

EFFECTS OF IMPERFECT DETECTABILITY ON INFERENCES FROM  
AVIAN MONITORING<sup>1</sup>:  
FINAL REPORT

6 October 2014

Graduate Research Assistant: ELIZABETH A. RIGBY, Natural Resources Science and Management Graduate Program, College of Food, Agricultural, and Natural Resources Sciences, University of Minnesota, St. Paul, Minnesota, USA.

Graduate Student Advisor: DOUGLAS H. JOHNSON, U.S. Geological Survey, Northern Prairie Wildlife Research Center, University of Minnesota, St. Paul, Minnesota, USA.

Principal Investigator: DAVID E. ANDERSEN, U.S. Geological Survey, Minnesota Cooperative Fish and Wildlife Research Unit<sup>2</sup>, 200 Hodson Hall, 1980 Folwell Avenue, St. Paul, Minnesota, USA.

---

<sup>1</sup>Research Work Order No. 83, Minnesota Cooperative Fish and Wildlife Research Unit

<sup>2</sup>Cooperators: U.S. Geological Survey, Minnesota Department of Natural Resources, University of Minnesota, The Wildlife Management Institute, and the U.S. Fish and Wildlife Service.

*Abstract:* Imperfect detectability can complicate analysis of bird survey data. Adjustment methods to account for imperfect detectability exist, but it is not clear how the benefits of these methods compare to their costs. Graduate student Elizabeth Rigby is constructing a computer simulation of bird surveys to evaluate the effects of survey method on survey conclusions. The computer simulation will create simulated birds, then conduct counts of these birds, taking into account realistic parameters of factors known to affect bird counts. This project is currently in the design and coding phase. In addition to the simulation, she conducted a field study of factors affecting detectability of birds in grasslands. The field study assessed the effects of distance to sound source, wind speed and direction, habitat structure and composition, and bird species on the detection of recorded bird songs. Mock surveys with over 9,000 opportunities to detect a recorded bird song were conducted in fall 2011 and 2012 with 4 observers. Detection of recorded songs was treated as a binary variable and analyzed with logistic regression and mixed models. Distance from the observer and an index of wind speed and direction were the strongest covariates to detection. Models used to predict detections of recorded songs performed well, correctly predicting detections 68-90% of the time (depending on species). Observer effects were important; odds of detection for inexperienced observers were only 26% of those of the primary observer. Detection around a sound source was asymmetrical and heavily affected by wind direction. Design and coding for the computer simulation, as well as analysis of field data, will continue in 2014.

---

Point counts are commonly used in bird surveys to achieve a number of objectives, including species abundance estimation and population monitoring. Point counts are ubiquitous in biological monitoring, yet there is significant debate regarding how count information can best be used. Of particular importance is the role played by detection probability. The expected value of the count ( $E(C)$ ) for any point is equal to the product of the number of birds present ( $N$ ) and the probability of detection ( $p$ ). Detection probability can be affected by a wide variety of factors, including behavioral (singing rates, volume, and motion of birds), environmental (precipitation, wind speed, ambient noise, visual obscurity), and observer effects (hearing ability, skill, distance from the source). Over the last 20 years, great effort has gone into crafting methods to account for detection probability in bird surveys (hereafter, “adjustment methods”), such as double observer surveys (Nichols et al. 2000), replicated samples (Royle 2004), distance sampling (Burnham et al. 1980; Buckland et al. 1993), and removal (Farnsworth et al. 2002) or time-of-detection (Allredge et al. 2007a) methods.

Although these adjustment methods are attractive on paper, there can be drawbacks to using them. Multiple observer methods (Nichols et al. 2000) require additional field technicians to make observations, at increased financial cost. In replicated samples (Royle 2004), the number of overall sites visited is reduced in favor of repeat visits to sites, resulting in reduced sample size. Distance sampling (Burnham et al. 1980; Buckland et al. 1993) requires estimating the distance to all birds, a potential source of error. Johnson (2008) argued that all adjustment

methods are “an assumption or a consequence of an assumption” and that their use is not universally preferable to index studies. Adjustment methods may entail additional sources of error, such as when distance must be estimated by observers (Alldredge et al. 2007b), consensus must be reached by multiple observers (Alldredge et al. 2006), or birds move or change their availability during time-of-detection surveys (Farnsworth et al. 2002, Alldredge et al. 2007a). How one surveys birds has the potential to affect the conclusions of surveys, but these effects have not been quantified, nor has consensus been reached on the best methods to use in different situations.

We have devised a 2-pronged approach to investigating effects of imperfect detection on survey results. First, we plan to use computer-simulated bird surveys to assess the effects of adjustment methods on survey results. By simulating surveys under different conditions, we hope to determine which survey methods are best for different situations and provide information that can improve the ability of monitoring programs to achieve their objectives. We also hope to make recommendations regarding the field use of adjustment methods based on situation, including species and habitats with known detectability problems (e.g., cryptic species, concealing habitat structure, or rare species). This project will be primarily be conducted by graduate student Elizabeth Rigby.

In addition to the computer simulation, Elizabeth has begun a field study on the factors affecting detectability of birds in grasslands. Despite the emphasis on the importance of detectability in bird surveys, there has been relatively little research to quantify factors affecting detection in the field. This gap is largely due to the difficulty of measuring factors affecting detectability of real birds in the field – calculating detectability is simple if true populations are known, but that is seldom, if ever, the case. Alldredge et al. (2007b) investigated effects on detectability in mature bottomland hardwood and mixed pine-hardwood forest, using a multi-speaker simulation system to broadcast bird songs to multiple observers. They estimated effects of singing rate, species, observer, and distance, as well as interactions among main effects. Pacifici et al. (2008) used a similar setup to estimate effects of cover type (deciduous forest vs. mixed pine-hardwood), presence/absence of foliage, ambient noise, observer, and distance. These studies remain the most intensive investigations to date. Grasslands have markedly different structure and species composition than the forests examined in previous studies of factors affecting detectability (Alldredge et al. 2007b; Pacifici et al. 2008), which could produce different effects on detectability. Grassland birds across North America have experienced widespread population declines for decades, increasing conservation concern for the group (Peterjohn and Sauer 1999). An understanding of factors affecting detectability in grasslands would guide and improve bird survey methodology for an increasingly imperiled group.

The objective of this field study was to assess the effects of distance to sound source, wind speed and direction, habitat structure and composition, and bird species on the detection of recorded bird songs in a grassland setting.

## Computer Simulation

### Methods

#### *Model Structure*

The bird survey simulation model will have a conceptual structure based on Nichols et al. (2009) and will be coded in Program R (R Development Core Team, Vienna, Austria, <http://www.R-project.org>). Surveys will be simulated for one species at a time. The model structure is derived from the equation

$$E(C) = pN ,$$

where the expected value of the count ( $E(C)$ ) for any point is equal to the product of the number of birds present ( $N$ ) and the probability of detection ( $p$ ). Nichols et al. (2009) decomposed  $p$  into 4 parts:  $p_s$ , the probability that a bird is in the area of inference;  $p_p$ , the probability that a bird is present in the surveyable area during a survey given that it is in the area of inference;  $p_a$ , the probability that a bird is available (vocalizes) during a survey, given that it is in the area of inference and present in the surveyable area; and  $p_d$ , the probability that a bird is detected, given that it is in the area of inference, present in the surveyable area, and available during the survey. The expected value for a count during a survey is thus

$$E(C) = p_s p_p p_a p_d N^* ,$$

where  $N^*$  is the entire continental population of the species, or superpopulation.

In addition to  $N^*$ , there are 4 other populations that may be useful in the discussion of detection.  $N_s$  is the population within the area of inference, where

$$N_s = p_s N^* .$$

$N_p$  is the population present within the surveyable area, where

$$N_p = p_s p_p N^* .$$

$N_a$  is the population available during a survey, where

$$N_a = p_s p_p p_a N^* .$$

$N_d$  is the population detected during a survey (also known as the count) where

$$N_d = p_s p_p p_a p_d N^* .$$

It is also useful to note that

$$N^* \geq N_s \geq N_p \geq N_a \geq N_d .$$

Each full run of the model will represent a “scenario”, which will include a suite of parameters designed to simulate a specific survey situation for a species. With each scenario, the model structure will include 5 nested levels: year ( $y = 1, 2, \dots, N_{Years}$ ), site ( $i = 1, 2, \dots, N_{SurveySites}$ ), bird ( $j = 1, 2, \dots, BirdsInHabitat.yi + BirdsInMatrix.yi$ ), replication ( $r = 1, 2, \dots, N_{Reps}$ ), and interval ( $k = 1, 2, \dots, N_{Intervals}$ ). A site represents a single surveyed area, though it can be surveyed multiple times if  $N_{Reps} > 1$ . An interval is a short period, akin to the duration of one bird song.

Within the model coding, R object names include an identifier, similar to a subscript, but instead connected with a “.”. For example, a year effect is coded with a “.y”, such as the mean arrival date for a species on the breeding grounds, *meanarrival.y* and an interval-specific effect is coded with a “.yijrk”, such as the location of bird *j* in replication *r* during interval *k* (*Location.yijrk*). Scenario-specific effects have no identifier, such as the number of years simulated in a scenario, *NYears*. To make reference to the R code easier, I will refer to variables in italics, as their R objects, rather than converting identifiers to subscripts.

