ABSTRACT

PACIFICI, JAMIAN KRISHNA. Effects of Vegetation and Background Noise on the Detection Process in Auditory Avian Point Count Surveys. (Under the direction of Theodore R. Simons and Kenneth H. Pollock.)

We used a system capable of simulating avian census conditions when birds are detected aurally to evaluate environmental effects on the detection process. We were interested in quantifying the effects of observers, species, and background noise on detection probability and maximum detection distance in two habitats (mixed pine/hardwood forest and deciduous forest) and two leaf conditions (leaves on and leaves off). We found significant effects of background noise, habitat, and leaf conditions on maximum detection distance. Maximum detection distance decreased on average by 36.61 m $\pm$ 5.44 with the addition of background noise, 29.52 m $\pm$ 6.25 with leaves on trees, and 35.68 m $\pm$ 5.58 between mixed pine/hardwood forest and deciduous forest. Average estimated detection probabilities varied greatly by factor combination and species, but in general they decreased with the addition of background noise, under leaf-on conditions, and in deciduous forest sites compared to mixed pine/hardwood sites. Average detection probabilities at 100 m ranged from 0 to 1 among species and under different environmental conditions. Average detection probability estimates never exceeded 0.19 for the Black-and-white Warbler (*Mniotilta varia*) at 100 m in deciduous forest. We found that a relative hearing index explained a maximum of 37% of the variation in observer detection probabilities. Interacting factors differed among species and were therefore difficult to predict. Environmental conditions can impart substantial bias in auditory point count data. We suggest estimating detection probability directly and incorporating this estimate in abundance estimates.

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

by
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A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the Degree of
Master of Science

ZOOLOGY

Raleigh, North Carolina

2007

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BIOGRAPHY

I was born in Roanoke, Virginia in 1979 and grew up in nearby Blacksburg, Virginia. Throughout my childhood I enjoyed being outdoors and spent extensive time in the mountains in southwestern Virginia and western North Carolina. I spent my summers in North Carolina backpacking in the mountains and spending all day outside.

After high school I moved out west to Tempe, Arizona to attend Arizona State University. I traveled during much of my time and enjoyed going to Flagstaff, the Grand Canyon, San Diego, Las Vegas, and Mexico. I worked for the Biology department at ASU and became involved in field work in the Gila River, which I thoroughly enjoyed. During my junior year at ASU I developed a rare illness and was forced to withdrawal from school. I spent the next year on dialysis with kidney failure and finally received a kidney transplant in 2000. After another year of regaining my strength I headed off to Raleigh, North Carolina to finish my bachelor's degree.

At NCSU I developed a great appreciation for wildlife biology and school in particular. With the help from the excellent faculty my interests quickly became focused around population biology and quantitative methods in wildlife sciences. I began volunteering on several projects at NCSU, which eventually led me to my master's project.

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INTRODUCTION

Point counts (Ralph et al. 1995) are used extensively in bird conservation and management. They are used to explore habitat relationships, understand environmental impacts, map species diversity and distribution, evaluate management decisions, and monitor abundance across space and time. Surveys in heavily vegetated habitats rely almost exclusively on auditory detections (Faanes and Bystrak 1981, Scott et al. 1981, Dejong and Emlen 1985) and typically the point count data are used to calculate an index of population abundance (Rosenstock et al. 2002, Diefenbach et al. 2003). Abundance indices assume that the proportion of individuals detected is constant over space and/or time, or that all factors affecting detection are known and can be accounted for by adjustments using measured covariates. Concerns about using counts as indices of abundance have been expressed in the literature for many years (see Burnham 1981, Nichols et al. 2000, Anderson 2001, Farnsworth et al. 2002, Rosenstock et al. 2002, Thompson 2002, Williams et al. 2002, Norvell et al. 2003, Buckland 2006, and Simons et al. 2007). Many researchers have shown that detection probabilities do vary over space and time (Nichols et al. 2000, Rosenstock et al. 2002, and Thompson 2002) and that it is generally impossible to adjust for all factors that influence detection probabilities.

Most biometricians now recommend estimating detection probabilities directly. Two general approaches exist: ad hoc procedures and statistically based methods (Thompson 2002). Ad hoc procedures rely on using information such as cue rates (Emlen 1977) to correct for variations in detection probabilities, or correction factors from studies conducted under similar conditions. Currently, four statistical methods are available to estimate detection probability: distance sampling (Buckland et al. 2001), multiple observer methods

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(Nichols et al. 2000, Alldredge et al. 2006), time of detection methods (Farnsworth et al. 2002, Alldredge et al. in press), and repeated count methods (Royle and Nichols 2003, Kery et al. 2005).

Many factors influence detection probabilities on avian point counts. They include time of season (Best 1981, Skirven 1981), time of day (Robbins 1981a, Skirven 1981), weather conditions (Robbins 1981b), habitat structure (Diehl 1981, Oelke 1981, McShea and Rappole 1997), and differences in observer ability (Faanes and Bystrak 1981, Sauer et al. 1994, Diefenbach et al. 2003). While these factors have been recognized and most sampling protocols (Ralph et al. 1995) attempt to control for them, not all factors affecting detection probability can be accounted for in a given protocol. For example, Simons et al. (2007) have recognized background noise as an important factor influencing detection probability, yet the collection of background noise as a covariate is rarely, if ever, done. Not measuring important covariates that affect detection probability can result in misleading estimates of population trends (Burnham 1981, Nichols et al. 2000, Thompson 2002, Norvell et al. 2003).

Estimating detection probability directly accounts for measured and unmeasured sources of variation, but these sources of variation are still poorly understood (Simons et al. 2007). Complications can arise when multiple factors are interacting (Simons et al. 2007, Alldredge et al. 2007) and the biases associated with these interactions can be difficult to predict.

Habitat conditions have long been recognized as an important factor affecting detection probability (Diehl 1981, Schieck 1997). Ideally, variation in habitat type can be accounted for during the design stage of a study by stratifying sampling effort by different habitat types (Morrison et al. 2001). Unfortunately, variation within a habitat type or among

similar habitats could potentially create variations in detection probabilities. Depending on the scale of the study, two habitats may not be classified as different, but in reality exhibit large differences in detection probability.

Schieck (1997) used playbacks of recorded calls to estimate the effects of vegetation on the maximum detection distance of several species of songbirds. Schieck (1997) found that at 50 m virtually all of the playbacks were still audible, but at 100 m roughly 27% were not detectable; detection was highest in white spruce (*Picea glauca*) forest and lowest in young aspen (*Populus* spp.) forest. Schieck (1997) noted significant differences among habitat types and leaf conditions. He used this information to adjust previously analyzed point count data to minimize detection bias associated with habitat, leaf conditions, and vegetation. Schieck (1997) suggested that the complexity of the vegetation might also differ within sites and these differences could influence detection probabilities. Unfortunately, Schieck (1997) only used one observer and songs were only played at two distances (50 m and 100 m). The use of one observer does not allow for evaluation of observer differences related to age-related hearing loss (Emlen and DeJong 1992), observer training (Kepler and Scott 1981), or multiple other factors (Davis 1981). Any biases associated with that one observer could not be assessed and could potentially bias Schieck's (1997) conclusions.

Sound attenuation and transmission have been shown to vary greatly among sites. Attenuation is affected by the ground surface (Wiley and Richards 1982), the amount and type of structures present (Morton 1975), and atmospheric conditions (Richards and Wiley 1980). Simons et al. (2007) suggested that the "active space" of signal recognition, which is influenced by factors affecting sound attenuation, is synonymous with detection probability. Therefore, these factors that affect the sound transmission and signal recognition for avian

communication could potentially have an effect on detection probability in auditory point counts.

Few studies have quantified how various factors affect detection probabilities because the size of a sampled population is almost never known. A notable exception is Nelson and Fancy (1999), who used radio-marked birds to evaluate distance sampling. Several studies have compared two or more methods against each other. Moore et al. (2004) compared the double dependent-observer method (Nichols et al. 2000) to a removal method (Farnsworth et al. 2002), and Buckland (2006) used territory mapping as a surrogate for true population size to compare three different applications of distance sampling (Buckland et al. 2001). In both cases the true population size was not known, which could potentially result in biased inferences about the best method to use.

We have developed a system for simulating avian census conditions when birds are detected aurally. The system uses a laptop computer to control a set of amplified MP3 players placed at known locations and distances. The system can realistically simulate bird songs under a range of varying factors that affect detection probability (Simons et al. 2007). Simons et al. (2007) were able to show how breezy conditions, background noise, and non-target background birds significantly affected detection probabilities. Using the same simulation system, Alldredge et al. (2007) were able to quantify the effects of singing rate, detection distance, species, and observer differences on detection probabilities and confirm interactions among several factors.

