

Abstract

STANISLAV, STEPHEN JOSEPH. Developments and Applications of a Closed Capture-Recapture Robust Design Model to Avian Point Count Data. (Under the direction of Kenneth H. Pollock.)

Here we review various methods of estimating detection probabilities for avian point counts; distance sampling, multiple observer methods, and recently proposed time-of-detection methods. We provide a general model of detection where the total probability of detection is made up of the probability of a bird singing (availability) and the probability of detecting a bird, conditional on its having sung. This approach is shown to be a special case of Pollock's robust capture-recapture design where the probability that a bird does not sing is equivalent to the probability that an animal is a temporary emigrant. We show that the time-of-detection method provides an estimate combining both probabilities and by combining the time-of-detection method with a multiple observer method it is possible to estimate the two components of the detection process separately. These results are presented in Chapter 1.

Chapter 2 presents the detailed model evaluation with model extensions and simulation studies. We report on the combined multiple-observer and time-of-detection method for estimation of the components of aural detection probabilities and population size through simulation. We focus on the dependent multiple-observer versus independent multiple-observer aspect of our combined method and evaluate which is the more effective in practice. We also evaluate the combined multiple-observer and time-of-detection method where the model assumptions may be violated.

Finally, Chapter 3 presents the development of several modeling approaches allowing for competing detection cues in estimation of population size and components of the competing cues, aural and visual, and then study these models through simulation. We also investigate advantages and disadvantages of the competing cue modeling versus the more conventional pooled cue modeling with evaluation through simulation. After the detailed explanations of our research methods and our simulated and real data results, we focus on the implications and importance of our work to field ornithologists designing point count studies and suggest possibilities for future research.

Developments and Applications of a Closed Capture-Recapture Robust Design Model
to Avian Point Count Data

by
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Dedication

To my family, friends and loving wife Teresa.

Without your support and encouragement, this never would have been possible.

Biography

Stephen Stanislav was born on March 30, 1982 to Bernadette and Stephen Stanislav in Youngstown, Ohio. In 2000, Stephen graduated from Cardinal Mooney High School in Youngstown and began his undergraduate work at Youngstown State University as an applied mathematics major. In May 2004, Stephen completed his Bachelor of Science degree in applied mathematics with minors in statistics and business. Stephen chose to pursue a graduate degree in statistics at North Carolina State University. There he received his Master of Statistics degree in 2006 and his doctoral degree in 2009 under the direction of Dr. Kenneth Pollock. As a graduate student, Stephen had the opportunity to serve as teaching assistant for undergraduate courses, work as a Mendenhall Teaching fellow and serve as the consulting research assistant to the College of Agriculture and Life Sciences. Stephen has also received the North Carolina State University Outstanding Teaching Assistant award in 2006 and the Francis G. Giesbrecht Statistical Consulting Enhancement Award in 2009. Now that he has completed his degree, Stephen is moving to Atlanta to work as a Research Scientist at Georgia Tech Research Institute.

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ment in times of need and their advice has gotten me through many tough situations.

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CHAPTER 1

Introduction to a Combined Multiple-Observer and Time-of-Detection Approach

1.1 Introduction

Point counts are very widely used to study the abundance and density of many bird populations (Ralph and Scott 1981, Ralph et al. 1995). The data are very easy to collect at larger spatial scales compared to mark and recapture methods that are frequently costly, and therefore, limited to studies on smaller spatial scales. Typically point counts have been viewed as indices of abundance and standardized protocols are emphasized to reduce variation in detection probability (Ralph et al. 1995). The weaknesses of this approach and the importance of estimating the detection probability have been noted for some time. Two recent overview papers by Thompson (2002) and Rosenstock et al. (2002) stress how important the estimation of the detection probability is to sound inference based on point counts.

We begin by developing a conceptual model for estimating detection probabilities when birds are detected by ear. We emphasize that detection probability for auditory cues includes the combined probability of a bird singing (availability) and the proba-

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bility of detecting a bird, conditional on its having sung. Further, a birds conditional probability of detection may decline with distance from an observer. We show how current methods fit into this conceptual framework, and briefly discuss their strengths and weaknesses. We then show how a combination of methods may lead to much stronger inferences.

In fixed radius point transects where all the birds are detected

$$D = N/a = n/k\pi w^2$$

where D denotes density, N denotes the number of birds in the sampled area, and n is the number of birds detected. Note that w is the radius of the circle around the point, and the area surveyed is therefore $a = k\pi w^2$ if k points are surveyed. Of course this is unrealistic in practice, because it is usually impossible to detect all birds within the sampled area. When some animals are undetected the result generalizes to:

$$\hat{D} = n/a\hat{p} = n/k\pi w^2\hat{p}$$

where p is the probability of detecting an animal in the circle.

The avian sampling literature now contains multiple approaches to estimating detection probability. Different methods make different assumptions about the detection process. One common approach is distance sampling (Ramsey and Scott 1979; Reynolds et al. 1980; Buckland et al. 2001). This method assumes that: detection is certain at the center of the point; that detection is a decreasing function of distance; and that nothing else influences detection. Alternatively double-observer approaches

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require that two observers detect birds simultaneously in the same sample area. Estimation then uses either a modified Lincoln-Petersen capture-recapture model based on the birds detected by both, or one of the two independent observers (Allredge 2004, Allredge et al. 2006) or by an extension of the 2-sample removal model (Zip-pin 1958, Williams et al. 2002) using the number of birds detected by two dependent observers (Cook and Jacobson 1979, Nichols et al. 2000). A third category of methods is based on the temporal sequence of detections during a count (Farnsworth et al. 2002, Allredge 2004, Allredge et al. 2007a) where individual birds detection histories are modeled using a closed capture-recapture or removal modeling approach (Williams et al. 2002). Repeated count methods (Royle and Dorazio 2008) are also useful for estimating detection probabilities.

In addition to developing new methods of estimating detection probability, our research group has carried out field tests using simulated populations of birds to validate several common methods of estimating detection probability based on auditory cues. The system uses a laptop computer to control up to 50 amplified MP3 players placed at known locations up to 200 *m* around a survey point (see Simons et al. 2007 for details). To date we have conducted over 4,000 simulated point counts with a large number of observers. The system can realistically simulate a known population of songbirds under a range of factors that affect the detection probabilities. The first experiments examined factors that influenced the detection probability (Allredge et al. 2007b) and measurement errors in detection distance (Allredge et al. 2007c). This experimental system is unique because it allows us to evaluate the performance of various sampling methods with populations of known size. We shall return to these

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experiments in Section 1.5 when we use experimental data to evaluate the combined time-of-detection/double-observer method discussed in this paper.

We develop a conceptual model for the detection process that includes both availability and detection given availability. Then we review three common sampling methods and show how they contribute to components of the detection model. The core of our paper where we present a combined time-of-detection and multiple observer methodology is developed and then illustrated with examples. We conclude with a general discussion and make suggestions for future research.

1.2 Modeling Overall Detection Probability

There are two conceptually distinct sources of bias in count-based population density (and abundance) estimates. These sources of bias are not new and they have been discussed, for example, by Marsh and Sinclair (1989) in an aerial survey context and more generally by Pollock et al. (2004). They are:

Availability bias

A bird is within the vicinity of an observer at a point but not available for detection (specifically, the probability of detection was 0) for some reason. For example, if a point is in a dense forest and all detections are auditory, then birds that do not sing during the survey period, have no chance of detection.

Perception bias

A bird is in the vicinity of an observer at a point and available for detection, but the observer simply fails to detect it. For example, if a point is located in a dense forest

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and all detections are auditory, even if the bird sings an observer may fail to hear or recognize it.

1.2.1 Components of Detection Probability

The overall probability of detection for an individual bird is comprised of an availability process (the probability a bird is available for detection), and a detection process (the probability a bird is detected, given that it is available for detection).

$$p = p_a p_d$$

where p , is the overall probability of detecting a bird that is present in the sampled area during the sampling period, p_a is the probability that such a bird is available for detection, and p_d is the conditional detection probability given availability.

Modeling the availability process involves estimating the probability an animal is available for detection (p_a). Because this process is very difficult to measure in the field most methods assume that p_a is 1 (in other words we condition our inference on the birds that are available for detection). Later when we consider the time-of-detection method, we show that we can estimate p_a under certain circumstances. The probability that an animal is detected given that it is available (p_d) can be estimated using either double-observer or distance sampling approaches.

1.2.2 Estimates of Population Size and Density

It is also often desirable to estimate population size and density for fixed radius plots. Typically we use the standard estimator of population size (e.g., see Seber 1982, Williams et al. 2002):

$$\hat{N} = n/\hat{p}$$

where n is the number of birds detected, and p is the overall probability of detection. This is converted to density using:

$$\hat{D} = \hat{N}/a = \hat{N}/k\pi w^2 = n/k\pi w^2 \hat{p}$$

where a is the area of the circle of radius w , and k is the number of circles or points at which point counts are conducted.

We can model individual bird covariates (a covariate value is obtained for each bird detection) using the generalized Horvitz-Thompson estimator of population size (Huggins 1989, 1991, Alho 1990). The estimator is:

$$\hat{N} = \sum_{i=1}^n [1/\hat{p}_i]$$

where n is the total number of birds detected, and the overall detection probability of each bird i is p_i which depends on the covariates.

1.3 Review of Current Methods

1.3.1 Point Transect Distance Method

One common method of estimating detection probability and density is distance sampling (Buckland et al. 2001). This method assumes that detection probability is a decreasing function of distance, and that no other factors influence detection. The standard results from Buckland et al. (2001, p.55) can be summarized as:

$$\hat{D} = n/a\hat{p}_d = n/k\pi w^2\hat{p}_d$$

where

$$p_d = 2 \int_0^w \frac{rg(r)}{w^2} dr$$

This latter expression is the probability of detection in a circle of radius r . It depends on a detection function, $g(r)$, which is the probability of detecting an animal given that it is distance r from the observer. Expressions developed in Buckland et al. (2001) and the DISTANCE software allows fitting complex detection functions (half normal, uniform, or hazard rate) and various adjustments (cosine, simple polynomial, or hermite polynomial).

The assumptions of point transect sampling are:

1. $g(0) = 1$, (i.e., certain detection at the point);
2. objects are detected at their initial location prior to any movement in response to the observer which implies a closed population;

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3. distances are measured accurately (ungrouped data), or objects are counted in the proper distance category (grouped data); and
4. objects are detected independently.

Certain detection at the point ($g(0) = 1$), is an important assumption of distance sampling. Violations of this assumption are probably common on avian point counts because birds may avoid observers or they may be difficult to see or hear when they perch high in the canopy overhead. Assumption 2 (no movement) may be violated in bird surveys especially if a longer count interval is used. Assumption 3 (accurate distance measurement) is also problematic in avian surveys where birds are primarily detected by ear (Allredge et al. 2007c) because observers may have trouble localising where the bird is perched. Distance sampling does not estimate the probability of availability (p_a). Therefore applications of the method either assume that p_a is 1, or that the estimate is a measure of the number of birds available.

1.3.2 Multiple Observer Methods

Two Independent Observers

The Lincoln-Petersen method (Williams et al. 2002) can be applied to information from two independent observers to estimate detection probabilities on point counts. The notation is as follows:

- $p_{d_1}(p_{d_2})$ is the probability of detection (given available) by the first (or second) observer;

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- X_{11} is number detected by both observers; X_{10} is number detected by the first observer only; X_{01} number detected by the second observer only; and $n_1(n_2)$ is the number detected by the first (or second) observer.

The probability of detection by each observer is estimated by:

$$\hat{p}_{d_1} = X_{11}/n_2 \text{ and } \hat{p}_{d_2} = X_{11}/n_1$$

The probability of detection by at least one observer (p_d) is the overall detection probability. It is the complement of the probability that both observers miss a particular bird:

$$\hat{p}_d = 1 - (1 - \hat{p}_{d_1})(1 - \hat{p}_{d_2})$$

The assumptions are:

1. Observers match their detections (X_{11}, X_{10}, X_{01}) accurately;
2. there are equal detection probabilities of all individual birds of each species for each observer;
3. the population is closed and there is no undetected movement out of the sampled area;
4. observers accurately assign birds to within or beyond the radius used for the fixed radius circle; and
5. the counts of the two observers are completely independent.

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Generalizations using Program MARK (White and Burnham 1999) or DOBSERV (Nichols et al. 2000) give the researcher the option to fit generalized Lincoln-Petersen models. These models allow the detection probability to depend on covariates such as species, observer, wind speed, distance etc. MARK and DOBSERV use the Akaike Information Criterion (AIC) to pick the simplest model that adequately explains the information in the data (Burnham and Anderson 2002).

While it is unlikely to be routinely used in practice, it is theoretically possible to use more than two observers. This approach enables one to use the closed capture-recapture models that allow for heterogeneity of detection probability. However, assuring independence of more than two observers may be difficult because observers may cue each other to the location of some birds. This can be reduced by the protocol used in the field. In particular, we suggest that observers begin the count with their backs to each other and with instructions to ignore the other observers. Alldredge (2004) and Alldredge et al. (2006) study this method in detail and give examples for data based on four independent observers.

The double observer method only estimates the probability of detection given that the animal is available. The estimator for p_{d_1} has the approximate expected value:

$$E(\hat{p}_{d_1}) \approx E(X_{11})/E(n_2) = Np_a p_{d_1} p_{d_2} / Np_a p_{d_2} = p_{d_1}$$

The probability of being available (p_a) cancels out of the expression. This is intuitively obvious because the two observers only have access to the same set of available birds. Therefore, the double-observer method only estimates the number of birds that are available for detection during the sample period. True abundance requires assuming

that p_a is 1.

Two Dependent Observers

Nichols et al. (2000) suggested applying a dependent double-observer method originally applied in an aerial survey context by Cook and Jacobsen (1979). To quote Nichols et al. (2000): “At each point count, a designated ‘primary’ observer indicates to another (‘secondary’) observer all birds detected. The secondary observer records all detections of the primary observer as well as any birds not detected by the primary observer. Observers alternate primary and secondary roles during the course of the survey. The approach permits estimation of observer specific detection probabilities and bird abundance.

The dependent double-observer approach can be viewed as an extension of the removal method (Zippin 1958, Seber 1982, p.309). Alldredge et al. (2006) showed that the independent double-observer approach is more efficient than the dependent approach, because capture-recapture methods are generally more efficient than removal methods (Seber 1982, p.324). In contrast, the dependent double-observer approach may reduce bias when independent observers are not really independent. The method also only estimates the conditional probability of detection given the availability of the animal (p_d).

1.3.3 Time-of-Detection Approaches

Temporal Capture-Recapture Approach

Farnsworth et al. (2002) developed a method which applied the removal method (Zip-pin 1958, Seber 1982) to the time when birds were first detected. A more efficient approach using a k -sample closed capture-recapture model based on full detection histories (the time intervals where a particular bird was detected and the time intervals where that same bird was not detected) has been developed by Alldredge (2004) and Alldredge et al. (2007a). Capture-recapture models also accommodate heterogeneity in detection probabilities better than removal models.

To illustrate, consider two equal-length time intervals and assume that it is possible to track individual birds and accurately record detections as occurring in period one and/or period two. Using the same notation as that for multiple observers, we could denote X_{11} , X_{10} , and X_{01} as the number of birds detected in; both time intervals, in time interval one only, and in time interval two only. For more than two samples we would have a more general set of capture histories ω and a vector of counts for each history X_ω . The probability of detection for each time interval is estimated by the Lincoln-Petersen equations (Seber 1982) provided for the two independent observer method in the previous section.

In this case, by examining the expected value of the estimate of detection probability we see that the probability of detection is not conditional on availability and we are able to estimate the overall detection probability.

$$E(\hat{p}_1) \approx E(X_{11})/E(n_2) = \frac{Np_{a_1}p_{d_1}p_{a_2}p_{d_2}}{Np_{a_2}p_{d_2}} = p_{a_1}p_{d_1} = p_1.$$

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This is a unique feature of the time-of-detection method (recall that both the multiple observer and distance methods cannot account for non availability of birds).

The ability to incorporate availability in the estimation of p for time-of-detection models emerges directly from the separation of individual detections by time intervals. It accounts for the possibility that a bird is available in one time interval but not in another. Of course this model is based on very strong assumptions that observers are able to accurately localize and track the location of individual birds throughout the count interval. This can be difficult if birds move frequently or if large numbers of birds are counted simultaneously.

Model assumptions are as follows:

1. There is no change in the population of birds within the detection radius during the point count (i.e., the population is closed and birds do not move in or out without being detected);
2. There is no double counting of individuals (i.e. the observer keeps track of individual birds without error);
3. All individual birds of a species have a constant per minute probability of being detected in each interval; and
4. Observers accurately assign birds to within the fixed radius circle.

If the probability of detection changes after the first detection (analogous to trap response in a true capture-recapture setting) then assumption 3 can be weakened. “Trap response” models may be useful and in this application recapture probabilities

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are likely greater than first capture probabilities because an observer will be anticipating that a individual bird of a species may call again and thus be more likely to be detected if it does call. Riddle (personal communication) found that trap response models were often chosen when he used the time-of-detection method on quail.

If the probability of detection varies among individual birds, then heterogeneity models may be used. Much has been written about these models in the capture-recapture literature (Burnham and Overton 1978, Otis et al. 1978, Pollock et al. 1990, Williams et al. 2002). Link (2003) has noted problems with identifiability problems when these models are used. Modeling heterogeneity in detection probability using covariates can reduce problems associated with identifiability (Huggins 1989,1991, Alho 1990).

