidity during each survey using a Kestrel 3000 (Kestrel Meters, Minneapolis, MN, USA). We played an airhorn from the beginning of the transect at the start of the recording period and subsequently clipped the recordings at the airhorn to synchronize the target vocalizations therein. We used the *seewave* package (Sueur et al. 2008) in R to clip each of 147 unmasked detections from each

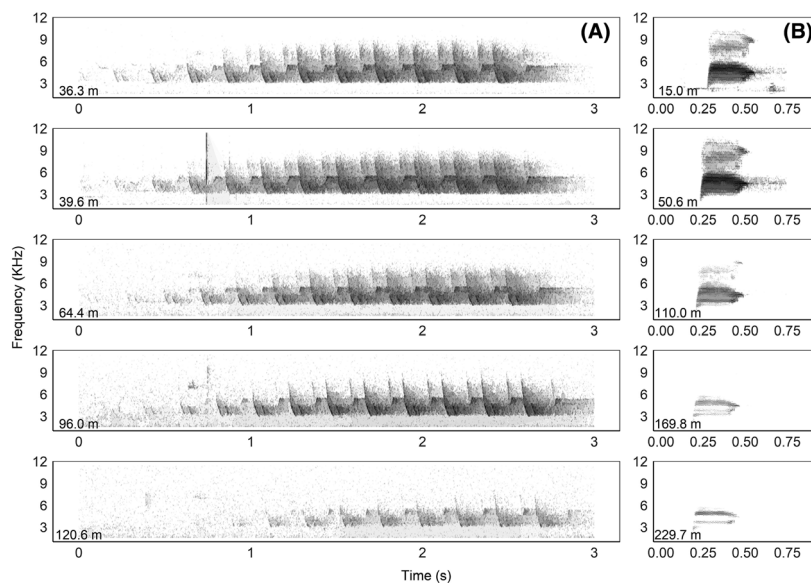
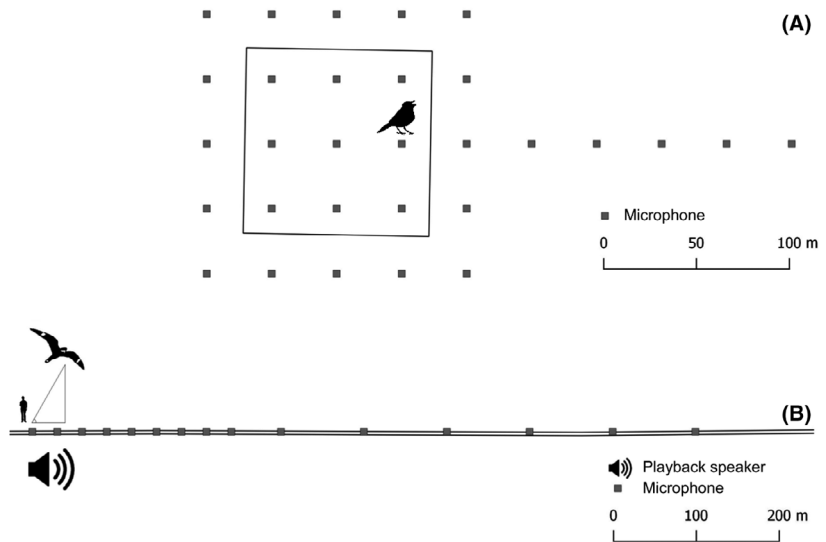


Figure 1. (A) Spectrograms of a single call of an individual Ovenbird (*Seiurus aurocapilla*; OVEN) recorded at five microphones at varying distances, as determined by acoustic localization from an array of autonomous recording units (ARUs). (B) Spectrograms of a single call of an individual Common Nighthawk (*Chordeiles minor*; CONI) recorded at five microphones at varying distances, as determined by attraction of the bird with conspecific broadcast calls to the beginning of a transect of ARUs.

Figure 2. (A) Autonomous recording unit (ARU) microphone array set-up at a wellsite (black square) for the localization of individual Ovenbird (*Seiurus aurocapilla*; OVEN) vocalizations. (B) Autonomous recording unit (ARU) microphone transect set-up along a linear feature (parallel lines) for the localization of individual Common Nighthawk (*Chordeiles minor*; CONI) vocalizations. An individual CONI was attracted with conspecific broadcast calls to the beginning of each transect, where an observer estimated the vertical and horizontal distance and bearing to the bird from the beginning of the transect for each vocalization.



of the 15 recordings along the transect as 0.7 s clips for a total of 2205 clips (Fig. 1).

Human estimated error

We extracted human observer error from the literature to compare to our RSL estimated distances. Of the four known field tests of human observer distance estimation error, Nadeau and Conway (2012) was the only paper from which it was feasible to extract raw data. We emphasize, however, that human observation distance estimation can vary based on a variety of factors (Simons et al. 2007; Nadeau and Conway 2012), and that this comparison may not be representative of all human observer distance estimation. We used WebPlotDigitizer (Rohatgi 2017) to extract raw data from Figure 1B, which depicted distance estimation error against measured distance. We tested for heteroscedasticity of the extracted data using a Breusch-Pagan test (Breusch and Pagan 1979) and found error to be homoscedastic ($BP = 0.013$, $P = 0.91$). Since distance estimation error from human surveyors did not significantly change with distance from observer, we used the mean and standard deviation of the extracted data to add error values randomly sampled from a normal distribution to every known distance value from the OVEN and CONI manual measurement datasets. We constrained the resultant distances (hereafter “human estimated distances”) to positive values.

