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EFFECTS OF VEGETATION AND BACKGROUND NOISE ON THE DETECTION PROCESS IN AUDITORY AVIAN POINT-COUNT SURVEYS

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ABSTRACT.—We used a bird-song simulation system to experimentally assess the effects of habitat, vegetation structure, and background noise on detection probability in aural avian point counts. We simulated bird songs of seven species in two habitats (mixed pine–hardwood forest and deciduous forest) and two leaf conditions (leaves on and leaves off) with two levels of background noise (~40 dB and ~50 dB). Estimated detection probabilities varied greatly among species, and complex interactions among all the factors existed. Background noise and the presence of leaves on trees decreased detection probabilities, and estimated detection probabilities were higher in mixed pine–hardwood forest than in deciduous forest. At 100 m, average estimated detection probabilities ranged from 0 to 1 and were lowest for the Black-and-white Warbler (*Mniotilta varia*) and highest for the Brown Thrasher (*Toxostoma rufum*). Simulations of expected counts, based on the best logistic model, indicated that observers detect between 3% (for the worst observer, least detectable species, with leaves on the trees and added background noise in the deciduous forest) and 99% (for the best observer, most detectable species, with no leaves on the trees and no added background noise in the mixed forest) of the total count. The large variation in expected counts illustrates the importance of estimating detection probabilities directly. The large differences in detection probabilities among species suggest that tailoring monitoring protocols to specific species of interest may produce better estimates than a single protocol applied to a wide range of species. Received 15 May 2007, accepted 17 November 2007.

Key words: aural detections, background noise, detection probability, habitat effects, point counts, population indices.

Efectos de la Vegetación y del Ruido de Fondo en el Proceso de Detección de Aves Mediante Registros Auditivos en Puntos de Conteo

RESUMEN.—Empleamos un sistema de simulación de cantos de aves para evaluar experimentalmente los efectos del hábitat, de la estructura de la vegetación y del sonido de fondo en la probabilidad de detección por audición de aves en puntos de conteo. Simulamos los cantos de siete especies de aves en dos ambientes (bosque mixto de pino y especies de madera dura, y bosque caducifolio) y dos condiciones de follaje (con y sin hojas) con dos niveles de sonido de fondo (~40 dB y ~50 dB). Las probabilidades de detección estimadas variaron marcadamente entre las especies, y existieron interacciones complejas entre todos los factores. El sonido de fondo y la presencia de hojas en los árboles disminuyó la probabilidad de detección, y las probabilidades de detección estimadas fueron más altas en los bosques mixtos que en los caducifolios. A 100 m, las probabilidades de detección estimadas promedio variaron entre 0 y 1, y fueron mínimas para *Mniotilta varia* y máximas para *Toxostoma rufum*. Las simulaciones de conteos esperados, basadas en el mejor modelo logístico, indicaron que los observadores detectaron entre el 3% (para el peor observador, las especies más difíciles de detectar, con hojas en los árboles y sonido de fondo agregado en el bosque caducifolio) y el 99% (para el mejor observador, las especies más fáciles de detectar, sin hojas en los árboles y sin sonido de fondo agregado en el bosque mixto) del conteo total. La gran variación en los conteos esperados ilustra la importancia de estimar las probabilidades de detección directamente. Las grandes diferencias en las probabilidades de detección entre las especies sugieren que los protocolos de monitoreo dirigidos a especies focales de interés pueden producir mejores estimados que un único protocolo aplicado a una amplio grupo de especies.

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POINT COUNTS ARE USED to explore avian habitat relationships, to map species diversity and abundance, and to evaluate the effects of management and environmental change on bird populations over space and time (Ralph et al. 1995). Surveys in heavily vegetated habitats rely almost exclusively on auditory detections (Faanes and Bystrak 1981, Scott et al. 1981, DeJong and Emlen 1985). Traditionally, point-count data are used to calculate indices of population abundance, which assumes that the proportion of individuals detected is constant over space, time, or both (Rosenstock et al. 2002, Diefenbach et al. 2003). This assumption is highly dubious, and most biometricians recommend using sampling methods that incorporate direct estimates of detection probability (for example, distance sampling [Buckland et al. 2001] or other methods as described by Simons et al. [2007]). Many field ornithologists, however, still use abundance indices (Rosenstock et al. 2002, Simons et al. 2007), arguing that standardized design protocols modeling measured covariates to control for variation in detection probability are sufficient.