In this paper we report on experiments to quantify the effects of species and observer under six environmental conditions: two habitats, two leaf conditions, and two levels of

background noise. We were interested in quantifying how these effects influenced maximum detection distance and detection probability.

METHODS

Study Sites

Experiments were conducted in Howell Woods, a natural area comprised of 1133 ha, in Johnston County, NC. Field experiments were established at two sites within Howell Woods: a mixed pine/hardwood forest and a deciduous forest located approximately 5 km apart. The mixed pine/hardwood forest is a 30-50 year old successional forest. Dominant species include oaks (*Quercus* sp.), pines (*Pinus* sp.), 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* sp., *Ilex* sp., and *Smilax* sp.. The deciduous forest is dominated by hickory (*Carya* sp.), sweetgum (*Liquidambar styraciflua*), and red maple (*Acer rubrum*) and is predominantly a single layered forest, 5-7 m high, with a dense understory, comprised of mainly *Smilax* sp.. 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 in each site (Avery and Burkhart 1983). 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 forested 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 the Licor LAI-2000 Plant Canopy Analyzer (LICOR, Lincoln, Nebraska, USA) at a height of 1 m to calculate an indirect index of total leaf area in the two study sites. LAI readings were collected at randomly selected points within both of the sites during both leaf conditions (leaves off and leaves on). We also used a 1.2 m coverboard (1.2 m height x 0.5 m width) constructed out of foam board and marked in a black-and-white checkerboard pattern (60 10x10 cm squares) to assess horizontal vegetation cover in 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 more than 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 was always facing the center of the site, where observers were located.

Hearing Index

We tested observer hearing using AUDIO-CD (Digital Recordings, Nova Scotia, Canada) which tests hearing thresholds of 24 frequencies between 20 Hz and 20 kHz. We used the hearing threshold information for each observer to create a relative hearing index.

We were interested in the range of frequencies (1-9 kHz) corresponding to the songs of our simulated bird species. We created the hearing index by summing the threshold level between 1-9 kHz for each observer (averaged between left and right ears). We calculated the ratio of each observer's threshold to the "normal" threshold reported by the manufacturer, such that the relative hearing index for each observer is

$$\text{R.H.I.} = \frac{\sum_{i=1}^{9} a_i}{\sum_{i=1}^{9} b_i}$$

where a = threshold level at frequency i for each observer, averaged across both left and right ears, b = threshold level at frequency i for the "normal" level, averaged across both left and right ears.

As there are accepted levels of deviation from the "normal" threshold levels we did not consider this as an absolute measure of hearing ability, but rather a relative index for our observers so we could rank each observer relative to others.

Bird Detection Experiments

We used a birdsong simulation system (Simons et al. 2007) to simulate the songs of seven species (Table 1) at 16 distances in two habitats under leaf-on and leaf-off conditions. In each habitat two replicate lines were created with 16 players placed 1 m above ground at 10 m intervals between 50-200 m. Songs were played directly toward the observers who stood approximately 50 m from the closest player. During each experiment seven species were played randomly at each of the 16 distances (7 species x 16 distances = 112 songs per line; Table 2). The experiment was then repeated on the same line with approximately 10 dB of background noise ("Brown" noise, frequency = $1 / f^2$; Table 2) played from three speakers

placed 5 m from the observers. We used brown noise because it contains more low-end

frequencies and resembles thunder or rushing water, we felt this was a fair simulation of

realistic environmental ambient noise as compared to 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 2).

A song was played once during each 10 second 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 a total of 12 observers during the

experiments, but only 3 observers were present for all combinations of experimental

conditions. We treated observations as binary responses where observers either identified the

song correctly or incorrectly at a given distance.

Analyses

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 local birds.

Observers knew the identities of the seven species before the experiment. Analyses will

focus on three species, Black and white Warbler (BAWW; *Mniotilta varia*), Black-throated

blue Warbler (BTBW; *Dendroica caerulescens*), and Brown Thrasher (BRTH; *Toxostoma*

rufum) which represent species with low, medium, and highly detectable songs, respectively.

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 as

quasi-experiments because we were able to control several important factors. Factors

include; observers, species, background noise, distance, habitat, and leaf condition (Table 2).

The two lines are considered as non-randomized replicates nested within each habitat type.

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Maximum Detection Distance: Because we were interested in examining the main factors and interactions influencing the maximum detection distance for a given species, we used a modified unbalanced split-split-split plot design, incorporating both observable factors (habitat and leaf condition) and controllable factors (background noise and observer) with maximum detection distance as the response variable. Habitat was the whole plot factor, leaves the sub-plot factor, background noise the sub-sub plot factor, and observer the sub-sub-sub plot factor. The design was unbalanced because the number of observers was not identical across all treatments. Model structure was similar to a split-split-split-plot design (Milliken and Johnson 1984) because line and background noise were not randomized, but only had two levels. Due to the unbalanced nature of the data, we used an iterative model selection process to uncover the appropriate model structure that used as much of the unbalanced data (observers) as possible. We included all of the main effects, two-way interactions, and the three-way interaction of the main effects (habitat, leaf condition, and background noise) in PROC GLM (SAS v. 9.1 2007). We then tested model assumptions (variance heterogeneity, residual normality, outliers) with the full model, including observer and all two-way observer interactions. We sequentially removed non-significant observer interactions using backwards elimination (P-value > 0.15) while checking that LSMEANS were estimable (the full model did not have estimable lsmeans). At each iteration we checked our type 3 tests of fixed effects against a balanced model (only three observers) to ensure that our model structure was appropriate. When the final model structure was determined we reran the model in PROC MIXED (SAS v. 9.1 2007) to obtain correct S.E.s (Littell et al. 1996) and we then ran F-tests using the Satterthwaite option for degrees of freedom (Littell et al. 1996). The linear model specified was:

$Y_{ijklm} = \mu + H_i + \alpha_{j(i)} + L_k + H{*}L_{ik} + \delta_{k(ij)} + N_l + H{*}N_{il} + L{*}N_{kl} + H{*}L{*}N_{ikl} + \gamma_{l(ijk)}$

$+ O_m + N{*}O_{lm} + \varepsilon_{m(ijkl)}$

where μ = overall average effect, and H = habitat with i = 1, 2, L = leaves with k = 1, 2, N =

background noise with l = 1, 2, O = observer with m = 1, 2, 3, 4, 5, 6 were fixed effects.

Random effects were; α = line(habitat) with j = 1, 2, δ = leaves*line(habitat), γ =

leaves*line*noise(habitat), and ε = residual error. All species had this model structure with

the exception of the BAWW, which included an additional interaction (observer*leaves).

Detection probability: 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. (2007), but modified for non-randomized 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 (SAS

v. 9.1 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 the same

variance functions used with independent data, but the covariance structure of the correlated

data is also incorporated into the model. PROC GENMOD (SAS v. 9.1 2007) 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 (pers. comm. Dr. Cavell

Brownie) to more accurately represent the true error structure. We used an independent

correlation type for the BRTH because neither the exchangeable nor 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 examined the relationship between detection probability and

observer separately using each observer's hearing information (post-hoc analysis).

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 only present Δ AIC (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 Δ 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 the greatest

importance (Burnham and Anderson 2002). The general form of the linear model including

only main effects was:

logit[π (*y*)] = $\beta_0 + \beta_1 x + \beta_2 H + \beta_3 L + \beta_4 N + \beta_5 O$

where π (*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.

RESULTS

The mixed pine/hardwood forest had higher estimated leaf area index and estimated

basal area (Table 3), while 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; Fig. 1). LAI ranged from 0.88 (SE = 0.04) in the deciduous forest with leaves off to 6.74

(SE = 0.09) in the mixed pine/hardwood forest with leaves on. LAI was significantly

different between habitats under both leaf conditions (t = 26.016, df = 58; $p < 0.0001$ leaves

on and t = 24.19, df = 58, $p < 0.0001$ leaves off) and between leaf conditions within a single

habitat (t = 171.73, df = 58, $p < 0.0001$ mixed pine/hardwood forest and t = 107.88, df = 58,

$p < 0.0001$ deciduous forest). Basal area was significantly different between habitats (t =

26.23, df = 48, $p < 0.0001$).

Observer age ranged from 27 to 55 and the relative hearing indices ranged from 0.29

for our youngest observer (observer 7 age 27) to 8.43 for our oldest observer (observer 12

age 55). We found a weak correlation between the relative hearing index and observer age

(correlation coefficient r = 0.42, Fig. 2).

Maximum detection distances varied by species and by factor combination (Table 4).