### *Abundance*

*Nstar* (the super population), the size of the area of inference (*AreaofInference*), and the proportion of *Nstar* that can be found in the area of interest (*Ps*) will be determined by the user, where  $N_s = N_{star} \times P_s$ . *Nstar* and *Ns* represent the true populations to which survey conclusions will be compared.

Each site *i* will have 1-2 landcover types: habitat and matrix. The proportion of habitat in the area of inference is *HabitatProportion.y*. The species’ preference for habitat is indicated by a specialist index, *SpecialistIndex*, where  $0 \leq SpecialistIndex \leq 1$ . A *SpecialistIndex* value of 0 indicates a generalist (no preference for habitat over matrix) and a value of 1 indicates a species found exclusively in habitat. The mean proportion of birds found in habitat within the area of inference is equal to  $HabitatProportion.y + SpecialistIndex (1 - HabitatProportion.y)$ . The density of birds in habitat within the area of inference, *HabitatDensity.y*, is therefore given by

$$\begin{aligned} & \textit{HabitatDensity.y} \\ = & \frac{N_s \times (\textit{HabitatProportion.y} + \textit{SpecialistIndex} (1 - \textit{HabitatProportion.y}))}{\textit{HabitatProportion.y} \times \textit{AreaofInference}} \end{aligned}$$

The density of birds in the matrix (*MatrixDensity.y*) is given by

$$\begin{aligned} & \text{MatrixDensity.y} \\ &= \frac{Ns - Ns(\text{HabitatProportion.y} + \text{SpecialistIndex}(1 - \text{HabitatProportion.y}))}{(1 - \text{HabitatProportion.y}) \times \text{AreaofInference}} \end{aligned}$$

It is useful to remember that  $\text{HabitatDensity.y} \geq \text{MatrixDensity.y}$  and the proportion of matrix in the area of inference,  $\text{MatrixProportion.y}$ , is equal to  $1 - \text{HabitatProportion.y}$ .

Proportion of habitat within the surrounding area of each site  $i$  ( $\text{PercentHabitat.yi}$ ) was modeled as a beta-distributed random variable, parameterized by a user-determined mean proportion of habitat in the area of inference ( $\text{HabitatProportion.y}$ ) and concentration parameter ( $\text{HabitatProportionTheta.y}$ ).

For site  $i$ , the total number of birds simulated for a survey will be generated as the sum of two Poisson-distributed random variables,  $\text{BirdsInHabitat.yi}$  (the number of birds found in habitat) and  $\text{BirdsInMatrix.yi}$  (the number of birds found in matrix). Surveys were spatially modeled in a 4000 m x 4000 m Cartesian grid centered on the observer, making the overall modeled survey area  $1.6 \times 10^7 \text{ m}^2$  for each site  $i$ .  $\text{BirdsInHabitat.yi}$  was described by the parameter  $\lambda = \text{HabitatDensity.y} \times 1.6 \times 10^7 \text{ m}^2 \times \text{HabitatProportion.y}$ .  $\text{BirdsInMatrix.yi}$  was described by the parameter  $\lambda = \text{MatrixDensity.y} \times 1.6 \times 10^7 \text{ m}^2 \times \text{MatrixProportion.y}$ .

### Spatial Modeling

Bird locations were modeled using a bivariate normal distribution, resulting in elliptical territories. For each survey area  $i$ , if  $N\text{Birds.yi} > 0$ , spatial parameters were generated for each bird  $j$  ( $\text{Spatial.yij}$ ): the center of the territory ( $\text{CenterX.yij}$ ,  $\text{CenterY.yij}$ ), the area of a 95% elliptical density contour ( $\text{Area.yij}$ ), the eccentricity of the ellipse ( $\text{Ecc.yij}$ ), and an angle of rotation ( $\text{Theta.yij}$ ).  $\text{CenterX.yij}$  and  $\text{CenterY.yij}$  were each drawn from a uniform distribution, (minimum = -2000, maximum = 2000).  $\text{Area.yij}$  was drawn from a lognormal distribution with parameters  $\mu$  (mean of  $\ln(\text{Area.yij})$ ) and  $\sigma^2$  (variance of  $\ln(\text{Area.yij})$ ). Empirical evidence was used to inform the size of the territories whenever possible. If estimates of territory size (expected value of area,  $E(X)$ , and variance,  $\text{Var}(X)$ ) were available for the species modeled,  $\mu$  and  $\sigma^2$  were calculated using

$$\begin{aligned} \mu &= \ln(E(X)) - \frac{1}{2} \ln(1 + \text{Var}(X) / (E(X))^2), \text{ and} \\ \sigma^2 &= \ln(1 + \text{Var}(X) / (E(X))^2). \end{aligned}$$

Each bird  $j$  had an interval-specific location  $\text{Location.yijrk}$  and distance from the observer  $\text{ObsDistance.yijrk}$ , calculated from the (x,y) coordinates in  $\text{Location.yijrk}$ . For each replication  $r$ , an initial location ( $\text{Location.yijr0}$ , with coordinating  $\text{ObsDistance.yijr0}$ ) was generated from

the bivariate normal distribution described in *Spatial.yij*. Some scenarios included a flush reaction by the bird to the arrival of the observer. In these scenarios, a Bernoulli-distributed random variable *DoesBirdMoveObs.yijr1* was generated via a probability of flushing (*PrBirdMovesObs.yijr1*), which is dependent on *ObsDistance.yijrk*. For  $k=1$ , if *DoesBirdMoveObs.yijr1* = 0, *Location.yijrk* = *Location.yijr0*. If *DoesBirdMoveObs.yijr1* = 1, new locations (*Location.yijrk*, with coordinating *ObsDistance.yijrk*) were generated from the bivariate normal distribution described in *Spatial.yij* for  $k=1$  until a location was obtained such that  $ObsDistance.yijr0 < ObsDistance.yijrk$ .

For each interval  $k>1$ , a Bernoulli-distributed random variable *DoesBirdMoveObs.yijrk* was generated via the mean probability that the bird moved (*PrBirdMoves.yijrk*), parameterized with movement information for the species. If *DoesBirdMoveObs.yijrk* = 1, a new *Location.yijrk* was generated from the bivariate normal distribution described in *Spatial.yij*. If *DoesBirdMoveObs.yijrk* = 0, *Location.yijrk* = *Location.yijr(k-1)*

In special cases, under a scenario where birds were not strictly territorial throughout all surveys within a year, spatial parameters were generated at the replication level (resulting in a list of spatial parameters, *Spatial.yijr*).

### *Availability*

Bird availability was modeled for each interval  $k$ , where availability *Sings.yijrk* = 1 indicated bird  $j$  sang during the interval and *Sings.yijrk* = 0 indicated no song. To produce temporal song patterns reflective of breeding males, I incorporated autocorrelation at 2 scales. Coarse-scale autocorrelation referred to bird  $j$  being in or out of “singing mode”, a state where vocalization is frequent and songs occur at regular intervals. If the bird was not in singing mode (i.e., if *SingingMode.yijrk* = 0), then bird  $j$  necessarily did not vocalize during interval  $k$  and *Sings.yijrk* = 0. If the bird was in singing mode, (i.e., if *SingingMode.yijrk* = 1), then *Sings.yijrk* could be 0 or 1: these vocalizations were modeled with fine-scale autocorrelation.

I modeled coarse-scale autocorrelation with a Markov chain, where the state of bird  $j$  at interval  $k$  is related to its state at interval  $k-1$ . The 2 possible states for bird  $j$  during interval  $k$  were to be in singing mode (1) or not in singing mode (0). The transition matrix  $P_{coarse}$  described the probabilities of remaining in or out of singing mode or switching modes, given the previous state (Table 1).

Unlike fine-scale autocorrelation, where song recordings can readily provide information about song and pause length, empirical data describing singing mode is scarce. Indeed, if singing mode is indeed a biological phenomenon, it may be impossible to accurately measure in the field; birds who are in singing mode but not currently singing may be indistinguishable from birds not in singing mode. There is, however, ample species-specific data describing the

probability that a bird sings at least once in a several minute period (e.g., Emlen 1977). For brevity, I will refer to this type of song rate information as the “singing probability”. By making some assumptions about the transition matrix, a Markov chain process can be created that will produce a population of simulated birds with the desired singing probability.