There is widespread evidence that many factors influence detection probabilities on avian point counts. These include habitat (Diehl 1981, Oelke 1981, McShea and Rappole 1997, Schieck 1997), time of day (Robbins 1981b, Skirvin 1981), weather conditions (Robbins 1981a), and observer ability (Faanes and Bystrak 1981, Sauer et al. 1994, Diefenbach et al. 2003). Schieck (1997) noted significant differences among habitat types and leaf conditions and suggested that variations in vegetation complexity among sites influences detection probabilities.

Unfortunately, it is very difficult to estimate detection probabilities accurately in the field, because true species diversity or abundance is usually unknown. Our research group has developed a system for simulating conditions on avian point counts when birds are detected by ear (Simons et al. 2007). This unique system can realistically simulate bird songs under a range of varying factors that affect detection probability, and it enables us to get accurate empirical estimates of detection probability under a wide range of conditions. Previous experiments have evaluated the effects of singing rate, number of species, and observer variability (Allredge et al. 2007b) and assessed current sampling methods, including distance estimation (Allredge et al. 2007a), multiple-observer methods (Allredge et al. 2008), and time-of-detection methods (Allredge et al. 2007c).

Here, we report on the application of our experimental system to study the effects of habitat, vegetation, and background noise on aural detection probabilities. We report empirical detection probability estimates under different combinations of these factors and discuss the implications of our results to the design of future point-count studies.

METHODS

Study sites.—Field studies were conducted in Howell Woods, a natural area comprising 1,133 ha, in Johnston County, North Carolina. Two sites were established within Howell Woods: a mixed pine-hardwood forest and a deciduous forest located ~5 km apart. The mixed pine-hardwood forest is a 30- to 50-year-old successional forest. Dominant species include oaks (*Quercus* spp.), pines (*Pinus* spp.), Sycamore (*Platanus occidentalis*), Blackgum (*Nyssa sylvatica*), and Red Maple (*Acer rubrum*), which create a two-layered forest

with an overstory roughly 20–25 m high and an understory dominated by *Vaccinium* spp., *Ilex* spp., and *Smilax* spp. The deciduous forest is dominated by hickory (*Carya* spp.), Sweetgum (*Liquidambar styraciflua*), and Red Maple and is predominantly a single-layered forest, 5–7 m high, with a dense understory dominated by *Smilax* spp. The deciduous forest contains early-successional communities that have emerged following a hurricane in 1996.

Vegetation indices.—Three vegetation indices—basal area, leaf area index, and coverboard density—were used to compare differences in vegetation structure and composition. Basal area was calculated using a wedge prism (metric units, basal area factor 2) at randomly selected points within each site (Avery and Burkhart 1983), and a paired *t*-test (Rao 1998) was used for comparisons between habitats and leaf conditions. Leaf area index (LAI) is the total one-sided foliage area per unit soil surface area. It provides a measure of the amount of light penetrating through the canopy (Gower and Norman 1991). In forest systems, direct and indirect measures of LAI are available. Indirect measures provide simple, easy ways to collect large amounts of data with minimal effort and have been found to provide rapid means of comparison for spatial and seasonal changes in leaf area (Brantley and Young 2007). Indirect measures of LAI can be made with a portable integrating radiometer, which uses canopy gap fraction to estimate LAI (Gower and Norman 1991). We used an LAI-2000 Plant Canopy Analyzer (LICOR Biosciences, Lincoln, Nebraska) at a height of 1 m to calculate an indirect index of total leaf area within the two study sites and compared estimates between habitats and leaf conditions using a paired *t*-test (Rao 1998). The LAI readings were collected at randomly selected points within both sites during both leaf conditions (leaves off and leaves on). We also used a 1.2-m coverboard (1.2 m height × 0.5 m width) constructed of foam board and marked in a black-and-white checkerboard pattern (sixty 10 × 10 cm squares) to assess horizontal vegetation cover within both sites and under both leaf conditions (Higgins et al. 1996). At each of five distances from the coverboard (2, 5, 10, 12, and 15 m), we calculated an index of horizontal vegetation cover. We counted the number of squares that were >50% obscured by vegetation at each distance to create this index. Instead of using a single optimal distance, we report vegetation indices from all five distances to more completely portray the total horizontal vegetation cover. The coverboard was placed at randomly located points within each site and always faced the center of the site, where observers were located.

