

A Field Evaluation of Distance Measurement Error in Auditory Avian Point Count Surveys

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ABSTRACT Detection distance is an important and common auxiliary variable measured during avian point count surveys. Distance data are used to determine the area sampled and to model the detection process using distance sampling theory. In densely forested habitats, visual detections of birds are rare, and most estimates of detection distance are based on auditory cues. Distance sampling theory assumes detection distances are measured accurately, but empirical validation of this assumption for auditory detections is lacking. We used a song playback system to simulate avian point counts with known distances in a forested habitat to determine the error structure of distance estimates based on auditory detections. We conducted field evaluations with 6 experienced observers both before and after distance estimation training. We conducted additional studies to determine the effect of height and speaker orientation (toward or away from observers) on distance estimation error. Distance estimation errors for all evaluations were substantial, although training reduced errors and bias in distance estimates by approximately 15%. Measurement errors showed a nonlinear relationship to distance. Our results suggest observers were not able to differentiate distances beyond 65 m. The height from which we played songs had no effect on distance estimation errors in this habitat. The orientation of the song source did have a large effect on distance estimation errors; observers generally doubled their distance estimates for songs played away from them compared with distance estimates for songs played directly toward them. These findings, which we based on realistic field conditions, suggest measures of uncertainty in distance estimates to auditory detections are substantially higher than assumed by most researchers. This means aural point count estimates of avian abundance based on distance methods deserve careful scrutiny because they are likely biased. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2759–2766; 2007)

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Estimating avian abundance is central to studies comparing spatial and temporal patterns of bird diversity and abundance (Kepler and Scott 1981, Scott et al. 1981). Distance sampling is one common method used to estimate avian abundance (Buckland et al. 2001). Distances are easily estimated for visual detections by using range finders or reference marks at each point. However, auditory detections make distance estimation more difficult. Such auditory detections can comprise 70% of observations in forested suburban landscapes (Sauer et al. 1994), 81% in tropical forests (Scott et al. 1981), and 94% of observations in deciduous forests (DeJong and Emlen 1985).

Understanding the measurement error associated with estimates of detection distance, especially for auditory detections, is critical to making valid inferences. Errors in distance estimation can bias estimates of the sampled area (Buckland et al. 2001, Burnham et al. 2004, Marques 2004).

We view the collection of distance data from auditory cues as having 2 error components, locating the cue and estimating the distance. Localization error, which is by far the most serious, reflects an observer's ability to accurately identify the location of the bird detected. Localization error is caused by different rates of sound attenuation and habitat-related reverberations (Morton 1975, Richards and Wiley 1980, Wiley and Richards 1982, Bibby and Buckland 1987). In habitats such as dense multilayered forests, detection is

primarily based on auditory cues and localization errors can be large. Distance estimation error that is conditional on a location is the ability of an observer to accurately estimate the distance to birds they have localized using visual cues. This error can be minimized by training observers (Scott et al. 1981) and by using range finders; it is far less problematic than the case where visual cues are lacking.

We use a bird song simulation system (Simons et al. 2007) to assess overall distance estimation error for five species of songbirds in a forested environment. The system allowed us to control the location, directionality, and intensity of song cues. Our objective was to experimentally evaluate the effects of species, observer, detection distance, song height, song direction, and observer training on distance estimation error in a natural field setting where true distance was known.

STUDY AREA

We conducted field evaluations at Howell Woods, a 1,133-ha natural area in Johnston County, North Carolina, USA. The site consisted of mature bottomland hardwood and mixed pine (*Pinus* spp.) hardwood forest with a dense understory. We conducted experiments between 0800 hours and 1600 hours on 12 and 26 February 2005 to minimize auditory interference from resident birds and insects. Average ambient noise levels on 12 February were 40.70 decibels (dB; SD = 3.10 dB) and 39.80 dB (SD = 2.72) on 26 February.

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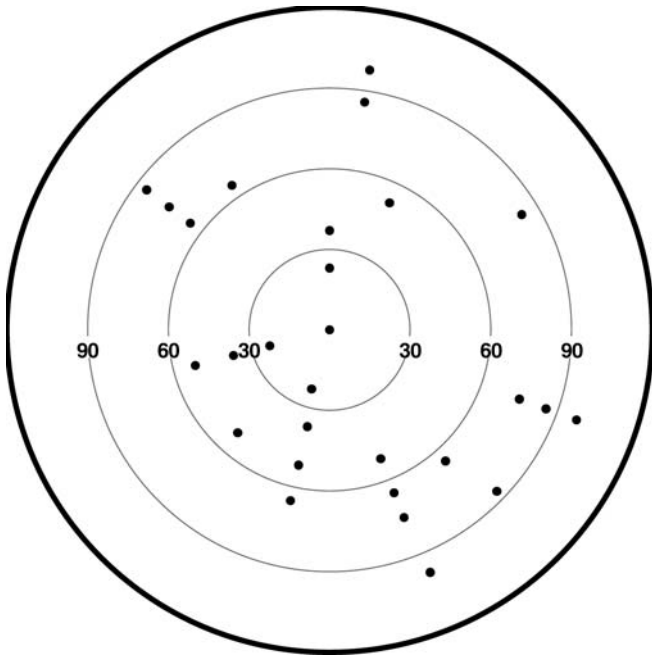


Figure 1. Arrangement of players used for distance estimation error experiment, located at Howell Woods, North Carolina, USA, and conducted in February 2005. Three players are located in each of seven distance bands (23 m, 37 m, 52 m, 65 m, 75 m, 86 m, and 98 m). One or 2 of the closest players may have been visible to some observers, but the radial alignment of players prevented observers from associating a given bearing with a specific distance. Players used in the orientation experiment were in the 23-m, 52-m, and 65-m distance bands, and players used in the height experiment were in the 52-m, 65-m, and 86-m distance bands, which added 2 players to each of these bands.