Animals with detection probabilities near 0 may be of special importance in time-of-detection applications. Alldredge (2004) and Brewster (2007) emphasize that avian singing rates may vary among individuals of the same species due to pairing status and other factors related to nesting phenology. Brewster (2007) estimated singing rates by following individual Ovenbirds (*Seiurus aurocapillus*) and Black-throated Blue Warblers (*Dendroica caerulescens*) for long periods. Some individuals had very low singing rates which made them almost impossible to detect.

There are different definitions of avian population size in this context:

1. The population of birds that sing at least once during the count.
2. The population of birds that have a probability of singing in an interval that is above 0; and

3. The total population of birds including those that do not sing frequently enough to detect.

The time-of-detection method estimates the total population defined in 2, however, there is difficulty in separating the population defined in 2 from that defined in 3 when there is heterogeneity in individual detection probabilities. We discuss this further at the end of the paper.

1.4 Combining Multiple Observers and Time-of-Detection Methods

Here we combine multiple-observer and time-of-detection methods into one design which allows separate estimation of the components of the detection process. Consider t time intervals and two independent observers where the birds are tracked throughout the count. We believe that in practice $t = 2 - 5$ time intervals are practical. This combined method is equivalent to a robust capture-recapture design (Pollock 1982, Williams et al. 2002) with t primary periods (the time intervals) and o secondary periods (the observers) within each primary period. In this case the population is assumed to be closed except for whether or not a bird is available (sings) in an interval. In the more general robust design, births and deaths and lack of availability (commonly referred to as temporary emigration) are also allowed. Modeling approaches already developed to account for temporary emigration (Kendall and Nichols 1995; Kendall et al. 1997) can be adapted for our application. The simplest model assumes that the temporal pattern of bird song follows a random process. An alternative approach

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assumes a Markovian process where the probability that a bird sings in an interval depends on whether it sang in the previous interval.

We focus on a general presentation of the simpler random temporary emigration or availability model. The robust design literature defines γ_i as the probability that an animal is a temporary emigrant in period i and this parameter does not depend on its value in previous periods. Thus $p_{a_i} = (1 - \gamma_i)$ $i = 1, \dots, k$. The conditional detection probabilities for each observer in each period (p_{d_1}, p_{d_2}) are also included in the model. Unlike the general robust design we are assuming that all animals survive during the point count so that $\varphi_i = 1$.

To illustrate, consider a detection history for two observers over two time periods. The history 11,01 denotes a bird detected by both observers in interval one and detected only by the second observer in interval two. This history has expected cell structure

$$p_{a_1}p_{d_{11}}p_{d_{21}}p_{a_2}(1 - p_{d_{12}})p_{d_{22}}.$$

Here the birds have to sing in each interval to be detected by at least one observer. However, another history 11,00 has the expected cell structure

$$p_{a_1}p_{d_{11}}p_{d_{21}}\{p_{a_2}(1 - p_{d_{12}})(1 - p_{d_{22}}) + (1 - p_{a_2})\}.$$

The 00 in the second interval means we have two components for the probability, the first where the bird sings but is missed by both observers and the second where the bird does not sing.

Based on the $k = 2^{t \circ}$ detection histories obtained in a study one can build a

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multinomial likelihood function and obtain parameter estimates and standard errors.

Where the observation of $(n_1, n_2, \dots, n_{k-1})$ gives the likelihood function

$$L(N; \theta) = \frac{N!}{n_1! \dots n_{k-1}!(N-n)!} p_1(\theta)^{n_1} \dots p_{k-1}(\theta)^{n_{k-1}} p_k(\theta)^{N-n} \quad (1.1)$$

where $n = \sum_{i=1}^{k-1} n_i$ denotes the number of observed detection histories, p_i represents the multinomial cell probabilities which are known functions of θ , the availability and detection probability parameters ($p_i(\theta) = f_i(\theta)$) and $p_k = 1 - \sum_{i=1}^{k-1} p_i$.

We use the conditional likelihood approach proposed by Sanathanan (1972) for estimation of the population size N , which writes the likelihood above as $L(N; \theta) = L_1(N; p_k(\theta))L_2(\theta)$ where

$$L_1(N; p_k(\theta)) = \frac{N!}{n!(N-n)!} (1 - p_k(\theta))^n p_k(\theta)^{N-n} \quad (1.2)$$

$$L_2(\theta) = \frac{n!}{n_1! \dots n_{k-1}!} q_1(\theta)^{n_1} \dots q_{k-1}(\theta)^{n_{k-1}} \quad (1.3)$$

with $q_i(\theta) = \frac{p_i(\theta)}{1-p_k(\theta)}$, with $i = 1, 2, \dots, k-1$.

We optimize the conditional likelihood function (1.3) to obtain estimates of the availability and detection probabilities then it follows from the work of Sanathanan (1972) that for any given \hat{p} that the estimate of the population size is $\hat{N} = \left\lfloor \frac{n}{1-\hat{p}_k} \right\rfloor$, the greatest integer $\leq \frac{n}{1-\hat{p}_k}$, which maximizes (1.2). The standard errors of the derived estimates can be obtained based on the second bootstrap method presented by Norris and Pollock (1996).

We computed maximum likelihood estimates directly through likelihood maximization. Standard errors are computed through bootstrap sampling (and could also be

used to construct confidence intervals). AIC can be used for model selection (Burnham and Anderson 2002, Williams et al. 2002). The estimated distance to each bird, detected by at least one observer, could be incorporated as an important covariate influencing the detection probability. Any number of observers and time intervals can be accommodated. This is the approach that we follow in the next section where we provide examples to illustrate the methodology.

1.5 Examples

To illustrate the potential of the combined method we use some data collected on one of our field experiments (Simons et al. 2007). Thirty five players were uniformly distributed with respect to an area surrounding a single point in a mixed pine-hardwood forest at Howell Woods Environmental Science Center in the Piedmont Region of North Carolina. The forest has a dense under story that limits visibility to 30 *m* or less in most directions. All players were placed on platforms 1 *m* above ground and were at radial distances between 0 and 120 *m*. Previous experiments demonstrated little effect due to height above ground (Alldredge et al. 2007b), therefore, we chose to eliminate this variable from our experiments although it could be important in other forested habitats. Songs for all species were played at a volume of approximately 90 *dB* at a distance of 1 *m*.

A total of 60, 8-minute point counts were simulated over two days in early March 2006. Points counts were broken into four, 2-minute intervals, and observers recorded birds using multi-colored pens to distinguish time intervals. Detection of a previously

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recorded bird in subsequent time intervals was recorded by circling the previous detection in the color designated for the interval. For this illustrative example, we present the results from just two observers. Here we know which ones the two observers saw in common whereas in standard point counts they would have had to use a matching rule.

Eight species of interest were simulated: Acadian Flycatcher (ACFL, *Empidonax virescens*), Black and White Warbler (BAWW, *Mniotiltavaria*), Black-throated Blue Warbler (BTBW), Black-throated Green Warbler (BTNW, *Dendroicavirens*), Hooded Warbler (HOWA, *Wilsoniacitрина*), Scarlet Tanager (SCTA, *Pirangaolivacea*), Ovenbird (OVEN), and Yellow-throated Warbler (YTWA, *Dendroicadominica*). Four other species were used to diversify the species list. None of the 12 species were found locally on the study area during our experiments. We focus first on the HOWA where a true population size of 100 birds within the 120 *m* radius circle was simulated over a total of 60 point counts. The singing rate was approximately 0.8 per minute or 0.96 per 2 minutes. All 100 birds sang at least once during the total 8-minute count interval. We also present results for OVEN based on singing rates measured empirically in the field (Brewster 2007). The empirical singing rate distribution for OVEN was extremely heterogeneous among individual birds, with a much lower mean singing probability than we simulated for the HOWA. We used those empirical singing rates to simulate a true population of 127 OVEN. Note that 27 birds with low singing rates never sang during the 8-minute count and thus only 100 birds were available to be counted by observers.

For HOWA, the AIC criteria selected a model with random temporary emigration constant over time intervals, and observer dependent detection probabilities (condi-

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tional on singing) that are also constant over time intervals (Table 1.1). The model with random temporary emigration, and constant detection probabilities (conditional on singing) that are also constant over time intervals was also competitive ($\Delta\text{AIC} = 4.86$). Parameter estimates for the best model (constant random temporary emigration, and observer dependent detection probabilities constant over time intervals) are presented for HOWA in Table 1.2. All of the estimates are very precise, presumably because this species has a loud, distinct, and easily localized call. Notice that the detection probabilities for each interval are very high, but they do vary between observer 1 (0.89) and observer 2 (0.95). The total population estimate for birds singing was 101.12, quite close to the simulated population size.

Table 1.1: *Model Selection for the Hooded Warbler using the AIC Criteria. The model set includes temporary emigration process being none or random. Conditional detection probability is interval varying (t), observer varying (o) and or constant (\cdot).*

Model	AICc	ΔAICc	AICc Weights	Parameters
$\gamma(\text{random}), p(\cdot, o)$	213.22	0	0.865	3
$\gamma(\text{random}), p(\cdot, \cdot)$	218.08	4.86	0.076	2
$\gamma(\text{random}), p(t, \cdot)$	218.67	5.45	0.057	5
$\gamma(\text{random}), p(t, o)$	225.12	11.9	0.002	9
$\gamma(\text{none}), p(\cdot, o)$	291.11	77.89	0	2
$\gamma(\text{none}), p(\cdot, \cdot)$	292.18	78.96	0	1
$\gamma(\text{none}), p(t, \cdot)$	296.18	82.96	0	4
$\gamma(\text{none}), p(t, o)$	304.15	90.93	0	8

Parameter estimates for the Ovenbird using the same model (constant random temporary emigration, and observer dependent detection probabilities constant over time intervals) are illustrated in Table 1.2. Notice that here the probability that an

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Ovenbird sings in a 2-minute interval is 0.74, much lower than for the HOWA. The conditional detection probabilities are very high for observer 1 (0.84) and observer 2 (0.91) but not as high as for the HOWA estimates presented in Table 2. The total available population is estimated to be 93.769, which is very close to the number of birds that actually sang (100). However, the estimate substantially underestimates the overall population of 127 birds.

Table 1.2: *A comparison of the Hooded Warbler and Ovenbird parameter estimates (standard errors) for a random singing model constant random temporary emigration model, with observer dependent detection probabilities constant over time intervals. The population of birds that sing at least once in 8 minutes is $N = 100$. Estimates and standard errors found with $B = 500$ bootstrap samples.*

Parameters	Parameter Estimates	
	Hooded Warbler	Ovenbird
N	101.12 (3.92)	93.769 (3.84)
p_a	0.9109 (0.0147)	0.7416 (0.0150)
p_{d_1}	0.8909 (0.0104)	0.8436 (0.0109)
p_{d_2}	0.9451 (0.0081)	0.9113 (0.0088)

We also considered an artificial dataset with lower availability and detection probabilities. The simulated dataset is designed to evaluate the relative performance of our method for populations that might not have such high values of model parameters. Our simulated dataset is generated from a random multinomial distribution with cell probabilities determined from the constant random temporary emigration model, with observer dependent detection probabilities constant over time intervals. Specifically $t = 4$ time intervals and two observers.

For this model we define the true population size (N) to be 100, the true probability

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that such a bird is available for detection, p_a , to be 0.45, the probability of detection by the first observer, p_{d_1} , is defined to be 0.5 and for the second observer (p_{d_2}) is 0.65.

Parameter estimates for this simulated data set of the same model are provided in Table 1.3. It is worthwhile to note, that even in this case with much lower availability and detection probability, our method performs quite well. The estimated probability that our simulated bird sings in a 2-minute interval is 0.42 lower than both the HOWA and OVEN. The conditional detection probabilities are much lower for observer 1 (0.45) and observer 2 (0.65) than in the cases of the HOWA and OVEN datasets, but are accurate estimates of the true probability values. The total available population is estimated at 102.27 birds. Once again our method provides yet another accurate estimate of the true population size of 100 birds, which is encouraging even given our simulated datasets low true values of the probability of availability and detection.

Table 1.3: *A comparison of the simulated dataset parameter estimates (standard errors) for a random singing model constant random temporary emigration model, with observer dependent detection probabilities constant over time intervals. The population of birds that sing at least once in 8 minutes is $N = 100$. Estimates and standard errors found with $B = 500$ bootstrap samples.*

Parameters	True Value	Parameter Estimates	Relative Bias (%)	RMSE
N	100	102.27(6.41)	2.2196	6.8001
p_a	0.45	0.4253 (0.0448)	-5.8077	0.0512
p_{d_1}	0.50	0.4952 (0.0424)	-0.9693	0.0427
p_{d_2}	0.65	0.6494 (0.0496)	-0.0924	0.0496

1.6 Discussion

Distance sampling and use of multiple observer methods are well known techniques of estimating detection probability that do not allow for birds not singing during the count. For situations when it is reasonable to assume that all birds sing they may be very profitably used and have been discussed at length in other papers and books. The time-of-detection method is one method that allows estimation of total detection probability and allows for birds to be unavailable when they do not sing. As there is a large literature that birds may not always have high singing rates (e.g. Brewster 2007 and references therein), we believe that the development of this method has been a significant advance in the field. Another method that allows for uncertain availability is the repeated counts method (Royle and Nichols 2003; Kery et al. 2005) and we believe that method also deserves future study, potentially in combination with other methods.

When using the time-of-detection method we recommend that the “capture-recapture” version which uses all times of detection be used. Counts would need to be long (10 minutes might be reasonable). We recommend the use of at least four time intervals and that they always be of equal length (say 5 intervals of 2 minutes each). The key assumption of the method is that the observer can keep track of individual birds without error. We believe that the method has great promise for species that have larger territories and that move little during a point count so that localization errors can be kept to a minimum. This will then mean that individuals can be tracked more accurately. For many point counts a large number of species may be detected and in those cases it may be necessary to just focus on a subset of the species that have lower

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localization errors. Our applications of the time-of-detection method have assumed that detection is by ear. In this case birds sing in discrete bouts and we have found it is possible to record in exactly which intervals birds sing and then are detected.

The combination of time-of-detection and multiple observer methods allows estimation of both components of the detection process. We have shown estimates for illustration for some simulated field data from our bird radio project. To our knowledge these are the first estimates of the components of detection probability for birds. We focused on the random temporary emigration model because they are simpler to interpret, more precise, and allow for easier computation of the total population of birds (including those not available in an interval). There could also be more study of Markovian models because we know that birds may sing in nonrandom bouts (Collins 2004) but the complexity of such models are likely to make them of limited usefulness in practice. We do not claim that the results in other studies will be as promising as those based on our data. The data from our bird radio study is unique in that we know exactly which birds were seen by each observer in each interval. In real point counts there could be additional matching errors between observers. One advantage, however, of our system is that we know truth and we are encouraged by the estimates we obtained especially for the HOWA. There is a need for more research on species that have very heterogeneous singing rates and this was exemplified by our Ovenbird estimates which were negatively biased.

Despite its additional expense and the potential for some counting and matching errors, we encourage field ornithologists to consider use of this combined time-of-detection method for at least a sub sample of their points to better understand the detection

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process in their field studies and potentially obtain better estimates of population abundance. Finally we note that it is possible to develop similar results for dependent observers combined with the time-of-detection method. We have explored that idea in collaboration with Jason Riddle of North Carolina State University. We have implemented the design for some point count surveys on bobwhite quail which we include in the Appendix.

CHAPTER 2

Statistical Methods of the Combined Multiple-Observer and Time-of-Detection Approach

2.1 Introduction

Bart (2005) estimated that there are over 1,000 independent organizations that gather long-term data on bird abundance in the United States and Canada alone. Many of their methods are based on simple point counts. Point counts are used for many purposes which include: measurement of spatial and temporal patterns in bird abundance, to evaluate change in abundance due to environmental change, to estimate species diversity and lastly, to assess species - habitat relationships. Point count studies are conducted annually in North America for a broad spectrum of research goals, from short-term site-specific studies to long-term continental-scale surveys, such as the North American Breeding Bird Survey (Sauer et al. 2005). Surveys of breeding birds rely heavily on auditory detections, which Simons et al. (2007) show are in the range of 70% of observations in suburban landscapes to 94% of observations in a closed-canopy forest.

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In fixed radius point transects, where all the birds are detected,

$$\hat{D} = N/a = n/k\pi w^2 \quad (2.1)$$

where D denotes density, N denotes the number of birds of a species in the sampled area, and n is the number of birds detected. Note that w is the radius of the circle around the point, and the area surveyed is therefore $a = k\pi w^2$ if k points are surveyed. Of course this is unrealistic in practice, because it is usually impossible to detect all birds within the sampled area. When some animals are undetected the result generalizes to:

$$\hat{D} = n/a\hat{p} = n/k\pi w^2 \hat{p} \quad (2.2)$$

where p is the probability of detecting an animal in the circle (Buckland et al. 2001). It is important to note that, while there may be multiple species present during a point-count, the analysis is carried out on a species-by-species basis.