Bird detection experiments.—We used a birdsong simulation system (Simons et al. 2007) to simulate the songs of seven species—Acadian Flycatcher (*Empidonax virescens*), Wood Thrush (*Hylocichla mustelina*), Brown Thrasher (*Toxostoma rufum*), Black-throated Blue Warbler (*Dendroica caerulescens*), Black-and-white Warbler (*Mniotilta varia*), Hooded Warbler (*Wilsonia citrina*), and Scarlet Tanager (*Piranga olivacea*)—at 16 distances in two habitats under leaf-on and leaf-off conditions. In each habitat, two replicate lines were created, with 16 players, mounted 1 m above ground, placed at 10-m intervals between 50 and 200 m. Songs were played directly toward the observers, who stood ~50 m from the closest player. During each experiment, seven species were played randomly at each of the 16 distances (7 species × 16 distances = 112 songs per line; Table 1). The experiment was then repeated on the same line, with ~10 dB background noise (“brown” noise, frequency = 1/f²; Table 1) played from three speakers placed

TABLE 1. Sample sizes (\pm SE) for each day, with and without simulated background noise. Experiments were run on two lines in each habitat (mixed forest and deciduous forest) one line at a time, with no noise, and then run again with simulated background noise added on the same line. Total songs simulated = 1,792 (448 per day). Player malfunctions resulted in 420–446 total observations each day.

	Day 1	Day 2	Day 3	Day 4
	Mixed forest	Deciduous forest	Mixed forest	Deciduous forest
No noise	36.65 \pm 1.08	38.38 \pm 2.86	36.49 \pm 1.68	41.50 \pm 2.48
With noise	46.50 \pm 0.98	47.35 \pm 1.85	46.68 \pm 1.03	48.76 \pm 2.01
Total observations	420	425	446	446

5 m from the observers. We used brown noise because it contains more low-end frequencies and resembles thunder or rushing water; we felt that this was a fair simulation of realistic environmental ambient noise as compared with higher-frequency white or pink noise. The experiment was then repeated on a second line in the same habitat. Experiments were conducted in both habitat types under leaf-on and leaf-off conditions (Table 1).

A song was played once during each 10-s interval, and observers were then given an auditory cue (“next”) alerting them to identify the next song. Sound intensity levels for all species were standardized to 90 dB at 1 m. We used 12 observers during the experiments, but only 3 observers were present for all combinations of experimental conditions. We treated observations as binary responses, whereby observers identified the song either correctly or incorrectly at a given distance.

The seven species simulated are not found at our study site, and experiments were conducted during months of the year when there was minimal interference from the calling of local birds. Observers knew the identities of the seven species before the experiment. The analyses presented here are focused on three species, the Black-and-white Warbler, Black-throated Blue Warbler, and Brown Thrasher, which represent three levels of detectability: low, medium, and high, respectively.

Analysis.—We analyzed each species separately to reduce the number of interacting factors in each analysis and to simplify the interpretation of results. We consider our field trials quasi-experiments, because we were able to control several important factors—observers, species, background noise, distance, habitat, and leaf condition (Table 2)—but not all relevant factors. Other factors inherent to each site, such as minor differences in habitat and vegetation structure or trivial differences in weather conditions (e.g., air temperature, humidity) among trials, could potentially influence sound transmission, creating uncontrolled

TABLE 2. Factors and factor levels in bird-detection experiments.

Main effects	Level	
Habitat (<i>H</i>)	Mixed pine–hardwood forest	Deciduous forest
Leaves (<i>L</i>)	Off	On
Background noise (<i>N</i>)	No	Yes
Observer (<i>O</i>)	12 total	
Distance (<i>x</i>)	Continuous variable	

variation in detection probability. The two lines are considered as nonrandomized replicates nested within each habitat type.

Our approach to modeling an empirical detection probability as a function of the main factors (habitat, leaves, noise, observer, and distance) is similar to that of Alldredge et al. (2007b) but modified for nonrandomized and nested factors. A logistic regression model explicitly assumes a binomially distributed error structure (Agresti 1990) that cannot incorporate correlated observations. Therefore, we used PROC GENMOD in SAS, version 9.1 (SAS Institute 2007), to fit a model with a binomially distributed error structure that incorporated the correlation of observations within habitats and observers. With this approach, correlated data are modeled using the same link function (logit), linear predictor variables, and variance functions used with independent data, but the covariance structure of the correlated data is also incorporated into the model. PROC GENMOD uses generalized estimating equations (GEE; Liang and Zeger 1986) to model the covariance structure using several different approaches (autoregressive [1], exchangeable, independent, *m*-dependent, and unstructured). We specified an exchangeable correlation type, which has commonly been used for repeated-measures and split-plot designs (C. Brownie pers. comm.) to more accurately represent the true error structure. We used an independent correlation type for the Brown Thrasher out of necessity, because neither the exchangeable nor the autoregressive (1) type provided estimable parameters.