RSL measurement

We measured RSL with two different methods: manual measurement and recognizer measurement. Ultimately, we were interested in using recognizer measurement to

automate RSL distance prediction, but wanted to confirm the RSL measurements were sufficiently precise via comparison with manually extracted measurements because the RSL measurement will ultimately depend on the accuracy of the temporal and frequency boundaries within which the measurement is taken.

Manual measurement

We measured RSL manually from the clips of known distance of both species in Raven Pro 1.5 (Charif et al. 2010) using a 512-point Hamming window spectrogram for visualization. We used the max power function to measure RSL for each vocalization by selecting the smallest possible area around the vocalization (Bioacoustics Research Program 2014). We measured RSL from all clips where the target individual was detected and the vocalization was not masked by vocalizations of non-target individuals. We only used data points at distances where the RSL exceeded the level of ambient background noise (≤ 200 m for OVEN, ≤ 500 m for CONI).

Recognizer measurement

We also used automated signal recognition to automate the RSL extraction process using convolutional neural network (CNN) recognizers (Knight et al. 2017). We trained one recognizer for each species as moving window recognizers in the TensorFlow (Abadi et al. 2015) framework with the Python API for model training and definition (Appendix S2). We then processed the clips of known distance with the corresponding species recognizer to measure RSL of each clip, excluding clips of known distance beyond the same distance thresholds used for

manual measurement. The recognizers output a time series of scores and RSL estimates generated from spectrogram inputs. We visually and aurally reviewed every hit for each species to confirm detections of the target individual and removed any hits where there was masking by non-target individuals. Analysis was conducted in Python (van Rossum 1995) version 3.5, using *librosa* (McFee et al. 2017) for audio loading and spectrogram generation, and *scipy* (Jones et al. 2001) for signal filtering.

Statistical analysis

Distance estimation

We fit generalized linear mixed models with a Gaussian distribution and log link function with known distance as the response and RSL as a second-order polynomial term for all four species–method datasets (hereafter referred to as: “OVEN manual”, “OVEN recognizer”, “CONI manual”, “CONI recognizer”). We selected a second-order polynomial term after preliminary comparison to linear and log models using small sample size corrected Akaike’s Information Criterion (AIC_c). We built global models that included time of day, score (recognizer only), vertical height (CONI only), and any relevant interactions (Appendix S3). We modeled horizontal distance with vertical height as a covariate for CONI instead of calculating and modeling euclidean distance because most applications of distance estimates, including distance sampling, require estimates of horizontal distance. In addition, we were interested in determining the relative importance of vertical distance in RSL distance prediction because in most applications of RSL distance prediction, vertical height will be unknown. All predictors, including RSL, were centered and standardized prior to modeling. We tested for collinearity between predictors by calculating the variance inflation factor (VIF) in a stepwise procedure for each predictor (Naimi et al. 2014). We retained all predictors for model selection (max VIF = 2.81). We excluded weather covariates to make this approach more generalizable because preliminary analyses indicated they were relatively small contributors to overall explained variance (Appendix S4). To further emphasize generalizability, we also calculated intraclass correlation coefficients (ICC) to determine importance of site, location within the ALS grid, and individual as random effects and removed any random effects with an ICC greater than 0.30 (A. Zuur and E. Ieno personal communication), leaving station as a random effect for both OVEN datasets (Appendix S5). We then used AIC_c to rank models and selected the model with the lowest AIC_c or the most parsimonious model when multiple candidate models had $\Delta AIC_c < 2$ (Arnold 2010; Appendix S3). We partitioned

relative importance of each variable included in the best model for each dataset using commonality analysis, which provides the unique variance explained by a predictor and common variance shared by two or more predictors (Nimon and Oswald 2013).

We used 10-fold cross-validation to build a dataset of RSL distances for each of the four species–method combinations by fitting the trained regression model to the withheld data from each fold (Mosteller and Tukey 1968). We excluded random effects from distance prediction to test the generalizability of our method beyond the calibration dataset. We calculated the magnitude of error (hereafter “distance estimation error”) as the absolute value of the difference between RSL predicted distance and known distance, and direction of mean error (hereafter “error bias”) as the RSL predicted distance minus known distance. We tested whether error bias differed from zero using a one-sample t-test for each dataset, and for differences in error bias between manual and recognizer approaches with independent two-sample t-tests for each species. Validation accuracy is reported as the mean adjusted R^2 between observed and fitted values from cross-validation.