Several approaches exist to estimate p , the probability of detection. Distance sampling (Buckland et al. 2001) requires that points be chosen randomly, detection is certain at the point, detection is a decreasing function with respect to distance, and that there is no movement before detection. Another approach, the multiple observer approach (see Alldredge et al. 2006 for details), requires that the observers detect the birds simultaneously at the same sample area and map their locations. Estimation is then based on a closed capture-recapture modeling approach for the detection histories. A key assumption is that there is no matching error. Also this method assumes that there are equal detection probabilities of all individual birds of each species for each

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observer, the population is closed and that there is no undetected movement out of the sampling area, observers assign birds accurately within or beyond the area, and the counts of the two observers are independent. Nichols et al. (2000) suggest a dependent double-observer variation on this method, based on early work of Cook and Jacobson (1979), which is likely to reduce the matching error problem. The time-of-detection approach requires that observers are able to accurately localize and track the location of individual birds throughout the count interval (Alldredge et al. 2007). Also other assumptions include that there is no double counting of individuals, all individual birds of a species have a constant per minute rate of being detected in an interval, and observers accurately assign birds to within or beyond the fixed radius circle. The focus of this paper is a new combined approach and its differences from the multiple-observer and time-of-detection methods.

The overall probability of detection of an individual animal is comprised of an availability process (the probability that an animal is available to be detected), and a detection process (the probability of an animal being detected, given that it is available for detection). Our work is focused on aural point counts so we represent this detection process by the following, $p = p_a p_d$, where p is the overall probability of detecting a bird that is present in the sampled circular area during the sample time period, p_a is the probability that such a bird is available for detection (i.e. - that it sang), and p_d is the conditional probability of detection given that a bird sang. Distance sampling and multiple observer methods assume that p_a is 1, that is, the inference is conditioned on only birds that have sung. The time-of-detection method allows for the estimation of the product $p = p_a p_d$. The combined multiple observer and time-of-detection method

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that is the focus of our research, allows the separate estimation of p_a and p_d . In Chapter 1 we presented the basic model with examples. Here we carry out a detailed model evaluation with model extensions and simulation studies.

Our set of models all have the same general framework using the multinomial distribution. Consider t time intervals (for example, each time interval may be two minutes in duration and if $t = 5$ there would be a total time of ten minutes for the point count) where the birds are tracked throughout the count. We assume o observers are used. Based on the information obtained from all of the $k = 2^{t \cdot o}$ detection histories where n_i , $i = 1, 2, \dots, k-1$ represents the number of birds that have the i^{th} detection history, we have the likelihood:

$$L(N; \theta) = \frac{N!}{n_1! \dots n_{k-1}!(N-n)!} p_1(\theta)^{n_1} \dots p_{k-1}(\theta)^{n_{k-1}} p_k(\theta)^{N-n} \quad (2.3)$$

where $n = \sum_{i=1}^{k-1} n_i$ denotes the total number of detected birds of a species, p_i represents the multinomial cell probabilities which are known functions of θ , the availability and detection probability parameters ($p_i(\theta) = f_i(\theta)$) and $p_k = 1 - \sum_{i=1}^{k-1} p_i$. For notation, we assume that the k^{th} detection history is the undetected history.

The basic model assumptions of the combined multiple-observer and time-of-detection approach are as follows:

1. Observers match their detections accurately;
2. there are equal detection probabilities of all individual birds of each species for each observer;
3. the population is closed and there is no undetected movement out of the sampled

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area; and

4. observers accurately assign birds to within or beyond the radius used for the sampling area.

These assumptions are not trivial because movement of individuals within the area during the count may cause violations of assumption 1. Movement in or out of the area that is not detected may cause violations of assumption 3, and difficulty in assigning distance of birds located aurally may cause violations of assumption 4. Furthermore, very little is known about the variability of singing rates in individual birds (assumption 2), but it seems apparent that it may be influenced by a wide array of factors (Gibbs and Wenny 1993).

Models that exist for capture-recapture settings that are built to allow for trap response and heterogeneity of capture probabilities could possibly be advantageously adapted to this setting. If the probability of detection changes after the first detection (analogous to trap response in a capture-recapture setting), then assumption 2 can be weakened. “Trap response models may be useful, and in this application, recapture probabilities are likely to be greater than first capture probabilities. An observer may anticipate that an individual bird may call again, and thus it would be more likely to be detected if it does call” (Alldredge et al. 2007a). If there is reason to believe that probability of detection varies among individual birds, then models which attempt to model such heterogeneity should strongly be considered.

Heterogeneity is likely because of variation in singing rates among individuals (Brewster 2007), which can be thought as heterogeneity on the probability of availability, as well as distance from the observer (Buckland et al. 2001), thought as hetero-

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geneity on the probability of detection, and many other factors. Much has been written about heterogeneity models in the capture-recapture literature (Burnham and Overton 1978, Otis et al. 1978, Pollock et al. 1990, Williams et al. 2002). Link (2003) has noted problems with identifiability when these models are used. Modeling heterogeneity in detection probability using covariates can reduce issues associated with identifiability (Huggins 1989, 1991, Alho 1990). One covariate of particular importance is distance from the observer to the bird.

Our models can be viewed as an extension to Pollock's robust design (Pollock 1982), as described in Chapter 1. The robust design model is a combination of the Jolly-Seber (JS) (Jolly 1965, Seber 1965) live open capture-recapture model and the closed capture models. The model is described in detail by Kendall et al. (1995, 1997). The key difference from the JS model is that instead of just 1 capture occasion between survival intervals, multiple (> 1) capture occasions are used. These occasions are close together in time, allowing the assumption that no mortality or temporary emigration occurs during these short time intervals. The closed encounter occasions are termed "trapping sessions", and each trapping sessions can be viewed as a closed capture survey. The power of this model is derived from the fact that the probability that an animal is captured at least once in a trapping sessions can be estimated from just the data collected during the session using capture-recapture models developed for closed populations, such as those summarized first by Otis et al. (1978).

Kendall et al. (1995, 1997) term the intervals between trapping sessions the primary sampling periods, and secondary sampling periods are the shorter intervals where the population is effectively closed to gains and losses. Our usage assumes t primary

periods (the time intervals) and two secondary periods (the observers) within each primary period and is a special case where an animal survival is guaranteed and there is no recruitment between primary periods, but there may be “temporary emigration” which in our situation would correspond to any animal being temporarily unavailable for detection.

The purpose of this paper is to report on the combined multiple-observer and time-of-detection method for estimation of the components of aural detection probabilities and population size through simulation. We will focus on the development of different models which contain different levels of complexity of the p_i 's. We will also focus on the dependent multiple-observer versus independent multiple-observer aspect of our method and evaluate through simulation which is the more effective in practice. We also evaluate the combined multiple-observer and time-of-detection method where the model assumptions may be violated. After a detailed explanation of our research methods and results, we focus on the implications and importance of our work to field ornithologists designing point-count studies and suggest possibilities for future research.

2.2 Summary of Model Types

For closed population models, there are four main factors that may affect detectability of animals. They are: a time/detection period effect (t); a response to detection effect (b); an observer effect (o); and a heterogeneity/differences between animals effect (h).

2.2.1 Independent Multiple Observers

Model structure is important for these model types, we consider effects due to observer, behavior, and time. It is important to note, model structure can effect both the probability of availability and the probability of detection, in our case we assume a constant probability of availability structure and vary on the probability of detection only. Below are models that are possible by combining these different effects:

Model M_0 : $p_{d_{ij}}$ is constant for all i . Capture probabilities are constant for all individuals and all capture periods.

Model M_o : The subscript o denotes observer effects in the model. $p_{d_{ij}}$ (or p_{a_j}) varies by observer, but not by time period.

Model M_t : The subscript t denotes time effects in the model. $p_{d_{ij}}$ (or p_{a_j}) varies by capture period, but not by individuals.

Model M_b : The subscript b denotes a behavioral effect in the population.

A “trap-effect” is assumed after the first detection, which changes the capture probability. An increase in the base detection probability is referred to as making an animal “trap-happy”. A decrease in the base detection probability is generally for situations when animals become “trap-shy” after first detection. Subsequent detections are assumed not to cause such an effect.

Model M_h : The subscript h denotes heterogeneity over individual animals in the population.

$p_{d_{ij}}$ (or p_{a_j}) varies by individual but not by capture period. This is often a realistic assumption, as some animals may be easier to capture than others (for example, the probability of capturing an animal may be different for animals of different ages).

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Other models are possible which combine the factors that may affect detectability. For example, in the M_{ot} model, $p_{d_{ij}}$ varies both by observer (by i) and by time period (by j).

In model M_0 , one assumes that $p_{d_{ij}}$ are constant across all time periods and all observers. That is, $p_{d_{ij}} = p_d$, where p_d is constant. To incorporate time effects for model M_t , one can assume $p_{d_{ij}} = p_{d_j}$. The same is true for the M_o model, incorporating an observer effect one assumes that $p_{d_{ij}} = p_{d_i}$. Similarly, behavioral effects for model M_b can be incorporated by using of $p_{d_{ij}} = p_d$ if the bird has not been detected before time period j , and $p_{d_{ij}} = c_d$ if the animal has been detected before time period j . For the more complex models such as the M_{ob} model, the observer effect is present both in the previously undetected case, $p_{d_{ij}} = p_{d_i}$ as well as in the previously detected case, $c_{d_{ij}} = c_{d_j}$.

In our combined multiple-observer and time-of-detection approach, modeling the effect due to differences between animals was met with complications. This will be discussed further in Section 2.4.

To illustrate the multinomial cell structure, consider a model composition for two independent observers and two time periods. Table 2.1 represents each corresponding detection history with its multinomial cell probability structure for each of the i^{th} detection histories.

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Table 2.1: *Multinomial cell structure for M_{ot} model with two independent observers and two time periods. Assuming constant availability probability structure.*

Detection History	Multinomial Cell Structure (p_i)
00,00	$\{p_a(1-p_{d_{11}})(1-p_{d_{21}}) + (1-p_a)\}\{p_a(1-p_{d_{12}})(1-p_{d_{22}}) + (1-p_a)\}$
00,01	$\{p_a(1-p_{d_{11}})(1-p_{d_{21}}) + (1-p_a)\}\{p_a(1-p_{d_{12}})p_{d_{22}}\}$
00,10	$\{p_a(1-p_{d_{11}})(1-p_{d_{21}}) + (1-p_a)\}\{p_ap_{d_{12}}(1-p_{d_{22}})\}$
01,00	$\{p_a(1-p_{d_{11}})p_{d_{21}}\}\{p_a(1-p_{d_{12}})(1-p_{d_{22}}) + (1-p_a)\}$
10,00	$\{p_ap_{d_{11}}(1-p_{d_{21}})\}\{p_a(1-p_{d_{12}})(1-p_{d_{22}}) + (1-p_a)\}$
11,00	$\{p_ap_{d_{11}}p_{d_{21}}\}\{p_a(1-p_{d_{12}})(1-p_{d_{22}}) + (1-p_a)\}$
10,10	$\{p_ap_{d_{11}}(1-p_{d_{21}})\}\{p_ap_{d_{12}}(1-p_{d_{22}})\}$
10,01	$\{p_ap_{d_{11}}(1-p_{d_{21}})\}\{p_a(1-p_{d_{11}})p_{d_{21}}\}$
01,10	$\{p_a(1-p_{d_{11}})p_{d_{21}}\}\{p_ap_{d_{12}}(1-p_{d_{22}})\}$
01,01	$\{p_a(1-p_{d_{11}})p_{d_{21}}\}\{p_a(1-p_{d_{12}})p_{d_{22}}\}$
00,11	$\{p_a(1-p_{d_{11}})(1-p_{d_{21}}) + (1-p_a)\}\{p_ap_{d_{12}}p_{d_{22}}\}$
11,10	$\{p_ap_{d_{11}}p_{d_{21}}\}\{p_ap_{d_{12}}(1-p_{d_{22}})\}$
11,01	$\{p_ap_{d_{11}}p_{d_{21}}\}\{p_a(1-p_{d_{12}})p_{d_{22}}\}$
10,11	$\{p_ap_{d_{11}}(1-p_{d_{21}})\}\{p_ap_{d_{11}}p_{d_{21}}\}$
01,11	$\{p_a(1-p_{d_{11}})p_{d_{21}}\}\{p_ap_{d_{12}}p_{d_{22}}\}$
11,11	$\{p_ap_{d_{11}}p_{d_{21}}\}\{p_ap_{d_{12}}p_{d_{22}}\}$

To illustrate, consider a detection history for two observers over two time periods with a M_{ot} model structure. The history 11,01 denotes a bird detected by both observers in interval one and detected only by the second observer in interval two. This history has expected cell structure

$$p_{a_1}p_{d_{11}}p_{d_{21}}p_{a_2}(1-p_{d_{12}})p_{d_{22}}.$$

Here the birds have to sing in each interval to be detected by at least one observer.

However, another history 11,00 has the expected cell structure

$$p_{a_1}p_{d_{11}}p_{d_{21}}\{p_{a_2}(1-p_{d_{12}})(1-p_{d_{22}}) + (1-p_{a_2})\}.$$

Notice that whenever a detection history has no detection of a bird, that is neither observer detected a bird in time period j , we have two components for the probability, the first where the bird is available but is missed by both observers and the second where the bird is just not available.

Once a structure, defined by the models listed above, is in place for the multinomial cells, maximization of (2.3) can be undertaken by numerical methods (Section 2.3).

2.2.2 Dependent Multiple Observers

In addition to having independent multiple observers for our combined method, we propose allowing the use of dependent double-observers as an alternative. Nichols et al. (2000) suggested originally the dependent double-observer method (based on the earlier work by Cook and Jacobson (1979)) where at each point count, the “primary” observer indicates to another (“secondary”) observer all birds detected. The secondary observer then records all detections of the primary observer as well as any other birds undetected by the primary observer. Observers alternate roles as the primary and secondary observer during the course of the point count survey.

While Alldredge et al. (2006) showed that the independent double-observer approach is more efficient than the dependent approach, we will allot a sample size cost to the independent double-observer method because it takes longer as the two observers have to stop and spend time reconciling their counts, and then compare the two approaches in Section 2.5. In addition, the dependent double-observer approach may reduce bias when independent observers are not really independent.

The model structures that were examined in Section 2.2.1 follow a similar form in

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the dependent double-observer setting although there is one major difference: there is no detection history where the primary observer detects the bird and the secondary observer does not, because the secondary observer role is to only add information (bird detections) that the primary observer may miss. Also for this modeling approach, not only do you have a probability structure for when observer one is the primary observer and the second observer is the secondary observer, but when their roles are reversed. Then for this dependent double-observer method a known parameter enters into the multinomial likelihood in Equation 2.3. This known parameter τ is the fraction of the detection histories where observer one is the primary observer and thus $1 - \tau$ is for the detection histories where the roles are reversed. It is important to note that while we include τ in the likelihood equation, it is a constant and does not affect analysis.

Consider t time intervals where the birds are tracked throughout the count, and 2 observers per time period, then based on the information obtained from the $k = 3^t$ detection histories for each primary observer case where $n_{i,j}$, $i = 1, 2, \dots, k-1$ represents the number of birds that have the i^{th} detection history detected when observer j is the primary observer, we have

$$L(N; \theta) = \frac{N!}{n_{1,1}! \dots n_{k-1,1}!(N-n)!} \tau \{p_{1,1}(\theta)^{n_{1,1}} \dots p_{k-1,1}(\theta)^{n_{k-1,1}}\} \\ \times \frac{1}{n_{1,2}! \dots n_{k-1,2}!} (1-\tau) \{p_{1,2}(\theta)^{n_{1,2}} \dots p_{k-1,2}(\theta)^{n_{k-1,2}}\} p_k(\theta)^{N-n} \quad (2.4)$$

where $n = \sum_{i=1}^{k-1} \sum_{j=1,2} n_{i,j}$ denotes the total number of detected birds, $p_{i,j}$ represents the multinomial cell probabilities which are known functions of θ , the availability and detection probability parameters ($p_{i,j}(\theta) = f_{i,j}(\theta)$) and $p_k = 1 - \sum_{i=1}^{k-1} \sum_{j=1,2} p_{i,j}$.

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For notation, we assume that the k^{th} detection history is the undetected history when either observer 1 or 2 is the primary observer, which is why it is not scaled. We can do this since in any time period when you have no detection the probability is the same regardless of which observer is the primary observer. Without loss of generality assume model M_{ot} structure with $t = 2$ time periods. If the first observer is the primary observer the probability of not being detected the length of the point-count is $\{p_a(1 - p_{d_{11}})(1 - p_{d_{21}}) + (1 - p_a)\}\{p_a(1 - p_{d_{12}})(1 - p_{d_{22}}) + (1 - p_a)\}$. The same is true if the second observer is the primary observer, just with non-detection terms transposed in each time period's probability, which makes no difference.

Modeling this way changes the multinomial cell structure quite dramatically for each of the i^{th} detection histories, which can be seen in Table 2.2.