The BAWW had the lowest maximum detection distances under all factor combinations

while the BRTH had the highest maximum detection distances. The BTBW showed the

largest difference in maximum detection distance among factor combinations (55.38 to

187.50 m) while the BRTH showed the smallest difference (118.26 to 193.33 m). The

maximum detection distance was generally lower in the deciduous forest and lower in leaf-on

conditions for all three species. We found an average effect of background noise on

maximum detection distance of 18.27 m ± 1.63 for the BAWW, 37.73 m ± 4.68 for the

BTBW, and 53.84 m ± 9.45 for the BRTH. The effect of background noise on maximum

detection distance was similar between habitats (mixed pine/hardwood forest 37.42 m ±

7.23, deciduous forest 35.81 m ± 8.8), but the effect was slightly larger for leaf-off

conditions (leaves off 40.29 m ± 8.29, leaves on 32.93 m ± 7.48). Leaf-on conditions

decreased the maximum detection distance by an average of 36.25 m ± 1.28 for the BAWW,

45.66 m ± 7.67 for the BTBW, and 6.65 m ± 9.62 for the BRTH. The effect of leaves was

similar under background noise conditions (33.21 m ± 9.3 with no noise and 25.84 m ± 8.9

with background noise). The effect of leaves on maximum detection distance was greater in

the mixed pine/hardwood forest than the deciduous forest (34.26 m ± 9.42 vs. 24.79 m ±

8.6). The effect of habitat on maximum detection distance was similar for the BAWW and

BTBW (42.5 m ± 1.51 and 48.95 m ± 6.33), but much less for the BRTH (15.58 m ±

9.58). Habitat had a larger effect under leaf-off conditions than leaf-on conditions (40.41 m

± 8.75 and 30.94 m ± 7.18), but had an insignificant effect under noise conditions (36.48 m

± 9.11 with no background noise and 34.87 m ± 8.16 with background noise). An

exception was the maximum detection distance increasing from leaf-off with noise

conditions to leaf-on with noise conditions for the BRTH in the deciduous forest. The BRTH

also produced a higher maximum detection distance in the deciduous forest than the mixed

pine/hardwood forest under leaf-on with noise conditions, contradicting the general pattern of

lower detection distances for the deciduous forest.

   Analyses confirmed the significance ($\alpha = 0.05$) of the main factors (habitat, noise,

leaves) with the exception of leaves for the BRTH (Table 5). Observer was a significant

factor for only the BAWW, but it was also significant in the noise*observer interaction for

the BRTH. Both the BAWW and the BRTH had significant interactions influencing

maximum detection distance while the BTBW had only significant main effects affecting

maximum detection distance (Table 5).

The selected logistic model for the BAWW included all main effects and all two-way

interactions and contained most of the support from the data (AIC weight = 0.64; Table 6).

Five models were within Δ AIC values <10 (Table 6) all of which included habitat*leaves

and habitat*distance interactions. AIC weights indicate the top two models contained almost

all of the support from the data (sum of AIC weights = 0.97) where the second best model

differed from the top model by the exclusion of a leaves*distance interaction. The variable

importance weights were all greater than 0.97 except for the leaves*distance interaction

suggesting it was the least supported by the data (Table 7).

The selected logistic model for the BTBW contained only three interactions,

noise*leaves, noise*distance, and leaves*distance (Table 6). Twenty-six models were within

Δ AIC values <10 (Table 6) with the top model only containing 0.18 of the support. Three

models had AIC weights greater than 0.10 while five other models had AIC weights greater

than 0.05 (Table 6). The noise*distance and leaves*distance interactions had the most

support from the data (variable importance weights > 0.82) while the noise*leaves,

habitat*distance, and habitat*noise interactions all had importance weights greater than 0.5

(Table 7). Only the habitat*leaves interaction contained an importance weight less than 0.5

indicating the least amount of support from the data (Table 7). Ten models had a Δ AIC

value <10, but contained AIC weights less than 0.01 indicating relatively no support from the

data.

The selected logistic model for the BRTH contained four interactions, habitat*noise, habitat*leaves, noise*leaves, and noise*distance (Table 6). Two models contained more than half of the support from the data (sum of AIC weights = 0.57) and only differed by three interactions, habitat*noise, habitat*distance, and leaves*distance (Table 6). The noise*leaves interaction was the only interaction with an importance weight = 1, but the noise*distance had an importance weight = 0.95 indicating strong support from the data as well (Table 7). The leaves*distance interaction was the least supported interaction, but still had an importance weight greater than 0.5 (Table 7).

Average estimated detection probabilities varied greatly by factor combinations and across species (Table 8). Looking specifically at 50 m and 100 m, average estimates ranged between 0 to 1 for both the BAWW and the BTBW, while BRTH estimates ranged from 0.65 to 1 (Table 8). Again looking specifically at 50 m and 100 m, the BAWW showed the greatest amount of variation in average detection probabilities in the mixed pine/hardwood forest at 100 m (Table 8). Both the BAWW and the BTBW exhibited differences in average estimated detection probabilities greater than 0.60 across the range of factors at 50 m and 100m while the largest difference for the BRTH was 0.32 (Table 8). The BAWW showed the largest amount of variation in average detection probabilities at both 50 m and 100 m ($\Delta = 0.37$ and 0.76, respectively, Table 8).

Average detection probabilities were generally higher for the BRTH and lowest for the BAWW. Adding background noise, leaves on trees, and moving from mixed pine/hardwood forest to deciduous forest generally resulted in decreased detection probabilities (Fig. 3). Each species' detection function varied among all possible factor combinations and between species (Fig. 3). Average detection probabilities declined rapidly

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for all three species (Fig. 3). The BAWW had the highest rate of decline in detection probability with distance while the BRTH had the slowest declining detection rates (Fig. 3). The BAWW in the mixed pine/hardwood forest with no leaves and no background noise was the only average detection probability greater than 0 at 150 m for this species (0.32; Fig. 3). The BTBW had higher overall detection probabilities than the BAWW, but still had large amounts of variation at 50 m, 100 m and 150 m (Fig. 3). The BRTH had the highest overall detection probabilities and exhibited the least amount of variation from 50 m up to 150 m, but had average detection probabilities between 0.06 and 0.99 at 150 m, illustrating the most variation at this distance among all three species (Fig. 3).

Observer variation generally increased with distance, the addition of background noise, and from leaf-off conditions to leaf-on conditions for all three species (Table 9). Neither habitat exhibited more observer variation than the other, although detection probability estimates were generally lower in the deciduous forest. The largest amount of observer variation within a single factor combination occurred in the mixed pine/hardwood forest with background noise under leaf-off conditions for the BAWW (Table 9). A single observer was responsible for all of the observed minimum detection probabilities for a species, but it was a different observer for each species (Observer 9-BAWW, Observer 12-BTBW, and Observer 8-BRTH).

The post-hoc analysis, examining hearing and variation in detection probability, only investigated factor combinations when observer variation in detection probability was greater than 0.4 at 50 m or 100 m. We found a weak negative linear relationship between hearing loss and detection probability for the BAWW and BTBW (range $R^2 = 0.15$ to 0.37). The relationship between observer hearing and detection probability was the same under each of

the conditions for each species, but the pattern differed between species (Fig. 4). The largest amount of variation was explained for the BTBW ($R^2 = 0.23$ to 0.37) while the least amount of variation was explained for the BAWW ($R^2 = 0.15$ to 0.18). The BRTH had three factor combinations that met our criteria, but displayed a weak positive linear relationship between hearing loss and detection probability (range $R^2 = 0.11$ to 0.12). Age did not explain more than 8% of the variation for any species under any of the conditions (Fig. 5).

DISCUSSION

Our results indicate that background noise, habitat, leaf condition, species, and observers have significant effects on detection probability and maximum detection distance. We found that the addition of background noise and the presence of leaves on trees decreased both detection probability and maximum detection distance. Both detection probability and maximum detection distance were higher in mixed pine/hardwood forest than deciduous forest. Basal area and leaf area index were higher for the mixed pine/hardwood forest, but the deciduous forest had more horizontal vegetation cover suggesting, for our study, that horizontal vegetation cover had the largest influence on detection probability and maximum detection distance. Given the height and location of our players (~1m off the ground), this conclusion is not surprising, and ideally players would need to be located at different heights in each of the habitats to fully understand the effect of vegetation. Wiley and Richards (1982) and Schieck (1997) found that sound transmission was improved at greater heights (less foliage at greater heights), but at a lower height, where sound is more susceptible to reflection, refraction, and diffraction (Wiley and Richards 1982), the openness of the canopy or vertical structure plays less of a role than horizontal cover in shaping sound travel.

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Simons et al. (2007) recently showed that background noise was an important factor influencing detection probability. Our results suggest that background noise can have a substantial effect on both detection probability and maximum detection distance (Table 4 and Table 8). Background noise is likely increasing in our environment (Wolkomir and Wolkomir 2001), but the degree to which it varies both spatially and temporally is still not known. Evidence exists that spatial variability in background noise may be extreme across large areas (figure 6 in Simons et al. in press). We therefore believe that, given the magnitude of the effect of background noise on both detection distance (overall average effect 36.61 m $\pm$ 5.44) and detection probability (Table 8), background noise should be recognized as a significant factor influencing avian sampling.

