

FACTORS AFFECTING AURAL DETECTIONS OF SONGBIRDS

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Abstract. Many factors affect the number of birds detected on point count surveys of breeding songbirds. The magnitude and importance of these factors are not well understood. We used a bird song simulation system to quantify the effects of detection distance, singing rate, species differences, and observer differences on detection probabilities of birds detected by ear. We simulated 40 point counts consisting of 10 birds per count for five primary species (Black-and-white Warbler *Mniotilta varia*, Black-throated Blue Warbler *Dendroica caerulescens*, Black-throated Green Warbler *Dendroica virens*, Hooded Warbler *Wilsonia citrina*, and Ovenbird *Seiurus aurocapillus*) over a range of 15 distances (34–143 m). Songs were played at low (two songs per count) and high (13–21 songs per count) singing rates. Detection probabilities averaged across observers ranged from 0.60 (Black-and-white Warbler) to 0.83 (Hooded Warbler) at the high singing rate and 0.41 (Black-and-white Warbler) to 0.67 (Hooded Warbler) at the low singing rate. Logistic regression analyses indicated that species, singing rate, distance, and observer were all significant factors affecting detection probabilities. Singing rate \times species and singing rate \times distance interactions were also significant. Simulations of expected counts, based on the best logistic model, indicated that observers detected between 19% (for the worst observer, lowest singing rate, and least detectable species) and 65% (for the best observer, highest singing rate, and most detectable species) of the true population. Detection probabilities on actual point count surveys are likely to vary even more because many sources of variability were controlled in our experiments. These findings strongly support the importance of adjusting measures of avian diversity or abundance from auditory point counts with direct estimates of detection probability.

Key words: auditory detection; detection probability; observer differences; point counts; singing rate; species difference; warblers.

INTRODUCTION

A point count survey, in which observers record all birds seen or heard at a point within a specified time interval (Ralph et al. 1995), is the most common counting method used in bird population studies (Rosenstock et al. 2002, Diefenbach et al. 2003). Hundreds of thousands of point counts are conducted annually in North America by federal, state, and private entities (Simons et al. 2007). Point counts are widely used to monitor spatial and temporal patterns in bird abundance, and to study species–habitat relationships and the response of populations to environmental change or management. Most researchers acknowledge the numerous factors affecting survey data, but without an assessment of the magnitude of these effects, it is not possible to judge the validity of abundance estimates derived for monitoring or research. We used a novel

experimental approach to quantify several factors that affect detection probabilities on point count surveys.

Surveys in heavily vegetated habitats rely almost exclusively on auditory detections (Faanes and Bystrak 1981, Scott et al. 1981, Dejong and Emlen 1985), and most use unadjusted counts as an index of population abundance (Rosenstock et al. 2002, Thompson 2002). The primary benefits of this approach are speed and low cost.

The problem with using count indices of population abundance is that many uncontrollable factors affect the detection probabilities of birds. Thus, observed differences among counts may represent either actual differences in abundance or differences in detection probability. Observer differences (Sauer et al. 1994, Kendall et al. 1996), habitat structure (Diehl 1981, McShea and Rappole 1997), meteorological conditions (Mayfield 1981, Robbins 1981), background noise (Simons et al. 2007), time of year (Best 1981, Skirvin 1981), and time of day (Robbins 1981, Skirvin 1981) are all factors known to affect detection probability. Any factor affecting the quality or quantity of a sound signal (such as masking, attenuation, or singing rate) can bias count indices by its affect on detection probability. For

Manuscript received 26 April 2006; accepted 23 June 2006; final version received 10 August 2006. Corresponding Editor: R. L. Knight.

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example, factors affecting the intensity of the sound reaching the observer will cause the maximum distance at which a bird can be identified to vary among sampling locations or years. Similarly, factors that affect singing rates of birds will directly affect the probability that a bird is detected by an observer.

Recognition of these factors has led to standardized methods for counts, including standards for the timing and environmental conditions under which counts are conducted (Ralph et al. 1995). The Breeding Bird Survey (Sauer et al. 2003) uses a standardized protocol specifying the time of year, time of day, weather conditions, and the location of survey points used each year. Standardized methods are often used to justify comparisons of unadjusted counts based on the assumption that the proportion of individuals detected is constant over space and time. This approach has been criticized because standardization cannot account for all of the factors that affect detection probabilities on counts, which can result in misleading inferences about bird abundance over space or time (Burnham 1981, Nichols et al. 2000, Thompson 2002, Norvell et al. 2003). For example, local background noise, habitat structure, and singing rate cannot be controlled by simply standardizing the environmental conditions and time of year under which counts are conducted.