Table 2.2: *Multinomial cell structure for M_{ot} model with dependent double-observers and two time periods. Assuming constant availability probability structure.*

Detection History	Multinomial Cell Structure ($p_{i,j}$)
00, 00	$\{p_a(1 - p_{d_{p1}})(1 - p_{d_{s1}}) + (1 - p_a)\}\{p_a(1 - p_{d_{p2}})(1 - p_{d_{s2}}) + (1 - p_a)\}$
00, 01	$\{p_a(1 - p_{d_{p1}})(1 - p_{d_{s1}}) + (1 - p_a)\}\{p_a(1 - p_{d_{p2}})p_{d_{s2}}\}$
01, 00	$\{p_a(1 - p_{d_{p1}})p_{d_{s1}}\}\{p_a(1 - p_{d_{p2}})(1 - p_{d_{s2}}) + (1 - p_a)\}$
11, 00	$\{p_a p_{d_{p1}}\}\{p_a(1 - p_{d_{p2}})(1 - p_{d_{s2}}) + (1 - p_a)\}$
01, 01	$\{p_a(1 - p_{d_{p1}})p_{d_{s1}}\}\{p_a(1 - p_{d_{p2}})p_{d_{s2}}\}$
00, 11	$\{p_a(1 - p_{d_{p1}})(1 - p_{d_{s1}}) + (1 - p_a)\}\{p_a p_{d_{p2}}\}$
11, 01	$\{p_a p_{d_{p1}}\}\{p_a(1 - p_{d_{p2}})p_{d_{s2}}\}$
01, 11	$\{p_a(1 - p_{d_{p1}})p_{d_{s1}}\}\{p_a p_{d_{p2}}\}$
11, 11	$\{p_a p_{d_{p1}}\}\{p_a p_{d_{p2}}\}$

Notation: The primary observer detection probability is denoted with a p subscript, and secondary observer with a s subscript.

To illustrate, consider a detection history for two observers over two time periods with a M_{ot} model structure, where $p_{d_{pj}}$ denotes the primary observer detection proba-

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bility and $p_{d_{sj}}$ denotes the secondary observer detection probability. The history 11,01 denotes a bird detected by both observers in interval one and detected only by the secondary observer in interval two. This history has expected cell structure

$$p_{a_1}p_{d_{p1}}\{p_{a_2}(1 - p_{d_{p2}})p_{d_{s2}}\}$$

Here the birds have to sing in each interval to be detected by at least one observer. However, another history 11,00 has the expected cell structure

$$p_{a_1}p_{d_{p1}}\{p_{a_2}(1 - p_{d_{p1}})(1 - p_{d_{s2}}) + (1 - p_{a_2})\}.$$

Notice that whenever a detection history has no detection of a bird, that is neither observer detected a bird in time period j , we have two components for the probability, the first where the bird is available but is missed by both observers and the second where the bird is just not available.

The model assumptions of the combined dependent double-observer and time-of-detection approach are as follows:

1. Observers are able to accurately decide if a detection is made by the primary or secondary observer;
2. there are equal detection probabilities of all individual birds of each species for each observer;
3. the population is closed and there is no undetected movement out of the sampled area;

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4. observers accurately assign birds to within or beyond the radius used for the sampling area; and
5. the detection probability is the same irrespective of whether an observer is in the primary or secondary role.

As with the independent double-observer method, these assumptions are not trivial because movement of individuals within the area during the count may again cause violations of assumption 1, but to less of a degree. It is presumed that variability of singing rates in individual birds (assumption 2) exists and can be impacted by many factors (Gibbs and Wenny 1993). Once again, movement in or out of the area that is not detected may cause violations of assumption 3, and difficulty in assigning distance of birds located aurally may cause violations of assumption 4. In addition, observers may be more likely to detect birds given the authority of their role as primary observer, or may be more (or less) likely to detect birds in their role as secondary observer, depending on the individual (assumption 5). Some secondary observers may become increasingly likely to detect birds, more actively attempting to find birds that the primary observer may miss, thus increasing their probability of detection. While other observers may turn lethargic in the role as the secondary observer, and consequently, decrease their probability of detection.

The method described here, with its likelihood in Equation 2.4, provides a unified structure which allows for joint estimation of the population size, N , the probability of availability, and the detection probabilities. One major benefit is that this structure allows us to compare the independent and dependent observer models which will be investigated in Section 2.5.

2.3 Estimation Method

Likelihood estimation for the combined multiple-observer and time-of-detection approach follows that presented by Sanathanan (1972) for estimation of the population size N . By conditioning on the sum of the detected birds, n , we may partition Equation 2.3 as $L(N; \theta) = L_1(N; p_k(\theta)) \times L_2(\theta)$ where

$$L_1(N; p_k(\theta)) = \frac{N!}{n!(N-n)!} (1 - p_k(\theta))^n p_k(\theta)^{N-n} \quad (2.5)$$

$$L_2(\theta) = \frac{n!}{n_1! \dots n_{k-1}!} q_1(\theta)^{n_1} \dots q_{k-1}(\theta)^{n_{k-1}} \quad (2.6)$$

with $q_i(\theta) = \frac{p_i(\theta)}{1-p_k(\theta)}$, with $i = 1, 2, \dots, k-1$.

The following lemma then provides the conditional estimate of N , which is known from the work of Chapman (1951).

Lemma 1. *For any given p , $\hat{N} = \left\lfloor \frac{n}{1-p_k} \right\rfloor$, the greatest integer $\leq \frac{n}{1-p_k}$, which maximizes $L_1(N; p_k(\theta))$, where $L_1(N; p_k(\theta))$ is defined in 2.5. If $1-p_k = n/\hat{N}$ for some integer \hat{N} , then \hat{N} and $\hat{N} - 1$ both maximize $L_1(N; p_k(\theta))$. Otherwise \hat{N} is the unique maximum.*

As noted by Sanathanan (1972), two estimates of N emerge in this method. The first is of course, the unconditional maximum likelihood estimate to be denoted \hat{N}_u defined by the condition that there exists a value $\hat{\theta}_u$ of θ such that $(\hat{N}_u, \hat{\theta}_u)$ maximizes $L(N; \theta)$ over all admissible values of $(N; \theta)$. The second is the estimation method we use, the conditional maximum likelihood estimate denoted here as \hat{N}_c defined by the condition that \hat{N}_c maximizes $L_1(N; \hat{p}_c)$ where $\hat{p}_c = p_k(\hat{\theta}_c)$ and $\hat{\theta}_c$ maximizes $L_2(\theta)$.

The reason we choose conditional likelihood maximization is that L_2 involves only θ

and not N and hence maximization of L_2 is much less computationally demanding than maximizing L . In addition, Sanathanan (1972) notes that the asymptotic distributions of \hat{N}_u and \hat{N}_c are shown to be the same. The presentation of Sanathanan's theorem and its details are presented in the Appendix.

Through use of the conditional likelihood maximization, an accessible approach for finding estimates of the availability and detection probabilities, along with the population size exists. Conditional likelihood estimates of parameters can be found directly from likelihood maximization procedures available in any software computing language, such as the *optim* function in *R*. For some instances one may require the use of constrained optimization to guarantee that probability estimates fall between 0 and 1, and in *R* the function *constrOptim* handles the task.

As Pledger et al. (2003) notes however, the Hessian matrix computed from the optimization does not provide reasonable estimates for standard errors. Our simulation evaluation uses the two-step method presented by Norris and Pollock (1996), by making use of simulated data sets generated for a particular model's structure, to estimate the standard errors. We use a two-step estimator approach in which the method assumes a good estimate for N (denoted by Norris and Pollock as \ddot{N}) exists. Then based on that first step; an estimate of $Var(T)$, the unconditional variance of the two-step estimator T can be obtained, where T is an estimate of a parameter of interest. The estimated variance of T is the variance of the computed bootstrap estimates of T .

For each bootstrap replication, \ddot{N} capture histories are drawn with the probability that detectable capture history i is drawn being n_i/\ddot{N} , for each subsequent draw, and the chance that the undetected capture history is drawn is $(\ddot{N} - n)/\ddot{N}$. For each

replication, the bootstrap sample is taken and \hat{N}_c is computed. The estimated variance of \hat{N}_c is the variance of the computed bootstrap estimates of \hat{N}_c . Norris and Pollock (1996) mention that while the estimated variance is not conditional on the number of detected birds, n , there is no smoothing of the estimated capture history probabilities. Implying that the estimated chances of bootstrap sampling of the observable detection histories are exactly the same as the relative number of birds which had these same detection histories. That is, if no birds have a certain observable detection history, then that detection history has no chance of occurring in the bootstrap replications.

Norris and Pollock (1996) also emphasize that n can differ from bootstrap replication to bootstrap replication so that the variability of n is appropriately incorporated in the estimated variability of \hat{N}_c ; thus this method estimates the unconditional variance of \hat{N}_c .

2.4 Heterogeneity in the Combined Approach

Typically, an effect due to differences between animals is considered for the model structure. However, complications arise when we model this heterogeneity in the animal population. Our structure which allows us to model animal availability, provides the opportunity to possibly model heterogeneity in multiple ways. One attempt is modeling heterogeneity on the probability that an animal is available. The motivation behind this is that some animals may be more likely to be available than others. In this condition, the M_h model might have $p_a = \lambda_i p_{a_i}$, where p_{a_i} represents the probability of availability for the i^{th} portion of the animal population and $\sum_{\forall i} \lambda_i = 1$. For example, consider a

two point mixture, to allow for animals with a high probability of being available and also those with a low availability, for such a case the probability of availability would be defined as:

$$p_a = \lambda_1 p_{a_1} + (1 - \lambda_1) p_{a_2}$$

Another attempt models heterogeneity on the probability that an animal is detected, motivation behind this approach is that certain animals may be more likely to be detected than others. Then similarly for this condition we have $p_d = \lambda_i p_{d_i}$, where p_{d_i} represents the probability of detection for the i^{th} portion of the animal population and $\sum_{\forall i} \lambda_i = 1$. However, each of these approaches does not allow for unique estimability of the finite mixture in the estimation technique we use, described in Section 2.3. More work is needed to determine how it is possible to incorporate heterogeneity in this combined multiple-observer and time-of-detection approach.

2.5 Simulation Studies

To evaluate our methods, simulation studies were carried out to investigate their accuracy and precision. In Section 2.5.1, we made a comparison of the combined multiple-observer and time-of-detection approaches when observers are viewed as dependent or independent double-observers, while not allowing for reconciliation time for the independent double-observer method. However, then reconciliation time is addressed through additional simulations which take the reconciliation into account for a wide range of reconciliation times. Next in Section 2.5.2, we examine what occurs when the assumption that observers' probability of detection is the same irrespective

of whether an observer is in the primary or secondary role is violated in the combined dependent double-observer and time-of-detection approach.

2.5.1 Model Evaluation Simulation Studies

Simulations were conducted for a variety of settings, first we examine Model M_b , which allows for a response due to capture, but no time effect (t) or observer effect (o). We examine the following combinations

$$\begin{array}{c} \text{Observer Assumption} \\ \left(\begin{array}{c} \text{Dependent Double-Observer} \\ \text{Independent Double-Observer} \end{array} \right) \end{array} \times \begin{array}{c} N \\ \left(\begin{array}{c} 500 \\ 1000 \end{array} \right) \end{array} \times \begin{array}{c} \text{Probability Components} \\ \left(\begin{array}{c} p_a = 0.30, p_d = 0.50, c_d = 0.60 \\ p_a = 0.60, p_d = 0.50, c_d = 0.70 \\ p_a = 0.75, p_d = 0.70, c_d = 0.85 \end{array} \right) \end{array}$$

and conducted simulations of our combined multiple-observer and time-of-detection method. For each combination, we performed 100 bootstrap replications on 100 randomly generated data sets which each consisted of generating N detection histories (based on the probability components above). These probability components represent settings where a bird is very difficult to detect, marginally difficult to detect, and very easy to detect. In each case, we assume that the trap-response allows for the birds to be more easily detected after its first detection. In each of the randomly generated 100 data sets, we then bootstrap resampled each data set 100 times. From these, we computed the conditional maximum likelihood estimates $(\hat{N}_c, \hat{\theta}_c)$ of (N, θ) , the two-step estimators. Then with each 100 bootstrap replications for each of the randomly generated data sets, we computed the estimated standard errors of \hat{N}_c and

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of the probability components of $\hat{\theta}_c$.

In Table 2.3, we report the mean estimates of the population size, N , and the probability components of θ , taken over all 10,000 estimates, along with their precision. Also reported are the mean standard error estimates for each component of the M_b model, taken over the 100 bootstrap two-step variance estimation method estimates, along with their precision. For each set of simulations grouped by population size N , as one might expect, the standard error estimates decrease the more easily it is for a bird to be detected. This is true regardless of which multiple-observer component is used in the study. Alldredge et al. (2006) showed that the independent double-observer approach is more efficient than the dependent approach, because capture-recapture methods generally are more efficient than removal methods (Seber 1982, p.324). In contrast, the dependent double-observer approach may reduce bias when independent observers are not really independent. It also may be easier to carry out in some field situations because observers don't have to spend time matching observations.

Regardless of which multiple-observer component is chosen, and what case of bird detectability; both methods estimate the population size with small bias and good precision. As we expected *a priori* that standard error estimates for our method with the independent double-observer component were smaller compared to those with the dependent double-observer component, due to the greater amount of information attained in the detection histories for the independent case. This arises due to the fact that in a time period where a bird is detected by both observers the proportion of the multinomial cell probability associated with that time period for the independent double-observer is $\{p_a p_{d_1} p_{d_2}\}$ versus $\{p_a p_{d_1}\}$ for the dependent double-observer case.

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This is just for the very simple M_o model, if a much more complex model structure is assumed, more information could be lost with, especially with regards to secondary observer parameters.

Table 2.3: *Simulation Study of Combined Multiple-Observer and Time-of-Detection Approach for M_b model for 100 data sets each with 100 bootstrap samples.*

Parameter	True Value	Dependent Observers		Independent Observers	
		Mean of Estimates	Mean of Std. Error Estimates	Mean of Estimates	Mean of Std. Error Estimates
N	100	100.67 (0.3472)	19.431 (0.6423)	103.30 (0.2461)	16.617 (0.6039)
p_a	0.30	0.3226 (8.937×10^{-4})	0.0612 (1.593×10^{-3})	0.3122 (7.997×10^{-4})	0.0548 (1.336×10^{-3})
p_d	0.50	0.5026 (1.109×10^{-3})	0.0784 (7.238×10^{-4})	0.4981 (9.363×10^{-4})	0.0638 (6.631×10^{-4})
c_d	0.60	0.5968 (1.443×10^{-3})	0.0947 (2.349×10^{-3})	0.5949 (1.251×10^{-3})	0.0894 (1.644×10^{-3})
N	100	101.33 (0.0941)	5.940 (0.0344)	100.46 (0.0611)	4.390 (0.1091)
p_a	0.60	0.6180 (7.904×10^{-4})	0.0539 (2.209×10^{-3})	0.6014 (5.253×10^{-4})	0.0381 (4.288×10^{-4})
p_d	0.50	0.4909 (1.232×10^{-3})	0.0802 (1.315×10^{-3})	0.5017 (6.786×10^{-4})	0.0487 (5.495×10^{-4})
c_d	0.70	0.6920 (1.031×10^{-3})	0.0701 (1.574×10^{-3})	0.6979 (5.827×10^{-4})	0.0399 (5.421×10^{-4})
N	100	99.55 (0.0140)	0.8534 (0.0432)	99.57 (0.0140)	0.7889 (0.0417)
p_a	0.75	0.7521 (3.915×10^{-4})	0.0267 (2.757×10^{-4})	0.7501 (3.460×10^{-4})	0.0254 (2.538×10^{-4})
p_d	0.70	0.7014 (8.203×10^{-4})	0.0585 (1.018×10^{-4})	0.7011 (6.245×10^{-4})	0.0390 (4.337×10^{-4})
c_d	0.85	0.8436 (4.829×10^{-4})	0.0330 (5.641×10^{-4})	0.8490 (2.930×10^{-4})	0.0211 (2.328×10^{-4})
N	500	509.45 (0.6121)	42.502 (1.031)	507.81 (0.4696)	31.871 (0.5318)
p_a	0.30	0.3046 (4.037×10^{-4})	0.0299 (7.108×10^{-4})	0.2990 (3.314×10^{-4})	0.0219 (2.496×10^{-4})
p_d	0.50	0.4941 (7.830×10^{-4})	0.0566 (6.705×10^{-4})	0.5009 (4.367×10^{-4})	0.0287 (2.037×10^{-4})
c_d	0.60	0.5953 (9.696×10^{-4})	0.0709 (1.190×10^{-3})	0.6023 (5.693×10^{-4})	0.0390 (3.980×10^{-4})
N	500	502.03 (0.1584)	10.789 (0.1822)	500.63 (0.1284)	9.125 (0.1102)
p_a	0.60	0.6000 (2.841×10^{-4})	0.0202 (2.405×10^{-4})	0.6043 (2.522×10^{-4})	0.0173 (1.349×10^{-4})
p_d	0.50	0.4984 (5.146×10^{-4})	0.0361 (4.044×10^{-4})	0.4978 (3.193×10^{-4})	0.0222 (1.977×10^{-4})
c_d	0.70	0.6984 (4.581×10^{-4})	0.0303 (3.625×10^{-4})	0.6966 (2.468×10^{-4})	0.0176 (1.270×10^{-4})
N	500	499.39 (0.0352)	2.387 (0.0306)	499.59 (0.0335)	2.278 (0.0287)
p_a	0.75	0.7499 (1.644×10^{-4})	0.0119 (9.492×10^{-5})	0.7496 (1.552×10^{-4})	0.0111 (8.782×10^{-5})
p_d	0.70	0.6992 (3.959×10^{-4})	0.0273 (2.736×10^{-4})	0.7019 (2.827×10^{-4})	0.0177 (1.466×10^{-4})
c_d	0.85	0.8492 (2.030×10^{-4})	0.0144 (1.294×10^{-4})	0.8500 (1.340×10^{-4})	0.0095 (7.686×10^{-5})
N	1000	1002.09 (0.7996)	54.885 (0.894)	1008.84 (0.6434)	44.449 (0.470)
p_a	0.30	0.3045 (2.857×10^{-4})	0.0197 (3.235×10^{-4})	0.3010 (2.161×10^{-4})	0.0157 (1.611×10^{-4})
p_d	0.50	0.4971 (5.470×10^{-4})	0.0396 (4.027×10^{-4})	0.4951 (2.794×10^{-4})	0.0208 (1.610×10^{-4})
c_d	0.60	0.5989 (6.526×10^{-4})	0.0488 (6.672×10^{-4})	0.5961 (4.185×10^{-4})	0.0282 (2.663×10^{-4})
N	1000	998.66 (0.2508)	15.932 (0.1818)	1001.382 (0.1912)	13.073 (0.1352)
p_a	0.60	0.5954 (1.979×10^{-4})	0.0132 (1.229×10^{-4})	0.6011 (1.694×10^{-4})	0.0121 (9.130×10^{-5})
p_d	0.50	0.5030 (3.809×10^{-4})	0.0264 (2.458×10^{-4})	0.4993 (2.354×10^{-4})	0.0158 (1.273×10^{-4})
c_d	0.70	0.6997 (3.414×10^{-4})	0.0234 (2.456×10^{-4})	0.7005 (1.783×10^{-4})	0.0125 (1.028×10^{-4})
N	1000	999.16 (0.0528)	3.375 (0.0383)	999.59 (0.0469)	3.309 (0.0320)
p_a	0.75	0.7505 (1.173×10^{-4})	0.0083 (6.478×10^{-5})	0.7492 (1.207×10^{-4})	0.0080 (5.762×10^{-5})
p_d	0.70	0.7015 (2.798×10^{-4})	0.0193 (1.499×10^{-4})	0.7007 (1.886×10^{-4})	0.0127 (8.944×10^{-5})
c_d	0.85	0.8502 (1.382×10^{-4})	0.0103 (8.939×10^{-5})	0.8493 (9.253×10^{-5})	0.0068 (5.499×10^{-5})

However, this direct comparison may not reflect the practical costs of the independent observers case. Between point-counts observers conducting a study using an in-

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dependent multiple-observer approach require time to compare and pair up (or match) their point-count data. The amount of time to match up information regarding the observed detection histories can take surprisingly long. Jason Riddle (personal communication) found that in cases where the number of species and individual birds is small the time for reconciliation might be say one-tenth of the time to do the count whereas it could sometimes be even longer than the count itself when there more animal species and individuals.