We showed that differences in detection probability and maximum detection distance between habitats can be extreme. Caution should be expressed when using a fixed radius plot (Ralph et al. 1995) because the maximum detection distance varies among species and habitats, making the use of a single fixed radius for an entire study unreliable. For example, in one location, a species may be detectable at 150 m, but in another location it may only be detectable at 50 m because of local habitat differences. Using a single fixed radius at both points will produce biased estimates because the size of the area sampled differs between habitats. Similarly, using a fixed radius plot assumes that detection probability is constant out to 50 m (Ralph et al. 1995) and in practice we have seen researchers extend this distance beyond 50 m up to 100 m. Our results suggest this assumption is violated under a range of environmental conditions. Detection probabilities at 50 m and 100 m were consistently below one under many conditions (Table 8) and they varied by species. Researchers interested in exploring bird-habitat relationships should acknowledge that different habitats

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affect detection probability and maximum detection distance differently for each species. The only way to account for these differences is to estimate detection probability directly and in most cases to also include an accurate measure of the actual area sampled (Nichols et al. 2000).

We showed large differences in maximum detection distance and detection probability between 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 habitat conditions similar to these found with and without leaves. For example, fire disturbance (Smucker et al. 2005), gypsy moth infestation (Bell and Whitmore 1997), and silvicultural practices such as thinning (Hayes et al. 2003) all result in pre- and post- situations similar to our leaf-off and leaf-on conditions. Failure to estimate detection probabilities directly could result in a biased inference because differences in pre- and post bird abundance attributed to the effect (e.g. fire, gypsy moths, or thinning) are confounded by differences in detection probability associated with the amount of vegetation. Repeated sampling at the same site takes place over a long period of time (several months to several years) while site characteristics are changing either by environmental factors, such as rain and strong wind or by man-made alterations. A directional difference (e.g. data collected before a storm vs. data collected after a storm) in the site characteristics (habitat structure, amount of vegetation present) could result in differences in detection probability and maximum detection distance, introducing a new source of bias in abundance unless detection probability is estimated directly and incorporated into abundance estimates.

The relative hearing index did a better job of explaining observed variation than age alone. Nevertheless we feel these results are only a first step in understanding the complexity

of observer differences in detecting birds. Age-related hearing loss is a commonly recognized phenomenon (Emlen and DeJong 1992), yet some of our older observers performed better on the hearing test and had higher estimated detection probabilities than our younger observers. Hearing is a more complex process than simply the ability to hear particular frequencies at various intensity levels. Our relative hearing index provided a measure of the rank of each of our observers, but did not completely explain the observed variation in detection probabilities under a range of environmental conditions. Other factors are influencing an observer's ability to detect individual birds that hearing and age alone cannot elucidate. Possible factors include experience (Sauer et al. 1994), familiarity with species, and skill.

Our results indicate that habitat, leaf conditions, background noise, observers, and species are interacting in their effect on detection probability and maximum detection distance (Table 7 and Fig. 3). All three species had different top models selected indicating that different interactions were important for each species (Table 6). Importance weights differed among species as well, indicating that no group of interactions was consistently more important for all three species (Table 7). For example, the habitat*leaves interaction was most important for the BAWW, but was the least important for the BTBW. The most detectable and least detectable species (BRTH and BAWW) had the fewest competing models and the BTBW did not have a single interaction with an importance weight greater than 86%. Species at the extremes of detectability may be influenced more by specific interactions that can be easily identified. Species that are not at the extremes of detectability may exhibit more uncertainty in identifying the factors that have the most influence on detection probability. The degree and type of factors interacting to effect detection

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probability and maximum detection distance vary among species. Unfortunately, most studies face habitat differences and observer differences, and most are interested in more than one species.

Correction factors, such as using double sampling (Bart and Earnst 2002), are useful if a sub-sample of plots can be completely censused and the correction factor is only used for the current study. Ad-hoc procedures such as the use of a correction factor from another study represents a poor approach to accounting for individuals present, but not detected. Our results show that detection probability varies under a range of environmental conditions, among species, and observers, indicating that a separate correction factor would have to be calculated for each condition and would not include the effect of factor interactions.

We used a unique approach to assess the effects of three factors (background noise, species, and observer) under varying environmental conditions (habitat and leaf condition). We could control for some of the factors in our study, and therefore believe our results provide accurate estimates of detection probability and maximum detection distance under a range of realistic conditions. We could not control for all sources of variation and minor differences still exist among days and observers. Unexplained sources of variation include spatial and temporal site differences, location of observers within a site (one observer might be closer to an opening in the vegetation and therefore be able to detect songs farther), and environmental differences between days (wind, temperature, and ambient noise). We showed that detection probability and maximum detection distance varied between habitats, leaf conditions, observers, species, and with the addition of background noise. We believe that reliable inference from auditory point counts must account for spatial and temporal

variation in detection probability and maximum detection distance by estimating detection

probability directly and incorporating this estimate into an abundance estimate.

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Table 1. Seven species simulated in field experiments and song length (seconds). Only three

species (BAWW, BTBW, BRTH) included in results. Songs from Peterson (1990), see

Simons et al. (2007) for specifications.

Species	Species Code	Song Length (sec.)
Acadian Flycatcher *Empidonax virescens*	ACFL	0.5
Black-and-white Warbler *Mniotilta varia*	BAWW	2
Brown Thrasher *Toxostoma rufum*	BRTH	5
Black-throated Blue Warbler *Dendroica caerulescens*	BTBW	1.4
Hooded Warbler *Wilsonia citrina*	HOWA	1.1
Scarlet Tanager *Piranga olivacea*	SCTA	2
Wood Thrush *Hylocichla mustelina*	WOTH	1.4

Table 2. Factors and factor levels in experiments. Design of experiments over four days including sample sizes for each day and ambient noise conditions with and without simulated background noise in dB (S.E.). Experiments were run one line at a time with no noise and then run again with simulated background noise added on the same line. Maximum detection distance analyses used six observers. Detection probability analyses used 12 observers.

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

	Day 1	Day 2	Day 3	Day 4
	Off Mixed pine/hardwood forest	Off Deciduous forest	On Mixed pine/hardwood forest	On Deciduous forest
	Line 1 No background noise Line 1 With background noise Line 2 No background noise Line 2 With background noise	Line 1 No background noise Line 1 With background noise Line 2 No background noise Line 2 With background noise	Line 1 No background noise Line 1 With background noise Line 2 No background noise Line 2 With background noise	Line 1 No background noise Line 1 With background noise Line 2 No background noise Line 2 With background noise
No noise	36.65 (1.08)	38.38 (2.86)	36.49 (1.68)	41.50 (2.48)
With noise	46.5 (0.98)	47.35 (1.85)	46.68 (1.03)	48.76 (2.01)
Total observations*	420	425	446	446

*Note: 1792 total songs simulated (448 per day). Player malfunctions resulted in 420-446 total observations each day.

Table 3. Total basal area (m^2/ha $\pm$ S.E.) for mixed pine/hardwood forest (n = 26) and

deciduous forest (n = 24). Indirect leaf area index, LAI (S.E.) for mixed pine/hardwood

forest (n = 30) and deciduous forest (n = 30) under leaf-off and leaf-on conditions. The

higher the index value, the greater the estimated leaf area.

		Mixed Forest	S.E.	Deciduous Forest	S.E.
	Total Basal Area	26.46	1.83	9.50	1.41
LAI	Leaf-on	6.74	0.09	5.41	0.19
	Leaf-off	1.41	0.08	0.88	0.04

Table 4. Least squares means (S.E.) for maximum detection distance. Three species
(BAWW, BTBW, BRTH) at each of the possible factor combinations.

		Mixed Forest		Deciduous Forest	
		Average	S.E.	Average	S.E.
BAWW	Leaf-off no noise	135.83	10.40	93.51	10.86
	Leaf-off with noise	116.67	10.40	74.01	10.86
	Leaf-on no noise	100.45	11.17	54.25	10.72
	Leaf-on with noise	79.55	11.17	40.75	10.72
BTBW	Leaf-off no noise	187.50	8.74	125.84	9.28
	Leaf-off with noise	140.00	8.74	82.28	9.28
	Leaf-on no noise	123.52	9.53	82.90	9.09
	Leaf-on with noise	91.18	9.53	55.38	9.09
BRTH	Leaf-off no noise	193.33	9.02	191.97	9.61
	Leaf-off with noise	155.00	9.02	118.26	9.61
	Leaf-on no noise	197.17	9.89	170.45	9.41
	Leaf-on with noise	130.91	9.89	133.41	9.41

Table 5. Factors affecting maximum detection distances for three species including p-values (F-value; numerator DF, denominator DF). An unbalanced design for all three species (BAWW, BTBW, BRTH) required an iterative process of fitting observer interactions, therefore the Leaves*observer effect was only included for BAWW.