METHODS

We played song recordings using a remotely operated simulation system consisting of a transmitter and 30 remote players with speakers facing in opposite directions (Simons et al. 2007). The study site had limited visibility (<30 m) in most directions. We placed speakers around a single census point and oriented both directly toward and away from observers. We placed 3 speakers along random bearings at each of 7 unique distances (23 m, 37 m, 52 m, 65 m, 75 m, 86 m, and 98 m; Fig. 1). We placed these 21 speakers (ground speakers) on platforms 1 m off the ground. We placed the remaining 9 speakers (tree speakers) in trees at a height of approximately 12 m at distances of 52 m, 65 m, and 86 m (3 speakers at each distance) along random bearings.

We played songs of Acadian flycatcher (*Empidonax virens*; ACFL), black-and-white warbler (*Mniotilta varia*; BAWW), black-throated green warbler (*Dendroica virens*; BTNW), red-breasted nuthatch (*Sitta canadensis*; RBNU), and wood thrush (*Hylocichla mustelina*; WOTH) at a sound pressure of 90 dB (dBA, ref uPa at 1 m) for all species. An individual trial involved playing the song of a single species at a particular location for a period of 30 seconds, allowing observers to focus on each song. During each 30-second playback period, we played 2 songs with a 6–10-second intersong interval. A minimum 10-second interval was

provided between trials for observers to finalize their distance estimates and record their field data.

Observers made 39 observations of each species: 21 from songs played toward them from ground players, 9 from songs played toward them from tree players, and 9 from songs played away from them from ground players at distances of 23 m, 52 m, and 65 m. We played the 195 trials (39 observations per species \times 5 species) in random order.

The 6 observers were experienced birders with extensive experience using distance sampling on avian point counts. Observers were not required to identify species in this experiment, because we identified the species played on each trial on data sheets.

We measured distance estimation error before and after training. We conducted the untrained observer component on the first day of the experiment with minimal training, which consisted of playing 2 songs for each species at distances of 50 m and 100 m. We then provided observers with additional training in distance estimation for the 5 species of interest. We played 15 songs for each species at distances ranging from 25 m to 120 m (we did not use experimental locations for training). After making their distance estimates, we immediately told observers the actual distance to the player. We played half of the training songs consecutively at 2 different locations so that observers could directly compare the sounds from different distances and species. We conducted additional training 2 weeks later just before the trained distance estimation component. In this session, we played 25 pairs of songs at several distances for each species.

We view our field evaluation as quasi-experimental for several reasons. First, we knew the true distance from the observers to each simulated song. Second, we were able to control factors such as song orientation, song height, song volume, habitat, and environmental conditions. Third, we were also able to randomize the location and order in which we played songs, because we used many more player locations in each experiment than were needed for an individual simulated count. Nevertheless, because we carried out our evaluation at one location, in one habitat type, during one season, we are unable to estimate the spatial or temporal variation in factors such as vegetation, topography, and background noise. The statistical analyses described next incorporate only the sources of variation we could estimate in our field evaluations.

For the 21 ground players with the speakers oriented at the observers, we used a split-plot analysis of variance (Steel et al. 1997), with distance error (d_e) as the response variable, and each individual song event as the whole-plot experimental unit. We considered species and distance whole-plot treatment factors. We treated observers as a split-plot treatment factor in this analysis, because each observer is hearing the same song at the same time. Because all observers were hearing the same birds at the same time in the same trial under exactly the same conditions, the variation of their measurements for the same song will be less variable than their measurements for different songs.

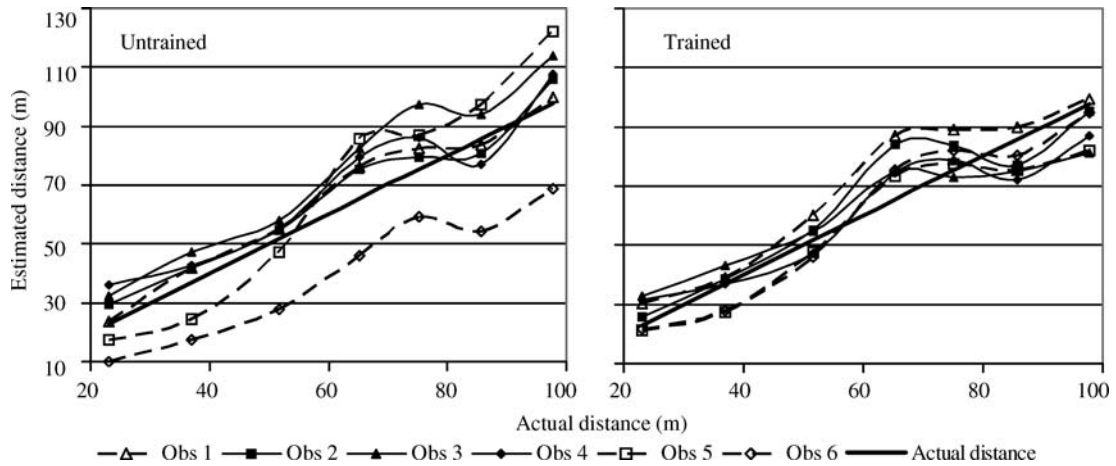


Figure 2. True distance and average estimated distance for each observer (Obs) averaged across species for both untrained and trained experiments at Howell Woods, North Carolina, USA, using only players located on the ground and oriented towards the observer. We collected data in February 2005.