To make impartial judgements on which multiple-observer component allows for better estimation, we will adjust the number of observable point-counts taken in our simulation study for the independent double-observer. The number of point-counts will be scaled by 90% (representing a relatively short reconciliation time period), 75% (moderate time period length), and 50% (lengthy reconciliation time period). Estimation is then carried out in a similar way. However, due to the fact the number of point-counts is knowingly diminished by a known proportion this will be reflected in the precision of the estimate of the population size. For this case, we revisit estimation of the density of the animal population in Equations 2.1 and 2.2 since we reduce the number of point-counts taken we might express the estimate of density as:

$$\hat{D} = \hat{N}/a_r = \frac{n}{\frac{1}{r}k\pi w^2} = \frac{rn}{k\pi w^2} \quad (2.7)$$

where a_r is defined to be the area surveyed allowing for the reconciliation time scale. Which then leads to the estimate of the population size, comparable to estimates with k point-counts as:

$$\hat{N} = a\hat{D} = \hat{D}/r \quad (2.8)$$

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Therefore, estimates calculated can be considered a population density estimate which can then be scaled back according to the reduction in the number of point-counts taken to estimate the size of the population. For example, for each bootstrap replication of each of the 100 randomly generated scaled data sets, if the number of observable point-counts were cut back by 75% then the estimate of the population size will be increased by $4/3$ to accommodate for the scaling factor. The probability components require no such scaling since we did not affect their estimation composition. We then computed the conditional maximum likelihood estimates $(\hat{N}_c, \hat{\theta}_c)$ of (N, θ) , the two-step estimators from these adjusted estimates. Then with each 100 bootstrap replications for each of the randomly generated data sets, we computed the estimated standard errors of \hat{N}_c and of the probability components of $\hat{\theta}_c$.

In Table 2.4, we report the mean estimates of the population size, N , and the probability components of θ , taken over all 10,000 estimates, along with their precision for the reconciled point-count data compared to the methods mentioned previously. Also reported are the mean standard error estimates for each component of the M_b model, taken over the 100 bootstrap two-step variance estimation method estimates, along with their precision. For this group of simulations, as expected, as less observed point-count information is collected in the combined independent double-observer and time-of-detection approach, the higher the standard error of the population size estimate. In our study, as reconciliation time for matching becomes longer due to a difficult environment, the dependent double-observer approach becomes a more viable option for estimation of population size. The standard error of the estimated population size, $(\widehat{SE}(\hat{N}_c) = 42.502)$, lies between the standard errors represented by a moderately easy

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matching reconciliation time condition (38.377) and the condition representing a more difficult reconciliation time (47.403).

Regarding the probability components of θ , as less observed point-count information is collected in the combined independent double-observer and time-of-detection approach, the higher the standard errors of the probability components estimates. As in the case of the estimate of the population size, as reconciliation time for matching becomes longer due to a difficult environment, the dependent double-observer approach becomes a more precise option in the estimation of the probability of availability, p_a . The standard error of the estimated probability of availability, $(\widehat{SE}(\hat{p}_a) = 0.0299)$, lies between the standard errors represented by a moderately easy matching reconciliation time condition (0.0260) and the condition representing a more difficult reconciliation time (0.0323). Concerning the estimation of the probability of detection, p_d and the trap-effect probability of detection, c_d , as less observed point-count information is collected in the combined independent double-observer and time-of-detection approach, the higher the standard error of the detection probability estimates. However, unlike in the case of the probability of availability, the cases related to the probabilities of detection do not have smaller standard errors for the dependent double-observer approach. This is due to the fact that less information is collected about the probability of detection in the dependent double-observer capture histories than in those for the independent double-observer method (eg - view Tables 2.1 and 2.2). Additional cases are presented in the Appendix.

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Table 2.4: *Simulation Study of Combined Multiple-Observer and Time-of-Detection Approach allowing for Reconciliation time for M_b model for 100 data sets each with 100 bootstrap samples. For the difficult to detect setting for a population of $N = 500$ birds.*

	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
	N	500	509.45 (0.6121)	42.502 (1.031)	57.080 (2.455)
DDO	p_a	0.30	0.3046 (4.037×10^{-4})	0.0299 (7.108×10^{-4})	0.0386 (1.314×10^{-3})
	p_d	0.50	0.4941 (7.830×10^{-4})	0.0566 (6.705×10^{-4})	0.0754 (2.266×10^{-3})
	c_d	0.60	0.5953 (9.696×10^{-4})	0.0709 (1.190×10^{-3})	0.0933 (2.802×10^{-3})
	N	500	507.81 (0.4696)	31.871 (0.5318)	44.676 (1.683)
(100%)	p_a	0.30	0.2990 (3.314×10^{-4})	0.0219 (2.496×10^{-4})	0.0315 (1.068×10^{-3})
	p_d	0.50	0.5009 (4.367×10^{-4})	0.0287 (2.037×10^{-4})	0.0419 (1.281×10^{-3})
	c_d	0.60	0.6023 (5.693×10^{-4})	0.0390 (3.980×10^{-4})	0.0549 (1.581×10^{-3})
	N	500	507.83 (0.5873)	34.382 (0.7242)	53.757 (2.528)
(90%)	p_a	0.30	0.3010 (4.171×10^{-4})	0.0238 (3.647×10^{-4})	0.0384 (1.645×10^{-3})
	p_d	0.50	0.5025 (5.292×10^{-4})	0.0302 (2.398×10^{-4})	0.0494 (1.943×10^{-3})
	c_d	0.60	0.5910 (7.682×10^{-4})	0.0420 (5.292×10^{-4})	0.0704 (3.248×10^{-3})
	N	500	511.04 (0.5873)	38.377 (0.8111)	57.242 (2.878)
(75%)	p_a	0.30	0.3012 (4.609×10^{-4})	0.0260 (4.410×10^{-4})	0.0421 (1.903×10^{-3})
	p_d	0.50	0.4987 (5.870×10^{-4})	0.0323 (2.692×10^{-4})	0.0546 (2.194×10^{-3})
	c_d	0.60	0.5971 (7.694×10^{-4})	0.0466 (7.449×10^{-4})	0.0726 (2.630×10^{-3})
	N	500	512.02 (0.7251)	47.403 (1.192)	65.443 (3.398)
(50%)	p_a	0.30	0.3001 (4.919×10^{-4})	0.0323 (5.596×10^{-4})	0.0465 (1.648×10^{-3})
	p_d	0.50	0.5044 (7.115×10^{-4})	0.0405 (3.343×10^{-4})	0.0660 (2.729×10^{-3})
	c_d	0.60	0.5943 (9.119×10^{-4})	0.0549 (8.450×10^{-4})	0.0853 (3.332×10^{-3})

2.5.2 Assumption Violation Simulation Studies

Primary-Secondary Observer Equal Detection Probability Assumption

The dependent double-observer method makes the assumption that the detection probability is the same irrespective of whether an observer is in the primary or secondary role. Referring back to Table 2.2, the first observer has the same probability of detection, $p_{d_{1t}}$, for a specific time period t whether they are the primary or secondary observer. Simulations were conducted for the following settings, initially we examine Model M_0 , which is the simplest model with probability components p_a , the probability

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of availability, and p_d , the probability of detection. For the data generation, we assume that when an observer is in the secondary role, their probability of detection is defined as q_d . We have begun with examining the following combinations for a population size of $N = 1000$.

Probability Components		
$p_a = 0.30, p_d = 0.40, c_d = 0.20$	$p_a = 0.60, p_d = 0.70, q_d = 0.50$	$p_a = 0.90, p_d = 0.70, c_d = 0.50$
$p_a = 0.30, p_d = 0.40, c_d = 0.40$	$p_a = 0.60, p_d = 0.70, q_d = 0.70$	$p_a = 0.90, p_d = 0.70, c_d = 0.70$
$p_a = 0.30, p_d = 0.40, c_d = 0.60$	$p_a = 0.60, p_d = 0.70, q_d = 0.90$	$p_a = 0.90, p_d = 0.70, c_d = 0.90$

For each combination, we performed 100 bootstrap replications on 100 randomly generated data sets which each consisted of generating N detection histories (based on the probability components above). These probability components represent settings where an observer is less likely to detect a bird in the secondary observer role than the primary observer role, the observer is as likely to detect a bird, and the observer is more likely to detect a bird. In each of the randomly generated 100 data sets, we then bootstrap resampled each data set 100 times. From these, we computed the conditional maximum likelihood estimates $(\hat{N}_c, \hat{\theta}_c)$ of (N, θ) , the two-step estimators, assuming that observers have the same detection probability regardless of whether an observer is in the primary or secondary role. Then with each 100 bootstrap replications for each of the randomly generated data sets, we computed the estimated standard errors of \hat{N}_c and of the probability components of $\hat{\theta}_c$.

In Table 2.5, we report the mean estimates of the population size, N , and the probability components of θ , taken over all 10,000 estimates, along with their precision. Also reported are the mean standard error and root mean square error (RMSE) estimates for each component of the M_0 model, taken over the 100 bootstrap two-step

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variance estimation method estimates, along with their precision.

Table 2.5: *Simulation Study testing the primary-secondary detection probability assumption violation for the Dependant Multiple Observer M_0 model for 100 data sets each with 100 bootstrap samples.*

Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
N	1000	1007.84 (0.9879)	67.196 (1.1142)	94.746 (2.9969)
p_a	0.30	0.1724 (1.987×10^{-4})	0.0134 (1.125×10^{-4})	0.1283 (1.464×10^{-3})
p_d	0.40	0.6999 (4.154×10^{-4})	0.0286 (3.209×10^{-4})	0.3013 (2.988×10^{-3})
q_d	0.20	-	-	-
N	1000	1005.26 (0.7333)	50.485 (0.6608)	69.274 (2.5264)
p_a	0.30	0.3014 (4.545×10^{-4})	0.0330 (8.930×10^{-5})	0.0431 (1.489×10^{-3})
p_d	0.40	0.4073 (6.113×10^{-4})	0.0444 (4.824×10^{-4})	0.0596 (1.631×10^{-3})
q_d	0.40	-	-	-
N	1000	1004.1 (0.5788)	39.748 (0.4965)	55.399 (1.7804)
p_a	0.30	0.8856 (1.670×10^{-3})	0.1123 (5.135×10^{-4})	0.6003 (1.034×10^{-2})
p_d	0.40	0.1465 (4.282×10^{-4})	0.0275 (1.424×10^{-4})	0.2556 (2.782×10^{-3})
q_d	0.60	-	-	-
N	1000	1001.60 (0.1283)	9.126 (0.0809)	12.374 (0.3873)
p_a	0.60	0.5331 (1.456×10^{-4})	0.0101 (8.056×10^{-5})	0.0676 (1.045×10^{-3})
p_d	0.70	0.7860 (1.727×10^{-4})	0.0125 (1.022×10^{-4})	0.0870 (1.180×10^{-3})
q_d	0.50	-	-	-
N	1000	999.61 (0.1080)	7.502 (0.0731)	10.358 (0.3184)
p_a	0.60	0.5998 (1.584×10^{-4})	0.0116 (9.530×10^{-5})	0.0152 (4.690×10^{-4})
p_d	0.70	0.7025 (2.135×10^{-4})	0.0153 (1.389×10^{-4})	0.0207 (6.157×10^{-4})
q_d	0.70	-	-	-
N	1000	998.60 (0.0968)	6.075 (0.0584)	9.149 (0.3519)
p_a	0.60	0.6861 (2.147×10^{-4})	0.0153 (1.585×10^{-4})	0.0875 (1.498×10^{-3})
p_d	0.70	0.6145 (2.573×10^{-4})	0.0181 (1.532×10^{-4})	0.0874 (1.808×10^{-3})
q_d	0.90	-	-	-
N	1000	999.80 (0.0248)	1.661 (0.0195)	2.368 (0.077)
p_a	0.90	0.8012 (1.086×10^{-4})	0.0082 (5.761×10^{-5})	0.0995 (7.200×10^{-4})
p_d	0.70	0.7859 (1.358×10^{-4})	0.0101 (8.395×10^{-5})	0.0865 (9.025×10^{-4})
q_d	0.50	-	-	-
N	1000	999.54 (0.0141)	0.893 (0.0335)	1.355 (0.0618)
p_a	0.90	0.9010 (1.391×10^{-4})	0.0100 (8.331×10^{-5})	0.0133 (4.191×10^{-4})
p_d	0.70	0.6993 (1.751×10^{-4})	0.0125 (1.066×10^{-4})	0.0170 (4.516×10^{-4})
q_d	0.70	-	-	-
N	1000	999.69 (0.0051)	0.4387 (0.0248)	0.8763 (0.0506)
p_a	0.90	0.9992 (3.531×10^{-5})	0.0017 (2.391×10^{-4})	0.0992 (1.907×10^{-4})
p_d	0.70	0.6384 (9.364×10^{-5})	0.0070 (1.397×10^{-4})	0.0620 (6.090×10^{-4})
q_d	0.90	-	-	-

As we expected *a priori*, estimation when $p_d = q_d$ preforms quite admirably; there

is good precision and accuracy in the estimates. However, when the probability of detection when the observer is in the secondary role, q_d , differs from the probability of detection when the observer is in the primary role, p_d , there is a large increase in the bias of the estimates of the probability components of the model. One unforeseen result is that it appears that the method estimates the population size adeptly. We believe this is due to the quantity of information provided from time period to time period allows the time-of-detection portion of our method to accurately estimate the population size N , through unbiased estimation of their product, $p = p_a p_d$. Further simulation cases examining different effect combinations should be investigated to examine this result.

Correct Matching Assumption

The independent double-observer method makes the assumption that the two (or more) observers match their detections accurately. However, this is not always the case often observers may incorrectly match their detections upwards to 20% of the detections (Allredge et al. 2007c). We will examine the most common case, that is, that given an individual bird and its corresponding detection history, we will investigate when it is in truth, two birds mistakenly matched. This can best be described in a two independent observer case where the observers detect two birds in close proximity. Then through discussion and survey protocols, the observers incorrectly match two birds as one individual.

We examine the combinations presented in Section 2.5.1 for the reconciliation time simulations. For each combination, we performed 100 bootstrap replications on 100 randomly generated data sets which each consisted of generating N detection histories.

Within each data set, we randomly allow for each of the N detection histories to be incorrectly matched by a specified matching error rate. If it is determined to be a matching error, the bird's detection history which was mistaken as another will be appended to the data set. This addition of birds will show how problematic the matching of observers' detections can be, by biasing results of the bird population.

As before, for each of the randomly generated 100 data sets, we then bootstrap resampled each data set 100 times. From these, in Tables 2.6 and 2.7, we report the computed the conditional maximum likelihood estimates $(\hat{N}_c, \hat{\theta}_c)$ of (N, θ) , the two-step estimators. Then with each 100 bootstrap replications for each of the randomly generated data sets, we computed the estimated standard errors and root mean square errors of \hat{N}_c and of the probability components of $\hat{\theta}_c$.