Effect	BAWW	BTBW	BRTH
Habitat	0.0003 (30.09; 1, 9.55)	<0.0001 (55.68; 1, 9.23)	0.0479 (5.26; 1, 8.86)
Leaves	0.0011 (22.68; 1, 8.93)	<0.0001 (50.56; 1, 8.49)	0.3456 (1; 1, 8.11)
Noise	0.04 (5.80; 1, 8.78)	0.0003 (33.86; 1, 8.81)	<0.0001 (64.35; 1, 8.43)
Observer	0.0211 (2.96; 5, 47.5)	0.1775 (1.60; 5, 52.5)	0.4721 (0.93; 5, 52.1)
Habitat*leaves	0.9996 (0; 1, 9.55)	0.1319 (2.77; 1, 8.67)	0.6171 (0.27; 1, 8.29)
Habitat*noise	0.8224 (0.05; 1, 9.05)	0.746 (0.11; 1, 9.23)	0.826 (0.05; 1, 8.86)
Leaves*noise	0.8903 (0.02; 1, 8.57)	0.2571 (1.48; 1, 8.49)	0.7507 (0.11; 1, 8.11)
Noise*observer	0.1232 (1.84; 5, 47.5)	0.822 (0.44; 5, 52.5)	0.0386 (2.55; 5, 52.1)
Leaves*observer	0.0302 (2.73; 5, 47.5)	-	-
Habitat*leaves*noise	0.8041 (0.07; 1, 8.69)	0.9734 (0; 1, 8.67)	0.0411 (5.84; 1, 8.29)

Table 6. Δ AIC and AIC weights (w_i) for logistic regression models of detection probability for each of three species with Δ AIC < 10.

BAWW

model	Δ AIC	w_i
$H + N + L + O + x +HN + HL + Hx + NL + Nx + Lx$	0.00	0.64
$H + N + L + O + x + HN + HL + Hx + NL + Nx$	1.33	0.33
$H + N + L + O + x + HL + Hx + NL + Lx$	6.94	0.02
$H + N + L + O + x + HN + HL + Hx + Nx + Lx$	8.90	0.01
$H + N + L + O + x + HL + Hx + Lx$	9.54	0.01

BTBW

model	Δ AIC	w_i
$H + N + L + O + x + NL + Nx + Lx$	0.00	0.18
$H + N + L + O + x + HN + Hx + NL + Nx + Lx$	0.68	0.13
$H + N + L + O + x +HN + HL + Hx + NL + Nx + Lx$	0.75	0.13
$H + N + L + O + x + Nx + Lx$	1.43	0.09
$H + N + L + O + x + HN + HL + Hx + NL + Nx$	1.74	0.08
$H + N + L + O + x + Hx + NL + Nx + Lx$	2.00	0.07
$H + N + L + O + x + HN + HL + Hx + NL$	2.00	0.07
$H + N + L + O + x + HN + HL + Hx + NL + Lx$	2.10	0.06
$H + N + L + O + x + Hx + Nx + Lx$	2.92	0.04
$H + N + L + O + x + HL + Nx + Lx$	3.37	0.03
$H + N + L + O + x + HN + Nx + Lx$	3.42	0.03
$H + N + L + O + x + HL + Hx + Nx + Lx$	4.40	0.02

Table 6 continued.

model	ΔAIC	w_i
$H + N + L + O + x + HN + HL + Nx + Lx$	5.37	0.01
$H + N + L + O + x + HN + Lx$	5.65	0.01
$H + N + L + O + x + HN + HL + NL + Nx + Lx$	5.95	0.01
$H + N + L + O + x + HN + HL + Lx$	6.75	0.01
$H + N + L + O + x + HL + Hx + Lx$	7.34	0.00
$H + N + L + O + x + HN + Hx + Lx$	7.60	0.00
$H + N + L + O + x + HN + NL + Lx$	7.62	0.00
$H + N + L + O + x + HN + HL + NL + Lx$	7.95	0.00
$H + N + L + O + x + HN + HL + Hx + Lx$	8.02	0.00
$H + N + L + O + x + Hx + Lx$	8.51	0.00
$H + N + L + O + x + Lx$	8.52	0.00
$H + N + L + O + x + HL + Hx + NL + Lx$	8.92	0.00
$H + N + L + O + x + HN + HL + Hx + Nx + Lx$	9.32	0.00
$H + N + L + O + x + HL + Lx$	9.49	0.00

BRTH

model	Δ AIC	w_i
$H + N + L + O + x + HN + HL + NL + Nx$	0.00	0.30
$H + N + L + O + x + HL + Hx + NL + Nx + Lx$	0.23	0.27
$H + N + L + O + x + HN + Hx + NL + Nx + Lx$	1.81	0.12
$H + N + L + O + x + HN + HL + Hx + NL + Nx + Lx$	2.04	0.11
$H + N + L + O + x + HN + NL + Nx$	3.43	0.05
$H + N + L + O + x + HN + HL + Hx + NL + Lx$	3.55	0.05

Table 6 continued.

$H + N + L + O + x + Hx + NL + Nx$	4.31	0.04
$H + N + L + O + x + HL + Hx + NL + Nx$	5.15	0.02
$H + N + L + O + x + Hx + NL + Nx + Lx$	5.65	0.02
$H + N + L + O + x + HN + HL + Hx + NL + Nx$	6.85	0.01

Table 7. Variable importance weights ($\sum w_i$) obtained by summing AIC weights for each model in which the predictor variable (main effects and two-way interactions) was found.

Predictor variable	BAWW	BTBW	BRTH
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 8. Average estimated detection probabilities (S.E.) for 12 observers at 50 m and 100 m for three species (BAWW, BTBW, BRTH). Estimates from the top AIC logistic regression model.
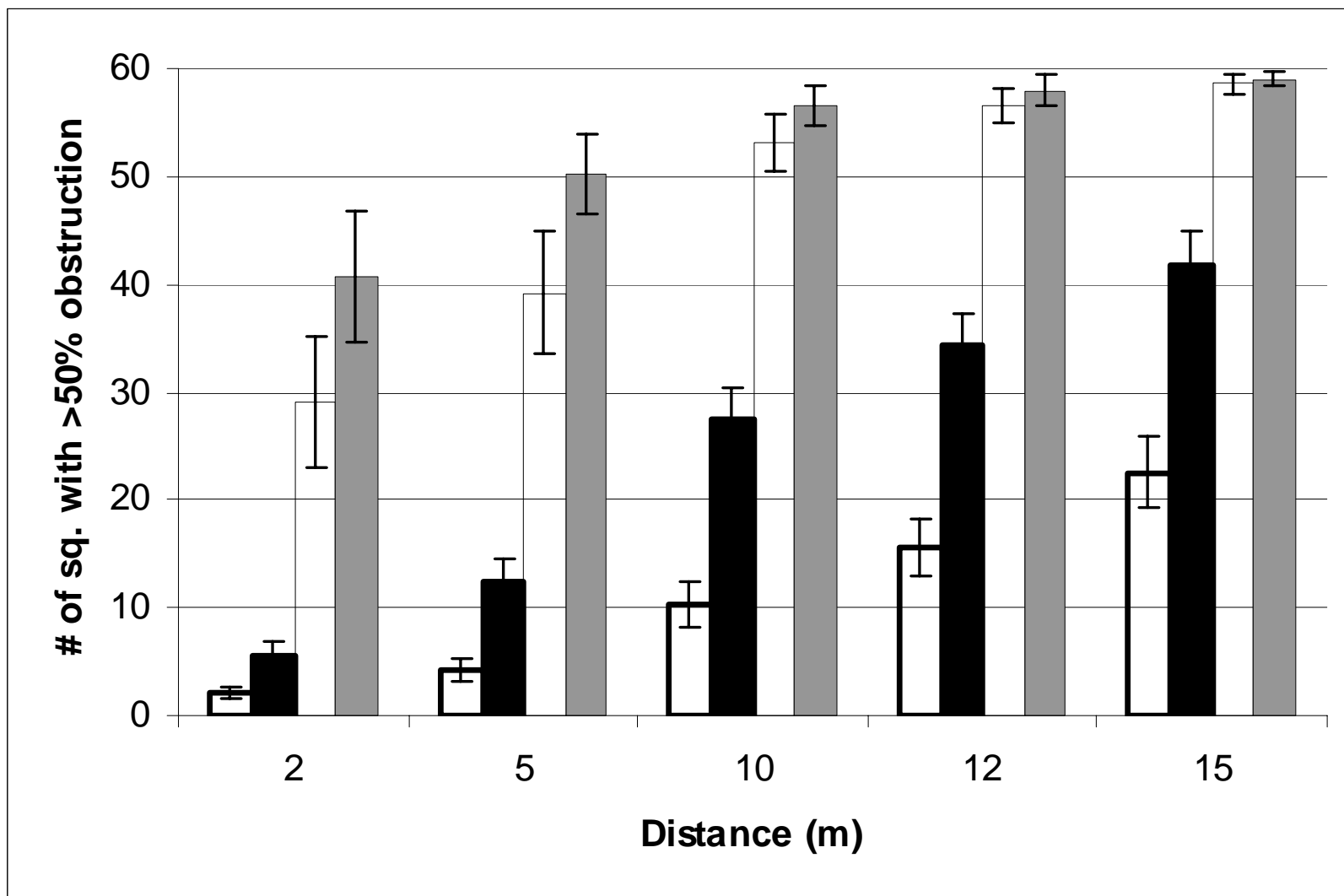
		Mixed Forest		Deciduous Forest	
	distance (meters)	50	100	50	100
BAWW	Leaf-off no noise	0.96 (0.02)	0.78 (0.07)	0.93 (0.04)	0.19 (0.03)
	Leaf-off with noise	1.00 (0.00)	0.68 (0.07)	0.97 (0.02)	0.02 (0.00)
	Leaf-on no noise	1.00 (0.00)	0.53 (0.07)	0.89 (0.05)	0.00 (0.00)
	Leaf-on with noise	1.00 (0.00)	0.02 (0.00)	0.56 (0.07)	0.00 (0.00)
BTBW	Leaf-off no noise	1.00 (0.00)	0.99 (0.00)	0.96 (0.01)	0.60 (0.05)
	Leaf-off with noise	1.00 (0.00)	0.94 (0.02)	0.91 (0.03)	0.16 (0.02)
	Leaf-on no noise	1.00 (0.00)	0.89 (0.03)	0.93 (0.02)	0.09 (0.01)
	Leaf-on with noise	1.00 (0.00)	0.34 (0.04)	0.69 (0.05)	0.00 (0.00)
BRTH	Leaf-off no noise	1.00 (0.00)	1.00 (0.00)	0.99 (0.00)	0.97 (0.01)
	Leaf-off with noise	1.00 (0.00)	0.95 (0.01)	0.99 (0.00)	0.74 (0.04)
	Leaf-on no noise	0.99 (0.00)	0.96 (0.01)	0.92 (0.02)	0.78 (0.04)
	Leaf-on with noise	0.99 (0.00)	0.87 (0.03)	0.98 (0.01)	0.65 (0.04)