Main effects, habitat (*H*), leaves (*L*), and background noise (*N*) were treated as categorical variables, and distance (*x*) was treated as a continuous variable. We included observer (*O*) as a main effect, using all 12 observers, but we did not consider observer interactions because we wanted to isolate the main effects of habitat, leaves, background noise, and distance. We present the range of observer estimates to give a rough idea of the magnitude of observer variation. Additional models were considered, including two-way interactions of all four main effects (excluding observer). The most parsimonious model was selected using Akaike’s information criterion (AIC; 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 the greatest importance (Burnham and Anderson 2002). The general form of the linear model including only main effects was $\text{logit}[\pi(y)] = \beta_0 + \beta_1 x + \beta_2 H + \beta_3 L + \beta_4 N + \beta_5 O$, where $\pi(y)$ is 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 , β_4 , and β_5 were estimated model parameters.

We used the selected logistic model to demonstrate the variability in raw count data generated by environmental conditions, species, and observer differences. We calculated expected counts for a hypothetical point-count survey for our “best” and “worst” observer under all eight environmental conditions (Table 2) and for three species (Black-and-white Warbler, Black-throated Blue Warbler, and Brown Thrasher). We did this by distributing (uniformly with respect to area) a simulated population of 1,000 birds at distances of 50, 100, 150, and 200 m and using the estimated detection probabilities from the logistic model for specific observers, distances, species, and environmental conditions to estimate expected counts.

TABLE 3. Total basal area ($m^2 ha^{-1} \pm SE$) for mixed pine–hardwood forest ($n = 26$) and deciduous forest ($n = 24$) and indirect leaf area index (LAI $\pm SE$) for mixed pine–hardwood forest ($n = 30$) and deciduous forest ($n = 30$) under leaf-off and leaf-on conditions. Note that the higher the index value, the greater the estimated leaf area.

	Mixed forest	Deciduous forest
Total basal area	26.46 \pm 1.83	9.50 \pm 1.41
LAI Leaf-on	6.74 \pm 0.09	5.41 \pm 0.19
LAI Leaf-off	1.41 \pm 0.08	0.88 \pm 0.04

RESULTS

The mixed pine–hardwood forest had higher estimated leaf area index and estimated basal area (Table 3), whereas the deciduous forest had a denser understory and more horizontal cover (Fig. 1). Both habitats exhibited similar trends between leaf-off and leaf-on conditions, with leaf-on conditions containing more estimated leaf area and more horizontal cover (Table 3 and Fig. 1). The LAI values were significantly different between habitats under both leaf conditions (leaf-on: $t = 26.016$, $df = 58$; $P < 0.0001$; leaf-off: $t = 24.19$, $df = 58$, $P < 0.0001$) and between leaf conditions within a single habitat (mixed pine–hardwood forest: $t = 171.73$, $df = 58$, $P < 0.0001$; deciduous forest: $t = 107.88$, $df = 58$, $P < 0.0001$). Basal area was significantly different between habitats ($t = 26.23$, $df = 48$, $P < 0.0001$).

The selected logistic model for detection probability for the Black-and-white Warbler included all main effects and all two-way interactions and contained most of the support from the data (AIC weight = 0.64; Table 4). Five models were within $\Delta AIC < 10$, all of

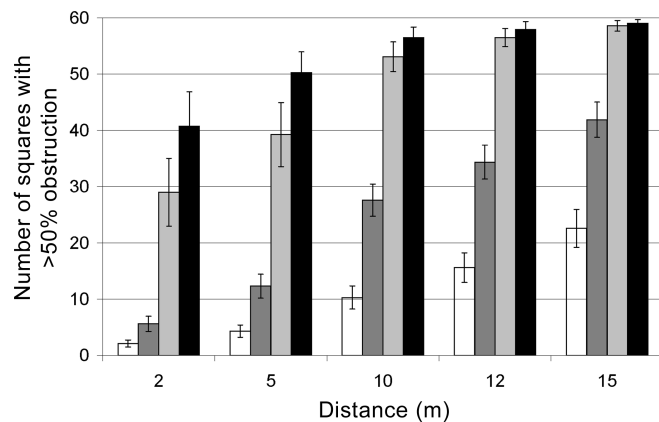


FIG. 1. Horizontal cover (includes SE bars) estimated using a 1.2-m (height) coverboard at five distances (2, 5, 10, 12, and 15 m) from the board in both the mixed pine–hardwood forest and the deciduous forest under leaf-off and leaf-on conditions. Cover is estimated as the number of squares (out of 60) with $\geq 50\%$ obstruction by vegetation. White bar represents mixed pine–hardwood forest under leaf-off conditions. Dark gray bar represents mixed pine–hardwood forest under leaf-on conditions. Light gray bar represents deciduous forest under leaf-off conditions. Black bar represents deciduous forest under leaf-on conditions.