We then used bootstrapping to determine the sampling effort required to create a suitable calibration dataset. We used a uniform distribution to randomly select a sample size for each species–method combination. We calculated absolute error using the same 10-fold cross-validation technique described above and calculated the coefficient of variation for different sample sizes at intervals of 20 samples. We estimated the sample size required to reach a coefficient of variation value of five, where variation in absolute error stabilized with increasing sample size.

Distance sampling

We used stochastic simulation to generate individual animal locations with a known population density to test whether RSL predicted distances produced accurate density estimates. We simulated OVEN and CONI locations within a 400-ha square survey plot with a random uniform distribution (Fig. 3). We imposed a minimum inter-individual distance of 40 m for OVEN and 100 m for CONI to represent territoriality. We determined the number of animal locations (i.e., population density) using random Poisson deviates with an average of 160 CONI (0.4 CONI/ha; *Knight unpublished data*) and 240 OVEN (0.6 OVEN/ha; Lankau et al. 2013). We repeated this simulation 50 times to represent a typical avian point count survey program.

Next, we simulated single-ARU point count locations at the center of the square survey plot. We calculated the known distance and probability of detection for each

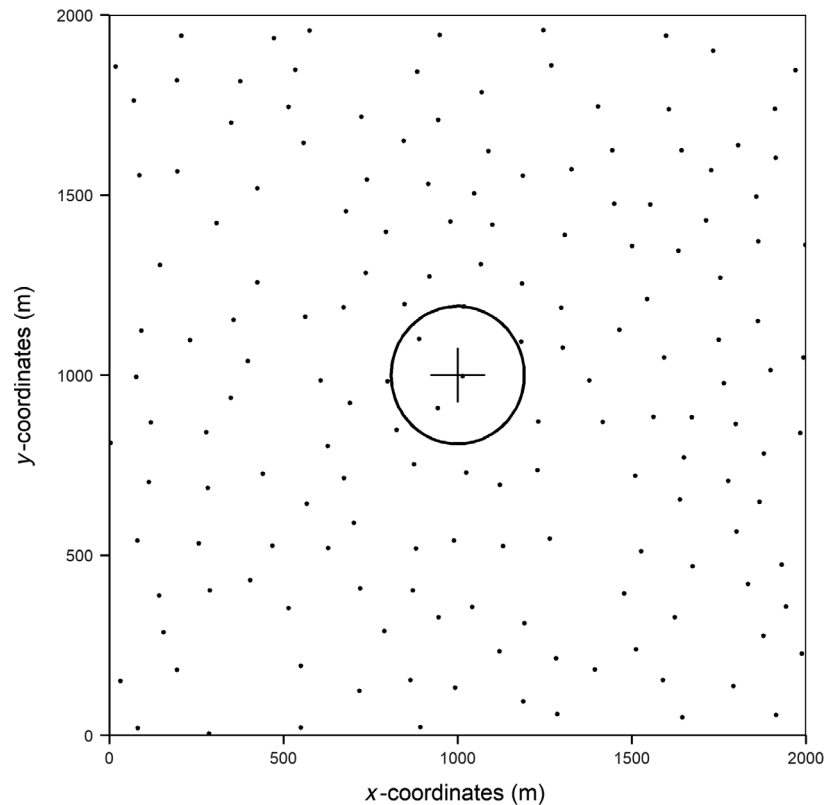


Figure 3. Example of CONI survey data generated through simulation. Each point represents the location of a vocalizing individual. The circle represents the effective detection radius for CONI at a survey location which is used to generate a set of detections and distances to individuals.

individual in each simulation. We calculated the probability of detection using a half-normal detection function generated from binomial recognizer results of OVEN and CONI vocalizations at known distances that were detected or missed (see Yip et al. 2017a for details). We used the distribution of errors from our distance estimation models to simulate RSL for each known distance using mean error bias and standard deviation as a function of distance. We then used those simulated RSL measurements in our previously fitted models for distance prediction to generate RSL predicted distances for each individual in each simulation. We also used the distribution of errors from the human estimated distances extracted from Nadeau and Conway (2012) to generate human estimated distances for each individual in each simulation.

Finally, we used distance sampling to estimate the density with point count surveys in each simulation using the known distances, RSL predicted distances, and human estimated distances. For each set of distances, we used AIC_c to rank, compare, and select conventional distance sampling models with combinations of uniform, half normal, and hazard rate key functions and cosine and polynomial adjustment terms (MRDS package; Thomas et al. 2010; Appendix S6). We used 83% confidence intervals to determine if there were statistical differences in density estimates produced from known distances, RSL predicted

distances, and human estimated distances (Krzyszowski and Altman 2013).

Results

We hand measured the RSL in 691 of the 1600 OVEN clips and 716 of the 2205 CONI clips. The maximum known distance that an individual was detected at with manual measurement was 187 m for OVEN and 500 m for CONI. After validation, the recognizer detected and measured RSL of 673 OVEN clips and 1223 CONI clips. The maximum known distance that an individual was detected at by the recognizer was 149 m for OVEN and 500 m for CONI.

We extracted 168 of 206 data points from Figure 1B in Nadeau and Conway (2012). We were unable to extract the remaining 38 data points due to overlap. The mean estimation error of the data we extracted was 42.5 m (± 84.8 m SD), which was similar to that reported in Nadeau and Conway (2012; 39 ± 79 m SD).