A hypothetical example will illustrate. If point counts are conducted on the same dates and times each year under standardized weather conditions, but ambient noise increases annually (e.g., due to increased traffic), or if vegetation becomes increasingly dense due to natural succession, then the effective area sampled by observers is likely to decrease over time, giving the appearance of declining populations. Similarly, many authors (Diehl 1981, Mayfield 1981, Wilson and Bart 1985, McShea and Rappole 1997) have hypothesized that differences in singing rates, which are related to an individual's breeding stage, cause differences in detection probabilities over the course of the breeding season. Trends in factors that influence singing rates in birds, such as climate (Both et al. 2006), can impose similar trends in detection probabilities, and the appearance of trends in true abundance (Simons et al. 2007). Biases due to factors affecting detection probabilities are thus problematic for almost all estimates of bird abundance.

Various sampling methods have been developed to adjust count data for biases caused by variations in detection probabilities. These include distance sampling (Buckland et al. 2001, Rosenstock et al. 2002), multiple-observer methods (Nichols et al. 2000, Alldredge et al. 2006), and time-of-detection methods (Farnsworth et al. 2002, Alldredge et al. 2007).

We have developed a system for simulating avian census conditions when most birds are identified by sound. The system uses a laptop computer to control a set of amplified MP3 players placed at known locations around a census point. The system can realistically simulate a known population of songbirds under a range

of factors that affect detection probabilities (Simons et al. 2007).

In this paper we report on experiments that used the bird song simulation system to quantify the effects of detection distance, singing rate, species differences, and observer differences on detection probabilities of birds detected by ear. We specifically tested the effect of two different singing rates on detection probabilities for five species of forest songbirds. We use logistic regression to obtain empirical estimates of detection probability including singing rate, species, distance, and observer as factors. We use these empirical estimates, and evidence of significant model factors, to make inferences about biases in standard point count methods that use unadjusted counts as indices of bird abundance.

METHODS

Point count simulation

We used a bird song simulation system (Simons et al. 2007) to simulate 40 3-minute point counts for seven skilled observers. All observers were experienced birders with extensive point count experience, and all were provided a species list and recordings of the songs used, prior to the experiment. Experiments were conducted in March 2005 to minimize auditory interference from resident birds. Field experiments were conducted at Howell Woods, a 1133-ha natural area in Johnston County, North Carolina, USA. The site consisted of mature bottomland hardwood and mixed pine-hardwood forest in an isolated rural setting. All counts were done at the same location and on the same day to minimize variations in detection probabilities associated with habitat or environmental differences. We simulated nine bird species that were not present in the study area at the time of the experiment. Most of the calls played were from the five species used for analysis: Black-and-white Warbler (BAWW), Black-throated Blue Warbler (BTBW), Black-throated Green Warbler (BTNW), Hooded Warbler (HOWA), and Ovenbird (OVEN). A small number of calls from four other species (Acadian Flycatcher *Empidonax virescens*, ACFL; Red-breasted Nuthatch *Sitta canadensis*, RBNU; Scarlet Tanager *Piranga olivacea*, SCTA; and Winter Wren *Troglodytes troglodytes*, WIWR) were also played at each point to maintain a diversity of species typical of field situations. We simulated 10 individual birds for every point count, chosen at random with a maximum of two birds for a given species at each point.

In total, 60 birds were simulated for BAWW, BTBW and HOWA, and 80 birds were simulated for BTNW and OVEN, for a possible 340 primary bird observations in the experiment (Table 1). Player malfunctions on three occasions resulted in an actual total of 337 primary birds. Songs were played at low (two songs per 3-minute count) and high (13–21 songs per 3-minute count) singing rates. Half of the total possible observations for each species were simulated at the high singing rate and half were simulated at the low singing rate. Sound

TABLE 1. Description of how songs were played during the experiment, including singing rates, total number of songs, birds per day, and height above ground for each of the nine species used during the experiment.