TABLE 4. AIC weights (w_i) and number of parameters (k) for top logistic regression models of detection probability for each of three species.

Species	Model	w_i	k
Black-and-white Warbler	$H + N + L + O + x + HN + HL + Hx + NL + Nx + Lx$	0.64	22
Black-throated Blue Warbler	$H + N + L + O + x + NL + Nx + Lx$	0.18	19
Brown Thrasher	$H + N + L + O + x + HN + HL + NL + Nx$	0.30	20

which included habitat*leaves and habitat*distance interactions (Pacifiçi 2007). The AIC weights indicate that the top two models contained almost all the support from the data (sum of AIC weights = 0.97); the second-best model differed from the top model by the exclusion of a leaves*distance interaction. The variable importance weights were all > 0.97 , except for the leaves*distance interaction, which suggests that this interaction was the least supported by the data (Table 5).

The selected logistic model for the Black-throated Blue Warbler contained only three interactions, noise*leaves, noise*distance, and leaves*distance (Table 4). Twenty-six models were within $\Delta AIC < 10$ (Pacifiçi 2007), the top model containing only 18% of the support. The noise*distance and leaves*distance interactions had the most support from the data (variable importance weights > 0.82), and the noise*leaves, habitat*distance, and habitat*noise interactions all had importance weights > 0.5 (Table 5).

The selected logistic model for the Brown Thrasher contained four interactions: habitat*noise, habitat*leaves, noise*leaves, and noise*distance (Table 4). Two models contained more than half the support from the data (sum of AIC weights = 0.57) and differed only by three interactions: habitat*noise, habitat*distance, and leaves*distance (Pacifiçi 2007). The noise*leaves interaction was the only interaction with an importance weight of 1, but the noise*distance interaction had an importance weight of 0.95, indicating that it had strong support from the data as well (Table 5). Average estimated detection probabilities varied greatly by factor combinations and across species (Table 6).

TABLE 5. 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	Black-and-white Warbler	Black-throated Blue Warbler	Brown Thrasher
H	1.00	1.00	1.00
N	1.00	1.00	1.00
L	1.00	1.00	1.00
O	1.00	1.00	1.00
x	1.00	1.00	1.00
HN	0.97	0.55	0.65
HL	1.00	0.43	0.77
Hx	1.00	0.61	0.64
NL	0.99	0.73	1.00
Nx	0.97	0.82	0.95
Lx	0.67	0.86	0.57

TABLE 6. Average (\pm SE) and minimum and maximum estimated detection probabilities for 12 observers at 50 m and 100 m for three species (estimates from the top AIC logistic regression model).

	Distance (m)	Mixed forest		Deciduous forest	
		50	100	50	100
Black-and-white Warbler	Leaf-off, no noise	0.96 \pm 0.02	0.78 \pm 0.07	0.93 \pm 0.04	0.19 \pm 0.03
	Minimum–maximum	0.74–0.99	0.17–0.93	0.57–0.99	0.01–0.31
	Leaf-off, with noise	1.00 \pm 0.00	0.68 \pm 0.07	0.97 \pm 0.02	0.02 \pm 0.00
	Minimum–maximum	0.98–1.00	0.09–0.87	0.81–1.00	0.00–0.03
	Leaf-on, no noise	1.00 \pm 0.00	0.53 \pm 0.07	0.89 \pm 0.05	0.00 \pm 0.00
	Minimum–maximum	1.00–1.00	0.04–0.74	0.41–0.98	0.00–0.00
	Leaf-on, with noise	1.00 \pm 0.00	0.02 \pm 0.00	0.56 \pm 0.07	0.00 \pm 0.00
	Minimum–maximum	1.00–1.00	0.00–0.03	0.05–0.77	0.00–0.00
Black-throated Blue Warbler	Leaf-off, no noise	1.00 \pm 0.00	0.99 \pm 0.00	0.96 \pm 0.01	0.60 \pm 0.05
	Minimum–maximum	1.00–1.00	0.97–1.00	0.83–0.99	0.16–0.80
	Leaf-off, with noise	1.00 \pm 0.00	0.94 \pm 0.02	0.91 \pm 0.03	0.16 \pm 0.02
	Minimum–maximum	1.00–1.00	0.75–0.98	0.63–0.97	0.02–0.31
	Leaf-on, no noise	1.00 \pm 0.00	0.89 \pm 0.03	0.93 \pm 0.02	0.09 \pm 0.01
	Minimum–maximum	1.00–1.00	0.59–0.97	0.70–0.97	0.01–0.17
	Leaf-on, with noise	1.00 \pm 0.00	0.34 \pm 0.04	0.69 \pm 0.05	0.00 \pm 0.00
	Minimum–maximum	0.98–1.00	0.06–0.56	0.23–0.87	0.00–0.01
Brown Thrasher	Leaf-off, no noise	1.00 \pm 0.00	1.00 \pm 0.00	0.99 \pm 0.00	0.97 \pm 0.01
	Minimum–maximum	1.00–1.00	0.99–1.00	0.96–1.00	0.88–0.99
	Leaf-off, with noise	1.00 \pm 0.00	0.95 \pm 0.01	0.99 \pm 0.00	0.74 \pm 0.04
	Minimum–maximum	0.99–1.00	0.80–0.97	0.94–0.99	0.35–0.84
	Leaf-on, no noise	0.99 \pm 0.00	0.96 \pm 0.01	0.92 \pm 0.02	0.78 \pm 0.04
	Minimum–maximum	0.95–0.99	0.85–0.98	0.69–0.96	0.40–0.87
	Leaf-on, with noise	0.99 \pm 0.00	0.87 \pm 0.03	0.98 \pm 0.01	0.65 \pm 0.04
	Minimum–maximum	0.98–1.00	0.57–0.93	0.91–0.99	0.24–0.76