To explain the mechanics of the coarse-scale autocorrelation, I will briefly assume that a bird with  $SingingMode.yijrk = 1$  will also have  $Sings.yijrk = 1$ . This assumption will be discarded when fine-scale autocorrelation is added. The probability that a bird  $j$  sings at least once in  $N_{intervals}$  intervals, or singing probability, is:

$$Z_{N_{intervals}} = q_1 + (1 - q_1) \times (1 - (1 - P(NS|NS))^{N_{intervals}}) ,$$

where  $q_1$  is the probability that bird  $j$  begins in singing mode (which is also the proportion of the population singing in any given interval, on average) and  $(1 - P(NS|NS))^{N_{intervals}}$  is the probability that the bird never switches into singing mode (given that it did not begin in singing mode). Each row of the transition matrix (Table 1) sums to 1, giving

$$P(S|S) + P(NS|S) = 1 ,$$

and

$$P(S|NS) + P(NS|NS) = 1 .$$

The steady state vector  $[q_1 \ q_2]$  can be determined from the transition matrix as  $[1 \ 0] [P_{coarse}] = [q_1 \ q_2]$ , or

$$[1 \ 0] \begin{vmatrix} P(S|S) & P(NS|S) \\ P(S|NS) & P(NS|NS) \end{vmatrix} = [q_1 \ q_2] .$$

Completing the matrix multiplication (above) produces

$$q_1(P(S|S) - 1) + q_2(P(S|NS)) = 0 ,$$

and

$$q_1(P(NS|S)) + q_2(P(NS|NS) - 1) = 0 .$$

Rearranging the above equations gives

$$q_1 = \frac{-P(S|NS)}{\quad}$$



$$\frac{P(S|S) - P(S|NS) - 1}{}$$

Therefore, the equation for  $Z_{Nintervals}$ , and  $P(S|NS) + P(NS|NS) = 1$  can be combined as

$$Z_{Nintervals} = \frac{-P(S|NS)}{P(S|S) - P(S|NS) - 1} + \left( 1 - \frac{-P(S|NS)}{P(S|S) - P(S|NS) - 1} \right) \times (1 - (1 - P(S|NS))^{Nintervals})$$

$Z_{Nintervals}$  can thus be determined by 3 parameters,  $P(S|S)$ ,  $P(S|NS)$ , and  $Nintervals$ .  $Nintervals$  is defined by the survey length, leaving 2 unknown parameters. I assumed that more variation in bird availability would be caused by variation in the probability of birds switching from non-singing mode into singing mode ( $P(S|NS)$ ) than by variation in the tendency for birds to stay in singing mode ( $P(S|S)$ ). I therefore decided to hold  $P(S|S)$  constant and vary  $P(S|NS)$  to achieve the desired  $Z_{Nintervals}$ . I investigated the relationship between  $P(S|S)$ ,  $P(S|NS)$ , and  $Z_{Nintervals}$  and decided that  $P(S|S) = 0.98$  allowed the best control over  $P(S|NS)$  for producing a desired value for  $Z_{Nintervals}$  (Figure 1).  $P(S|S) > 0.98$  produced too few transitions (birds in singing mode almost never transitioned out) and  $P(S|S) < 0.98$  produced birds that transitioned too quickly (birds were so likely to transition into singing mode that  $q_1$  had to be kept very low and variability in realized  $Z_{Nintervals}$  was high).

I therefore held constant  $P(S|S) = 0.98$  for all simulations. The  $P(S|NS)$  needed to produce a desired singing probability was determined using optimization using function `optimize()` in program R. Because values of  $P(S|NS)$  were very small, the optimization process was sensitive to starting values; all analyses used a starting interval of 0 - 0.05 for  $P(S|NS)$ .

For example, a species with an interval length of 2 seconds and a desired singing probability (probability that a bird sings at least once in 10 minutes)  $Z_{Nintervals} = 0.6$  could be produced by using  $P(S|S) = 0.98$  and  $P(S|NS) = 0.0037$ , creating the transition matrix

$$P_{coarse} = \begin{vmatrix} P(S|S) = 0.98 & P(NS|S) = 0.02 \\ P(S|NS) = 0.0037 & P(NS|NS) = 0.9963 \end{vmatrix} .$$

The resulting proportion of birds singing in any given interval was  $q_1 = 0.14$ .

Fine-scale autocorrelation was modeled with a Markov chain to produce a pattern of songs and pauses similar to those occurring in audio recordings for the species. I assumed that a recorded bird was in singing mode for the duration of the recording. For each species modeled, I listened to recordings of that species from the Macaulay Library at Cornell University and timed the songs and pauses to obtain mean song length and mean pause length. Interval length was adjusted so that the length of an interval roughly equaled the length of a song. At a fine scale, songs were negatively autocorrelated: songs rarely occurred back-to-back and instead included pauses in between.

Fine-scale autocorrelation was modeled only for intervals with  $SingingMode.yijrk = 1$  (for all intervals with  $SingingMode.yijrk = 0$ ,  $Sings.yijrk = 0$ ). To model this autocorrelation, I used a Markov chain with 2 states: singing (1) or not singing (0). The ratio of mean song length: mean pause length was used to create the steady state vector  $[q_1 \ q_2]$ , where  $q_1$  represents the average proportion of birds singing at any given time and  $q_2$  is the average proportion of birds not singing. The ratio was scaled so that  $q_1 + q_2 = 1$ , or  $[q_1 \ q_2] = [\text{mean song length}/(\text{mean song length} + \text{mean pause length}) \ \text{mean pause length}/(\text{mean song length} + \text{mean pause length})]$ . For example, if a species had a mean song length of 2 seconds and a mean pause length of 6 seconds, it could be modeled with an interval length of 2 seconds, a 1 : 3 ratio of song length : pause length, and steady state vector of  $[0.25 \ 0.75]$ .

A transition matrix  $P_{fine}$  for the fine-scale Markov chain was selected to produce the desired steady state matrix. The matrix  $P_{fine}$  described the probabilities of state 0 or 1 at interval  $k$  (i.e.,  $Sings.yijrk = 0$  or  $Sings.yijrk = 1$ ), given the state at the previous interval,  $k-1$  (Table 2).

Parameters for the fine-scale transition matrix  $P_{fine}$  were as follows. I defined  $P(S|S)$  as 0.001 to make back-to-back songs unlikely.  $P(NS|S)$  was therefore 0.999, because  $P(S|S) + P(NS|S) = 1$  (above). The remaining transition probabilities were calculated such that  $P_{fine}$  produced the steady state vector  $[q_1 \ q_2]$ , where  $[1 \ 0] [P_{fine}] = [q_1 \ q_2]$ . Using the example above, a species with a steady state vector of  $[0.25 \ 0.75]$  would have fine-scale transition matrix

$$P_{fine} = \begin{vmatrix} P(S|S) = 0.001 & P(NS|S) = 0.999 \\ P(S|NS) = 0.333 & P(NS|NS) = 0.667 \end{vmatrix} .$$

The next step was to combine the coarse-scale autocorrelation with the fine-scale. If I simply used the transition matrices above, the realized singing probability in simulations ( $\hat{Z}_{Nintervals}$ ) would be slightly lower on average than the desired singing probability ( $Z_{Nintervals}$ ). This discrepancy is caused by simulations where birds are in singing mode at some point in the survey but do not actually sing. To compensate for this, I ran simulations to determine the discrepancy ( $Z_d$ ), where

$$Z_d = Z_{Nintervals} - \hat{Z}_{Nintervals} .$$

I then added this percent discrepancy to the desired singing probability to get an adjusted desired singing probability:

$$Z_{NintervalsAdj} = Z_{Nintervals} + Z_d .$$

*SingingMode.yijrk* was then modeled by calculating  $P_{coarse}$  that would produce  $Z_{NintervalsAdj}$ , as in

$$Z_{NintervalsAdj} = \frac{-P(S|NS)}{P(S|S) - P(S|NS) - 1} + \left( 1 - \frac{-P(S|NS)}{P(S|S) - P(S|NS) - 1} \right) \times (1 - (1 - P(S|NS))^{Nintervals})$$

*Sings.yijrk* was modeled using  $P_{fine}$  (unchanged). Simulations were run to ensure that the realized singing probability of simulations was within 1% of the desired singing probability after incorporating  $Z_{NintervalsAdj}$ .

#### *Availability Parameterization*

Whereas autocorrelation was incorporated via the structure of the model (as outlined previously) other factors affecting availability were incorporated as effects on the parameter singing probability, *SingingProbability.yijrk*. For every interval  $k$ , *SingingProbability.yijrk* was modeled as a function of phenology and time of day. Phenology-specific singing probability information is available for some species (e.g., Emlen 1977; Figure 2) and can be approximated for others based on general species information. For migratory species, arrival and departure dates (*Arrival.yij* and *Departure.yij*) were selected for each bird  $j$  from normal distributions. Mean Julian date for arrival and departure was selected based on Birds of North America data (e.g., Evans et al. 2011) for each species and standard deviation was 7 days. Although migration is surely a spatial issue (i.e., it mainly concerns  $p_s$ ), it was more convenient to address this issue through availability ( $p_a$ ) because singing probability was modeled as a function of phenology. For bird  $j$ , *SingingProbability.yijrk* was constrained to zero before *Arrival.yij* and after *Departure.yij*. Time of day information is available from Rosenberg and Blancher (2005), who provide relative song rate information based on BBS surveys (Figure 3). These two factors were combined to produce an average singing probability for any given interval, *AverageSingingProbability.yijrk* (Figure 4).

Other covariates such as effects of weather or day, habitat type or quality, and distance to and abundance of conspecifics were used as weights on the average singing probability, so that  $SingingProbability.yijrk = AverageSingingProbability.yijrk \times \Pi$  weights. The weight for weather and day effects (*weather.yijr*) was replication-specific, the weight for habitat type and

quality (*habitat.yi*) was site-specific, and the weight for conspecifics effects (*conspecifics.yjrk*) was interval-specific. Distributions for these effects were scenario-specific. If an effect was not of interest for the scenario, its weight was set to equal 1.

### *Perceptibility*

Bird perceptibility was modeled as a Bernoulli-distributed event with probability *perceptibility.yjrk<sub>o</sub>* that detection *DetectedYN.yjrk<sub>o</sub>* = 1 (indicating bird *j* was detected by observer *o* during interval *k*, replication *r*, and year *y*). If *DetectedYN.yjrk<sub>o</sub>* = 0, no detection was indicated.