Compared to the estimates for the dependent double-observer method in Table 2.3, these estimates of the combined time-of-detection and independent multiple-observer allowing for matching error do not perform well based on the root mean square error comparison of the population size estimates.

2.6 Discussion

The combination of time-of-detection and multiple observer methods allows estimation of both components of the detection process. We do not claim that the results in other studies will be as promising as those based on our data. However, through simulation studies we know the true values of the parameters of interest and are encouraged in their results. We focused on the random availability model because they are simpler

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to interpret, more precise, and allow for easier computation of the total population of birds (including those not available in an interval). There could also be more study of Markovian models because we know that birds sing in nonrandom bouts (Collins 2004), but as noted, the complexity of such models are likely to make them of limited usefulness in practice. In addition, there is a great interest in future research regarding modeling heterogeneity with this combined approach.s

Despite its additional expense and the potential for some counting and matching errors, we encourage field ornithologists to consider use of this combined double-observer and time-of-detection method for at least a sub-sample of their points to better understand the detection process in their field studies and potentially obtain better estimates of population abundance. If the cost of using the combined independent double-observer and time-of-detection method is of concern, we have shown that use of the combined dependent double-observer and time-of-detection method provides comparable accuracy and precision when you take into account reconciliation time that is required with independent observers.

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Table 2.6: *Simulation Study testing the matching error assumption violation for the Independent Multiple Observer M_b model for 100 data sets each with 100 bootstrap samples. Population size of $N = 500$.*

	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
5%	N	500	526.42 (0.5086)	34.575 (0.5684)	52.880 (2.2488)
	p_a	0.30	0.3038 (3.405×10^{-4})	0.0227 (2.546×10^{-4})	0.0325 (1.125×10^{-3})
	p_d	0.50	0.4753 (4.433×10^{-4})	0.0291 (1.940×10^{-4})	0.0472 (1.910×10^{-3})
	c_d	0.60	0.5767 (5.643×10^{-4})	0.0400 (3.984×10^{-4})	0.0580 (1.967×10^{-3})
10%	N	500	546.05 (0.5319)	36.850 (0.6437)	63.969 (2.9677)
	p_a	0.30	0.3103 (3.745×10^{-4})	0.0242 (2.865×10^{-4})	0.0361 (1.467×10^{-3})
	p_d	0.50	0.4482 (4.276×10^{-4})	0.0289 (2.306×10^{-4})	0.0625 (2.484×10^{-3})
	c_d	0.60	0.5496 (6.031×10^{-4})	0.0412 (3.666×10^{-4})	0.0726 (3.054×10^{-3})
20%	N	500	588.84 (0.6400)	43.345 (0.8412)	101.178 (4.2283)
	p_a	0.30	0.3236 (4.013×10^{-4})	0.0272 (4.057×10^{-4})	0.0422 (1.994×10^{-3})
	p_d	0.50	0.3974 (4.191×10^{-4})	0.0287 (2.012×10^{-4})	0.1070 (2.924×10^{-3})
	c_d	0.60	0.5004 (6.125×10^{-4})	0.0430 (5.004×10^{-4})	0.1103 (3.938×10^{-3})
5%	N	500	522.84 (0.1503)	10.248 (0.1073)	25.528 (0.9889)
	p_a	0.60	0.6110 (2.607×10^{-4})	0.0176 (1.670×10^{-4})	0.0265 (1.017×10^{-3})
	p_d	0.50	0.4682 (3.165×10^{-4})	0.0219 (1.579×10^{-4})	0.0419 (1.637×10^{-3})
	c_d	0.70	0.6673 (2.755×10^{-4})	0.0186 (1.593×10^{-4})	0.0396 (1.615×10^{-3})
10%	N	500	545.05 (0.1681)	11.546 (0.1379)	46.582 (1.2042)
	p_a	0.60	0.6185 (2.741×10^{-4})	0.0190 (1.656×10^{-4})	0.0309 (1.211×10^{-3})
	p_d	0.50	0.4407 (3.032×10^{-4})	0.0212 (1.701×10^{-4})	0.0637 (1.965×10^{-3})
	c_d	0.70	0.6396 (2.775×10^{-4})	0.0199 (1.850×10^{-4})	0.0639 (1.841×10^{-3})
20%	N	500	592.68 (0.2196)	13.982 (0.1726)	93.744 (1.6976)
	p_a	0.60	0.6457 (3.298×10^{-4})	0.0215 (2.179×10^{-4})	0.0521 (2.166×10^{-3})
	p_d	0.50	0.3863 (3.177×10^{-4})	0.0207 (1.460×10^{-4})	0.1157 (2.379×10^{-3})
	c_d	0.70	0.5742 (3.241×10^{-4})	0.0221 (2.105×10^{-4})	0.1278 (2.355×10^{-3})
5%	N	500	524.68 (0.0632)	2.646 (0.0334)	24.827 (0.5739)
	p_a	0.75	0.7530 (1.641×10^{-4})	0.0117 (1.092×10^{-4})	0.0161 (4.640×10^{-4})
	p_d	0.70	0.6590 (2.878×10^{-4})	0.0180 (1.463×10^{-4})	0.0466 (1.857×10^{-3})
	c_d	0.85	0.8113 (1.694×10^{-4})	0.0115 (8.628×10^{-5})	0.0406 (1.201×10^{-3})
10%	N	500	548.40 (0.0815)	3.077 (0.0392)	48.496 (0.7572)
	p_a	0.75	0.7596 (1.719×10^{-4})	0.0118 (9.641×10^{-5})	0.0184 (6.968×10^{-4})
	p_d	0.70	0.6212 (2.931×10^{-4})	0.0183 (1.473×10^{-4})	0.0812 (2.223×10^{-3})
	c_d	0.85	0.7740 (2.063×10^{-4})	0.0132 (1.253×10^{-4})	0.0772 (1.576×10^{-3})
20%	N	500	597.20 (0.1067)	3.917 (0.0498)	97.285 (0.9970)
	p_a	0.75	0.7854 (2.057×10^{-4})	0.0137 (1.248×10^{-4})	0.0384 (1.421×10^{-3})
	p_d	0.70	0.5462 (2.938×10^{-4})	0.0183 (1.250×10^{-4})	0.1549 (2.295×10^{-3})
	c_d	0.85	0.6939 (2.468×10^{-4})	0.0162 (1.446×10^{-4})	0.1570 (1.864×10^{-3})

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Table 2.7: *Simulation Study testing the matching error assumption violation for the Independent Multiple Observer M_b model for 100 data sets each with 100 bootstrap samples. Population size of $N = 1000$.*

	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
5%	N	1000	1046.71 (0.7120)	48.486 (0.6052)	77.946 (3.4826)
	p_a	0.30	0.3051 (2.244×10^{-4})	0.0164 (1.745×10^{-4})	0.0220 (6.987×10^{-4})
	p_d	0.50	0.4696 (2.842×10^{-4})	0.0206 (1.512×10^{-4})	0.0388 (1.528×10^{-3})
	c_d	0.60	0.5727 (4.256×10^{-4})	0.0288 (2.606×10^{-4})	0.0469 (1.922×10^{-3})
10%	N	1000	1089.17 (0.7375)	52.251 (0.6048)	107.556 (4.3224)
	p_a	0.30	0.3122 (2.396×10^{-4})	0.0174 (1.626×10^{-4})	0.0256 (8.539×10^{-4})
	p_d	0.50	0.4402 (2.745×10^{-4})	0.0206 (1.554×10^{-4})	0.0636 (1.705×10^{-3})
	c_d	0.60	0.5429 (4.212×10^{-4})	0.0294 (2.447×10^{-4})	0.0665 (2.484×10^{-3})
20%	N	1000	1199.35 (0.7761)	60.127 (0.6137)	202.192 (5.219)
	p_a	0.30	0.3214 (2.658×10^{-4})	0.0211 (1.542×10^{-4})	0.0312 (1.021×10^{-3})
	p_d	0.50	0.4187 (2.541×10^{-4})	0.0217 (1.626×10^{-4})	0.0847 (1.989×10^{-3})
	c_d	0.60	0.5142 (4.169×10^{-4})	0.0315 (2.238×10^{-4})	0.0872 (3.172×10^{-3})
5%	N	1000	1046.74 (0.2268)	14.510 (0.1492)	49.244 (1.6731)
	p_a	0.60	0.6067 (1.759×10^{-4})	0.0126 (1.024×10^{-4})	0.0178 (6.300×10^{-4})
	p_d	0.50	0.4699 (2.319×10^{-4})	0.0154 (1.154×10^{-4})	0.0356 (1.342×10^{-3})
	c_d	0.70	0.6713 (1.967×10^{-4})	0.0133 (9.823×10^{-5})	0.0324 (1.279×10^{-3})
10%	N	1000	1090.38 (0.2591)	16.048 (0.1668)	91.852 (2.0281)
	p_a	0.60	0.6155 (1.862×10^{-4})	0.0133 (9.343×10^{-5})	0.0225 (9.203×10^{-4})
	p_d	0.50	0.4426 (2.304×10^{-4})	0.0152 (1.049×10^{-4})	0.0597 (1.633×10^{-3})
	c_d	0.70	0.6416 (1.986×10^{-4})	0.0143 (1.207×10^{-4})	0.0602 (1.361×10^{-3})
20%	N	1000	1192.78 (0.2931)	19.813 (0.2102)	198.992 (3.421)
	p_a	0.60	0.6238 (2.219×10^{-4})	0.0142 (8.871×10^{-5})	0.0287 (1.181×10^{-3})
	p_d	0.50	0.4103 (2.911×10^{-4})	0.0155 (1.021×10^{-4})	0.0651 (1.982×10^{-3})
	c_d	0.70	0.6239 (2.012×10^{-4})	0.0176 (1.117×10^{-4})	0.0763 (1.398×10^{-3})
5%	N	1000	1047.99 (0.0870)	3.825 (0.0383)	48.143 (0.7835)
	p_a	0.75	0.7530 (1.304×10^{-4})	0.0082 (6.194×10^{-5})	0.0125 (4.755×10^{-4})
	p_d	0.70	0.6593 (1.937×10^{-4})	0.0128 (8.478×10^{-5})	0.0430 (1.372×10^{-3})
	c_d	0.85	0.8116 (1.225×10^{-4})	0.0081 (6.771×10^{-5})	0.0393 (9.109×10^{-4})
10%	N	1000	1097.33 (0.1186)	4.379 (0.0465)	97.437 (1.1079)
	p_a	0.75	0.7597 (1.310×10^{-4})	0.0085 (6.655×10^{-5})	0.0152 (6.086×10^{-4})
	p_d	0.70	0.6189 (1.888×10^{-4})	0.0131 (1.045×10^{-4})	0.0821 (1.358×10^{-3})
	c_d	0.85	0.7729 (1.478×10^{-4})	0.0096 (6.742×10^{-5})	0.0777 (1.131×10^{-3})
20%	N	1000	1197.48 (0.1499)	5.575 (0.0540)	197.565 (1.3991)
	p_a	0.75	0.7850 (1.556×10^{-4})	0.0100 (8.190×10^{-5})	0.0366 (1.147×10^{-3})
	p_d	0.70	0.5438 (1.911×10^{-4})	0.0129 (8.411×10^{-5})	0.1568 (1.417×10^{-3})
	c_d	0.85	0.6922 (1.731×10^{-4})	0.0116 (7.684×10^{-5})	0.1583 (1.289×10^{-3})

CHAPTER 3

An Extension of Combined Multiple-Observer and Time-of-Detection Models to Multiple Cues

3.1 Introduction

A very important method for estimating detection probability in avian point counts is the time of detection method (Farnsworth et al. 2002, Alldredge et al. 2007ab). A problem usually ignored in those models is that birds may give both sound and visual cues and usually detections from all cue types are pooled. Here we develop overall models that allow detections from each cue type to be modeled separately. As subsequent detections often require separate detection parameters (observer behavioral response) we focus on the simpler time to first detection and thus these models can be viewed as extensions to the models of Farnsworth et al. (2002). Development of these models involves assuming that there are multiple cue types – visual and aural – which compete for an observers attention. Furthermore each detection is then categorized as either aural or visual and a joint likelihood developed.

We borrow from the competing risks survival analysis literature and introduce notation presented by Crowder (2001) in that context. We let T be a continuous random

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variable representing survival time. We assume that when failure occurs it may be one of m distinct types indexed by $j \in \{1, 2, \dots, m\}$, and we let J be a random variable representing the type of failure. We also let x be a vector of covariates.

We define the overall hazard rate as

$$\lambda(t, x) = \lim_{dt \rightarrow 0} \frac{\Pr\{t \leq T < t + dt | T \geq t, x\}}{dt}$$

We will also define a cause-specific hazard rate, representing the instantaneous risk of becoming removed by cause j

$$\lambda_j(t, x) = \lim_{dt \rightarrow 0} \frac{\Pr\{t \leq T < t + dt, J = j | T \geq t, x\}}{dt}$$

Which in other words, we have calculated the conditional probability that a subject is removed in the interval $[t, t + dt)$ and the cause of removal is the j^{th} cause, given that the subject was not removed just before time t . The probability is then converted into a rate by the division by dt and then taking the limit as $dt \rightarrow 0$.

By the law of total probability, we have

$$\lambda(t, x) = \sum_{j=1}^m \lambda_j(t, x)$$

because removal must be due to one (and only one) of the m causes.

The overall survival function can be defined as

$$S(t, x) = e^{-\lambda(t, x)}$$

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and the function $S(t, x)$ has a clear meaning as the probability of surviving all types of failure up to time t .

The competing risk concepts provide a basic framework for our multiple competing cues models. We will alter some of the traditional competing risks terminology to better clarify its purpose in this animal population estimation setting. While the following is a basic reinterpretation of terminology, it may be expanded to the forthcoming developed models. To begin, a failure or removal in the traditional definition can be viewed as the *animal's first detection*, due to the fact that once it is detected in the time of first detection methodology the animal has no further detection history information. The type of failure is redefined as the specific cue, either aural or visual, which compete for the observers' detection. Then the cause-specific hazard rates are also specific to the types of cues competing for the observers' first detection are now termed the *aural or visual hazard rates*. The survival function is then the probability an animal is not detected, as a survival is a non-failure (non-detection).

Usually the assumption is made that all such risks are independent in estimation of the survival function (survival probability). However, if the competing risks are not independent, then there is generally no known acceptable way to estimate the survival function. There has been considerable work done towards this problem of dependent competing risks, starting with the early observation by Cox (1959), that there was a difficulty in the interpretation of bivariate data in the competing risk context. Tsiatis (1975) proved a non-identifiability theorem which concluded that a dependent risk model is indistinguishable from some specific independent risk model and that any analysis of data should be a careful analysis of biological circumstances.

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Peterson (1976) argued that serious errors can be made in estimating the survival function in the competing risk problem because one can never know from the data whether the competing risks are independent or not. Crowder (1991) elaborates on the non-identifiability when information on the pair, T and the marginal distribution of the independent risk is known. He shows that even when such additional information on the independent risk is known, by possible means of controlled experimental situations, that the joint survival function of the independent and dependent risks is still not identifiable. Slud (1992) shows how the marginal distribution of survival time T can be nonparametrically identifiable when only the data (T, x) are observed, where x is an observed covariate such that the competing risk event time and x are conditionally independent given T .

Therefore, due to non-identifiability complications regarding dependent competing risks we focus on independent competing risks when constructing our models. While this assumption may not be realistic in practice it is possible to refine observer techniques to avoid potential violations of the independence assumption. In addition, creation of a potential proxy independent competing risks model in the spirit of Tsiatis (1975), which would mimic the dependence relationship is another possible course of action.

The purpose of this paper is to develop several modeling approaches allowing for competing cues in estimation of population size and components of the competing cues, aural and visual, and then study these models through simulation. In Section 3.2, we focus on the development of the independent competing cues models starting with a basic time to first detection approach, which categorizes detection in a tradition point

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count region as an aural or visual detection. We then examine a combined dependent multiple-observer and time to first detection approach in Section 3.3, which along with detection cue categorization provides for multiple observers during the duration of the point count. Next in Section 3.4, we undertake modeling for the case where we make allowances for visual cue limitations and for deterioration or improvement of aural cues in a 2-region approach. In the subsequent section, we extend this concept to allow for further degradation of aural cues in a r -region approach. Finally, we investigate advantages and disadvantages of the competing cue modeling versus the more conventional pooled cue modeling with evaluation through simulation. After the detailed explanation of our research methods and our results, we focus on the implications and importance of our work to field ornithologists designing point count studies and suggest possibilities for future research.