This is accounted for in the split-plot model. Our analysis does not account for any carryover effects from one song-calling event to the next; however, we did randomize the order and location from which we presented songs.

If we found species–observer interactions, we then analyzed our results by species to simplify the presentation. We based mixed model F tests on Kenward–Roger’s adjusted degrees of freedom (Kenward and Roger 1997). The statistical model for a single species with only ground speakers oriented toward the observers is as follows:

$$D_{e(ijk)} = \mu + d_i + (wp)_{ik} + o_j + (do)_{ij} + (sp)_{ijk}$$

where d_i ($i = 1, \dots, 7$) is the distance band, o_j ($j = 1, \dots, 6$) is the observer, and $k = 1, \dots, 3$ represents the replicate within each distance band. The random effects associated with the whole-plot unit is given by $(wp)_{ik} \sim N(0, \sigma_{wp}^2)$, and the random effects associated with the split-plot units are given by $(sp)_{ijk} \sim N(0, \sigma_{sp}^2)$.

We used a similar split-plot analysis to determine the effect of player orientation on distance estimation, in particular to assess any bias associated with the orientation of the sound source. We used a similar model with species and distance as whole-plot factors, but both observers and orientation were split-plot factors. We also presented analyses by species when we found significant species–observer interactions.

The final split-plot analysis examined whether player height was associated with differences in the direction or magnitude of distance estimation bias. We used observations from the 9 ground players at 52 m, 65 m, and 86 m, and the 9 tree players at the same distances for this analysis. Species and distance were whole-plot factors, and height and observers were split-plot factors in these analyses. We reported analyses by species when we found significant species–observer interactions.

RESULTS

We recorded 1,170 total data points in both the untrained observer and trained observer distance estimation experi-

ments. Average distance estimates for each observer showed similar patterns among observers and between the untrained and trained components (Fig. 2). The average estimated distance for each observer increased as the actual distance increased for distances between 23 m and 65 m. Average estimated distances did not increase at the 65-m, 75-m, and 86-m distances for any observer but estimated distances increased at 98 m.

Distance estimation errors were substantial and highly variable (Table 1). The average error across all distances, species, and observers was 9.0 m (SD = 25.8 m) for the untrained observer experiment and 7.6 m (SD = 21.4 m) for the trained observer experiment. In both the trained and untrained observer experiments, distance was overestimated at a distance of 23 m, slightly underestimated at a distance of 37 m, and overestimated at intermediate distances between 52 m and 75 m, when we combined speaker orientations and heights. Distance was underestimated in the trained observer experiments at distances of 86 m and 98 m, except for tree speakers at a distance of 86 m. Overestimation at distances of 23 m, 52 m, and 65 m was greater for songs directed away from observers than for songs directed toward observers. Distance estimation errors ranged from underestimates of 72.8 m (player distance = 98 m) to overestimates of 202.2 m (player distance = 98 m) for the untrained observer experiment and forward-oriented speakers. Distance estimation errors for the trained observer experiment were smaller, ranging from underestimates of 67.8 m (player distance = 98 m) to overestimates of 59.7 m (player distance = 65 m) for forward-oriented speakers. Standard deviations were large for all estimates of the average distance estimation error, demonstrating the large amount of variability in estimates.

An analysis based only on songs from ground speakers oriented toward observers showed similar patterns in estimation error across distance categories, species, and observer training (Fig. 3). For all species and experiments, we observed an increase in distance estimates with increasing true distance up to the 65-m distance. However, distance estimation bias was not consistent for observers

Table 1. Average, standard deviation, minimum, and maximum distance estimation errors combined over all observers and species, reported by song orientation (toward observers = front; away from observers = back), height, and combined for each distance category for the trained and untrained experiments. All distances are reported in meters. We collected data at Howell Woods, Johnston County, North Carolina, USA, on February 2005.