Modeling of bird perceptibility(*perceptibility.yjrk<sub>o</sub>*) was based on a logit link. Specifically,

$$\text{Logit}(\textit{perceptibility.yjrk}_o) = \log\left(\frac{\textit{perceptibility.yjrk}_o}{1-\textit{perceptibility.yjrk}_o}\right) = \beta_0 + \beta_p X_p,$$

for *p* covariates *X*. Coefficient values for covariates investigated by Pacifici et al. (2008) were thus useful to parameterize the model. Covariates for perceptibility included distance to the observer, ambient noise, observer skill, and habitat features such as forest type and presence of leaves on deciduous trees.

To incorporate the possibility of species misidentification or double-counting, an additional step models the observer's interpretation of a detected bird song. For *DetectedYN.yjrk<sub>o</sub>* = 1, *CorrectID.yjko* was a Bernoulli-distributed random with probability *PrCorrectID.yjrk<sub>o</sub>*. Similarly, if *CorrectID.yjko* = 1, *DoubleCount.yjrk<sub>o</sub>* was a Bernoulli-distributed random with probability *PrDoubleCount.yjrk<sub>o</sub>*.

For each loop of the simulation, *Count.yjrk<sub>o</sub>* = 0, 1, or 2. *Count.yjrk<sub>o</sub>* = 0 could result from any lack of detection, from a model bird that did not sing (*SingYN.yjrk* = 0) to a bird that sang and was detected, but was incorrectly identified (*SingYN.yjrk* = 1, *DetectedYN.yjrk<sub>o</sub>* = 1, *CorrectID.yjrk<sub>o</sub>* = 0). If *Count.yjrk<sub>o</sub>* = 1, then necessarily *SingYN.yjrk* = 1, *DetectedYN.yjrk<sub>o</sub>* = 1, *CorrectID.yjrk<sub>o</sub>* = 1, etc.

## Scenario 1: Black-Throated Blue Warblers

The first experiment I designed using the previously-described model was to investigate detection of black-throated blue warblers (BTBW, *Setophaga caerulescens*). The species was ideal for a preliminary analysis in several ways. First, nesting densities have been shown to be correlated with density of shrubs (Steele 1992, Steele 1993, Holmes et al. 2005), which aligned nicely with the model's assignment of abundance to sites based on an underlying habitat covariate. BTBW are relatively well-studied, with ample spatial information available (Holmes 2005), so parameters were based in reality. BTBW exhibit stable or increasing population trends across its range (Holmes et al. 1996, Sauer et al. 2014), making it a non-controversial choice for an example species. Finally, recordings of BTBW songs were used by Pacifici et al. (2008), Alldredge et al. (2007b), and Simons et al. (2007) in their estimations of perceptibility, allowing a more accurate parameterization of the perceptibility process than would be possible for most species.

For each analysis method (distance sampling, removal, multiple observer, and replicated counts) we ran the simulation 10 times with the same parameters ( $N_{Years} = 10$ ). To estimate song length, I listened to the first minute of 4 BTBW recordings from the Macaulay Library (1992, 1994, 2000, 2010) and timed songs and pauses to the nearest second. Mean song length was 2.11 seconds, mean pause length was 6.64 seconds. I therefore used  $IntervalLength = 2$ ,  $SongLength = 2.1/IntervalLength$ , and  $PauseLength = 6.6/IntervalLength$ . We modified  $NSurveySites$ ,  $NReps$ , and  $SurveyLength$  to use approximately the same amount of human effort in each survey type (Table 3). Results of this analysis are pending.

## Field Study

### Study Area

In 2011, field work was carried out on Waterfowl Production Areas (WPAs) in the Morris Wetland Management District near Morris, Minnesota. Land cover in this region is highly fragmented, with agriculture (primarily corn and soybeans) dominant. Historically, this region was part of the tallgrass prairie ecosystem that stretched from Canada to Texas, though modern prairie in Minnesota has declined an estimated 99.6% from historical area (Samson and Knopf 1994). WPAs are protected for the dual purpose of waterfowl production and public recreation opportunities, including hunting (Morris Wetland Management District 2011). WPAs usually include a wetland for adult waterfowl and brood habitat and upland habitat for nesting (Morris Wetland Management District 2011). This study focused on upland prairie, though wetlands were included incidentally. In 2012, field work was performed on land owned by the Belwin Conservancy near Afton, MN, Carver Park Reserve near Victoria, MN and Murphy-Hanrehan Park Reserve near Burnsville, MN. These sites were managed as grasslands to provide habitat for wildlife and for recreation.

### Methods

#### *Field Work*

Survey sites in the Morris Wetland Management District were selected within a 30-km radius of Morris, Minnesota in Pope, Grant, Stevens, and Swift counties, with supplemental sites up to 70 km from Morris to provide a wider diversity of habitat conditions. Survey sites in 2012 were selected within a 30-mile radius of the St. Paul campus of the University of Minnesota. Sites were chosen using aerial photography (U.S. Department of Agriculture 2010). Eligible sites were 150-m radius circles contained within accessible land that did not intersect with roads or other manmade structures and included at least 50% prairie habitat. Site perimeters were within 200 m of a road to ensure access, but were located at least 500 m from highways to reduce noise interference. Roads adjacent to sites were seldom traveled, with passing traffic rates under 10 automobiles per hour. Actively grazed sites were eliminated, as were sites with elevation changes > 10 m, and sites with tree cover > 20%. Survey sites in 2011 were selected to have a wide range of habitat conditions, from lightly vegetated, recently grazed sites to heavily vegetated shrubby sites. Surveys were performed under a variety of wind conditions, with winds recorded from 0-9 m/s.

The sampling array at each site was set up as follows: 6 sampling “legs” radiated from the central point, spaced 60° apart (Figure 5). The first leg of each site was oriented directly into the wind, or due north when there was no detectable wind. Surveys took place at “sampling points” located along each leg at 30, 60, 90, 120, and 150 m from the central point (as measured with a GPS). In 2011, surveys were conducted at all survey sites and all 6 legs (30 sampling points per site). In 2012, surveys were conducted at all surveys sites on only 4 legs (legs at

either 60° and 120° or 240° and 300° were eliminated as redundant, 20 sampling points per site). Sampling points were eliminated if obstacles (ditches, deep water, heavy forest) prohibited observer access, but such eliminations were rare. When suitable prairie habitat was adjacent to non-suitable habitat (forested or wetland habitat), surveys were performed on suitable legs and omitted on non-suitable legs. Survey sites were eliminated if < 50% of legs could be surveyed.

In 2011, recorded bird songs were broadcast from the central point of survey sites with an Apple ipod mp3 music player connected to Poly-Planar MA4055 marine speakers via a Poly-Planar ME-60 amplifier. Speakers were positioned at the beginning of each survey leg to broadcast toward the observer. In 2012, the speakers were replaced with a TIC GS 5P OmniSpeaker, which broadcasts 360° to allow simultaneous listening by observers in multiple orientations. All speakers were mounted such that they stood at 1-m height during surveys (roughly representative of perch height in grasslands).

Song recordings from the Macaulay Library at Cornell University were used for 10 species that inhabit grasslands in Minnesota: horned lark (*Eremophila alpestris*, HOLA, ML Audio 41134), bobolink (*Dolichonyx oryzivorus*, BOBO, ML Audio 42237), eastern meadowlark (*Sturnella magna*, EAME, ML Audio 94367), vesper sparrow (*Pooecetes gramineus*, VESP, ML Audio 42228), savannah sparrow (*Passerculus sandwichensis*, SAVS, ML Audio 42219), grasshopper sparrow (*Ammodramus savannarum*, GRSP, ML Audio 50283), Henslow's sparrow (*Ammodramus henslowii*, HESP, ML Audio 73945), Le Conte's sparrow (*Ammodramus leconteii*, LCSP, ML Audio 42207), dickcissel (*Spiza Americana*, DICK, ML Audio 50234), and sedge wren (*Cistothorus platensis*, SEWR, ML Audio 50277). Songs recordings in .WAV format were trimmed to 6-second files using Program Audacity (open source, <http://audacity.sourceforge.net>). To ensure that all songs were played at the same volume regardless of species, song volume was adjusted using the function Amplify in Program Audacity. Selected songs produced a maximum volume of 90 dB ( $\pm 1.5$  dB) (Brackenbury 1979, Simons et al. 2007) when measured 1 m from the speaker system using a Martel Electronics model 325 mini sound level meter (Derry, NH, <http://www.martelcorp.com>). Within years, once consistent volume was achieved, the same 10 songs were used for all surveys. Song volume was checked at each survey site to make sure that songs were played at 90 dB at 1 m, with the sound level meter positioned upwind of the speakers.

Each sampling event consisted of a 1-minute listening period during which a playlist of 10 6-second audio files was played through the speaker system. Each audio file contained either a bird song or silence, with 1-10 songs played in each sampling event. Number of songs was randomly selected from a uniform distribution and species of songs was assigned randomly, with replacement, from a list of 10 species. Songs and pauses were ordered randomly, but playlists with consecutive songs of the same species were eliminated to avoid confusion. Playlists were constructed in Program R (R Development Core Team, Vienna, Austria, <http://www.R-project.org>) and played with Program iTunes (Apple Inc., Cupertino, CA, <http://www.apple.com/itunes>).