Table 9. Minimum and maximum (min – max) estimated detection probabilities for 12 observers under all possible factor combinations. Estimates obtained from the top AIC logistic regression model for three species (BAWW, BTBW, BRTH) at 50 meters and 100 meters.

		Mixed Forest		Deciduous Forest	
	distance (meters)	50	100	50	100
BAWW	Leaf-off no noise	0.74 - 0.99	0.17 - 0.93	0.57 - 0.99	0.01 - 0.31
	Leaf-off with noise	0.98 - 1.00	0.09 - 0.87	0.81 - 1.00	0.00 - 0.03
	Leaf-on no noise	1.00 - 1.00	0.04 - 0.74	0.41 - 0.98	0.00 - 0.00
	Leaf-on with noise	1.00 - 1.00	0.00 - 0.03	0.05 - 0.77	0.00 - 0.00
BTBW	Leaf-off no noise	1.00 - 1.00	0.97 - 1.00	0.83 - 0.99	0.16 - 0.80
	Leaf-off with noise	1.00 - 1.00	0.75 - 0.98	0.63 - 0.97	0.02 - 0.31
	Leaf-on no noise	1.00 - 1.00	0.59 - 0.97	0.70 - 0.97	0.01 - 0.17
	Leaf-on with noise	0.98 - 1.00	0.06 - 0.56	0.23 - 0.87	0.00 - 0.01
BRTH	Leaf-off no noise	1.00 - 1.00	0.99 - 1.00	0.96 - 1.00	0.88 - 0.99
	Leaf-off with noise	0.99 - 1.00	0.80 - 0.97	0.94 - 0.99	0.35 - 0.84
	Leaf-on no noise	0.95 - 0.99	0.85 - 0.98	0.69 - 0.96	0.40 - 0.87
	Leaf-on with noise	0.98 - 1.00	0.57 - 0.93	0.91 - 0.99	0.24 - 0.76

Figure 1. Horizontal cover (includes S.E. bars) estimated using a 1.2 meter (height) coverboard at five distances (2, 5, 10, 12, and 15 m) from the board in both the mixed pine/hardwood forest and deciduous forest under leaf off and leaf on conditions. Cover is estimated as the number of squares (out of 60) with at least 50% obstruction by vegetation. Solid open rectangle represents mixed pine/hardwood forest under leaf-off conditions. Solid filled rectangle represents mixed pine/hardwood forest under leaf-on conditions. Light open rectangle represents deciduous forest under leaf-off conditions. Light gray-filled rectangle represents deciduous forest under leaf-on conditions.
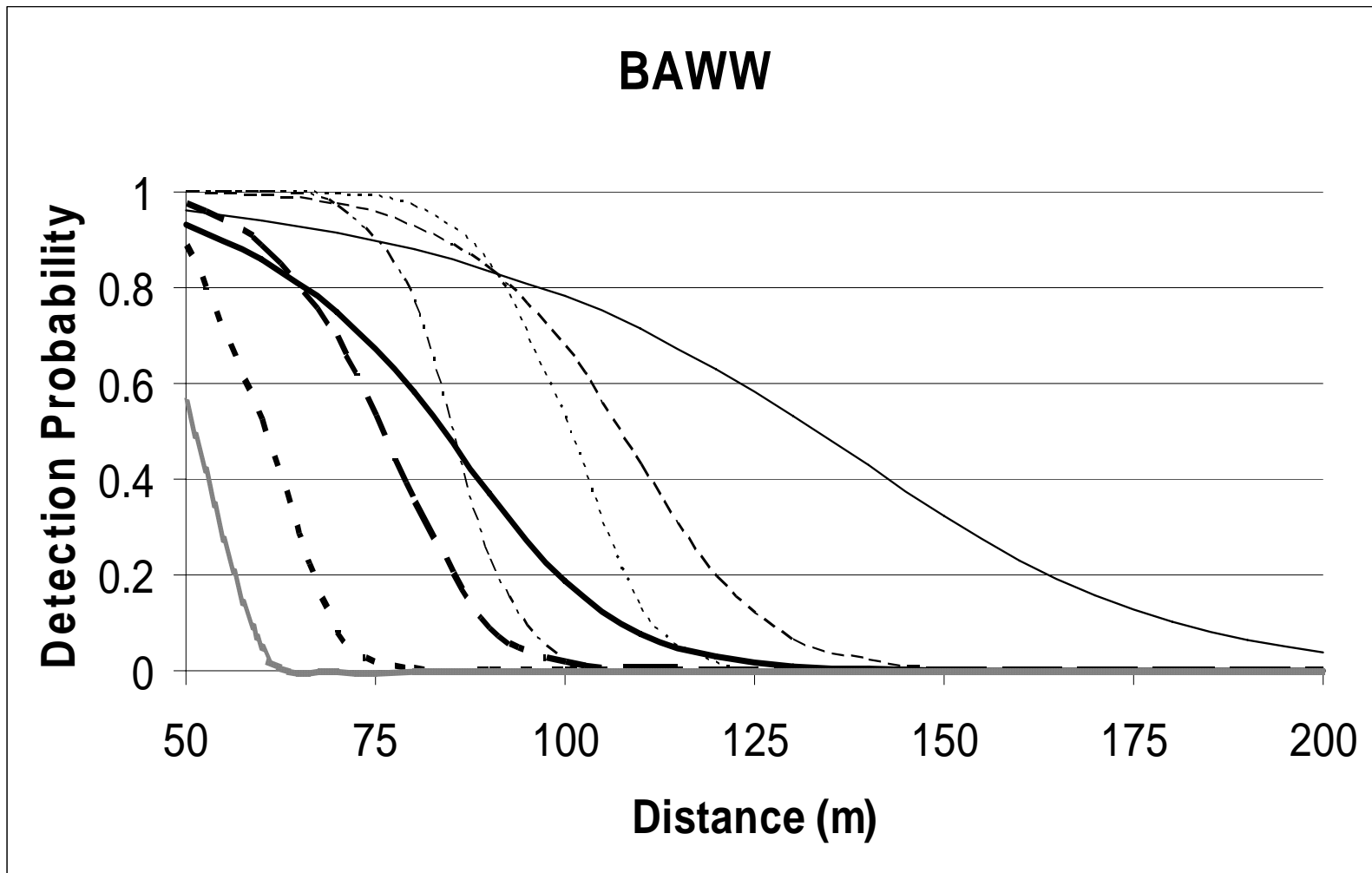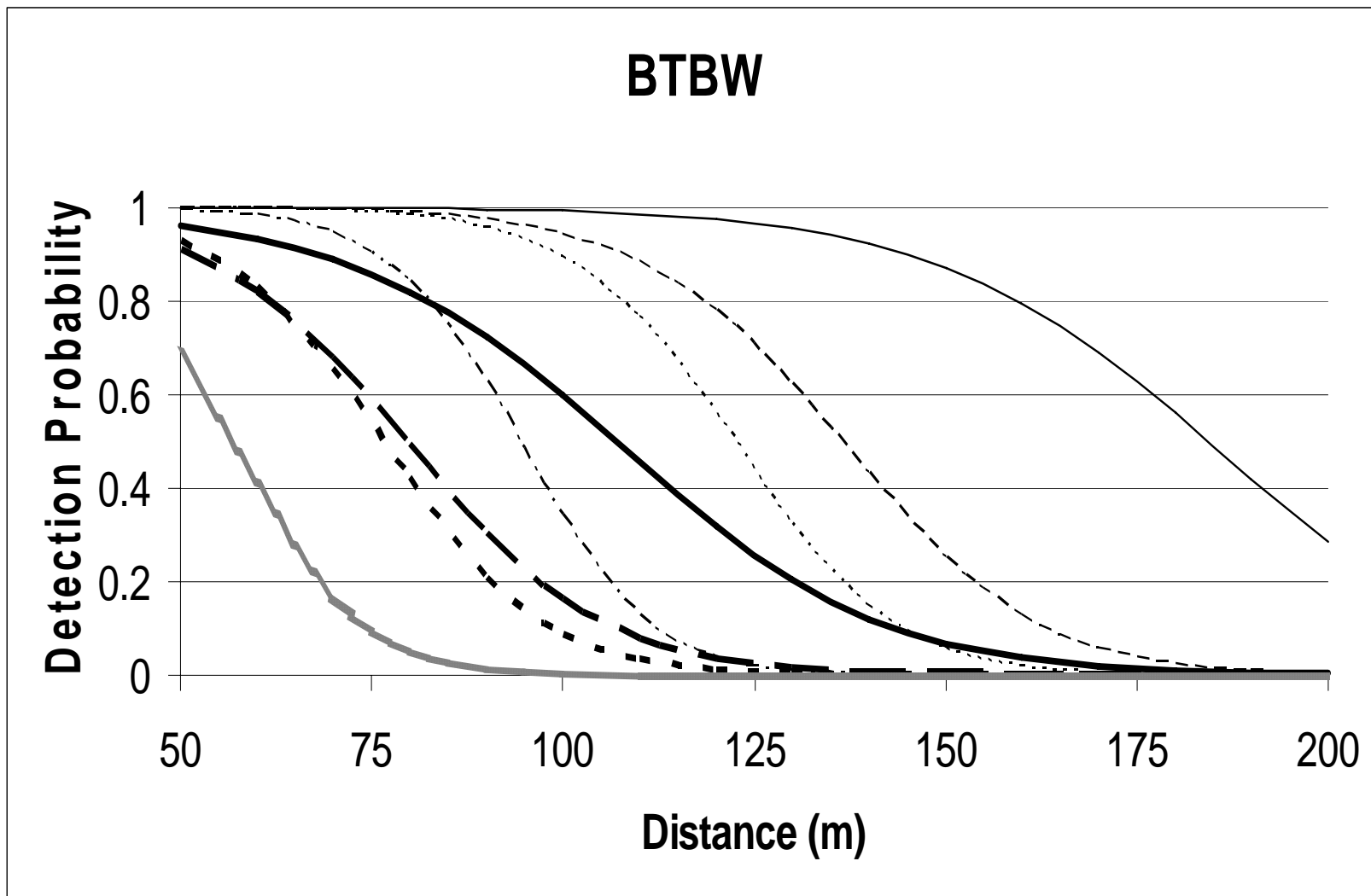
Figure 2. Age versus relative hearing index for all 12 observers ($R^2 = 0.17$).