Player type	Distance	Untrained experiment				Trained experiment			
		\bar{x}	SD	Min.	Max.	\bar{x}	SD	Min.	Max.
Front		1.8	11.3	-18.0	32.0	4.1	8.5	-8.0	32.0
Back	23	30.5	18.1	-3.0	78.0	32.8	15.2	2.0	77.0
Overall		16.2	20.8	-18.0	78.0	18.5	18.9	-8.0	77.0
Front—Overall	37	-1.1	16.9	-32.0	43.0	-1.6	11.0	-17.0	33.0
Front		-2.0	18.3	-36.7	43.3	0.1	14.2	-31.7	48.3
Back	52	33.7	23.1	-21.7	98.3	31.7	17.3	-1.7	78.3
Tree		-1.5	20.2	-41.4	68.6	-5.1	13.9	-31.4	30.6
Overall		9.9	26.6	-41.4	98.3	8.8	22.3	-32.3	78.3
Front		8.9	21.5	-65.3	49.7	13.0	17.0	-30.3	59.7
Back	65	36.2	21.8	-20.3	134.7	34.3	14.7	-15.3	64.7
Tree		-1.2	22.6	-52.9	65.1	-2.7	16.1	-39.9	35.1
Overall		14.6	27.1	-65.3	134.7	14.8	22.1	-40.3	64.7
Front—Overall	75	6.8	22.1	-50.2	74.8	5.5	19.2	-40.2	54.8
Front		-4.5	26.9	-65.7	74.3	-7.4	18.2	-50.7	44.3
Tree	86	6.2	22.9	-53.4	66.6	5.1	14.9	-33.4	31.6
Overall		-0.1	25.3	-65.7	74.3	-2.1	17.4	-50.7	44.3
Front—Overall	98	5.2	31.2	-72.8	202.2	-7.9	16.8	-67.8	32.2
Front		2.1	22.3	-72.8	202.2	0.8	16.8	-67.8	59.7
Back	All	33.5	21.2	-21.7	134.7	32.9	15.7	-15.3	78.3
Tree		1.2	22.1	-53.4	68.6	-0.9	15.6	-39.9	35.1
Overall		9.0	25.8	-72.8	202.2	7.6	21.4	-67.8	78.3

across species, which produced the species by observer interaction. For example, both observers 1 and 2 consistently overestimated distances to black-throated green warbler and red-breasted nuthatch songs, but only observer 2 overestimated distances to wood thrush songs.

Observer differences in distance estimation error were significant (ACFL $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-25.8, 20.3]$, $F_{5,10} = 68.76$, $P < 0.001$; BAWW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-9.2, 3.8]$, $F_{5,10} = 7.00$, $P = 0.005$; BTNW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-18.2, 23.7]$, $F_{5,10} = 29.35$, $P < 0.001$; RBNU $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-29.4, 11.1]$, $F_{5,10} = 16.13$, $P < 0.001$; WOTH $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-26.5, 21.6]$, $F_{5,10} = 75.86$, $P < 0.001$) for all species in the untrained experiment. Distance ($P > 0.31$; ACFL most significant, $F_{6,14} = 1.33$, $P = 0.31$) and distance by observer interactions were not significant ($P > 0.12$, WOTH most significant, $F_{30,14.4} = 1.80$, $P = 0.12$) factors for any of the species in the untrained experiment.

We also found significant distance estimation errors among trained observers (ACFL $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-13.2, 8.6]$, $F_{5,10} = 18.78$, $P < 0.001$; BAWW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-9.2, 5.4]$, $F_{5,10} = 10.52$, $P = 0.001$; BTNW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-14.7, 8.9]$, $F_{5,10} = 27.81$, $P < 0.001$; RBNU $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-4.3, 11.1]$, $F_{5,10} = 12.05$, $P = 0.0006$; WOTH $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-4.6, 10.2]$, $F_{5,10} = 9.36$, $P = 0.002$). Distance from the observer was also a significant factor affecting distance estimates for the wood thrush ($\bar{d}_{obs}[\text{min.}, \text{max.}] = [-12.3, 14.2]$, $F_{6,14} = 4.39$, $P = 0.011$). We observed a distance by observer interaction for the red-breasted nuthatch ($F_{30,14.4} = 13.68$, $P < 0.001$), indicating bias in distance estimation changed differently for observers as distance increased.

Our next analysis demonstrated that distance estimates for songs played away from observers were approximately

double those for songs played toward observers, even for observers that consistently underestimated distances to songs played toward them. Estimation bias for songs played away from observers was much greater than that for songs played toward observers (Fig. 4).

Song direction for the untrained (ACFL $\bar{d}_{dir}[\text{front, back}] = [3.8, 33.9]$, $F_{1,9.5} = 21.04$, $P = 0.0011$; BAWW $\bar{d}_{dir}[\text{front, back}] = [2.3, 32.9]$, $F_{1,11.4} = 65.21$, $P < 0.001$; BTNW $\bar{d}_{dir}[\text{front, back}] = [0.3, 32.8]$, $F_{1,12} = 39.73$, $P < 0.001$; RBNU $\bar{d}_{dir}[\text{front, back}] = [8.2, 36.7]$, $F_{1,9.4} = 56.96$, $P < 0.001$; WOTH $\bar{d}_{dir}[\text{front, back}] = [5.1, 33.1]$, $F_{1,11.6} = 41.87$, $P < 0.001$) and trained (ACFL $\bar{d}_{dir}[\text{front, back}] = [4.9, 36.3]$, $F_{1,4.72} = 68.23$, $P < 0.001$; BAWW $\bar{d}_{dir}[\text{front, back}] = (3.9, 31.8)$, $F_{1,12} = 61.73$, $P < 0.001$; BTNW $\bar{d}_{dir}[\text{front, back}] = [4.6, 30.8]$, $F_{1,9.0} = 62.07$, $P < 0.001$; RBNU $\bar{d}_{dir}[\text{front, back}] = [9.7, 34.4]$, $F_{1,7.4} = 29.76$, $P < 0.001$; WOTH $\bar{d}_{dir}[\text{front, back}] = [5.6, 31.4]$, $F_{1,2.3} = 66.45$, $P < 0.009$) and observer for the untrained (ACFL $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-4.5, 26.4]$, $F_{5,8} = 82.09$, $P < 0.001$; BAWW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [6.9, 25.8]$, $F_{5,8} = 4.41$, $P = 0.03$; BTNW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-1.9, 37.2]$, $F_{5,8} = 26.16$, $P < 0.001$; RBNU $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-2.7, 34.2]$, $F_{5,8} = 13.56$, $P = 0.001$; WOTH $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-4.4, 31.4]$, $F_{5,8} = 13.41$, $P = 0.0010$) and trained (ACFL $\bar{d}_{obs}[\text{min.}, \text{max.}] = [11.1, 27.4]$, $F_{5,8} = 12.68$, $P = 0.001$; BAWW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [0.8, 28.3]$, $F_{5,8} = 6.9$, $P = 0.009$; BTNW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [7.2, 25.1]$, $F_{5,8} = 41.71$, $P < 0.001$; RBNU $\bar{d}_{obs}[\text{min.}, \text{max.}] = [13.8, 30.7]$, $F_{5,8} = 5.54$, $P = 0.017$; WOTH $\bar{d}_{obs}[\text{min.}, \text{max.}] = [14.2, 29.0]$, $F_{5,8} = 3.92$, $P = 0.043$) experiments were significant factors affecting distance estimation errors for all species. Distance by observer ($F_{10,10} = 5.54$, $P = 0.006$) and distance by observer by song direction ($F_{10,10} = 4.48$, $P = 0.010$) were significant interactions for the