Distance estimation

RSL decreased with increasing distance and explained at least 93.4% of the total partitioned R^2 in all models except the OVEN recognizer model, where RSL and score

combined explained 95.2% of total partitioned R^2 (Fig. 4; Appendix S4 and S7). The selected models for OVEN distance estimation included a negative effect of time of day. The selected models for CONI included estimated vertical height of CONI as a positive predictor and time after sunset. Both models for recognizer measurement also included score. Adjusted R^2 between fitted and observed data in cross-validation was between 0.61 and 0.73 for all models.

Distance estimation error was significantly greater than zero for all datasets but was lower for OVEN than CONI (Fig. 5; Appendix S8). Distance estimation error from manual measurements was higher than error from recognizer measurements for CONI ($P < 0.001$), but not for OVEN ($P = 0.187$; Appendix S8). Absolute distance estimation error was 14.69 m (± 12.24 m SD) for OVEN manual measurement, 13.85 m (± 10.75 m SD) for OVEN recognizer measurement, 47.64 m (± 40.83 m SD) for CONI manual measurement, and 37.62 m (± 38.19 m SD) for CONI recognizer measurement.

Mean error bias was significantly greater than zero for OVEN but not for CONI ($P < 0.001$, $P > 0.05$; Fig. 5; Appendix S8). There was no significant difference in error bias between manual measurement and recognizer measurement for either species (all $P > 0.05$; Appendix S8). Mean error bias was 5.66 m (± 18.27 m SD) for OVEN

manual measurement, 4.15 m (± 17.04 m SD) for OVEN recognizer measurement, -0.31 m (± 62.76 m SD) for CONI manual measurement, and 0.39 m (± 53.61 m SD) for CONI recognizer measurement.

Variation in estimates of absolute error decreased with sample size (Fig. 6). A sample size of approximately 300 measurements was sufficient to reach the a priori threshold coefficient of variation ($CV = 5$) for all datasets (OVEN manual: 350; OVEN recognizer: 290; CONI manual: 250, CONI recognizer: 340).

Distance sampling

There was no significant difference between the density estimates produced with known distance and RSL predicted distance; however, the density estimate from manually measured RSL distance estimates was lower than true simulation density for OVEN (Fig. 7). Density estimates produced from human estimated distances were lower than density estimates from known distance and true simulation density for both species.

Discussion

We show that relative sound level (RSL) can be used to estimate distance from autonomous recording units

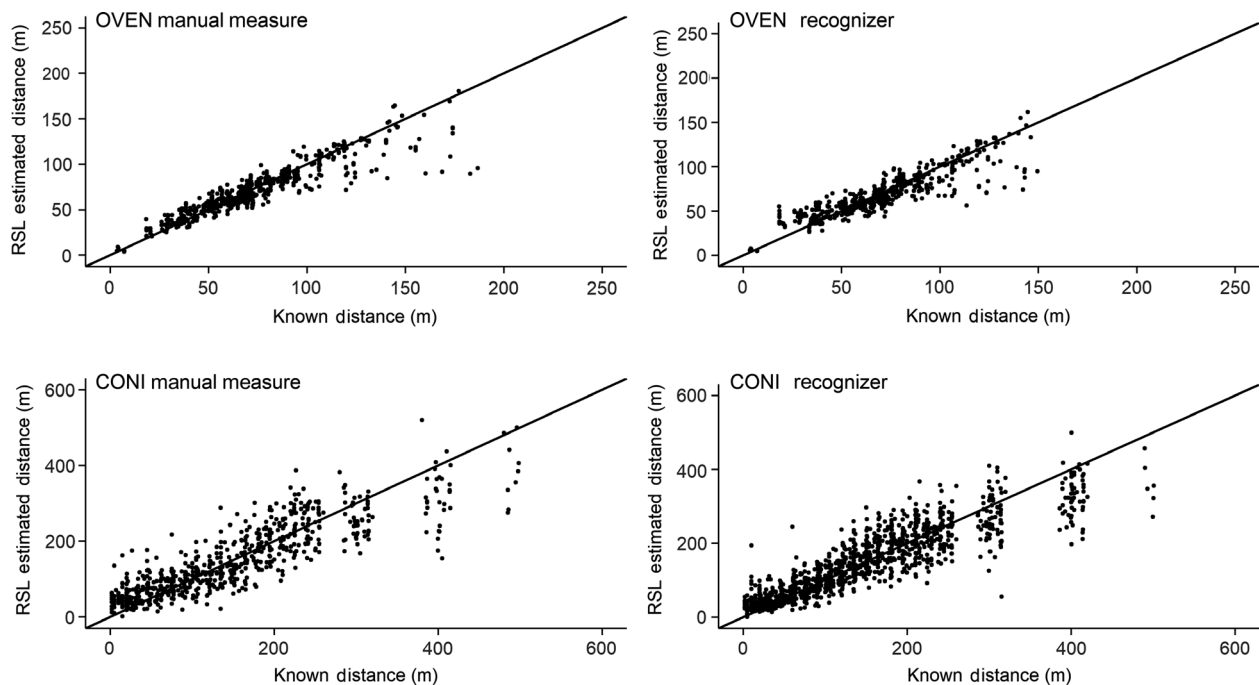


Figure 4. Relative sound level (RSL) estimated distance relative to known distance for Ovenbird (*Seiurus aurocapilla*; OVEN) and Common Nighthawk (*Chordeiles minor*; CONI) measured manually and with a recognizer. RSL predicted distance was predicted from generalized linear models for each species-method combination. Black line indicates no bias or error between known distance and RSL predicted distance.