Average detection probabilities were generally highest for the Brown Thrasher and lowest for the Black-and-white Warbler. Adding background noise, adding leaves on trees, and moving from mixed pine–hardwood forest to deciduous forest generally resulted in decreased detection probabilities (Fig. 2). Looking specifically at 50 m and 100 m, average estimates ranged between 0 and 1 for both the Black-and-white Warbler and the Black-throated Blue Warbler, whereas Brown Thrasher estimates ranged from 0.65 to 1.00 (Table 6). Both the Black-and-white Warbler and the Black-throated Blue Warbler exhibited differences in average estimated detection probabilities of >0.60 across the range of factors at 50 m and 100 m, whereas the largest difference for the Brown Thrasher was 0.32 (Table 6). The Black-and-white Warbler showed the largest amount of variation in average detection probabilities at both 50 m and 100 m (difference among conditions = 0.44 and 0.76, respectively; Table 6).

Observer variation generally increased with distance, with the addition of background noise, and from leaf-off conditions to leaf-on conditions for all three species (Table 6). Neither habitat exhibited more observer variation than the other, though detection probability estimates were generally lower in the deciduous forest. The largest amount of observer variation within a single combination of factors occurred in the mixed pine–hardwood forest with background noise under leaf-off conditions for the

Black-and-white Warbler (Table 6). A single observer was responsible for all the observed minimum detection probabilities for a species, but it was a different observer for each species (observer 9: Black-and-white Warbler; observer 12: Black-throated Blue Warbler; observer 8: Brown Thrasher).

Detection probabilities from the selected logistic model were determined for the best and worst observers for all three species and under all eight environmental conditions at distances of 50, 100, 150, and 200 m (Table 7). Applying these detection probabilities, expected counts for a simulated population of 1,000 birds ranged from 63 birds (Black-and-white Warbler; leaf-on with background noise and worst observer) to 996 birds (Brown Thrasher; leaf-off with no background noise and best observer) in the mixed forest and from 3 birds (Black-and-white Warbler; leaf-on with background noise and worst observer) to 921 birds (Brown Thrasher; leaf-off with no background noise and best observer) in the deciduous forest. Differences in counts with leaves off and no background noise ranged from 38 birds (Black-and-white Warbler; worst observer and deciduous forest habitat) to 996 birds (Brown Thrasher; best observer and mixed forest habitat) across both habitats. Differences in counts with leaves on and with background noise ranged from 3 birds (Black-and-white Warbler; worst observer and deciduous forest habitat) to 335 birds (Brown Thrasher; best observer and mixed forest habitat) across both habitats.