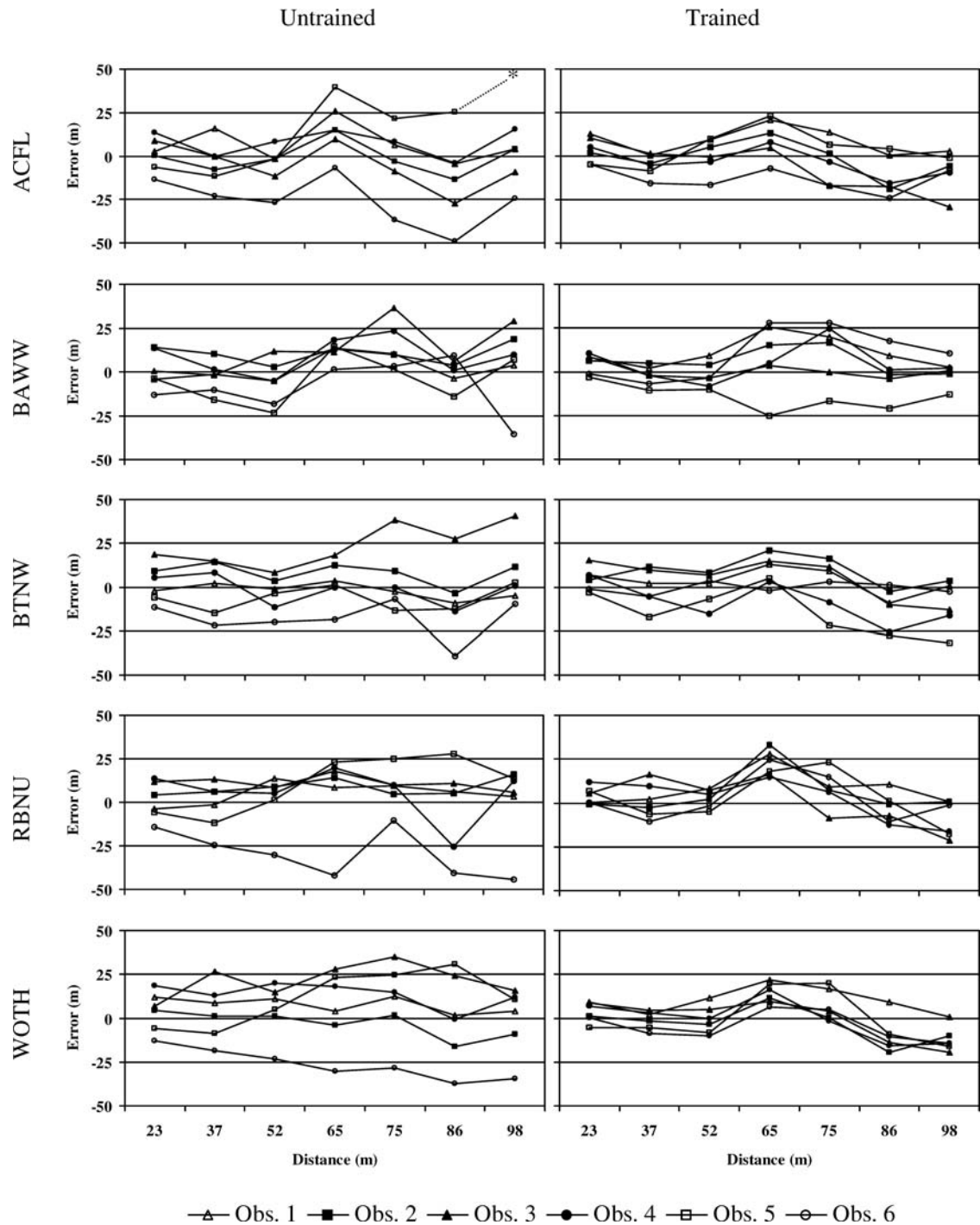


Figure 3. Average distance estimation error across the 3 players oriented toward the observer within each distance category for each observer (Obs) and species. Experiment conducted at Howell Woods, North Carolina, USA, in February 2005. ACFL = Acadian flycatcher, BAWW = black-and-white warbler, BTNW = black-throated green warbler, RBNU = red-breasted nuthatch, and WOTH = wood thrush.