One observer (Elizabeth Rigby) performed surveys in 2011; four observers performed surveys simultaneously in 2012. Two of the observers were experienced with identifying grassland bird songs in the field (primary observer and experienced observer) and 2 were not, although they had identified songs of other birds in the field (inexperienced observers). Surveys began with all observers at the site's center point. The primary observer then triggered playback of playlists for the first leg and observers walked from the central point to their first sampling points, 30 m away along a survey leg. The primary observer always began by surveying the leg directly upwind. Other observers (if present) simultaneously performed surveys along legs in different directions. Each observer performed one survey at each sampling point along each survey leg once and only once per site.

Playlists were set to play automatically throughout a leg, with walking time (94 seconds in 2011, 60 seconds in 2012) allowed before each 1-minute listening period. Loud beeps sounded at 9 seconds before the listening period and immediately before the listening period. The observers wrote down all recorded bird songs heard during the listening periods, recorded if the audible warnings were heard, and recorded if extraneous noise interfered with their observation ability. The primary observer also measured average wind speed over a 10-second period using a Kestrel 2000 anemometer (Birmingham, MI). No audible warning was given at the end of the listening period, requiring the observers to time the 1-minute interval. When listening periods at all 5 sampling points of the first leg were complete the observers returned to the central point to begin subsequent survey legs.

Habitat characteristics were measured using 2-m-high profile boards divided into 6, 0.33-m sections by alternating black and white paint (Nudds 1977). A board was staked into the ground 1 m to the left or right of each sampling point and 1 m from the central point. Care was taken not to trample vegetation in front of each board. Horizontal cover for each profile board section was estimated by the primary observer to the nearest 5% from 30 m and was intended as an index of vegetation that might affect sound attenuation between the speakers and the observer. The horizontal cover measurements for the 30-m sampling point, for example, were taken with the observer standing at 30 m from the central point and estimating percent visibility of the profile board stationed at the central point. When conditions were too windy for profile boards to be used, song detections were recorded as usual and habitat conditions were recorded on a calmer day, no more than 1 week later.

### *Analysis*

To allow for an iterative model selection process, we divided the data into 3 groups. Initial analyses were performed using 25 randomly chosen sites from 2011 (Group 1), with 10 sites from 2011 withheld for validation purposes (Group 2). Data from 2012 constituted Group 3.



Group 1 data were analyzed with logistic regression with mixed models, using correct detection of a broadcast song as the binary response variable. Survey site was included as a random effect and species were analyzed separately. All input variables were rescaled via mean centering and dividing by 2 standard deviations (Gelman 2007). Fixed effects included wind speed in m/s ( $S$ ), wind speed squared ( $S^2$ ), a wind index ( $W$ , where  $W = \cos(180^\circ - \text{wind direction}) \times S$ , which ranged from  $S$  to  $-S$ ), distance from the sound source to the observer in meters ( $D$ ), distance from the sound source to the observer squared ( $D^2$ ), habitat index ( $H$ ), and observer-indicated binary variables for manmade noise ( $M$ ), bird noise from real birds ( $B$ ), and other noise ( $N$ ). We created 197 logistic regression models with 0 to 6 covariates each. The set of models was created by including all combinations of covariates that fit the following rules:

- (1) A model could include  $S$ ,  $S^2$ , both, or neither.
- (2) A model could include  $D$  or  $D^2$ , or neither.
- (3) A model could include  $M$  or  $B$  or  $N$  or no noise covariate.
- (4) A model could include  $H$  or not.
- (5) A model could include  $W$  or not.
- (6) All models included the random effect of survey site.

Models were ranked by Akaike Information Criterion (AIC) values and variable importance weights (VIW) were calculated for each fixed effect, where  $VIW_i = \Sigma \text{AIC weights for models in which fixed effect } i \text{ appeared}$  (Burnham and Anderson 2002). Mean  $VIW_i$  was calculated across species. Fixed effects with mean  $VIW_i < 0.5$  were designated “unimportant” and were not included in further model selection steps.

To analyze Group 2 data, we created 6 prediction models using fixed effects with  $VIW \geq 0.5$  ( $D$ ,  $W$ ,  $S$ ,  $S^2$ , and  $H$ ). The set of models included all combinations of covariates that fit the following rules:

- (1) All prediction models included  $D$  and  $W$ .
- (2) A model could include  $S$ ,  $S$  and  $S^2$ , or neither.
- (3) A model could include  $H$  or not.

These logistic regression prediction models were parameterized with fixed effects estimates from the previous analysis and used to predict detection separately for each species using Group 2 data. All input variables were rescaled via mean centering and dividing by 2 standard deviations (Gelman 2007). We assessed the ability of the models to predict detection by calculating the proportion of correct predictions by model and by species. We visually examined plots of

model-predicted probability of detection and actual detections as a function of distance and wind index to assess model fit.

Distance had a negative relationship with probability of detection for 7 of 10 species, but fit was often poor. Wind index was positively related to probability of detection, but fit was poor, suggesting a possible quadratic effect.

While distance and wind index clearly affected detection, we considered the model fit poor for many species and elected to test additional models of those covariates. Our goal was to create a model that could be used to visualize probability of detection up to 150 m from the sound source under various wind conditions.

To analyze Group 3 data and select a “best” model of wind and distance effects for this visualization, we created our final model set. In an attempt to better fit the effect of distance, we created 3 distance functions: linear ( $D$ ), quadratic ( $D + D^2$ ), and cubic ( $D + D^2 + D^3$ ). We also were able to investigate the effect of observer ( $O$ ), as 4 observers were used to collect Group 3 data. We created combinations of wind variables using both  $W$  and  $S$ . Due to the high VIW of  $W$  in Group 1 analysis,  $W$  was included in all models. The set of 30 models included all combinations of covariates that fit the following rules:

- (1) All models included a wind index covariate ( $W$ ), an observer covariate ( $O$ ), and the random effect of survey site.
- (2) All models included 1 of 3 distance functions:  $D$ ,  $D + D^2$ , or  $D + D^2 + D^3$ .
- (3) A model could include  $W^2$ ,  $W^2 + W^3$ ,  $W^2 + S$ ,  $S$ ,  $S + S^2$ , or none of these terms.
- (4) A model could include a distance and wind index interaction ( $D \times W$ ) or not.

Survey site was included as a random effect and species were analyzed separately. Models were ranked by Akaike Information Criterion (AIC) values. We used model-averaging to obtain predicted detections around a single sound source and plotted these predictions to visualize a “detection zone” under different wind conditions. To visualize detection around an observer, the “perceptibility zone”, model- averaged predictions for detection were produced for a 4 m by 4 m grid of hypothetical sound sources extending to 200 m from the observer.

## Results

Sites were surveyed from 9 September - 11 October 2011 and from 7 September – 21 October 2012. There were nearly 9000 binary opportunities for detection across the 2-year study (Table 4). Top models, based on AIC, varied across species for the Group 1 analysis. Distance and WindIndex were the covariates with the highest VIW (Table 5) and appeared in all models with  $\Delta AIC < 5$  for all species.

The six prediction models used in Group 2 analysis all performed well, with 68-90% correctly predicted detections (Table 6). EAME was the most predictable species, with 87-90% correctly predicted detection among the 6 models. HESP was the least predictable, with 68-73% correctly predicted detections. There was more variation among species than within models. We were not satisfied with model fit for linear distance and wind effects, so we included quadratic and cubic effects in the model set for Group 3 analysis.

In the Group 3 analysis, the primary observer and experienced observer had the highest detection rate. The odds of detection for the experienced observer was 81% of the primary observer. Inexperienced observers had a lower detection rate (odds of detection were 26% of the primary observer).

Detection zones (the area around the sound source where songs could be detected) were asymmetrical and differed with wind speed (Figure 6). Detection was more likely downwind of the sound source during light to medium winds. During high winds, detection was tightly constricted to a small area downwind of the sound source. Perceptibility zone results are pending.

## Literature Cited

- Allredge, M.W., K.H. Pollock, and T.R. Simons. 2006. Estimating detection probabilities from multiple-observer point counts. *Auk* 123: 1172-1182.
- Allredge, M.W., K.H. Pollock, T.R. Simons, J.A. Collazo, and S.A. Shriner. 2007a. Time-of-detection method for estimating abundance from point-count surveys. *Auk* 124: 653–664.
- Allredge, M.W., T.R. Simons, and K.H. Pollock. 2007b. Factors affecting aural detections of songbirds. *Ecological Applications* 17: 948-955.
- Brackenbury, J.H. 1979. Power capabilities of the avian sound-producing system. *Journal of Experimental Biology* 78:163-166.
- Buckland, S.T., K.P. Burnham, D.R. Anderson, and J.L. Laake. 1993. Distance sampling: estimation of abundance of biological populations. Chapman and Hall, London, United Kingdom.
- Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York, USA.
- Evans, M., E. Gow, R.R. Roth, M.S. Johnson and T.J. Underwood. 2011. Wood Thrush, *In The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu/bna/species/246>, accessed 26 February 2014.
- Farnsworth, G.L., K.H. Pollock, J.D. Nichols, T.R. Simons, J.E. Hines, and J.R. Sauer. 2002. A removal method for estimating detection probabilities from point-count surveys. *Auk* 119: 414–425.
- Holmes, R.T., P.P. Marra, and T.W. Sherry. 1996. Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology* 65:183-195.
- Holmes, R.T., N.L. Rodenhouse, and T.S. Sillett. 2005. Black-throated Blue Warbler, *In The Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu/bna/species/087>, accessed 7 October 2014.
- Macaulay Library. 1992. Black-throated Blue Warbler: *Setophaga caerulescens*. <http://macaulaylibrary.org/audio/73987>, accessed 7 October 2014.
- Macaulay Library. 1994. Black-throated Blue Warbler: *Setophaga caerulescens*. <http://macaulaylibrary.org/audio/76520>, accessed 7 October 2014.