3.2 Independent Cues Model

We begin by assuming that there are two cue types, V (visual) and A (aural), which compete for an observers attention. Further each detection is categorized as a V or A type detection. We can define an instantaneous rate for visual cues resulting in a detection of V and the corresponding instantaneous rate for an aural cue of A . If we assume that we have t intervals of equal unit length then the probability of an animal not being detected during a time period is:

$$1 - p = e^{-(V+A)}$$

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and the probability of an animal not being detected during the entire point count being:

$$p_0(t) = (1 - p)^t = (e^{-(V+A)})^t = e^{-t(V+A)}$$

Therefore the probability of detection from either cue during a time period is:

$$p = 1 - e^{-(V+A)}$$

The probability of detection visually (aurally) in the first interval is:

$$p_V(1) = \{V/(V + A)\} [1 - e^{-(V+A)}]$$

$$p_A(1) = \{A/(V + A)\} [1 - e^{-(V+A)}]$$

Similarly the probabilities of first being detected visually (aurally) in the second interval is:

$$p_V(2) = e^{-(V+A)} \{V/(V + A)\} [1 - e^{-(V+A)}]$$

$$p_A(2) = e^{-(V+A)} \{A/(V + A)\} [1 - e^{-(V+A)}]$$

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Therefore for first detection in the t^{th} interval the probabilities are:

$$\begin{aligned}
 p_V(t) &= \{e^{-(V+A)}\}^{t-1} \{V/(V+A)\} [1 - e^{-(V+A)}] \\
 &= e^{-(t-1)(V+A)} \{V/(V+A)\} [1 - e^{-(V+A)}] \\
 p_A(t) &= \{e^{-(V+A)}\}^{t-1} \{A/(V+A)\} [1 - e^{-(V+A)}] \\
 &= e^{-(t-1)(V+A)} \{A/(V+A)\} [1 - e^{-(V+A)}]
 \end{aligned}$$

Thus the likelihood is multinomial based on these cell probabilities, and the cell probability for undetected animals. Consider t time intervals where the birds are tracked throughout the count, then based on the information obtained from the detection histories where $n_{h,i}$, for $h \in \{A, V\}$ and $i = 1, 2, \dots, t$ represents the number of birds detected in the i^{th} time period by cue type h , which gives the likelihood:

$$\begin{aligned}
 L(N; A, V) &= \frac{N!}{n_{A,1}! \dots n_{A,t}!(N-n)!} \{p_A(1)^{n_{A,1}} \dots p_A(t)^{n_{A,t}}\} \\
 &\quad \times \frac{1}{n_{V,1}! \dots n_{V,t}!} \{p_V(1)^{n_{V,1}} \dots p_V(t)^{n_{V,t}}\} p_\emptyset(t)^{N-n} \quad (3.1)
 \end{aligned}$$

where $n = \sum_{h \in \{A, V\}} \sum_{i=1}^t n_{h,i}$ denotes the total number of detected birds of a species, p_h represents the multinomial cell probabilities which are known functions of t , and $p_\emptyset(t) = 1 - \sum_{h \in \{A, V\}} \sum_{i=1}^t p_{h,i}$, the probability that a bird goes undetected aurally or visually through the duration of the point count.

Model assumptions are as follows:

1. There is no change in the population of birds within the detection radius during the point count (i.e., the population is closed and birds do not move in or out

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without being detected);

2. there is no double counting of individuals (i.e. the observer keeps track of individual birds without error);
3. all individual birds of a species have a constant per minute probability of being detected in each interval;
4. observers accurately assign birds to within the fixed radius circle; and
5. observers accurately determine the type of detection once a bird is first detected.

These assumptions are not trivial because movement of individuals within the area during the count may cause violations of assumption 1. This should be less of a problem for small breeding songbirds, like Wood Warblers (*Phylloscopus sibilatrix*), with their relatively small breeding territories but is more likely to be violated with larger ranging species like Pileated Woodpecker (*Dryocopus pileatus*) and Bar-tailed Godwit (*Limosa lapponica*). However, this assumption is less likely to be violated for point counts of shorter duration, provided the point count is divided into shorter intervals.

The somewhat long duration of the point counts may lead to violation of assumption 2. However, if observers are trained to be conservative in their counting and even if counting errors may exist, they are not unique to this method. Furthermore, very little is known about the variability of singing rates in individual birds (assumption 3), but it seems apparent that it may be influenced by a wide array of factors (Gibbs and Wenny 1993). In addition, the incorporation of visual detectability may lessen the potential factors for violations of assumption 3.

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In order to estimate the population size or density, some measure of area sampled is necessary. Movement in or out of the area that is not detected may cause violations of assumption 4, and difficulty in assigning distance of birds located aurally may also cause violations of the assumption. Again, this assumption is also required for distance sampling and many other methods of density estimation. In addition to this time till first detection model assumptions, the assumption that observers accurately determine the type of detection is necessary for this method. While dependency of cues are likely to exist, focusing on a first detection will likely minimize potential problems, as the dependency between visual and aural cues is likely to compound over subsequent detections. Riddle (personal communication) found that it is quite common for highly skilled and experience observers to keep a record of the type of detection, therefore the added effort to record the different detections is meager.

The method has been described here, with it's likelihood in Equation 3.1. Estimation can be undertaken by numerical methods as we have shown earlier in Section 2.3. This allows for joint estimation of the population size, N , the rate of aural cues, the rate of visual cues, and thus, the overall probability of detection.

3.3 Combined Dependent Double-Observer and Independent Cues Model

A possible extension of the multiple cue model development is to consider incorporating it into the combined dependent double-observer and time-of-first-detection approach. Model structure is important for these model types, we consider effects due to observer,

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time and potentially heterogeneity of individuals. Possible models are similar to those mentioned in Section 2.2.1, however effects now may have specific impact on visual detection and/or aural detection.

Again borrowing from the competing risks literature (Crowder 2001) we can define an instantaneous rate for visual cues resulting in a detection of V and the corresponding instantaneous rate for an aural cue of A . We will assume a M_o model structure, as a simple M_0 in this setting is equivalent to a basic independent cues model from Section 3.2. If we assume that we have t intervals of equal unit length with two dependent observers then the probability of an animal not being detected by the primary and secondary observers (denoted with p and s subscripts respectively) during a time period is:

$$1 - p_p = e^{-(V_p + A_p)}$$
$$1 - p_s = e^{-(V_s + A_s)}$$

and the probability of an animal not being detected during the entire point count being:

$$p_\phi(t) = \{(1 - p_p)(1 - p_s)\}^t = \left(e^{-(V_p + A_p + V_s + A_s)}\right)^t = e^{-t(V_p + A_p + V_s + A_s)}$$

Therefore the probability of detection from either cue during a time period is:

$$p_p = 1 - e^{-(V_p + A_p)}$$
$$p_s = 1 - e^{-(V_s + A_s)}$$

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The probability of detection visually (aurally) in the first interval by the primary observer is:

$$p_{V_p}(1) = \{V_p/(V_p + A_p)\} [1 - e^{-(V_p+A_p)}]$$
$$p_{A_p}(1) = \{A_p/(V_p + A_p)\} [1 - e^{-(V_p+A_p)}]$$

and for the secondary observer:

$$p_{V_s}(1) = \{V_s/(V_s + A_s)\} [1 - e^{-(V_s+A_s)}] e^{-(V_p+A_p)}$$
$$p_{A_s}(1) = \{A_s/(V_s + A_s)\} [1 - e^{-(V_s+A_s)}] e^{-(V_p+A_p)}$$

The probability of detection visually (aurally) in the second interval by the primary observer is:

$$p_{V_p}(2) = \{V_p/(V_p + A_p)\} [1 - e^{-(V_p+A_p)}] e^{-(V_p+A_p)} e^{-(V_s+A_s)}$$
$$p_{A_p}(2) = \{A_p/(V_p + A_p)\} [1 - e^{-(V_p+A_p)}] e^{-(V_p+A_p)} e^{-(V_s+A_s)}$$

and for the secondary observer:

$$p_{V_s}(2) = \{V_s/(V_s + A_s)\} [1 - e^{-(V_s+A_s)}] e^{-(V_p+A_p)^2} e^{-(V_s+A_s)}$$
$$p_{A_s}(2) = \{A_s/(V_s + A_s)\} [1 - e^{-(V_s+A_s)}] e^{-(V_p+A_p)^2} e^{-(V_s+A_s)}$$

Similarly, as before, for first detection in the t^{th} interval the probabilities for the primary

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observer are:

$$\begin{aligned}
 p_{V_p}(t) &= \{V_p/(V_p + A_p)\} [1 - e^{-(V_p+A_p)}] e^{-(V_p+A_p)^{t-1}} e^{-(V_s+A_s)^{t-1}} \\
 &= \{V_p/(V_p + A_p)\} [1 - e^{-(V_p+A_p)}] e^{-(t-1)\{V_p+A_p+V_s+A_s\}} \\
 p_{A_p}(t) &= \{A_p/(V_p + A_p)\} [1 - e^{-(V_p+A_p)}] e^{-(V_p+A_p)^{t-1}} e^{-(V_s+A_s)^{t-1}} \\
 &= \{A_p/(V_p + A_p)\} [1 - e^{-(V_p+A_p)}] e^{-(t-1)\{V_p+A_p+V_s+A_s\}}
 \end{aligned}$$

then for the secondary observer:

$$\begin{aligned}
 p_{V_s}(t) &= \{V_s/(V_s + A_s)\} [1 - e^{-(V_s+A_s)}] e^{-(V_p+A_p)^t} e^{-(V_s+A_s)^{t-1}} \\
 &= \{V_s/(V_s + A_s)\} [1 - e^{-(V_s+A_s)}] e^{-(t-1)\{V_p+A_p+V_s+A_s\}+\{V_p+A_p\}} \\
 p_{A_s}(t) &= \{A_s/(V_s + A_s)\} [1 - e^{-(V_s+A_s)}] e^{-(V_p+A_p)^t} e^{-(V_s+A_s)^{t-1}} \\
 &= \{A_s/(V_s + A_s)\} [1 - e^{-(V_s+A_s)}] e^{-(t-1)\{V_p+A_p+V_s+A_s\}+\{V_p+A_p\}}
 \end{aligned}$$

Thus the likelihood is multinomial based on these cell probabilities when each observer takes their turn fulfilling the primary observer role. Consider t time intervals where the birds are tracked throughout the count, then based on the information obtained from the detection histories where $n_{h,i}$, for $h \in \{A_p, V_p, A_s, V_s\}$ and $i = 1, 2, \dots, t$ represents the number of birds detected in the i^{th} time period by cue type h , which

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gives the likelihood:

$$L(N; A_p, V_p, A_s, V_s) = \frac{N!}{\prod_{i=1}^t n_{A_p,i}! \prod_{i=1}^t n_{V_p,i}! (N-n)!} \left\{ \prod_{i=1}^t p_{A_p}(i)^{n_{A_p,i}} \prod_{i=1}^t p_{V_p}(i)^{n_{V_p,i}} \right\} \\ \times \frac{1}{\prod_{i=1}^t n_{A_s,i}! \prod_{i=1}^t n_{V_s,i}!} \left\{ \prod_{i=1}^t p_{A_s}(i)^{n_{A_s,i}} \prod_{i=1}^t p_{V_s}(i)^{n_{V_s,i}} \right\} p_\phi(t)^{N-n} \quad (3.2)$$

where $n = \sum_h \sum_{i=1}^t n_{h,i}$ denotes the total number of detected birds of a species, p_h represents the multinomial cell probabilities which are known functions of t , and $p_\phi(t) = 1 - \sum_h \sum_{i=1}^t p_{h,i}$, the probability that a bird goes undetected through the duration of the point count.

The model assumptions of the combined multiple-observer and independent cues approach are as follows:

1. Observers are able to accurately decide if a detection is made by the primary or secondary observer;
2. there are equal detection probabilities of all individual birds of each species for each observer;
3. the population is closed and there is no undetected movement out of the sampled area;
4. observers accurately assign birds to within or beyond the radius used for the sampling area;
5. the detection probability is the same irrespective of whether an observer is in the primary or secondary role; and

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6. observers accurately determine the type of detection once a bird is first detected.

As with the independent cues and dependent double observer methods before them, these assumptions are not trivial because movement of individuals within the area during the count may again cause violations of assumption 1, but to less of a degree. It is presumed that variability of singing rates in individual birds (assumption 2) exists and can be impacted by many factors (Gibbs and Wenny 1993). Once again, movement in or out of the area that is not detected may cause violations of assumption 3, and difficulty in assigning distance of birds located aurally may cause violations of assumption 4. In addition, observers may be more likely to detect birds given the authority of their role as primary observer, or may be more (or less) likely to detect birds in their role as secondary observer, depending on the individual (assumption 5). Some secondary observers may become increasingly likely to detect birds, more actively attempting to find birds that the primary observer may miss, thus increasing their probability of detection. While other observers may turn lethargic in the role as the secondary observer, and consequently, decrease their probability of detection. Identifying the type of detection is necessary (assumption 6), but with experienced observers and a “heads-up” approach to distinguish bird detections types, this assumption can be implemented successfully. Once again, these assumptions are also required for distance sampling and many other methods of density estimation.

The dependent-observers aspect in this setting is viewed in the removal model foundation developed by Cook and Jacobson (1979), as it may work in conjunction with the time-to-first-detection removal process presented here. While we have combined dependent-observers with the simple independent cues model from Section 3.2, it is

possible to apply this aspect to the forthcoming models.

3.4 Independent Cues Model Allowing for Visual Limitations

In this modeling approach, we draw upon the initial work of independent cues in Section 3.2 and divide the point count sampling area into two regions. Here we examine a circular sampling area with a circular inner region. Motivation for this approach lies with the fact that the visual cue detection may have a range of effectiveness much less than that for aural cues. Therefore, detection via independent cues, aurally and visually, might be possible in the inner region with radius R_1 ; while in the outer region

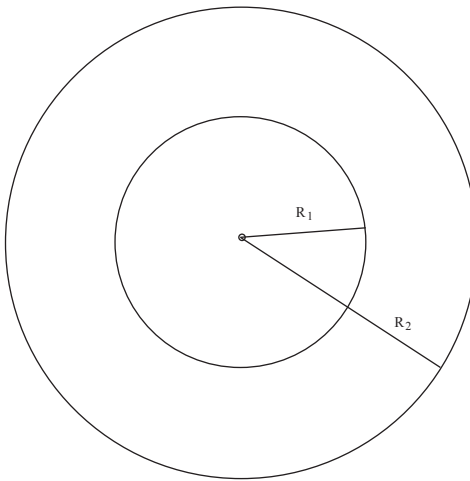


Figure 3.1: *Potential sampling area for avian point counts for Independent Cues Allowing for Visual Limitations Model.*

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between radii R_1 and R_2 an observer focuses only on aural detection. We present the possibility for only aural detection in the outer region, however, it make be useful in the case of soaring birds with strong visual presence, such as California Condor (*Gymnogyps californianus*) and the Northern Goshawk (*Accipiter gentilis*), to allow for visual cues only in the outer region.

We begin by assuming that there are multiple cue types V (visual) and A_1 (aural) which compete for an observers attention within the inner sampling region. Furthermore, each detection in the inner region is categorized as a visual or aural type detection. Therefore we can define an instantaneous rate for visual cues resulting in a detection of V and the corresponding instantaneous rate for an aural cue of A_1 as before. If we assume that we have t intervals of equal unit length then the probability of an animals not being detected in the inner region is:

$$1 - p_I = e^{-(V+A_1)}$$

with therefore the probability of detection from either cue being:

$$p_I = 1 - e^{-(V+A_1)}$$

Similarly for the outer sampling region we can define an instantaneous rate for aural cues, A_2 , then the probability of an animals not being detected in the outer region is:

$$1 - p_O = e^{-A_2}$$

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with the probability of detection from aural cues being:

$$p_O = 1 - e^{-A_2}$$

From earlier model development, we see the probability of detection aurally in the t^{th} interval in the inner region, $0 \leq d < R_1$ is:

$$\begin{aligned} p_{A_1}(t) &= \frac{A_1}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{\text{Area of Inner Region}}{\text{Area of Total Region}} \\ &= \frac{A_1}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{\pi R_1^2}{\pi R_2^2} \\ &= \frac{A_1}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{R_1^2}{R_2^2} \end{aligned}$$

Similarly, the probability of detection visually in the t^{th} interval in the inner region, $0 \leq d < R_1$ is:

$$\begin{aligned} p_V(t) &= \frac{V}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{\text{Area of Inner Region}}{\text{Area of Total Region}} \\ &= \frac{V}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{\pi R_1^2}{\pi R_2^2} \\ &= \frac{V}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{R_1^2}{R_2^2} \end{aligned}$$

Then the probability of detection aurally in the t^{th} interval in the outer region, $R_1 <$

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$d < R_2$ defined as:

$$\begin{aligned}
 p_{A_2}(t) &= (1 - e^{-A_2}) e^{-(t-1)*A_2} \times \frac{\text{Area of Outer Region}}{\text{Area of Total Region}} \\
 &= (1 - e^{-A_2}) e^{-(t-1)*A_2} \times \frac{\pi R_2^2 - \pi R_1^2}{\pi R_2^2} \\
 &= (1 - e^{-A_2}) e^{-(t-1)*A_2} \times \left(1 - \frac{R_1^2}{R_2^2}\right)
 \end{aligned}$$

Finally, the probability of an animal going undetected during the entire point count (t time intervals) being:

$$\begin{aligned}
 p_\phi(t) &= e^{-t(A_1+V)} \times \frac{\pi R_1^2}{\pi R_2^2} + e^{-tA_2} \times \frac{\pi R_2^2 - \pi R_1^2}{\pi R_2^2} \\
 &= e^{-t(A_1+V)} \times \frac{R_1^2}{R_2^2} + e^{-tA_2} \times \left(1 - \frac{R_1^2}{R_2^2}\right)
 \end{aligned}$$

Thus the likelihood is multinomial based on these cell probabilities, and the undetected occurrence. Consider t time intervals where the birds are tracked throughout the count, then based on the information obtained from the detection histories where $n_{h,i}$, for $h \in \{V, A_1, A_2\}$ and $i = 1, 2, \dots, t$ represents the number of birds detected in the i^{th} time period by cue type h , which gives the likelihood:

$$\begin{aligned}
 L(N; V, A_1, A_2) &= \frac{N!}{\prod_{i=1}^t n_{A_1,i}! \prod_{i=1}^t n_{V,i}! (N-n)!} \underbrace{\prod_{i=1}^t p_{A_1}(i)^{n_{A_1,i}} \prod_{i=1}^t p_V(i)^{n_{V,i}}}_{\text{Inner Region Cells}} \\
 &\quad \times \frac{1}{\prod_{i=1}^t n_{A_2,i}!} \underbrace{\prod_{i=1}^t p_{A_2}(i)^{n_{A_2,i}}}_{\text{Outer Region Cells}} p_\phi(t)^{N-n} \quad (3.3)
 \end{aligned}$$

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where $n = \sum_h \sum_{i=1}^t n_{h,i}$ denotes the total number of detected birds of a species, p_h represents the multinomial cell probabilities which are known functions of t , and $p_o(t) = 1 - \sum_h \sum_{i=1}^t p_{h,i}$, the probability that a bird goes undetected through the duration of the point count.