Figure 3. Logistic regression models for each of the three focal species (BAWW, BTBW, BRTH) averaged across 12 observers demonstrating differences among species and each of the eight factor combinations. The eight treatments are combinations of habitat (mixed pine/hardwood forest, deciduous forest), leaf condition (off, on), and added background noise (no, yes). Heavier weighted lines represent deciduous forest and lighter weighted lines represent mixed pine/hardwood forest. Continuous lines (⟍) represent leaf-off conditions with no background noise. (⟍) represent leaf-off conditions with background noise. (⟍) represent leaf-on conditions with no background noise. (⟍) represent leaf-on conditions with background noise in the mixed pine/hardwood forest and (⟍) represent leaf-on conditions with background noise in the deciduous forest.
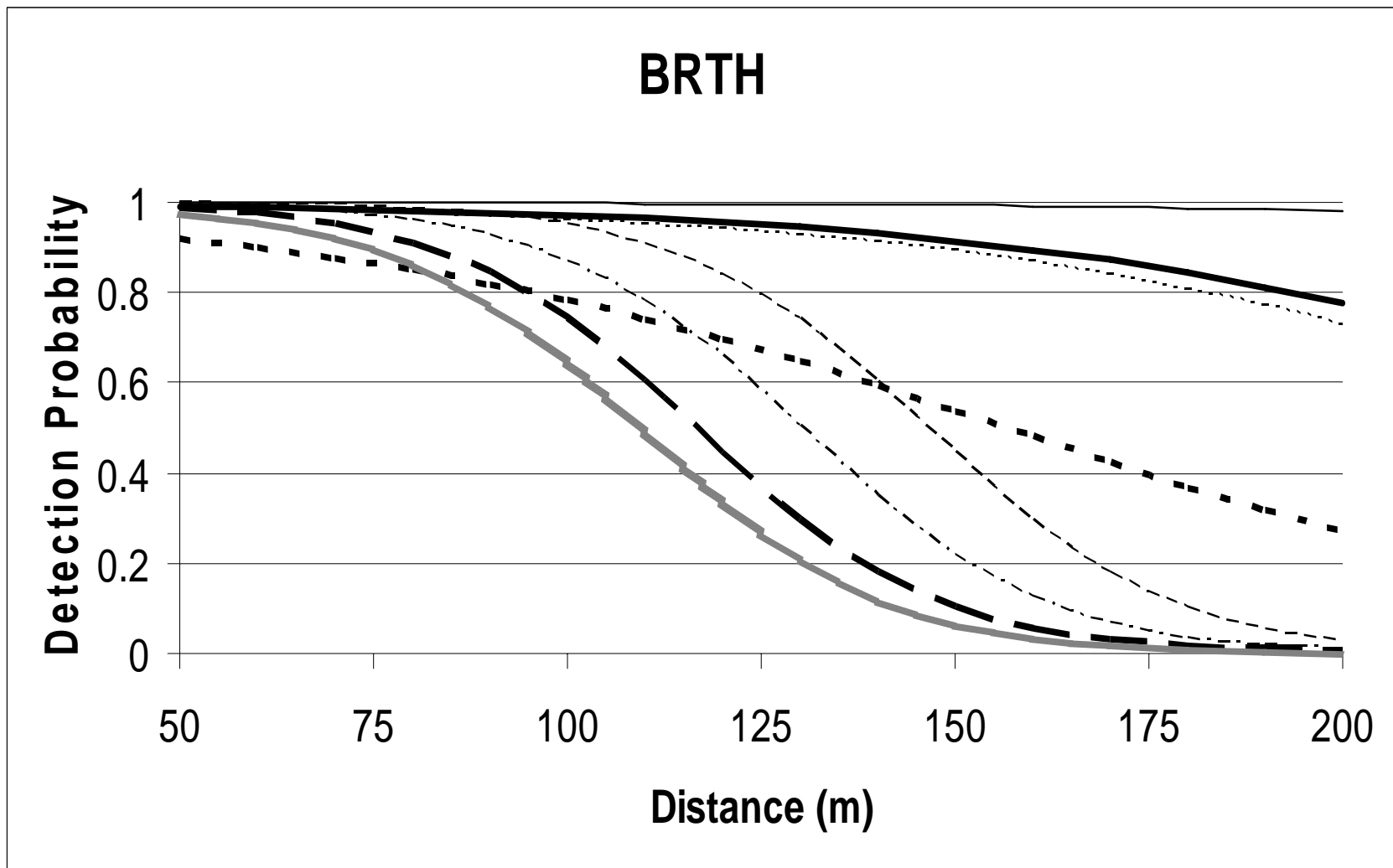
BAWW