- Macaulay Library. 2000. Black-throated Blue Warbler: *Setophaga caerulescens*.  
<http://macaulaylibrary.org/audio/107391>, accessed 7 October 2014.
- Macaulay Library. 2010. Black-throated Blue Warbler: *Setophaga caerulescens*.  
<http://macaulaylibrary.org/audio/140091>, accessed 7 October 2014.
- Morris Wetland Management District. 2011. Waterfowl Production Areas.  
<http://www.fws.gov/midwest/morris/wpa.html>, accessed 5 January 2012.
- Nichols, J.D., J.E. Hines, J.R. Sauer, F.W. Fallon, J.E. Fallon, and P.J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *Auk* 117: 393-408.
- Nichols, J.D., L. Thomas, and P.B. Conn. 2009. Inferences about landbird abundance from count data: recent advances and future directions. Pages 201–235 in D.L. Thomson, E.G. Cooch, and M.J. Conroy, editors. *Modeling demographic processes in marked populations*. Springer-Verlag, New York, New York, USA.
- Nudds, T.D. 1977. Quantifying the vegetative structure of wildlife cover. *Wildlife Society Bulletin* 5: 113-117.
- Pacifici, K., T.R. Simons, K.H. Pollock. 2008. Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. *Auk* 125:600-607.
- Peterjohn, B.G., and J.R. Sauer. 1999. Population status of North American grassland birds from the North American breeding bird survey, 1966-1996. *Studies in Avian Ecology* 19:27-44.
- Royle, A. J. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60: 108-115.
- Samson, F.B., and F.L. Knopf. 1994. Prairie conservation in North America. *Bioscience* 44: 418–421.
- Sauer, J.R., J.E. Hines, J.E. Fallon, K.L. Pardieck, D.J. Ziolkowski, Jr., and W.A. Link. 2014. *The North American Breeding Bird Survey, Results and Analysis 1966 - 2012*. Version 02.19.2014. USGS Patuxent Wildlife Research Center, Laurel, MD, USA.  
<http://www.mbr-pwrc.usgs.gov/bbs/>, accessed 7 October 2014.
- Simons, T.R., M.W. Alldredge, K.H. Pollock, J.M. Wettröth. 2007. Experimental analysis of the auditory detection process on avian point counts. *Auk* 124: 986-999.
- Steele, B.B. 1992. Habitat selection by breeding black-throated blue warblers at two spatial scales. *Ornis Scandinavica* 23:33-42.

Steele, B.B. 1993. Selection of foraging and nesting sites by black-throated blue warblers: their relative influence on habitat choice. *Condor* 95:568-579.

U.S. Department of Agriculture. 2010. National Agricultural Imagery Program Mosaic, Geospatial Data Gateway. <http://datagateway.nrcs.usda.gov>, accessed 23 August 2011.

Table 1: Transition matrix definitions for a Markov chain modeling autocorrelation for coarse-scale bird availability.

		<b>State at interval <math>k</math></b>	
		Bird $j$ is in singing mode in interval $k$ .	Bird $j$ is not in singing mode in interval $k$ .
<b>State at interval <math>k-1</math></b>	Bird $j$ was in singing mode in interval $k-1$ .	$P(S S)$ Probability that bird $j$ is in singing mode in interval $k$ , given that it was in singing mode in interval $k-1$ .	$P(NS S)$ Probability that bird $j$ is not in singing mode in interval $k$ , given that it was in singing mode in interval $k-1$ .
	Bird $j$ was not in singing mode in interval $k-1$ .	$P(S NS)$ Probability that bird $j$ is in singing mode in interval $k$ , given that it was not in singing mode in interval $k-1$ .	$P(NS NS)$ Probability that bird $j$ is not in singing mode in interval $k$ , given that it was not in singing mode in interval $k-1$ .

Table 2: Transition matrix definitions for a Markov chain modeling autocorrelation for fine-scale bird availability.

		<b>State at interval <math>k</math></b>	
		Bird $j$ sings in interval $k$ .	Bird $j$ does not sing in interval $k$ .
<b>State at interval <math>k-1</math></b>	Bird $j$ sang in interval $k-1$ .	$P(S S)$ Probability that bird $j$ sings in interval $k$ , given that it sang in interval $k-1$ .	$P(NS S)$ Probability that bird $j$ does not sing in interval $k$ , given that it sang in interval $k-1$ .
	Bird $j$ did not sing in interval $k-1$ .	$P(S NS)$ Probability that bird $j$ sings in interval $k$ , given that it did not sing in interval $k-1$ .	$P(NS NS)$ Probability that bird $j$ does not sing in interval $k$ , given that it did not sing in interval $k-1$ .



Table 3: Parameter values for BTBW surveys under the first simulated scenario. Logistical concerns (man hours, travel to/from sites) were considered and we attempted to keep overall effort constant across analysis method.

Analysis Method	NSurveySites	NReps	SurveyLength (minutes)	NSimultaneousObservers
Distance Sampling	30	1	3	1
Multiple Observer	15	1	3	2
Replicated Counts	10	3	3	1
Removal / Time of Detection	20	1	10	1

Table 4: Occasions for detection of recorded bird songs in grasslands near Morris, MN (2011) and near the Minneapolis - St. Paul, MN metro area (2012).

Year	Sites	Observers	Legs	Sampling Points	Detection Occasions
2011	35	1	192	942	4445
2012	12	4	48	240	4481

Table 5: Variable importance weights (VIW) for covariates used in 197 models of detection of recorded bird songs in Minnesota grasslands, using Group 1 data. VIW were calculated as the sum of the Akaike information criterion (AIC) weights for the models in which the covariate appeared. Species were analyzed separately; reported VIW were averaged across species.

Covariate	Mean	Range
Distance	0.97	(0.91 - 0.99)
WindIndex	0.78	(0.55 - 0.96)
WindSpeed	0.61	(0.53 - 0.71)
(WindSpeed) <sup>2</sup>	0.52	(0.47 - 0.60)
HabitatIndex	0.50	(0.48 - 0.55)
Noise	0.26	(0.23 - 0.33)
BirdNoise	0.26	(0.22 - 0.29)
ManmadeNoise	0.24	(0.23 - 0.25)
(Distance) <sup>2</sup>	0.02	(0.003 - 0.04)

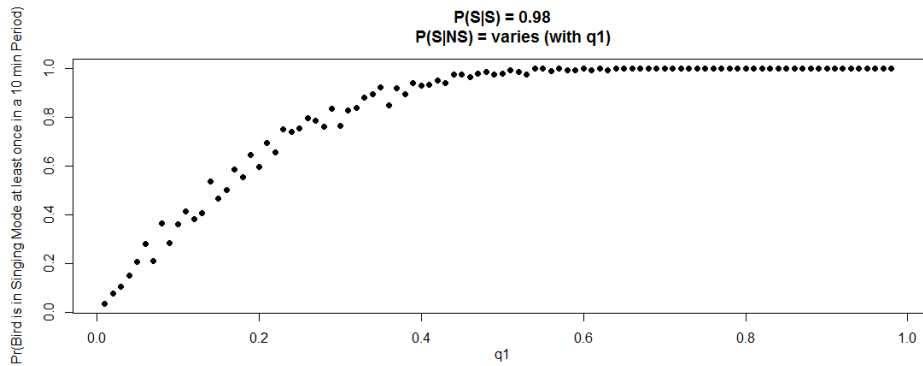
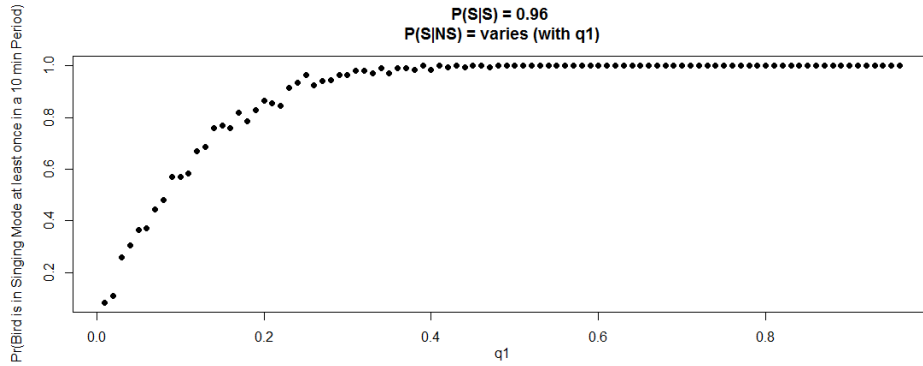
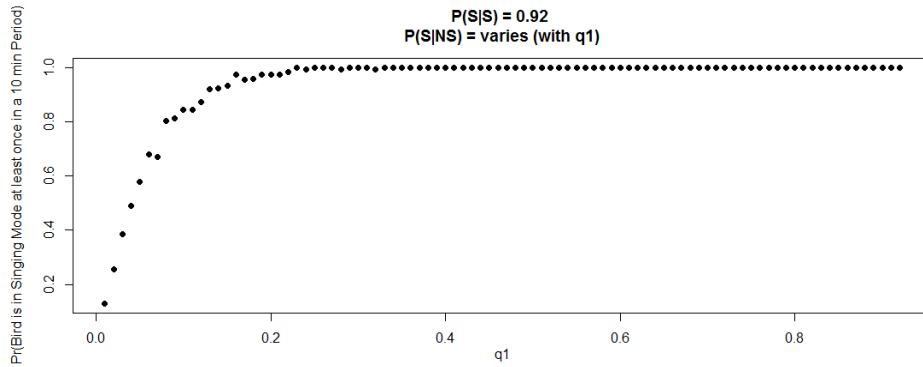
Table 6: Detection was predicted for Group 2 data using 6 logistic regression models, parameterized with fixed effects estimates from Group 1 data. The proportion of correct predictions are summarized by species and model.