Acadian flycatcher in the untrained observer experiment. Distance by song direction ($F_{2,11.4} = 4.86$, $P = 0.030$) was a significant interaction for the black-and-white warbler in the untrained observer experiment, associated with increasing overestimation at larger distances for songs oriented towards the observers. Song direction by observer were significant interactions for both the red-breasted nuthatch ($F_{5,8} = 4.82$, $P = 0.025$) and the wood thrush ($F_{5,8} = 7.97$, $P = 0.006$) in the trained observer experiment.

Our final analysis showed little effect of speaker height on distance estimation error. Mean distance estimation error, pooling across all distances, was similar between the ground and tree player locations for all observers (Fig. 5). Observer differences were significant (ACFL $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-29.5, 9.6]$, $F_{5,12} = 51.17$, $P < 0.001$; BAWW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-6.3, 9.0]$, $F_{5,12} = 4.74$, $P = 0.013$; BTNW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-21.0, 20.7]$, $F_{5,12} = 74.32$, $P < 0.001$; RBNU $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-33.7, 11.2]$, $F_{5,12} = 14.80$, $P <$

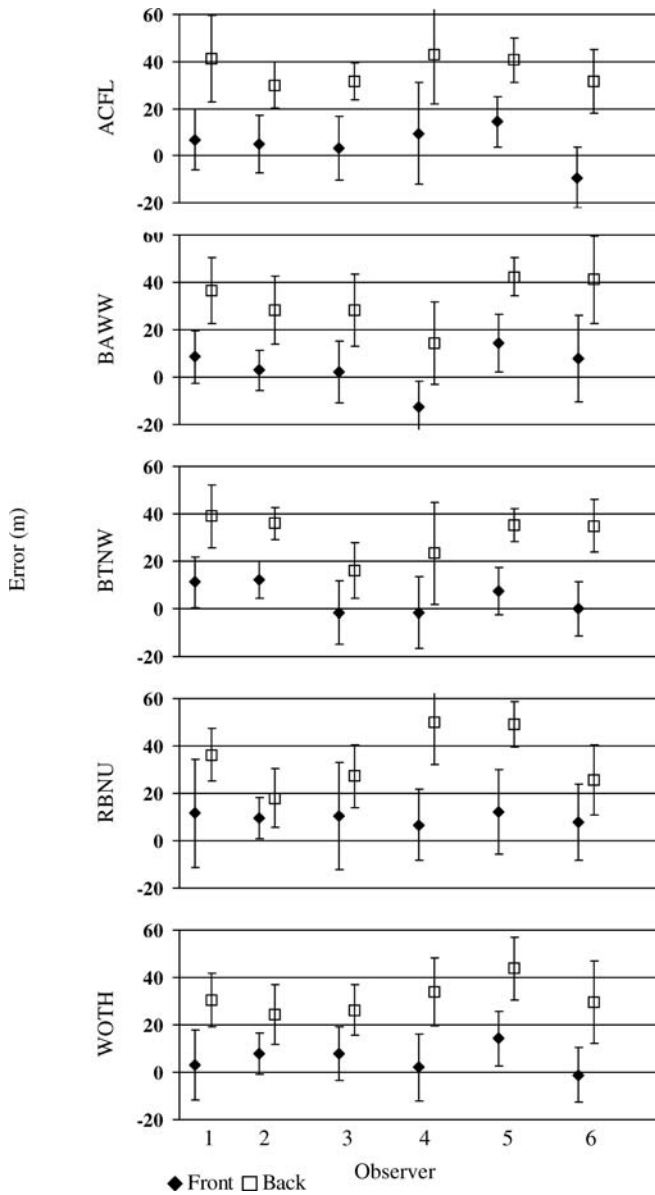


Figure 4. Average distance estimation error for observers 1 through 6 averaged across the 23-m, 52-m, and 65-m distance categories depicting differences in measurement errors for songs oriented toward the observers (front) compared with those oriented away from observers (back). We conducted the experiment at Howell Woods, North Carolina, USA, in February 2005. ACFL = Acadian flycatcher, BAWW = black-and-white warbler, BTNW = black-throated green warbler, RBNU = red-breasted nuthatch, and WOTH = wood thrush.

0.001; WOTH $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-31.0, 25.7]$, $F_{5,12} = 63.34$, $P < 0.001$) for all species except the black-and-white warbler for the untrained observer experiment and for all species (ACFL $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-13.8, 9.6]$, $F_{5,12} = 28.75$, $P < 0.001$; BAWW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-18.0, 15.3]$, $F_{5,12} = 20.44$, $P < 0.001$; BTNW $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-16.6, 7.4]$, $F_{5,12} = 57.79$, $P < 0.001$; RBNU $\bar{d}_{obs}[\text{min.}, \text{max.}] = [1.8, 16.8]$, $F_{5,12} = 5.74$, $P = 0.006$; WOTH $\bar{d}_{obs}[\text{min.}, \text{max.}] = [-4.5, 10.4]$, $F_{5,12} = 10.65$, $P < 0.001$) in the trained observer experiment. Distance by observer was a significant interaction for the Acadian flycatcher ($F_{10,12} = 3.43$, $P = 0.024$), black-and-white warbler ($F_{10,12} = 2.83$, $P = 0.046$),