Species	Intersong interval (s)	Singing rate	Total no. songs	Total no. birds	Height (m)
Black-and-white Warbler	8	low	2	30	12.2
		high	14	30	12.2
Black-throated Blue Warbler	13	low	2	30	12.2
		high	13	30	12.2
Black-throated Green Warbler	9	low	2	40	12.2
		high	18	40	12.2
Hooded Warbler	8	low	2	30	3.0
		high	21	30	3.0
Ovenbird	8	low	2	40	3.0
		high	21	40	3.0
Acadian Flycatcher	8	low	1	15	3.0
		high	21	15	3.0
Red-breasted Nuthatch	12	low	1	15	3.0
		high	10	15	3.0
Scarlet Tanager	11	low	2	15	12.2
		high	15	15	12.2
Winter Wren	12	low	2	15	3.0
		high	14	15	3.0

intensity levels for all species were standardized to 90 dBA at 1 m (decibels frequency-weighted to the A curve, used to express the intensity of a sound wave, equal to 20 times the common logarithm of the ratio of the pressure produced by the sound wave to a reference pressure). Ambient sound levels during the experiment averaged 39.2 ± 2.26 (mean \pm SE). Points 27, 28, and 29 were redone after completing the original 40 points, because military jets flying overhead produced sound levels in excess of 80 dBA. All songs were played from speakers facing directly toward the observers at random distances ranging from 34 m to 143 m, which were located along random bearings (Fig. 1). Speakers were placed at heights characteristic for the simulated species

(between 3.0 m and 12.2 m; Table 1). In total, there were 2359 potential observations by our seven observers for the five primary species.

Analysis

Data were scored as binary dependent variables determined by whether or not individual observers detected or failed to detect individual simulated birds. We modeled the data using logistic regression, which explicitly assumes a binomially distributed error structure (Agresti 1990). Singing rate (*R*), species (*S*), and observer (*O*) effects were included as independent categorical variables, whereas distance from observer (*x*) was treated as a continuous independent variable.

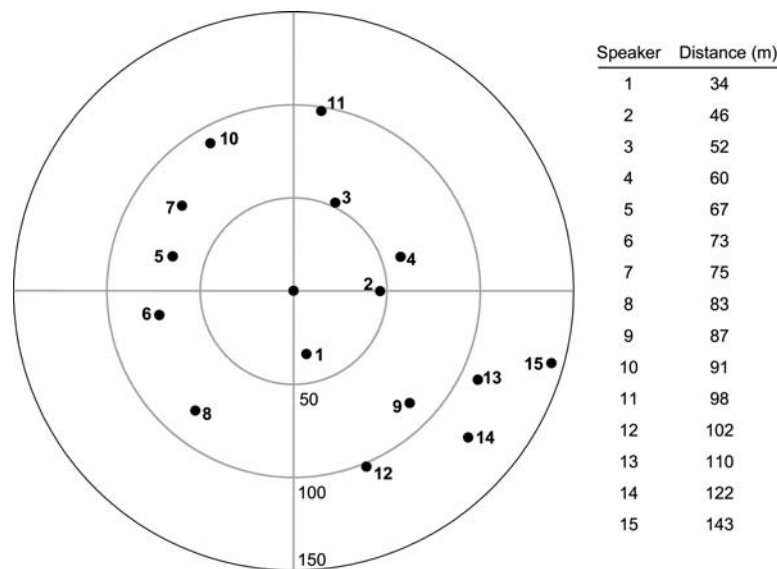


FIG. 1. Locations and radial distance for the 30 speakers used for the detection probability estimation experiment. Each location had one speaker at 3 m and another at 12.2 m above ground.

The general form of the main-effects model used for the logistic regression was

$$\text{logit}[\pi(y)] = \beta_0 + \beta_1 x + \beta_2 R + \beta_3 S + \beta_4 O$$

where $\pi(y)$ was the probability that y was 1 (song detected by an observer), given fixed values of the independent variables, and β_0 , β_1 , β_2 , β_3 , and β_4 were the estimated model parameters. Additional models were parameterized by considering interactions among the independent variables. Only the five primary species were analyzed, due to sample size limitations.

We assumed that species, observer, singing rate, distance, and interactions among these variables were biologically relevant factors affecting detection probabilities. We considered a null model with an intercept only and models with subsets of main effects (16 models). We then considered models of all possible two-way interactions, and we used AIC (Burnham and Anderson 2002) to select the most appropriate model. If a model was selected with multiple two-way interactions, we then examined the importance of potential three-way interactions.