Species	% Correct Predictions	
	Mean	SD
EAME	0.897	0.013
VESP	0.858	0.009
LCSP	0.850	0.014
HOLA	0.846	0.009
DICK	0.832	0.012
GRSP	0.792	0.013
BOBO	0.772	0.008
SEWR	0.766	0.011
SAVS	0.757	0.018
HESP	0.747	0.008

Model	% Correct Predictions	
	Mean	SD
Detection ~ D + W + H + S + S <sup>2</sup>	0.820	0.054
Detection ~ D + W + S + S <sup>2</sup>	0.818	0.049
Detection ~ D + W + S + H	0.817	0.053
Detection ~ D + W	0.808	0.051
Detection ~ D + W + H	0.806	0.053
Detection ~ D + W + S	0.803	0.052

1) Figure 1: Singing Probability ( $Z_{Nintervals}$ , the probability that a bird sings at least once in several minutes) is a function of  $P(S|S)$  (the probability that a bird sings, given that it sang in the previous interval) and  $P(S|NS)$  (the probability that a bird sings, given that it did not sing in the previous interval).  $P(S|S)$  is constant within each plot.  $P(S|NS)$  and  $q_1$  (the average proportion of total birds singing at any given interval) are interchangeable on the x-axis;  $q_1$  is shown to provide an intuitive sense of how many birds must sing at once to produce the desired  $Z_{Nintervals}$ , given  $P(S|S)$ . For  $P(S|S)=0.92$ , birds transition frequently to non-singing from singing, resulting in singing probability  $\sim 1$  if more than 10% of birds sing in any given interval. For  $P(S|S)=0.99$ , few birds transition between modes. As  $P(S|S)$  approaches 1, singing probability approaches  $q_1$  and transitions between states approaches 0.  $P(S|S)=0.98$  was chosen for all simulations.



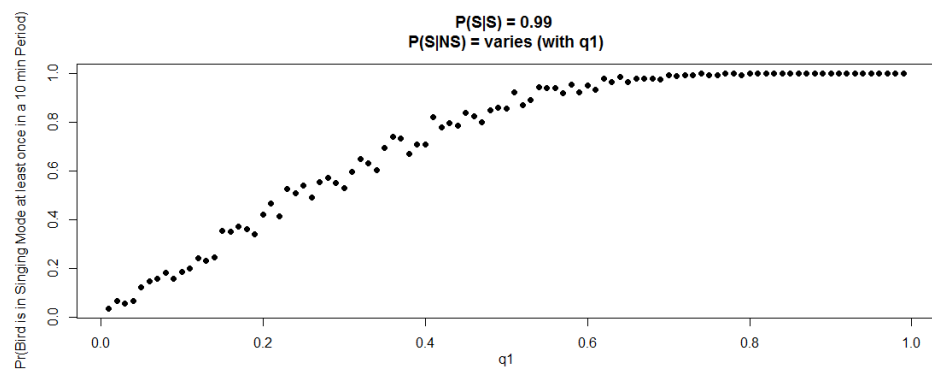


Figure 2: Phenological information for singing probability was available for many species. Here, singing probability was reported for Wood Thrush (*Hylocichla mustelina*) in Wisconsin (Emlen 1977). Time of arrival to and departure from the breeding grounds (Evans et al. 2011) are marked with vertical dashed lines and singing probability is constrained to zero outside those lines.

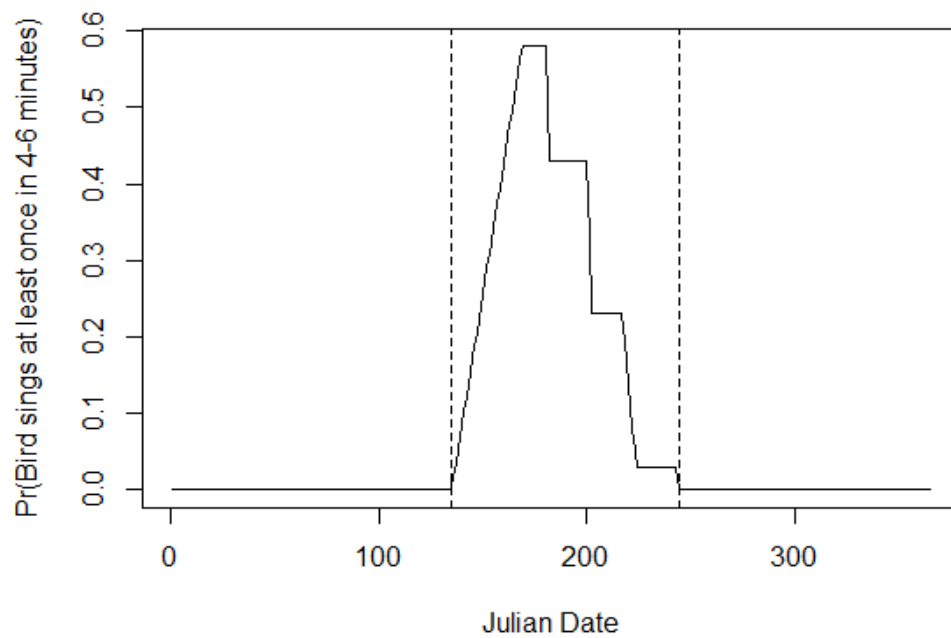


Figure 3: Time of day detection information was available from Rosenberg and Blancher (2005). Here, information for Wood Thrush is given, where 2.30 is the time of day adjustment (maximum detection / average detection) used in that study. Because this information reflects relative singing rate, it can be incorporated directly with phenological singing probability information.

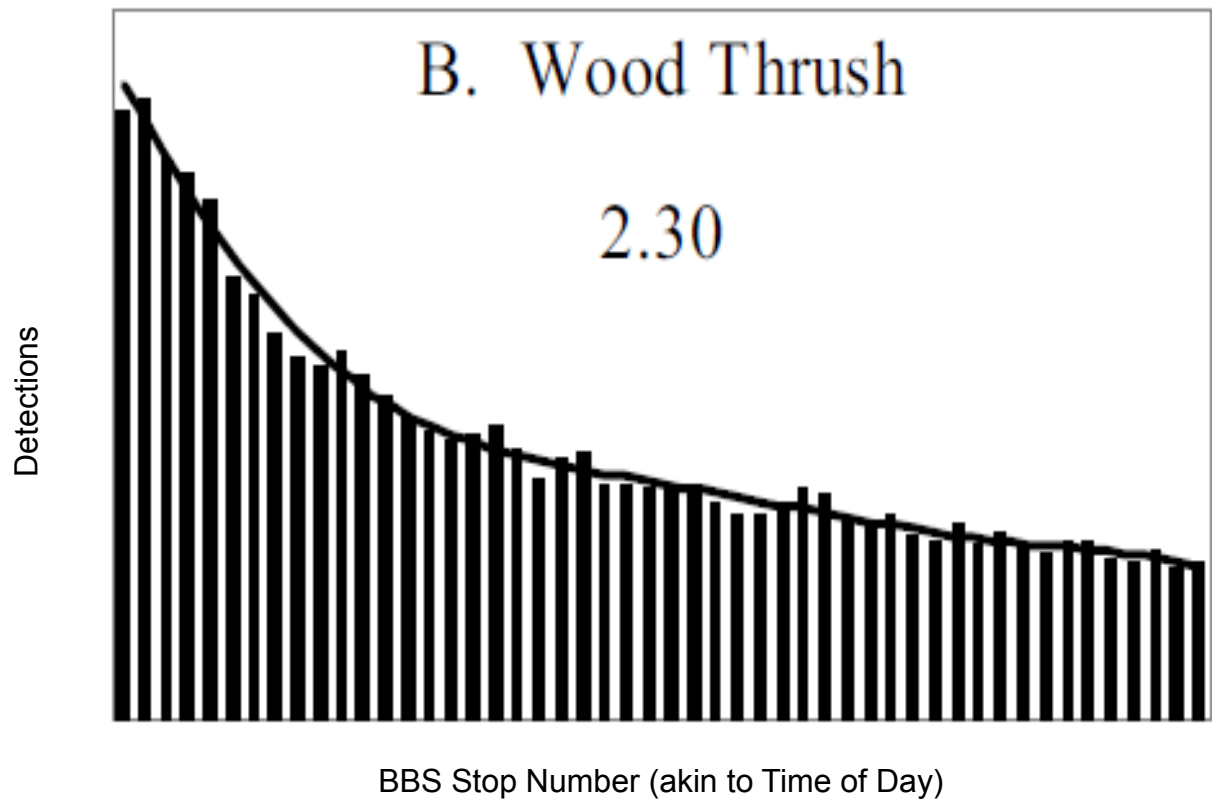




Figure 4: Singing probability was modeled as a function of phenological and time-of-day information to create an average singing probability throughout the year. The four plots below show different angles of the same 3-dimensional function. Average singing probability was parameterized for the Wood Thrush as a function of phenology (Figure 2) and relative time-of-day information (Figure 3).