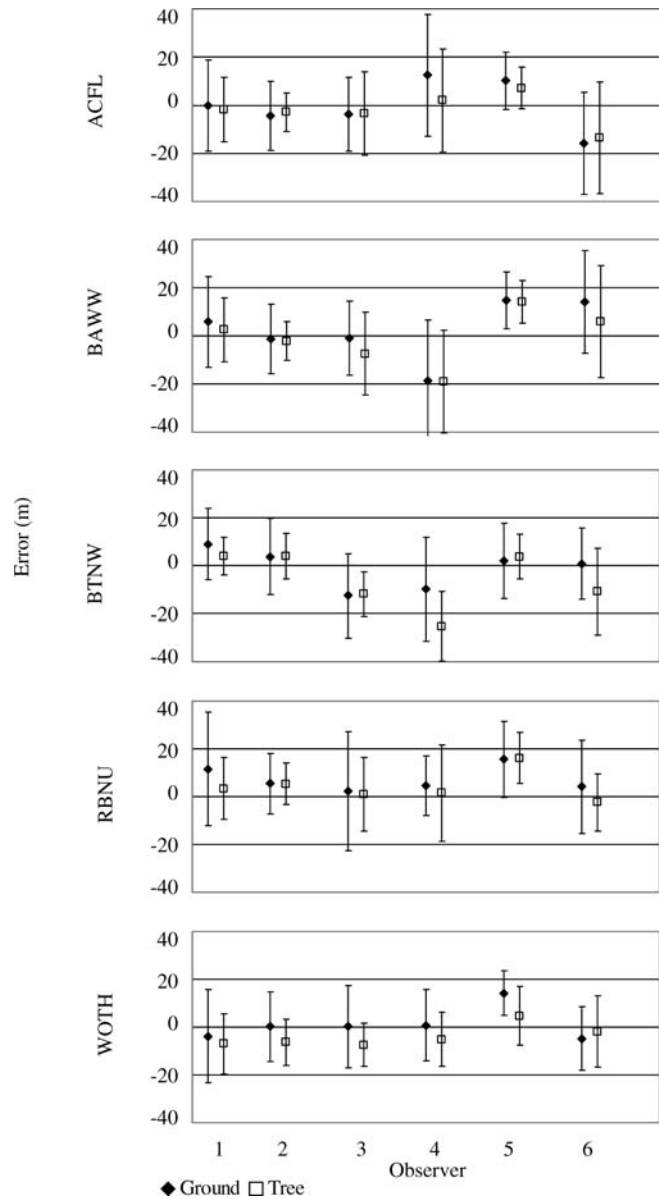


Figure 5. Average distance estimation error for observers 1 through 6 averaged across the 52-m, 65-m, and 86-m distance categories depicting differences between measurement errors for songs played from ground speakers compared to tree speakers. We conducted the experiment at Howell Woods, North Carolina, USA, in February 2005. ACFL = Acadian flycatcher, BAWW = black-and-white warbler, BTNW = black-throated green warbler, RBNU = red-breasted nuthatch, and WOTH = wood thrush.

and wood thrush ($F_{10,12} = 6.31$, $P = 0.002$) in the untrained observer experiment. Height by observer was a significant interaction for the Acadian flycatcher ($F_{5,12} = 3.53$, $P = 0.034$) and black-and-white warbler ($F_{5,12} = 3.49$, $P = 0.035$) for the untrained observer experiment, which related to some observers overestimating distance for tree speakers at close distances. Distance by observer was a significant interaction for the black-and-white warbler ($F_{10,12} = 5.12$, $P = 0.005$) and the red-breasted nuthatch ($F_{10,12} = 3.15$, $P = 0.032$) for trained observers. Height was not a significant factor for any species for either untrained or trained observers ($P > 0.16$, most significant was for WOTH in

trained experiment, $F_{1,12} = 2.18$, $P = 0.167$), with the largest average distance occurring for the wood thrush in the trained experiment ($\bar{d}_{ground} = 2.14$, $SE = 2.46$; $\bar{d}_{tree} = -2.99$, $SE = 2.46$)

DISCUSSION

We think that our results are very important because they provide some of the first field measurements of distance measurement errors for aural detections. Nevertheless, there are practical limitations to our approach. For example, we were not able to replicate our measurements in different habitats, during different seasons of the year, or by using different variations of species' calls. Thus, our analyses using the split-plot model only incorporates variation among observers and bird species. Also, we have had to ignore possible carryover effects of observers' behavior changing from call to call.

Our results reflect the magnitude of distance estimation errors in a somewhat simplified and partially controlled field setting. We provided trained observers with multiple examples of a single known species under low-ambient-noise, leaf-off conditions, and we gave them ample time to evaluate each song and estimate distances. Thus, our mean measures of distance estimation errors should be considered conservative in comparison with errors expected under actual census conditions when observers attempt to rapidly estimate distances to many individuals and species under highly variable levels of ambient noise at different spatial points. Furthermore, our variance estimates are likely highly conservative, because they do not include spatial variation. Nevertheless, we were surprised by the magnitude of distance estimation errors, even for songs played toward observers at relatively small distances. For example, when we played songs at a distance of 23 m, observers underestimated and overestimated the distance by as much as 35% and 96%, respectively.