Given the number of candidate models, we only present ΔAIC (the difference between the AIC value for a given model and that of the best model) and AIC weights (the weight of evidence for a given model) for models with $\Delta\text{AIC} < 10$ (Burnham and Anderson 2002). We calculated variable importance weights for each variable by summing the AIC weights for each model in which the predictor variable appeared (main effects and two-way interactions). Variable importance weights allow a direct comparison of variables by ranking each variable on a scale from 0 to 1, with 1 indicating greatest importance (Burnham and Anderson 2002).

We used the selected logistic model to demonstrate the variability in raw count data by estimating the expected counts for a hypothetical point count survey. We calculated expected counts for our “best” and “worst” observer, the least detectable and most detectable species, and the highest and lowest singing rates. We did this by distributing (uniformly with respect to area) a simulated population of 1000 birds at distances of 30, 60, 90, 120, and 150 m, and using the estimated detection probabilities from the logistic model for specific observers, distances, species, and singing rates to estimate expected counts.

RESULTS

The proportion of birds detected varied by species, observer, and singing rate (Fig. 2). No observer consistently detected a higher proportion of birds, indicating that observer abilities differed among species. Average detection probabilities for all observers and species ranged from 0.60 (BAWW) to 0.83 (HOWA) at the high singing rate, and from 0.41 (BAWW) to 0.67 (HOWA) at the low singing rate.

The proportion of birds detected by observer 7 was very low (<0.18) for three of the primary species. The

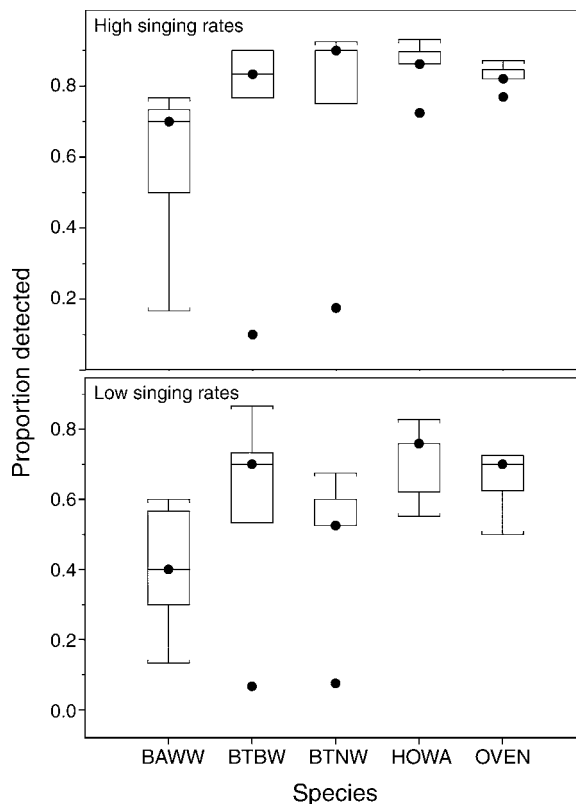


FIG. 2. Box plots for each species of interest showing the average proportion detected and the amount of variability in the proportion detected for both high (upper panel) and low (lower panel) singing rates. The box depicts the median (solid line in box) and the upper and lower 25% quartiles, whiskers represent the data range; outliers (values outside the whiskers of the box plot) are shown. Species abbreviations are: BAWW, Black-and-white Warbler; BTBW, Black-throated Blue Warbler; BTNW, Black-throated Green Warbler; HOWA, Hooded Warbler; OVEN, Ovenbird.

detection probability for observer 7 was considered an outlier (outside 1.5 times the standard range) for four species at the high singing rate and two species at the low singing rate (Fig. 2). This may have been the result of high-frequency hearing loss, and this observer was dropped from subsequent analyses. The average proportion detected across all species for the six other observers was 0.82 ± 0.096 (mean \pm SE) for the high singing rate and 0.63 ± 0.131 for the low singing rate.

The selected logistic model included all main effects and singing rate \times distance and singing rate \times species interactions. Nine models had ΔAIC values <10 (Table 2), all of which included the main effects and the singing rate \times distance interaction effect. The top six models also included a singing rate \times species interaction effect. AIC weights indicated that the top three models were best supported by the data (sum of AIC weights for these models is 0.891). The two alternate models added either an observer \times distance or an observer \times singing rate interaction effect to the selected model. The AIC

TABLE 2. Δ AIC and AIC weights (w_i) for logistic regression models of detection probability with Δ AIC values <10.