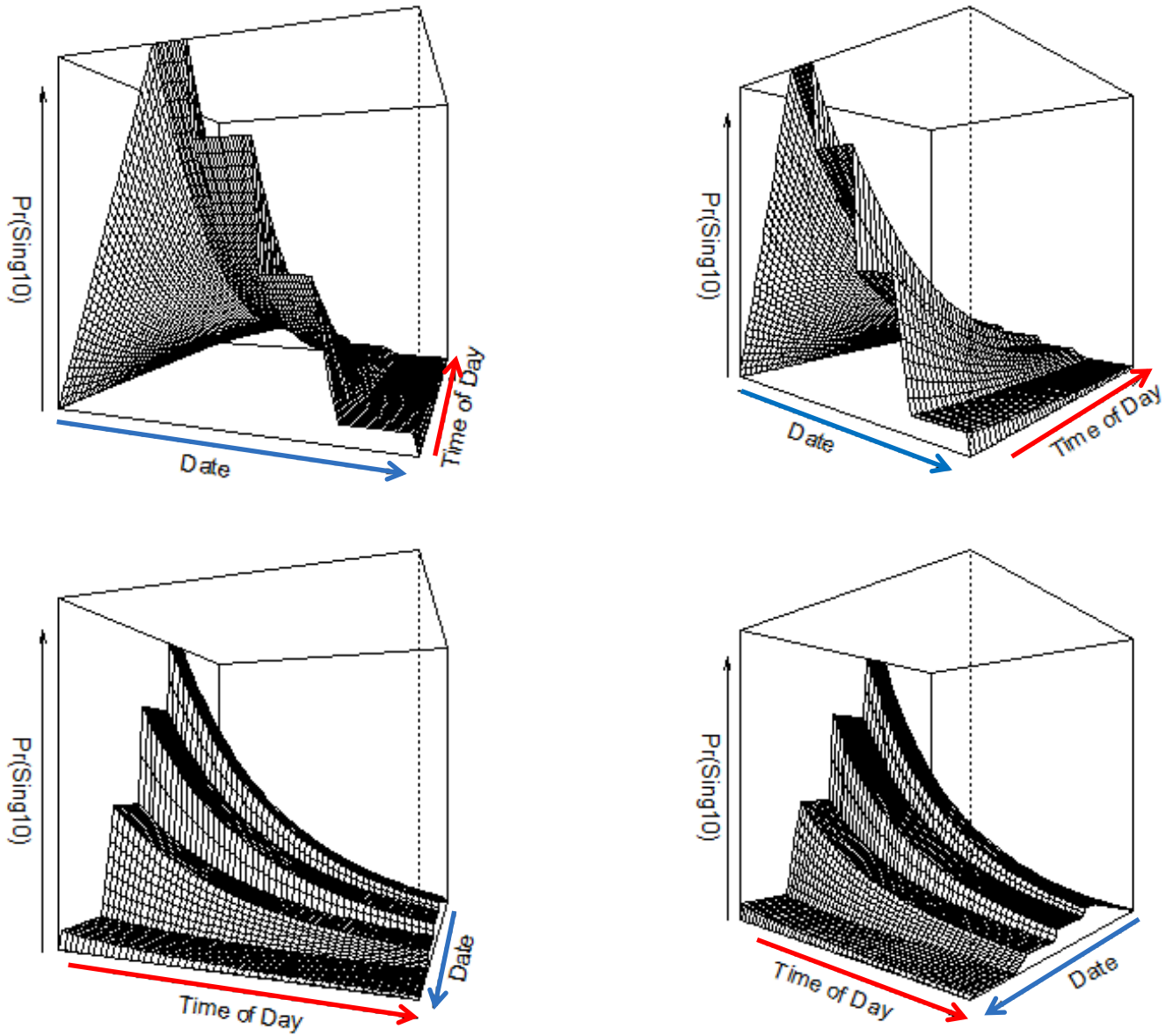


Figure 5:

Survey site layout. The central point of the survey site (filled dot) is surrounded by 6 survey legs in a radial arrangement. Sampling points lie along the legs, spaced 30 m apart. Speakers broadcast bird songs from the central point and the detection observations are made at each sampling point. Orientation of the sub-survey legs was determined by wind direction (first survey will extend directly into the wind).

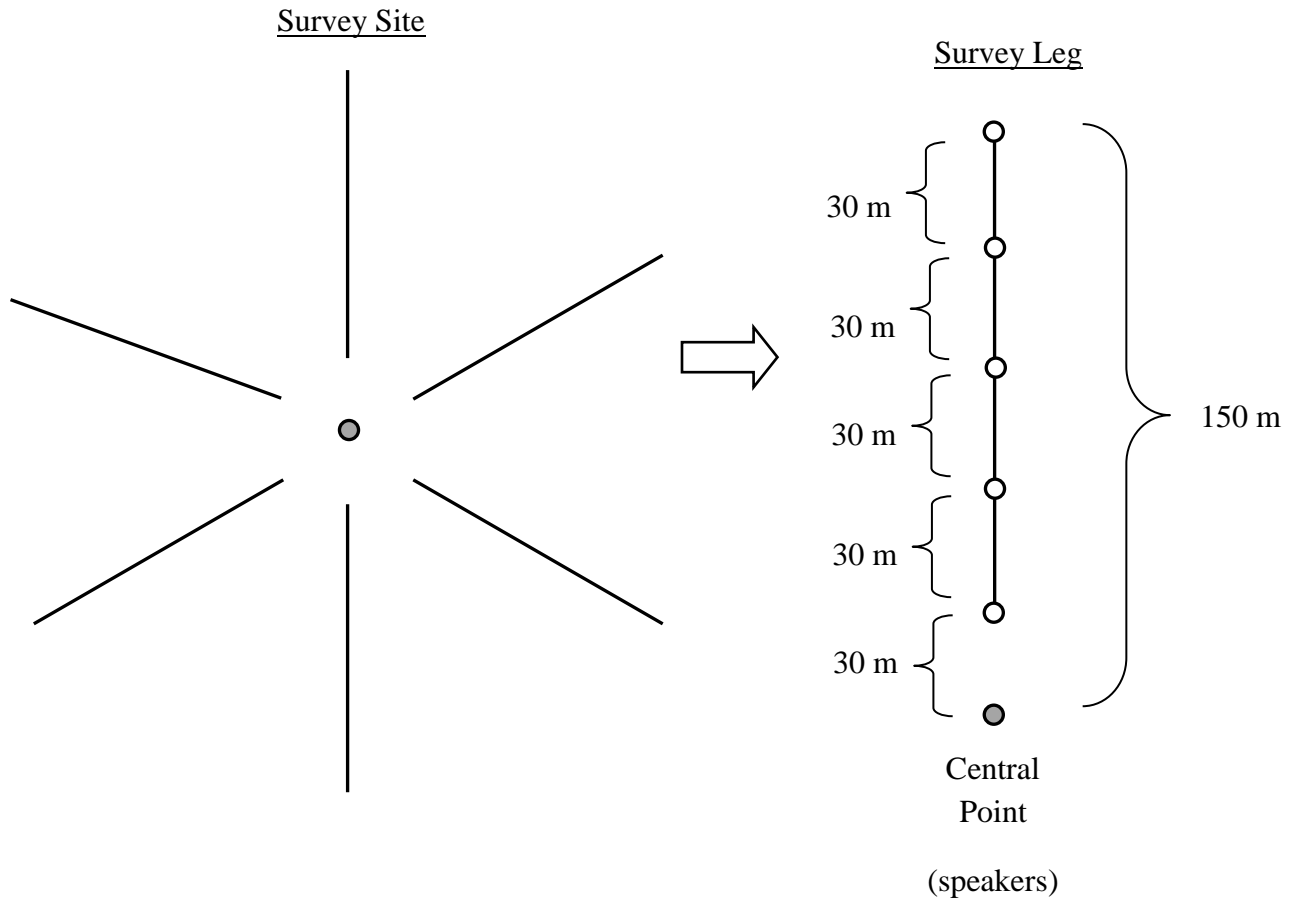


Figure 6: Predicted detection zones (the area around the sound source where recorded songs could be detected) were asymmetrical and differed with wind speed in grasslands. Here, detection zones are predicted for dickcissel (DICK). Protocol for the Breeding Bird Survey recommends surveying when wind speed is at or below a 3 on the Beaufort scale, though surveys performed under Beaufort 4 conditions are permissible in grassland locations.