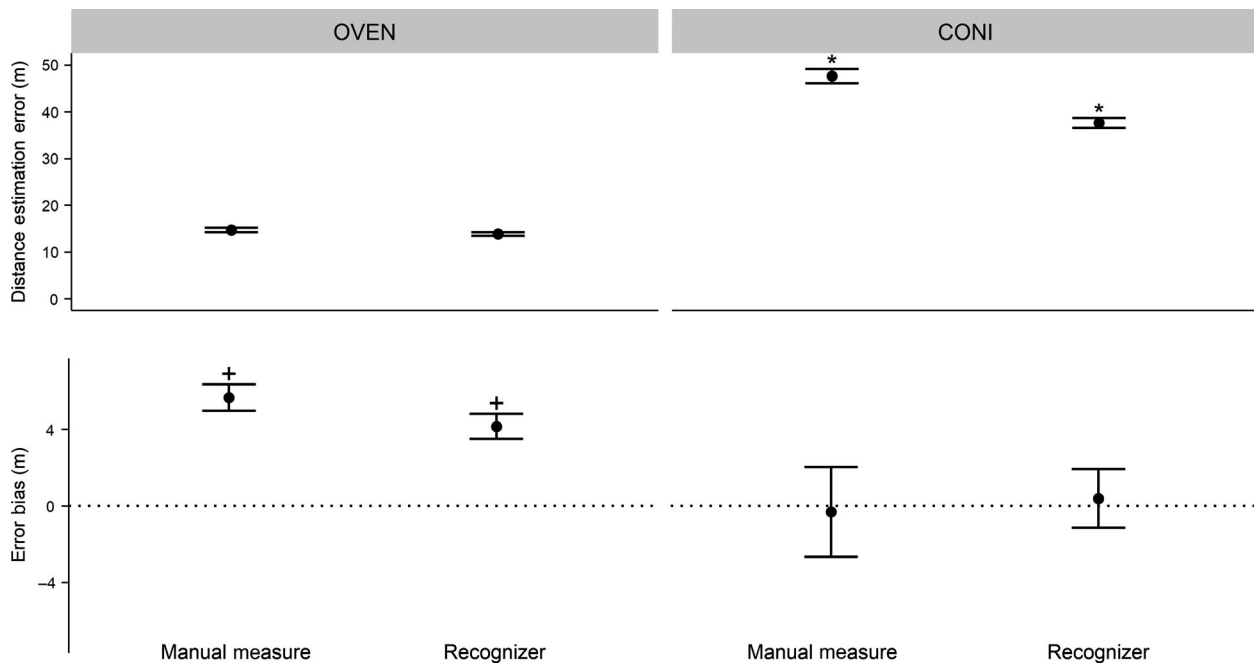


Figure 5. Distance estimation error and error bias of relative sound level (RSL) estimated distance for Ovenbird (*Seiurus aurocapilla*; OVEN) and Common Nighthawk (*Chordeiles minor*; CONI) measured manually and with a recognizer. Distance estimation error was calculated as the absolute value of the difference between RSL predicted distance and known distance. Error bias was calculated as the RSL predicted distance minus known distance. Known distances for both species were calculated as distance between the autonomous recording unit (ARU) and the individual bird at the time of vocalization. Error bars represent standard error. * indicate significant differences between measurement methods for distance estimation error and + indicates significant difference (relative to zero) for error bias.

(ARUs) and is an improvement over human distance estimation. Distance estimation by observers in the field can be inaccurate with systematic or clumped error due to differences in skill, perception, and time since training (Alldredge et al. 2007; Camp 2007; Nadeau and Conway 2012). We found RSL distances were not clumped, and while models slightly overestimated smaller distances and underestimated greater distances, there was no significant error bias in CONI datasets and low error bias in OVEN datasets relative to reported error bias from human estimates of distance. Previous studies have reported mean error bias for human surveyors of -10.1% to 9.0% for distances up to 70 m (Scott et al. 1981), 7.6 m (± 21.4 m SD) for distances up to 98 m (Alldredge et al. 2007), -9 m (± 47 m SD) for distances up to 239 m (Nadeau and Conway 2012), and 53.3 m (± 58.6 m SD) for distances up to 500 m (Murray et al. 2011). Significant error bias in our RSL distances was 5.66 m (± 18.27 m SD) for OVEN manual measurement and 4.15 m (± 17.04 m SD) for OVEN recognizer measurement. Additionally, RSL provides individual distances instead of distance bins commonly used in bird counts. Our method of estimating error bias through cross-validation may provide optimistic results compared to distances predicted from a

separate dataset but suggests less error than human surveyors. We note, however, that the human error that we extracted and compared to our RSL distance estimates is a case study and may not be representative because human observation distance estimation can vary based on a variety of factors (Simons et al. 2007; Nadeau and Conway 2012). In fact, the error bias reported in Nadeau and Conway (2012) is lower than the other case studies summarized above.