When observers estimate distances based solely on song characteristics, such as sound intensity and sound quality, errors (due primarily to the difficulty of localization) are likely due to variations in sound intensity, attenuation, and reverberations related to habitat structure, and local environmental factors such as wind, topography, and ambient noise (Richards and Wiley 1980, Wiley 1991, Slabbekoorn 2004, Simons et al. 2007). Under ideal conditions, sound attenuates by 6 dB for each doubling of distance, but attenuation rates vary substantially in natural environments because higher frequency sounds attenuate faster than lower frequency sounds, and because the effects of reverberations vary from site to site due to differences in forest structure (Morton 1975, Wiley and Richards 1982, Bibby and Buckland 1987).

Errors also reflect the limitations of human hearing. The frequency range of most birds, 3–4 kHz (Richards and Wiley 1980), is within the range where humans have the greatest difficulty localizing sound sources. Low-frequency sounds are localized by binaural time differences derived from the phase differences of sound waves arriving at each

ear. High-frequency sounds are located by the binaural differences in sound intensity (Casseday and Neff 1973). Casseday and Neff (1973) found that sound localization by humans is relatively accurate below 1,000 Hz, decays steadily above 1,000 Hz, and then begins to increase again as frequency is raised above 4,000 Hz. The difficulty our observers had localizing bird songs at distances greater than 65 m may be explained in part by the overlap between the frequency range of bird song and the frequency range where the ability of humans to localize sound is most degraded.

We expected that playing songs from locations 12 m high in trees would reduce distance estimation errors due to lower signal interference from the ground and vegetation. However, we found no significant effect of song height on distance estimation errors. This may, in part, reflect the leaf-off habitat conditions under which we conducted the experiment.

Estimation errors were larger when we oriented songs away from observers. The distance estimates of songs played away from observers ($\bar{x} = 32.9$ m, $SD = 15.7$) were at least double those for songs played toward observers ($\bar{x} = 5.7$ m, $SD = 14.7$). Assuming that the orientation of wild birds with respect to observers is essentially a random process, we can expect large distance estimation errors of the order of 19 m ($SD > 15$ m, 95% $CI = 0$ –49 m), even under ideal sampling conditions.

Distance estimation error was reduced at all seven distance categories after our observers received training (e.g., observer 6 in Fig. 2). Nevertheless, overall distance errors were still large and highly variable following training (overall \bar{x} error = 7.6 m, $SD = 21.4$ m). The benefit of training may be limited because observers apparently cannot discriminate differences in singing distance when birds are >65 m from an observer (Fig. 2).

The observed bias in distance estimates, between 65 m and 86 m, even after training, may indicate that observers were unable to differentiate songs within this distance range. Estimates did increase, as expected, at distances beyond 86 m, perhaps because observers associated very faint songs with their expected maximum detection distance for particular species.

The distance estimation errors observed in this experiment have implications for the use of unlimited-radius and fixed radius point counts. Distance estimation errors will produce errors in the estimated area sampled on a point count. Random, unbiased distance estimation errors will inflate counts of fixed radius plots because the number of birds outside the fixed radius that are mistakenly included will be greater than the number of birds occurring inside the fixed radius that are mistakenly omitted from the count (Buckland et al. 2001). Simulating a count based on the errors observed in this study suggests that, given perfect detection of birds and a 100-m fixed radius plot, a raw count would be $17 \pm 3.2\%$ greater than the actual population occurring within the fixed plot radius.

Density estimates based on distance sampling methods are similarly affected by distance estimation errors because the

number of birds in any distance interval increases with distance. Therefore, random errors in distance estimates result in a net transfer of animals toward smaller distances (Buckland et al. 2001). For example, consistently overestimating distance by 10% results in a 17% underestimate of density. Underestimating distance by 10% results in 23% overestimate of density (Buckland et al. 2001). The inability of observers to estimate the distances to songs played between 65 m and 86 m suggests that “heaping” (the tendency for estimates to cluster around particular values; Buckland et al. 2001:34) will also be a problem with auditory distance estimates. Simulation of actual point counts using distance sampling procedures has demonstrated that heaping is a problem and that density estimates overestimate true density by 79% (SE = 10.0%) on average.

Our research shows that accounting for distance measurement error on auditory point counts is crucial because the magnitude of the error is large. New developments in statistical methodology have extended distance sampling to model distance measurement errors in ways that do not produce bias in density estimates (Burnham et al. 2004). However, we are not convinced this approach will provide practical improvements in abundance estimates. Current models that correct for distance estimation errors assume either an additive error structure (Chen 1998, Chen and Cowling 2001) or a multiplicative error structure (Marques 2004). The error structure of our data is neither additive nor multiplicative, but closer to quadratic in nature (Fig. 2). Therefore, our research indicates that the statistical measurement error modeling will need to be more complex than the current literature suggests.

MANAGEMENT IMPLICATIONS

Distance sampling is the predominant method used to account for variations in detection probability and to estimate sampled area on avian point counts. The method assumes distances are measured accurately and most current practitioners assume that training and the use of range-finders obviates the need to account for measurement error. Ours is the first empirical evaluation of distance measurement error on auditory point counts. Measurement error was substantial, even under our simplified field conditions, which implies high uncertainty exists in derived estimates of avian diversity and abundance based on such distance sampling data. We recommend that practitioners distinguish between visual and auditory detections in the analysis of point count data and avoid distance sampling methods on avian point counts when most detections are auditory. We also look forward to the development of realistic measurement error models if distance sampling based on auditory detections is unavoidable.

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