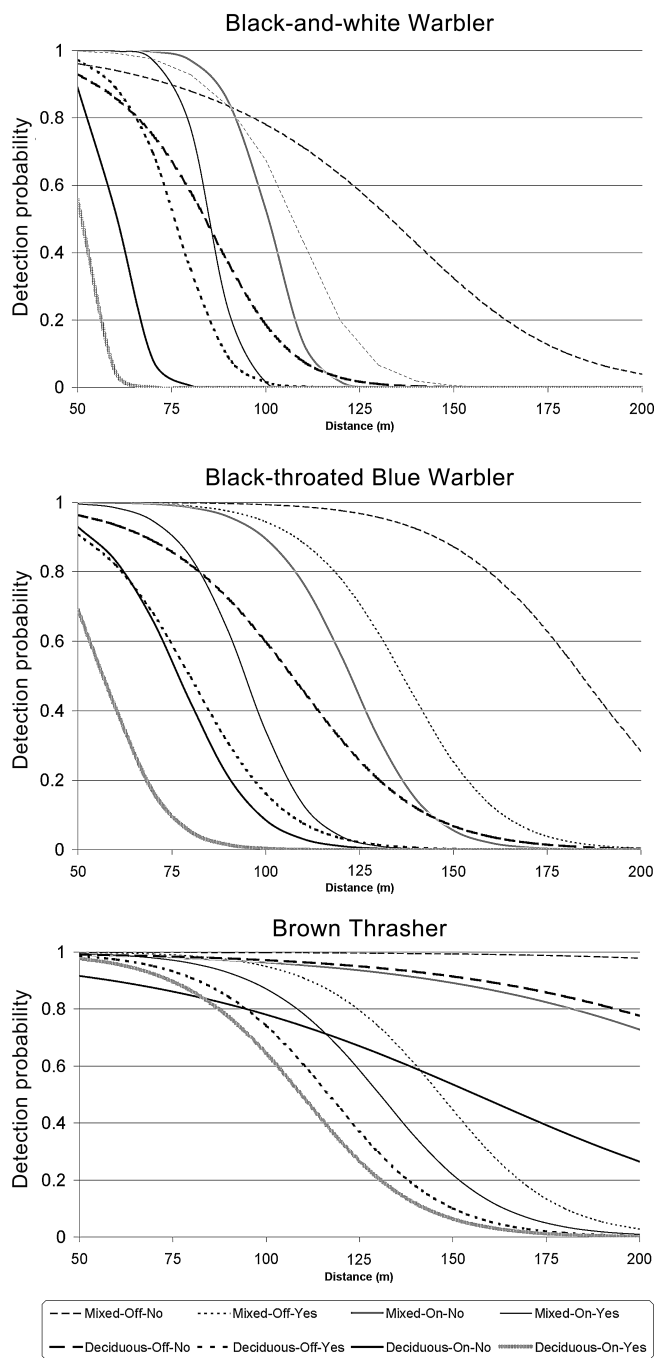


FIG. 2. Logistic regression models for each of the three focal species, Black-and-white Warbler, Black-throated Blue Warbler, and Brown Thrasher, averaged across 12 observers, demonstrating differences among species and each of the eight factor combinations. Legend corresponds to the combinations of habitat (mixed pine–hardwood forest, deciduous forest), leaf condition (off, on), and added background noise (no, yes).

DISCUSSION

These results provide direct empirical estimates of detection probability for known populations of birds under different environmental conditions. Although we could not control for all sources of variation, our results indicate that background noise, habitat, leaf condition, species, and observers have significant effects on detection probability. Background noise and the presence of leaves on trees decreased detection probabilities. Detection probabilities were higher in mixed pine–hardwood forest than in deciduous forest. Although basal area and LAI were higher for the mixed pine–hardwood forest, the deciduous forest had more horizontal vegetation cover, which suggests that horizontal vegetation cover had the largest influence on detection probability in our habitats. We would expect horizontal vegetation cover to have a large effect in these experiments, because our players were located ~1 m off the ground. The structure of the forest canopy probably has a greater influence on the detection probability of songs transmitted from greater heights, but we did not evaluate this relationship in these experiments.

We found large differences in detection probability between the two habitats we sampled. Unfortunately, because of the limited number of habitats and species in our study, we cannot generalize our results to all studies in all environmental conditions. Ideally, this study would be replicated over multiple habitats to allow us to make inference about detection probability under a broad range of habitat conditions encountered in avian surveys. Our results suggest that practitioners should not assume that fixed-radius plots (Ralph et al. 1995) ensure that detection probabilities are comparable among sampling sites. For example, in the mixed forest with leaves on and no background noise, the Black-and-white Warbler was detectable at 100 m (average estimated $p = 0.53 \pm 0.07$), but in the deciduous forest, under similar environmental conditions, it was not detectable at 100 m (average estimated $p = 0.00 \pm 0.00$). Using a single fixed-radius plot at both locations will produce biased estimates, because the effective area sampled differs between locations.