RSL distance prediction removes human subjectivity from distance estimation, and we suggest that automating extracting RSL estimates with recognizers further removes human subjectivity. We found that both distance estimation error and error bias were lower when we measured RSL with a recognizer. In contrast, the distance estimation error from manually measured RSL was large enough to significantly reduce the density estimate for OVEN. We suggest that automated RSL measurement with a recognizer is more accurate than manual measurement because it removes human subjectivity, variation, and error. Automated RSL measurement also improves the efficiency of the distance estimation process.

The improvement in distance estimation accuracy resulted in more accurate density estimates from distance

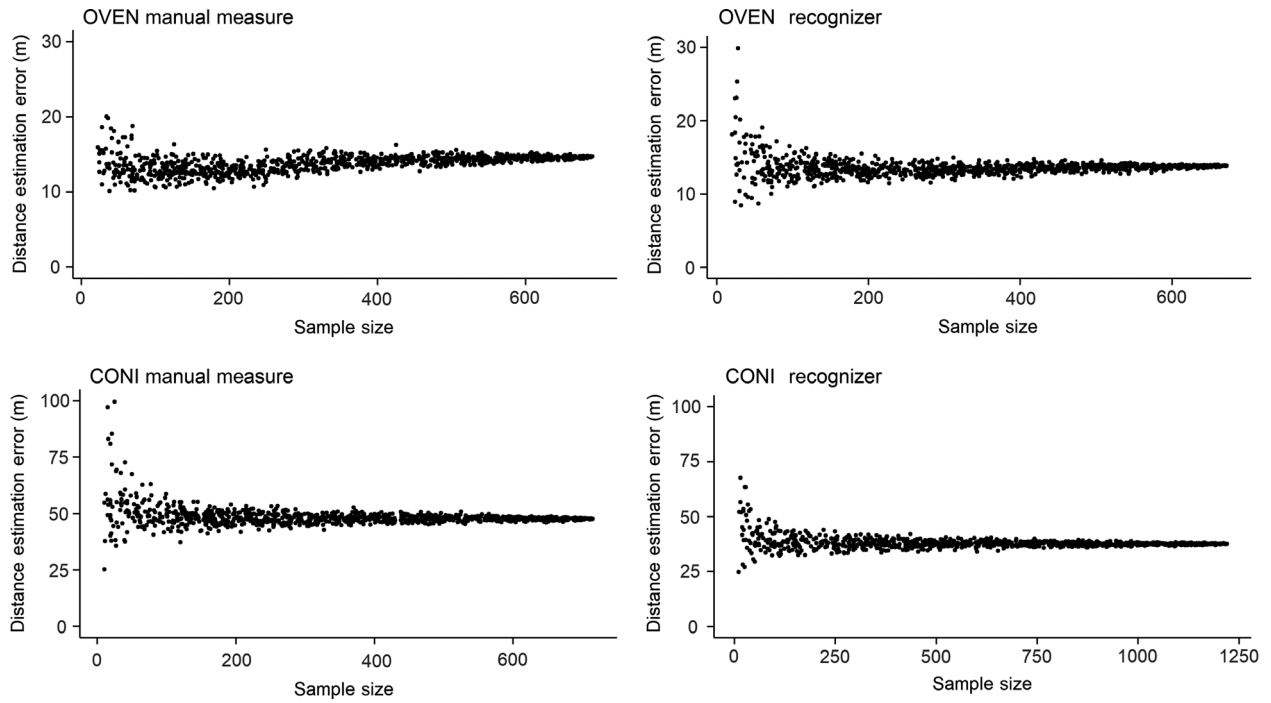


Figure 6. Bootstrapped distance estimation error for manual and recognizer RSL measurements of Ovenbird (*Seiurus aurocapilla*; OVEN) and Common Nighthawk (*Chordeiles minor*; CONI) recordings relative to sample size.