Model	Δ AIC	w_i
O + R + S + D + R × D + R × S	0.00	0.396
O + R + S + D + R × D + R × S + O × D	0.43	0.319
O + R + S + D + R × D + R × S + O × R	1.62	0.176
O + R + S + D + R × D + R × S + D × S	4.89	0.034
O + R + S + D + R × D + R × S + O × R + O × D	5.35	0.027
O + R + S + D + R × D + R × S + O × D + D × S	5.36	0.027
O + R + S + D + R × D	8.08	0.007
O + R + S + D + R × D + O × D	8.50	0.006
O + R + S + D + R × D + O × R	9.92	0.003

Note: Candidate models consisted of main effects (O, Observer; R, singing rate; S, Species; and D, Distance) and two-way interactions.

value for a model adding a three-way interaction to the selected two-way interaction model was larger (difference in AIC = 3.2), indicating a lack of support for the three-way interaction model.

The selected model fit the data reasonably well (maximum-rescaled $R^2 = 0.49$). The variable importance weights for all of the predictor variables in the selected model were near 1.00 (Table 3), indicating that these variables were very important in explaining the variability in data. All other variable importance weights were <0.38, indicating lower importance for these two-way interaction predictor variables.

Observer 1 detected the highest proportion of birds and was used as the reference observer. Therefore, the parameter estimates for all other observers were negative, indicating lower overall detection probabilities (Table 4). Parameter estimates and standard errors showed similarity among observers 2, 3, and 6. Observers 4 and 5 had much lower detection probabilities than the other observers. Using the high singing rate as a reference, the parameter estimate for singing rate was negative, indicating a significantly lower detection probability for the low singing rate (Table 4). The parameter estimate for distance indicated that detection probability declined with distance from observers (Table 4). Parameter estimates indicate that BAWW had the lowest detection probability overall, but the other four species had relatively similar detection

TABLE 3. Variable importance weights (Σw_i) obtained by summing AIC weights for each model in which the predictor variable (main effects and two-way interactions) was found.

Predictor variable	Σw_i
Observer	1.00
Singing rate	1.00
Distance	1.00
Species	1.00
Observer × singing rate	0.21
Observer × distance	0.38
Observer × species	0.00
Rate × distance	1.00
Rate × species	0.98
Distance × species	0.07

Note: Variable importance weights near 1.00 indicate greater variable importance.

probabilities at the high singing rate (Table 4). The parameter estimate for the singing rate × distance interaction was positive, indicating that the effect of singing rate declines with increasing distance (Table 4). BTNW showed the only significant singing rate × species interaction, indicating that the effect of singing rate on detection probability was similar among all other species (Table 4).

Model results for a single observer further illustrate these patterns (Fig. 3). Detection probabilities for each species were higher for the high singing rate than the low singing rate (singing rate main effect). High singing rate detection probabilities were similar among all species except BAWW and were near 1.00 out to ~100 m. Detection probabilities for BAWW at the high singing rate began to fall off at 60 m (species main effect primarily associated with BAWW). At the low singing rate, detection probabilities declined more rapidly than at the high singing rate (distance × singing rate inter-

TABLE 4. Parameter estimates and standard errors for the selected model with main effects (species, distance, observer, and singing rate), and interactions.

Parameters	Estimate	SE
Main effects		
Intercept	8.053	0.5811
Observer 2	-0.590	0.2281
Observer 3	-0.319	0.2310
Observer 4	-0.937	0.2258
Observer 5	-0.755	0.2268
Observer 6	-0.469	0.2293
Low singing rate	-3.741	0.6420
Distance	-0.077	0.0056
BTBW	1.698	0.3513
BTNW	2.062	0.3480
HOWA	2.339	0.3885
OVEN	1.548	0.3253
Interactions		
Distance × singing rate	0.028	0.0066
Singing rate × BTBW	-0.264	0.4397
Singing rate × BTNW	-1.498	0.4187
Singing rate × HOWA	-0.749	0.4736
Singing rate × OVEN	-0.299	0.4054

Note: The intercept parameter is based on the reference values for the model (Observer 1, BAWW, high singing rate, 34 m).