BTBW

BRTH

Figure 4. Estimated detection probabilities for 12 observers plotted against each observer's relative hearing index for three species (BAWW, BTBW, and BRTH); general pattern is similar under all conditions. Detection probabilities are from top AIC logistic regression model demonstrating largest R^2 values for each species (BAWW 0.18, BTBW 0.37, BRTH 0.12). Note that BAWW and BTBW displayed negative relationships between detection probability and hearing while BRTH displayed a positive relationship. (□) represents BAWW, (○) BTBW, and (✕) BRTH.
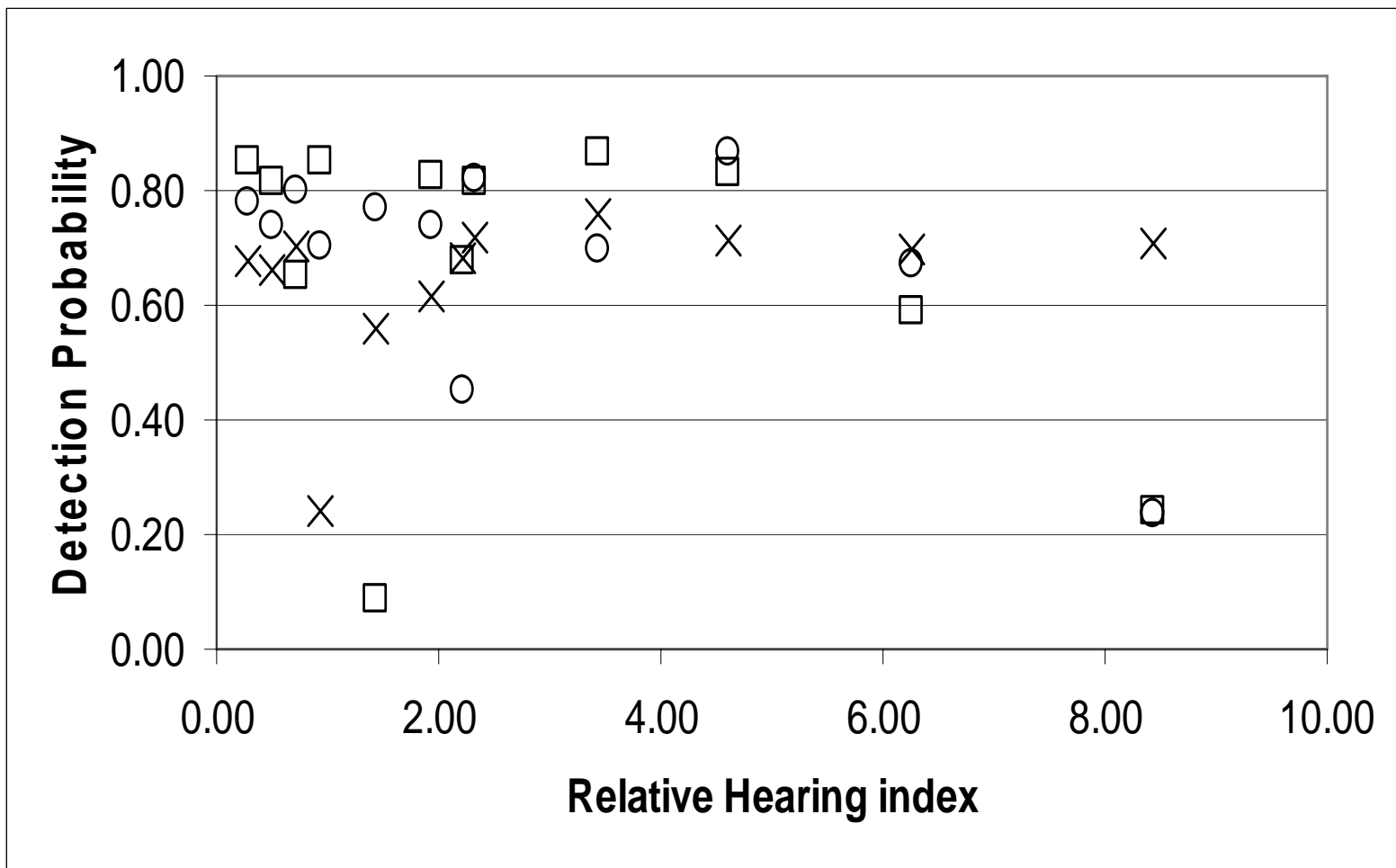
Figure 5. Estimated detection probability for 12 observers plotted against each observer's age for one species (BTBW) with the highest R^2 (0.08) value. Detection probabilities are from the top AIC logistic regression model at 50 m under leaf-on conditions with additional background noise in the deciduous forest.
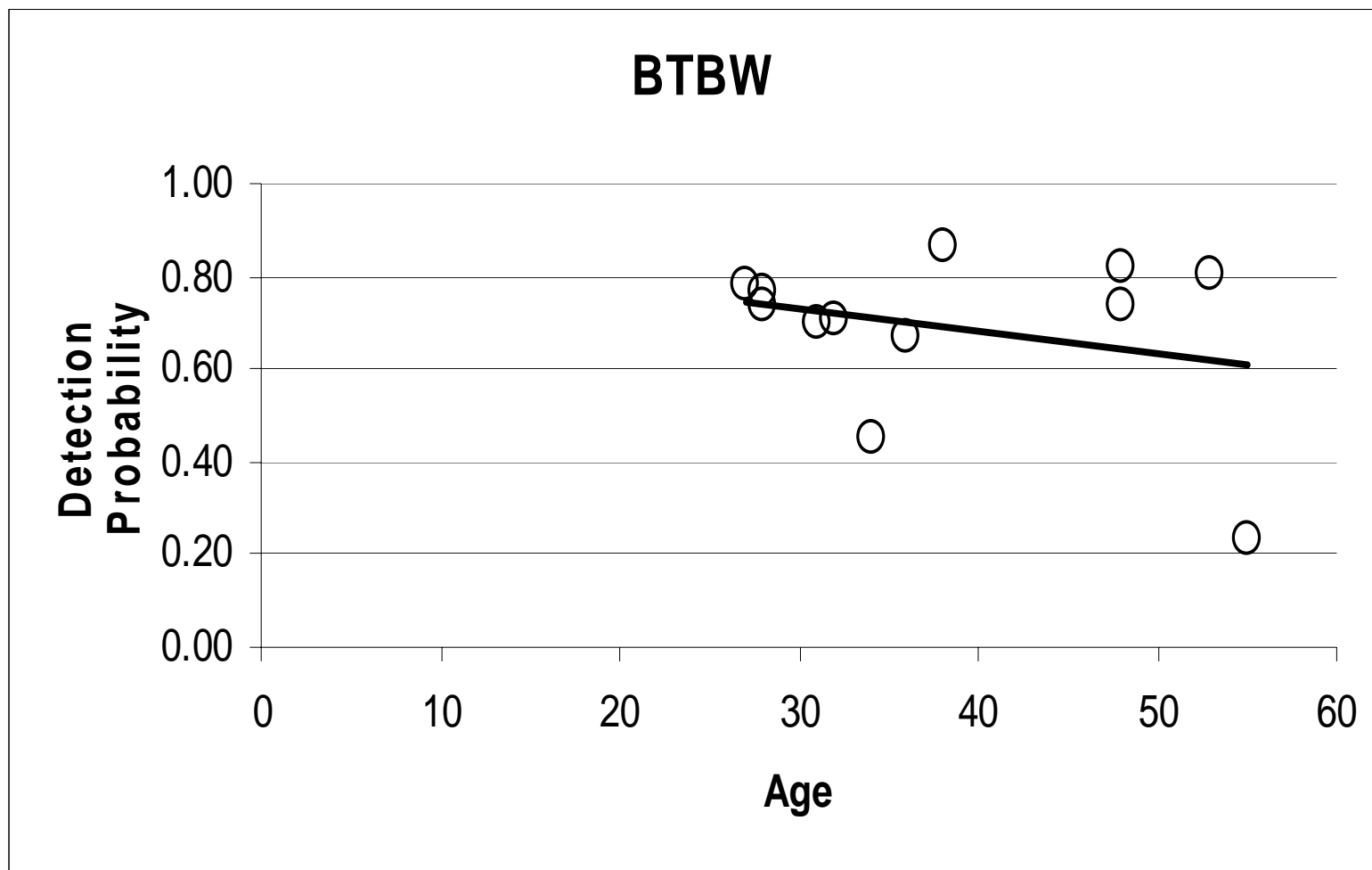
BTBW

Figure 6. Measured levels of ambient noise on 23 North Carolina Breeding Bird Surveys in 2006. Observers conduct 50 3-minute unlimited radius point counts along a 40 km route. Dots represent the mean of three sound pressure readings measured along each route using a Martel Electronics model 325 sound level meter (accuracy $\pm$ 1.5 dB). Weighted rectangle represents the reference range of ambient noise conditions for our study. Adapted from Simons et al. (2007).