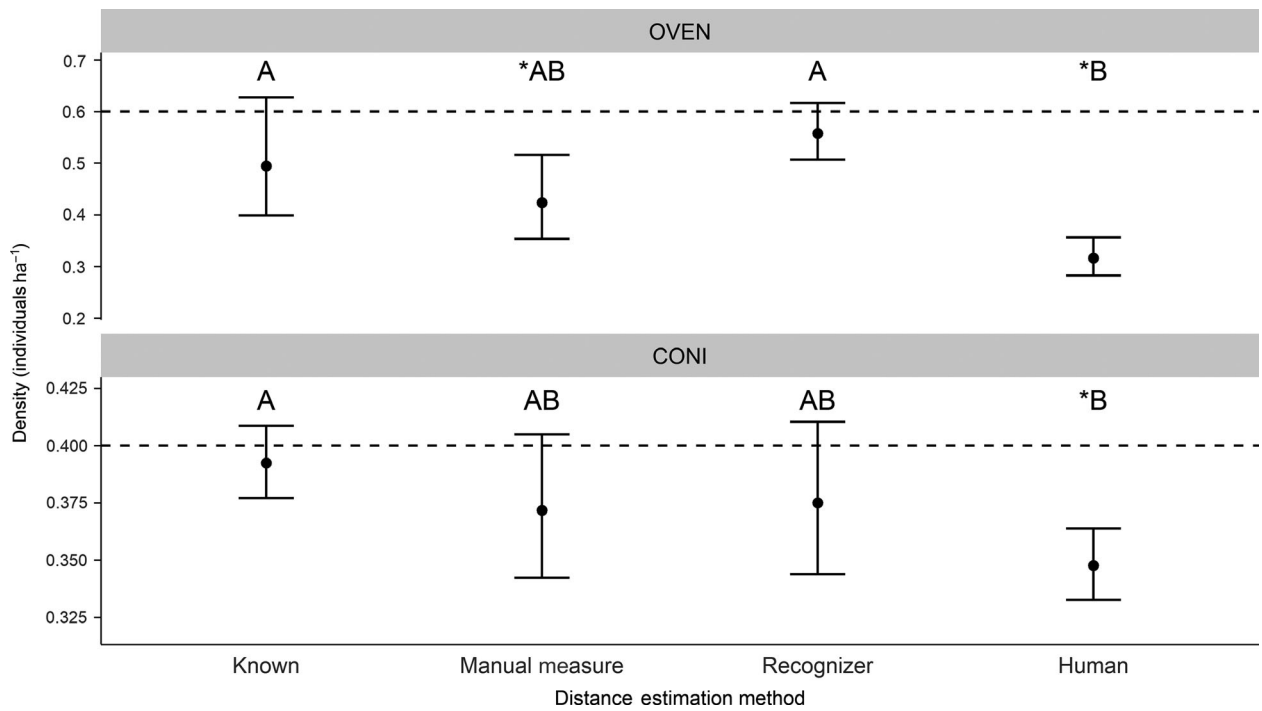


Figure 7. Density estimates of simulated Ovenbird (*Seiurus aurocapilla*; OVEN) and Common Nighthawk (*Chordeiles minor*; CONI) distributions using known distances, distances estimated from relative sound level (RSL) measured manually, with recognizer, and human surveyor distance estimation error. Mean error is presented with 83% confidence intervals. * indicate significant difference of density estimate from true simulation density represented by dashed line. Density estimates with different letters are significantly different.

sampling. We used simulation to show that the density estimates derived from RSL estimated distances did not differ from density estimates derived from known distances, despite the presence of some error and bias. Our results suggest that RSL distance prediction does not violate the assumption of distance sampling that distances are measured without error (Table 1). Density estimates should be relatively unaffected if distance estimation is unbiased on average, unless error in distance estimation is large (Buckland et al. 2001). In comparison, density estimates from human estimated distances were significantly lower than density estimates from known distance, likely due to human overestimation of distance in the dataset extracted from Nadeau and Conway (2012). We suggest that application of RSL distance prediction to real field recordings would improve compliance with the distance estimation assumption of distance sampling (Table 1), which is normally violated when using distances estimated by human surveyors (Buckland et al. 2001). RSL distance prediction also removes the subjectivity of human estimation, which can exacerbate bias in distance estimates (Sebastián-González et al. 2018). Future work should test whether distance sampling models that statistically incorporate quantified error in RSL estimated distance can further improve the accuracy of density estimates (Borchers et al. 2010).

Despite the improvement in distance estimates and density estimates from RSL distance prediction, some error remained in the RSL predicted distances. We investigated the residuals of the fitted models and found no correlation with any of our measured covariates, which suggests the remaining bias is due to an unmeasured covariate. The distance estimation error in our RSL distances is likely due to variation in individual acoustic behavior, such as vocalization directionality, height, and intensity. Animal vocalizations are not omnidirectional and the amount of spherical spreading can vary with signal type (Patricelli et al. 2007; Catchpole and Slater 2008). Sebastián-González et al. (2018) argue that directionality will not lead to biased density estimation if cues are oriented randomly relative to the ARU because they will average out. Height can also affect RSL because sounds emitted at greater heights suffer less attenuation than sounds emitted near the ground (Marten and Marler 1977), and we found that including vertical height as a covariate improved the parsimony of RSL distances. Alldredge et al. (2007) found that directionality of broadcast calls affected human surveyor estimation error, but height did not; however, they only tested to 12 m height, compared with up to 100 m height for our CONI. We also found that distance predictions were affected by time of day, which may be due to behavioral variation in the amplitude of bird song, with stronger levels earlier in the day (Porneluzi et al. 2011). This time-varying effect is also related to the assumption of

perfect observability at zero distance, as availability and behavioral components are known to affect overall detectability (Sólymos et al. 2013). Finally, vegetation structure could also contribute to variation in RSL (Johnson 2008). We controlled for vegetative structure within each dataset by selecting study sites with similar vegetation, but there may have been differences between sites that introduced some variation in RSL distances.