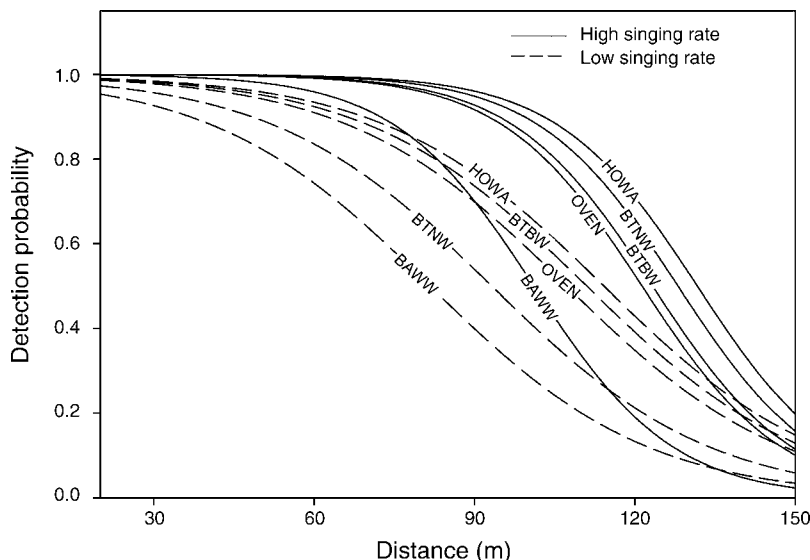


FIG. 3. Logistic regression models for a single observer demonstrating the differences among all five species and high and low singing rates.

action). For all species except BTNW, detection probabilities at high and low singing rates were similar (no singing rate \times species interaction). However, as illustrated by the greater separation between the high and low singing rate curves, the effect of singing rate on detection probability was much greater for BTNW (Fig. 3).

Detection probabilities from the selected logistic model were determined for the best and worst observers, for the least and most detectable species (BAWW and HOWA), for high and low singing rates, and for distances of 30, 60, 90, 120, and 150 m (Table 5). Applying these detection probabilities, the expected counts from a simulated population of 1000 birds ranged from 190 birds (least detectable species, lowest

singing rate, and worst observer) to 653 birds (most detectable species, highest singing rate, and best observer). Differences in counts between observers ranged from 88 to 147 birds, within species and singing rate. Differences in counts between singing rates ranged from 87 to 147 birds, within species and observer. Differences in counts between species ranged from 192 to 271 birds, within singing rates and observer.

DISCUSSION

We used a novel experimental approach to qualitatively and quantitatively assess four factors affecting detection probabilities on point count surveys. Our goal is to improve the quality of bird abundance data

TABLE 5. Detection probabilities at distances from 30 m to 150 m, and expected counts for a simulated population of 1000 birds, by observer and singing rate (low vs. high).

Species and distance (m)	No. birds	Worst observer		Best observer	
		Low	High	Low	High
BAWW					
30	40	0.87	0.99	0.94	1.00
60	120	0.61	0.92	0.80	0.97
90	200	0.26	0.55	0.48	0.75
120	280	0.08	0.11	0.17	0.23
150	360	0.02	0.01	0.05	0.03
Expected count		190	294	295	382
HOWA					
30	40	0.97	1.00	0.99	1.00
60	120	0.88	0.99	0.95	1.00
90	200	0.64	0.93	0.82	0.97
120	280	0.29	0.55	0.51	0.76
150	360	0.08	0.11	0.19	0.24
Expected count		382	538	529	653

Notes: Detection probabilities are based on the logistic models for BAWW (least detectable species) and HOWA (most detectable species) using the best and worst observers and both high and low singing rates.

collected for ecological research and population monitoring. We believe that our findings have important implications for how point count surveys are conducted, and how count data are interpreted.

As we expected, species, singing rate, observer, and distance from the observer were all significant factors affecting detection probabilities on auditory avian point counts. Testing these factors in a controlled experimental framework provides a clear understanding of their effects on the detection process. By experimentally controlling some of the factors affecting the detection process, we have eliminated numerous sources of variability that are normally present in actual bird point count surveys. All of our bird songs were played at the same volume, from speakers facing directly toward the center of the point, and at the same height for a given species. Spatial variation in factors (habitat or topographic differences, changes in ambient noise, and so on) was minimized because the same point was used throughout the experiment. Therefore we would expect greater differences in detection probabilities and greater variability among counts on actual point count surveys than we observed in these experiments.