We found large differences in detection probabilities under leaf-off and leaf-on conditions. Most bird surveys are conducted under leaf-on conditions when birds are breeding, but they are also used to evaluate bird–habitat relationships following disturbances such as fire (Smucker et al. 2005), Gypsy Moth (*Lymantria dispar*) infestation (Bell and Whitmore 1997), and silvicultural practices such as thinning (Hayes et al. 2003). Each of these forms of disturbance produces conditions similar to our leaf-off habitats. In these situations, failure to estimate detection probabilities directly could bias inferences. For example, without direct estimates of detection probabilities it is impossible to know whether differences between pre- and post-treatment bird abundances are caused by the treatment (e.g., fire, gypsy moths, or thinning) or if they are simply attributable to differences in the ability of observers to see or hear birds.

Our results reinforce those of Simons et al. (2007), who found that background noise can have a substantial effect on detection probabilities. Background noise is likely increasing in our environment (Wolkomir and Wolkomir 2001), but the degree to which it varies both spatially and temporally is not well understood.

TABLE 7. Range of estimated detection probabilities for worst and best observer by species, environmental condition, and habitat at distances from 50 m to 200 m. Expected counts were calculated for a simulated population of 1,000 birds uniformly distributed. Number of birds represents the true number of simulated birds in each distance band.

Species	Distance (m)	Number of birds	Leaf-off, no noise	Leaf-off, with noise	Leaf-on, no noise	Leaf-on, with noise
Mixed forest						
Black-and-white Warbler	0–50	63	0.74–0.99	0.98–1.00	1.00–1.00	1.00–1.00
	51–100	187	0.17–0.93	0.09–0.87	0.04–0.74	0.00–0.03
	101–150	312	0.02–0.51	0.00–0.01	0.00–0.00	0.00–0.00
	151–200	438	0.00–0.07	0.00–0.00	0.00–0.00	0.00–0.00
Expected count		1,000	85–426	79–229	70–201	63–69
Black-throated Blue Warbler	50	63	1.00–1.00	1.00–1.00	1.00–1.00	0.98–1.00
	100	187	0.97–1.00	0.75–0.98	0.59–0.97	0.06–0.56
	150	312	0.53–0.96	0.04–0.44	0.01–0.12	0.00–0.00
	200	438	0.04–0.49	0.00–0.01	0.00–0.00	0.00–0.00
Expected count		1,000	427–764	216–388	176–282	73–168
Brown Thrasher	50	63	1.00–1.00	0.99–1.00	0.95–0.99	0.98–1.00
	100	187	0.99–1.00	0.80–0.97	0.85–0.98	0.57–0.93
	150	312	0.97–1.00	0.12–0.57	0.62–0.94	0.04–0.30
	200	438	0.91–0.99	0.00–0.04	0.33–0.83	0.00–0.01
Expected count		1,000	949–996	249–440	557–902	181–335
Deciduous forest						
Black-and-white Warbler	50	63	0.57–0.99	0.81–1.00	0.41–0.98	0.05–0.77
	100	187	0.01–0.31	0.00–0.03	0.00–0.00	0.00–0.00
	150	312	0.00–0.00	0.00–0.00	0.00–0.00	0.00–0.00
	200	438	0.00–0.00	0.00–0.00	0.00–0.00	0.00–0.00
Expected count		1,000	38–120	51–69	26–62	3–49
Black-throated Blue Warbler	50	63	0.83–0.99	0.63–0.97	0.70–0.97	0.23–0.87
	100	187	0.16–0.80	0.02–0.31	0.01–0.17	0.00–0.00
	150	312	0.01–0.14	0.00–0.00	0.00–0.00	0.00–0.00
	200	438	0.00–0.01	0.00–0.00	0.00–0.00	0.00–0.00
Expected count		1,000	85–260	43–119	46–93	14–57
Brown Thrasher	50	63	0.96–1.00	0.94–0.99	0.69–0.96	0.91–0.99
	100	187	0.88–0.99	0.35–0.84	0.40–0.87	0.24–0.76
	150	312	0.69–0.95	0.02–0.15	0.16–0.66	0.01–0.09
	200	438	0.39–0.86	0.00–0.01	0.06–0.36	0.00–0.00
Expected count		1,000	611–921	131–271	194–587	105–233

Given the observed interaction of factors affecting detection probability and that no group of factor interactions was consistently more important for all three species, it is unlikely that the use of standardized correction factors could provide a plausible alternative to estimating detection probabilities directly.

Observers detected between 3% and 99% of the total count of a simulated population. The large variation in expected counts among observers and environmental conditions illustrates the importance of estimating detection probabilities directly, especially when monitoring programs use many observers to collect data on many species over large spatial areas. Sampling methods and assumptions appropriate for species with very high detection probabilities (e.g., Brown Thrasher) may not be appropriate for less detectable species. These differences suggest that tailoring monitoring protocols to specific species of interest or to several

important “focal” species would produce better estimates than a single protocol applied to a wide range of species.

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