Distance sampling from single point count ARUs has been infrequently attempted because the sampling radius of ARUs is typically unknown and may vary depending on recorder technology, vegetation, weather, and species (Yip et al. 2017b; Darras et al. 2018a). We found RSL was the main predictor of distance (93.4–99.7% total partitioned R^2), and several recent studies suggest that a reliable relationship between RSL and distance can be established for various taxa. Darras et al. (2018b) found that human listeners can estimate distance from recordings with 0.76–0.96 correlation with true distance for five species. Sebastián-González et al. (2018) found that sound power explained 37.45% of deviance in known distance of Hawai'i 'Amakihi (*Chlorodrepanis virens*). Both studies, however, did not quantify distance estimation error and only included known distances up to 80 and 40 m, respectively. We suggest that distance sampling with RSL predicted distances from ARU recordings may be an easier method of density estimation than the spatially explicit capture-recapture (SECR) method because RSL distance prediction requires only one microphone (Dawson and Efford 2009). RSL distance prediction may also improve efficiency of distance estimation, as ARU deployment generally requires less time than field observations conducted by trained observers (Holmes et al. 2014).

RSL distance prediction does, however, require calibration recordings to establish the relationship between RSL and distance for the focal species. Calibration recordings can also be used for other applications, such as estimating distance by ear (Darras et al. 2018b) or setting recognizer classification thresholds (Knight and Bayne 2018). We showed that although RSL prediction error was smallest when we fit our model with our entire dataset (673–1223 clips), the reduction in error was minimal for datasets greater than 300 calibration recordings. We therefore suggest that the time required to collect calibration recordings for RSL distance should not be prohibitive for most species. We emphasize that calibration datasets for RSL distance prediction should be representative of the field recordings that the predictive model will be applied to. Distance estimation models should not be used across habitat types because attenuation varies with vegetation unless effective detection radius is tested for generalizability across vegetation types or corrected for with standardized variation (Yip et al. 2017a,b) or incorporating an

attenuation coefficient (Royle 2018). Further, microphones for collecting calibration data and field recordings should be calibrated to the same standards to avoid bias in RSL measurements.

There are three known methods for developing calibration datasets. The first and most precise method, which we used here for OVEN, uses triangulation from an acoustic location system (ALS); however, this method is laborious to set up and post-process to obtain individual locations. We do not suggest this “ALS method” for anyone who does not already use an ALS for their focal species. The second method, introduced here for CONI, uses broadcast calls to attract an individual to a transect of recorders and a human surveyor to estimate bird location relative to that transect. This “transect method” requires only 2–3 h of time each day for several days, produces an even distribution of known distances, and can also be used to control the known distances measured. The disadvantage of this method is that the precision of known distances is lower than triangulation, but precision could be improved if the focal species is one that sings from a perch and thus can be located with a laser rangefinder and compass. The third method, presented by Sebastián-González et al. (2018), involves walking the study area and manually recording vocalizing individuals that are visually detected while simultaneously measuring distance with a laser range-finder. A similar variant, presented by Darras et al. (2018b), involves conducting a point count survey with a human observer and an ARU, and measuring distance to any visual detections of vocalizing individuals. This “opportunistic method” requires a similar amount of field time as the broadcast-transect method, and likely has similar precision of known distances. The disadvantage of the haphazard method is that there is little control over the range of known distances recorded, and it may be difficult to obtain recordings at close range and far range, resulting in a RSL distance prediction model that does not perform well across all distances. We therefore recommend using the broadcast-transect method unless the acoustic behavior of the focal species is altered by broadcast calls. Similar transect designs have been used in other acoustic studies to understand the effects of sound attenuation (Meyer et al. 2013; Yip et al. 2017a).

We thus conclude that RSL distance prediction is an accessible method that can be used to remove subjectivity, improve accuracy, and reduce bias of distance estimates and density estimates for most species. RSL distance prediction can also be used to improve the efficiency of density estimation because it can be applied to ARU recordings in an automated fashion. RSL predicted distances can be used in distance sampling to produce unbiased density estimates and thus not violate the assumption that distances are measured without error.

Minimizing error in distance estimation is important for reducing error in density predictions from distance sampling (Buckland et al. 2001) and may prevent erroneous conclusions about wildlife populations.

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Conflict of Interest

The authors have no competing interests to disclose and the work complies with all ethics and permitting requirements associated with the University of Alberta and the Province of Alberta.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Detailed calibration data collection materials & methods.

Appendix S2. Detailed recognizer training and automated relative sound level (RSL) estimation.

Appendix S3. Model selection for GLMs predicting distance.

Appendix S4. Commonality analysis.

Appendix S5. Intraclass correlation coefficients (ICC) for selecting random effects in GLMs.

Appendix S6. Distance sampling model selection.

Appendix S7. Model Coefficients for GLMs predicting distance.

Appendix S8. Distance estimation error and post-hoc comparisons.