Differences in detection probabilities among species were expected and were similar to those reported from field studies (Nichols et al. 2000, Diefenbach et al. 2003, Alldredge et al. 2006). These differences are attributable to differences in sound intensity (Emlen and DeJong 1981), sound attenuation (Richards 1981, Wiley and Richards 1982), and singing rates (Mayfield 1981, Read and Weary 1992, McShea and Rappole 1997). Differences among species in this experiment presumably reflect differences in sound attenuation, because sound intensity was similar for all species (~90 dB). The Black-and-white Warbler, the species with the highest frequency song of our primary species, was the least detectable species in our experiment. Morton (1975) has shown how higher frequency songs attenuate more rapidly in forest habitats.

Observer differences in detection probability were also expected. Observer differences have been attributed to both experience (Sauer et al. 1994, Kendall et al. 1996) and hearing loss (Emlen and DeJong 1981, 1992). All of the observers used in this experiment were experienced, but high-frequency hearing loss may have been a source of observer variability, as indicated by the greater standard range in the box plot for the Black-and-white Warbler compared to the other primary species. Although Diefenbach et al. (2003) documented a large range of observer-specific detection probabilities (0.43–1.00) for Henslow's Sparrow, most published studies assume that detection probabilities are similar among observers (Rosenstock et al. 2002). Our results indicate that observer differences are due to differences in the rate at which detection probabilities decline with distance (i.e., that detection probabilities for "better" observers remain high at greater distances, the observer \times distance interaction effect).

The relationship between detection distance and detection probability was also expected. Distance sampling methods are based on the monotonic decline in detection probability with increasing distance from the observer (Buckland et al. 2001, Rosenstock et al. 2002). This relationship was clear at high singing rates. With the exception of the Black-and-white Warbler, detection probabilities were near 1.0 out to a distance of ~100 m and then declined rapidly. Detection probabilities for the Black-and-white Warbler began at smaller detection distances and they declined more gradually, presumably due to higher rates of sound attenuation. We found much greater variability in the relationship between detection probability and distance at the low singing rate. This may reflect observers failing to detect a song due to masking by other species, the distraction of observers, random environmental noise, and so on.

Mayfield (1981), Wilson and Bart (1985), and McShea and Rappole (1997) have documented the effects of singing rate on detection probability. We demonstrated this in our experiment as well, and showed the relationship between singing rate and distance from the observer. Our two levels of singing rate represent the extremes that might be realized in an actual survey. Singing rate variation within a species can be attributed to the proximity of the observer (McShea and Rappole 1997), breeding stage (Mayfield 1981, Wilson and Bart 1985), time of day (Mayfield 1981), time of year (Best 1981, Skirvin 1981), habitat (Diehl 1981, McShea and Rappole 1997), and differences among individual birds (Mayfield 1981). Given the magnitude of the singing rate effect, and the number of factors influencing it, we believe that it is a major determinant of detection probabilities on avian point counts.

Expected counts varied up to 344% among observers, singing rates, and species, producing total counts of between 19% and 65% of the simulated population. Variability for typical point count surveys may be even greater as additional sources of variability may affect the detection of birds, such as habitat, topography, and environmental factors. Given the variety and magnitude of these sources of variability, and the difficulties of constraining them by standardization, it is apparent that valid spatial or temporal comparisons of avian auditory point count data must account for variations in detection probability.

ACKNOWLEDGMENTS

This project was funded by the U.S. Geological Survey and the National Park Service. We thank our wonderful set of observers for their time and support. We also thank K. Pacifici, J. Marsh, and M. Foster for their technical support and assistance with this project and two anonymous reviewers whose comments helped to clarify and improve this manuscript.

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ERRATA

In the paper by N. Thompson Hobbs and Ray Hilborn (2006) published as part of the “Contemporary Statistics and Ecology” Invited Feature, *Ecological Applications* 16(1):5–19, the equations published for Eqs. 6 and 7 were incorrect. The text spanning pp. 8–9 should read as follows:

... The likelihood of model i given the data is

$$\mathcal{L}(g_i|\mathbf{Y}) = e^{-\frac{1}{2}\Delta_i} \quad (6)$$

and the Akaike weight, w_i , is calculated for each model as

$$w_i = \frac{e^{-\frac{1}{2}\Delta_i}}{\sum_{r=1}^R e^{-\frac{1}{2}\Delta_r}}. \quad (7)$$