Model assumptions are as follows:

1. There is no change in the population of birds within the detection radius during the point count (i.e., the population is closed and birds do not move in or out without being detected);
2. there is no double counting of individuals (i.e. the observer keeps track of individual birds without error);
3. all individual birds of a species have a constant per minute probability of being detected in each interval;
4. observers accurately assign birds to within the inner or outer regions of the sampling region circle; and
5. observers accurately determine the type of detection once a bird is first detected.

These assumptions are similar to those from the simple independent cues model presented in Section 3.2, and are not trivial because movement of individuals within the area during the count may cause violations of assumption 1. Again, this assumption is less likely to be violated for point counts of shorter duration, provided the point count is divided into shorter intervals.

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The somewhat long duration of the point counts may lead to violation of assumption 2. However, if observers are trained to be conservative in their counting and even if counting errors may exist, they are not unique to this method. Furthermore, very little is known about the variability of singing rates in individual birds (assumption 3), but it seems apparent that it may be influenced by a wide array of factors (Gibbs and Wenny 1993). In addition, the incorporation of visual detectability may lessen the potential factors for violations of assumption 3.

In order to estimate the population size or density, some measure of area sampled is necessary. Movement in or out of the area that is not detected may cause violations of assumption 4, and difficulty in assigning distance of birds located aurally may also cause violations of the assumption. Again, this assumption is also required for distance sampling and many other methods of density estimation. In addition to this time till first detection model assumptions, the assumption that observers accurately determine the type of detection is necessary for this method. While dependency of cues are likely to exist, focusing on a first detection will likely minimize potential problems, as the dependency between visual and aural cues is likely to compound over subsequent detections. Riddle (personal communication) found that it is quite common for highly skilled and experienced observers to keep a record of the type of detection, therefore the added effort to record the different detections is meager.

3.5 Independent Cues Model Allowing for Aural Cue Rate Decay

In this modeling approach, we draw upon the initial work of independent cues in Section 3.4 and divide the point count sampling area further in into r regions. Again we examine a circular sampling area with a circular inner region and additional ring regions. Motivation for this approach stems from the 2-ring approach and for the reason that the visual cue detection may have a range of effectiveness much less than that for aural cues. In addition, by sectioning the outer sampling region from the 2-ring approach, we account for the possibility that the aural cue will diminish the further a bird is from the observer. Therefore, detection via independent cues, aurally and visually, might be possible in the inner region with radius R_1 ; while in the outer regions an observer focuses only on aural detection. Again also, while we present the possibility for only aural detection in the outer region, however, it make be useful in the case of soaring birds with strong visual presence. Furthermore, while we do not present it here, it would be possible to allow for an extension of visual cues farther out into the detection region, and allow for their diminishment as well, but not on the same rate that of the aural cues.

As before, we assume that there are multiple cue types V (visual) and A_1 (aural) which compete for an observers attention within the inner sampling region. Furthermore, each detection in the inner region is categorized as a visual or aural type detection. Therefore we can define an instantaneous rate for visual cues resulting in a detection of V and the corresponding instantaneous rate for an aural cue of A_1 as

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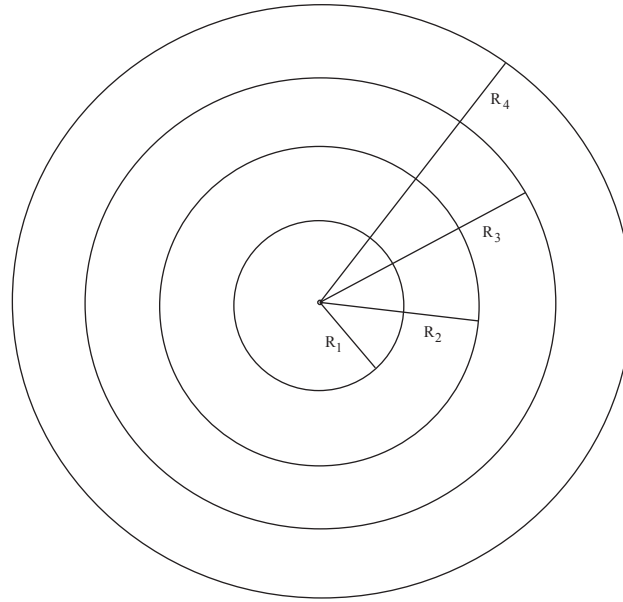


Figure 3.2: *Potential sampling area for avian point counts for Independent Cues Allowing for Aural Cue Rate Decay Model.*

before. If we assume that we have t intervals of equal unit length and $r = 4$ rings creating the sampling regions, then the probability of an animal not being detected in the inner region is:

$$1 - p_I = e^{-(V+A_1)}$$

with therefore the probability of detection from either cue being:

$$p_I = 1 - e^{-(V+A_1)}$$

Similarly for the outer sampling regions we can define an instantaneous rate for aural

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cues, A_j , then the probability of an animal not being detected in the j^{th} region is:

$$1 - p_{O_j} = e^{-A_j}$$

with the probability of detection from aural cues being:

$$p_{O_j} = 1 - e^{-A_j}$$

where

$$A_i = A_1 e^{\sigma \frac{\text{Midpoint Distance of } j^{th} \text{ Region}}{\text{Midpoint Distance of } r^{th} \text{ Region}}}, \quad \text{for } j = 2, \dots, r$$

with the j^{th} region defined by the ring created by the circles of radii R_j and R_{j-1} , and σ , a scale parameter.

Just as with previous model development, we see the probability of detection aurally in the t^{th} interval in the inner region, $0 \leq d < R_1$ is:

$$\begin{aligned} p_{A_1}(t) &= \frac{A_1}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{\text{Area of Inner Region}}{\text{Area of Total Region}} \\ &= \frac{A_1}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{\pi R_1^2}{\pi R_2^2} \\ &= \frac{A_1}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{R_1^2}{R_2^2} \end{aligned}$$

Similarly, the probability of detection visually in the t^{th} interval in the inner region,

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$0 \leq d < R_1$ is:

$$\begin{aligned}
 p_V(t) &= \frac{V}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{\text{Area of Inner Region}}{\text{Area of Total Region}} \\
 &= \frac{V}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{\pi R_1^2}{\pi R_r^2} \\
 &= \frac{V}{A_1 + V} \{1 - e^{-(A_1+V)}\} e^{-(t-1)*(A_1+V)} \times \frac{R_1^2}{R_r^2}
 \end{aligned}$$

Then the probability of detection aurally in the t^{th} interval in the j^{th} region, $R_{j-1} < d < R_j$ defined as:

$$\begin{aligned}
 p_{A_j}(t) &= (1 - e^{-A_j}) e^{-(t-1)*A_j} \times \frac{\text{Area of } j^{\text{th}} \text{ Region}}{\text{Area of Total Region}} \\
 &= (1 - e^{-A_j}) e^{-(t-1)*A_j} \times \frac{\pi R_j^2 - \pi R_{j-1}^2}{\pi R_r^2}
 \end{aligned}$$

Finally, the probability of an animal going undetected during the entire point count (t time intervals) being:

$$p_\emptyset(t) = e^{-t(A_1+V)} \times \frac{\pi R_1^2}{\pi R_r^2} + \prod_{j=2}^r e^{-tA_j} \times \frac{\pi R_j^2 - \pi R_{j-1}^2}{\pi R_r^2} \quad (3.4)$$

Thus the likelihood is multinomial based on these cell probabilities, and the undetected occurrence. Consider t time intervals where the birds are tracked throughout the count, then based on the information obtained from the detection histories where $n_{h,i}$, for $h \in \{V, A_1, A_2, \dots, A_r\}$ and $i = 1, 2, \dots, t$ represents the number of birds detected

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in the i^{th} time period by cue type h , which gives the likelihood:

$$L(N; V, A_1, A_2, \dots, A_r) = \frac{N!}{\prod_{i=1}^t n_{A_1,i}! \prod_{i=1}^t n_{V,i}! (N-n)!} \underbrace{\prod_{i=1}^t p_{A_1}(i)^{n_{A_1,i}} \prod_{i=1}^t p_V(i)^{n_{V,i}}}_{\text{Inner Region Cells}} \times \prod_{j=2}^r \underbrace{\frac{1}{\prod_{i=1}^t n_{A_j,i}!} \prod_{i=1}^t p_{A_j}(i)^{n_{A_j,i}}}_{\text{Outer Region Cells}} p_\phi(t)^{N-n} \quad (3.5)$$

where $n = \sum_h \sum_{i=1}^t n_{h,i}$ denotes the total number of detected birds of a species, p_h represents the multinomial cell probabilities which are known functions of t , and $p_\phi(t) = 1 - \sum_h \sum_{i=1}^t p_{h,i}$, the probability that a bird goes undetected through the duration of the point count.

Model assumptions are as follows:

1. There is no change in the population of birds within the detection radius during the point count (i.e., the population is closed and birds do not move in or out without being detected);
2. there is no double counting of individuals (i.e. the observer keeps track of individual birds without error);
3. all individual birds of a species have a constant per minute probability of being detected in each interval;
4. observers accurately assign birds to within the inner or outer regions of the sampling region circle; and
5. observers accurately determine the type of detection once a bird is first detected.

These assumptions are similar to those from the simple independent cues model presented in Section 3.4, and are not trivial, especially assumption 4. However, we are confident that highly skilled and experienced observers will become accustomed to these new survey methods. Also as noted previously, it is quite common for observers to keep a record of the type of detection, therefore the added effort to record the different detections proposed is meager and promotes a more “heads-up” survey method.

3.6 Simulation Studies

To evaluate our methods, simulation studies were carried out to investigate their accuracy and precision. As the models developed in this chapter are similar in structure, we will examine the last and most complex model, the independent cues model which allows for aural cue rate decay. Then in Section 3.6.2, we make a comparison of the multiple cue model in a aural decay 4-ring setting versus a more traditional pooled cue setting. We will examine a comparison of the estimates of the population size, N , and the probability of detection, p_d , along with their standard errors and root mean square

3.6.1 Model Evaluation

Simulations were conducted for a variety of settings, we examine the independent cues model which allows for aural cue rate decay, with $r = 4$ rings. Several constants through the course of these simulations are: the radii distances ($R_1 = 50, R_2 = 100, R_3 = 150, R_4 = 200$), the scale parameter, $\sigma = 2/3$ and $t = 4$ time periods. We then examine the following parameter combinations

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$$\begin{array}{c} N \\ \left(\begin{array}{c} 500 \\ 1000 \end{array} \right) \end{array} \times \begin{array}{c} \text{Probability Components} \\ \left(\begin{array}{c} V = 0.35, A_0 = 0.75 \\ V = 0.75, A_0 = 0.35 \\ V = 0.35, A_0 = 0.35 \end{array} \right) \end{array}$$

and conducted simulations of our multiple cue method. For each combination, we performed 100 bootstrap replications on 100 randomly generated data sets which each consisted of generating N detection histories (based on the parameters above). These probability components represent settings where a bird has a high singing rate and a low rate of visual availability, a low singing rate and a high rate of visual availability and low singing rate and a low rate of visual availability. In each of the randomly generated 100 data sets, we then bootstrap resampled each data set 100 times. From these, we computed the conditional maximum likelihood estimates $(\hat{N}_c, \hat{\theta}_c)$ of (N, θ) , the two-step estimators. Then with each 100 bootstrap replications for each of the randomly generated data sets, we computed the estimated standard errors of \hat{N}_c and of the probability components of $\hat{\theta}_c$.

In Table 3.1, we report the mean estimates of the population size, N , and the cue rate components of θ , taken over all 10,000 estimates, along with their precision. Also reported are the mean standard error estimates for each component of the aural cue rate decay model, taken over the 100 bootstrap two-step variance estimation method estimates, along with their precision. For each set of simulations grouped by population size N , as one might expect, the standard error estimates of the population size estimates are quite large in the models which have low rates of both aural and visual cues. These low cue rates correspond to a very difficult to detect setting for the observer, which attributes to the higher standard error of the population size estimate.

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Table 3.1: *Simulation Study of Independent Cues Model Allowing for Aural Cue Rate Decay for 100 data sets each with 100 bootstrap samples.*

Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates
N	500	508.48 (0.9831)	68.943 (3.2570)
V	0.35	0.3612 (1.699×10^{-3})	0.1260 (3.550×10^{-3})
A_0	0.35	0.3407 (1.155×10^{-3})	0.0808 (1.653×10^{-3})
σ	2/3	0.6245 (3.219×10^{-3})	0.2390 (4.720×10^{-3})
N	500	486.66 (0.2760)	19.277 (0.3953)
V	0.35	0.3822 (1.884×10^{-3})	0.1342 (3.480×10^{-3})
A_0	0.75	0.7428 (1.556×10^{-3})	0.1129 (1.990×10^{-3})
σ	2/3	0.6473 (2.900×10^{-3})	0.2108 (4.740×10^{-3})
N	500	495.95 (0.7480)	52.929 (1.2851)
V	0.75	0.7696 (2.092×10^{-3})	0.1470 (4.341×10^{-3})
A_0	0.35	0.3524 (1.075×10^{-3})	0.0767 (1.639×10^{-3})
σ	2/3	0.6194 (3.221×10^{-3})	0.2358 (5.523×10^{-3})
N	1000	979.49 (1.1402)	81.509 (1.9282)
V	0.35	0.3560 (1.152×10^{-3})	0.0842 (1.624×10^{-3})
A_0	0.35	0.3519 (7.943×10^{-4})	0.0596 (8.598×10^{-4})
σ	2/3	0.6294 (2.598×10^{-3})	0.1849 (2.899×10^{-3})
N	1000	973.28 (0.4063)	27.509 (0.4730)
V	0.35	0.3576 (1.255×10^{-3})	0.0874 (1.987×10^{-3})
A_0	0.75	0.7524 (1.219×10^{-3})	0.0863 (8.937×10^{-4})
σ	2/3	0.6599 (2.193×10^{-3})	0.1649 (2.110×10^{-3})
N	1000	983.50 (1.0865)	73.911 (1.3121)
V	0.75	0.7506 (1.711×10^{-3})	0.1163 (2.124×10^{-3})
A_0	0.35	0.3484 (7.821×10^{-4})	0.0565 (9.063×10^{-4})
σ	2/3	0.6323 (2.534×10^{-3})	0.1882 (3.296×10^{-3})

Secondly, we may draw from the table that the model which has a higher magnitude decaying aural cue rate and a low visual cue rate, has a lower standard error estimate of the population size estimate than that of the model with the lower magnitude decaying aural cue rate and a higher visual cue rate. The lower decaying cue rate will yield even smaller aural cue rates in the outer regions, which in turn may lead to fewer detected animals and an increased standard error.

3.6.2 Model Comparison - Multiple Cues versus Pooled Cues

Motivation for our work with multiple competing cues is to examine potential advantages, as well as potential disadvantages, of this approach compared to the traditional method of pooling cue types. We will take the cases examined in Section 3.6.1 and report analysis of the same data, generated in a multiple cue model framework, alongside it. This pooled cue model has a two parameters: the population size, N , and the pooled cue rate, P , which is found from a weighted calculation similar to that in Equation 3.4.

For each combination, we performed 100 bootstrap replications on 100 randomly generated data sets which each consisted of generating N detection histories (based on the parameters from Section 3.6.1). In each of the randomly generated 100 data sets, for each cue setting, we then bootstrap resampled each data set 100 times. From these, we once again compute the conditional maximum likelihood estimates $(\hat{N}_c, \hat{\theta}_c)$ of (N, θ) , the two-step estimators. Then with each 100 bootstrap replications for each of the randomly generated data sets, we computed the estimated standard errors of \hat{N}_c and of the probability components of $\hat{\theta}_c$. Results which include the multiple cue rates comparatively with the pooled cue rates are presented in Table 3.2.

To accurately compare these two model settings, we then find the probability of detection for each case. For the pooled case, the calculation is simply

$$p_d = 1 - e^{-P}.$$

For the multiple cue setting, the probability of detection is once again found similarly

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Table 3.2: *Simulation Study of Independent Cues Model Allowing for Aural Cue Rate Decay examining cue rates and their estimates compared to pooled time of first detection model for 100 data sets each with 100 bootstrap samples.*

Parameter	True Value	Multiple Cues		Pooled Cues	
		Mean of Estimates	Mean of Std. Error Estimates	Mean of Estimates	Mean of Std. Error Estimates
N	500	508.48 (0.9831)	68.943 (3.2570)	486.82 (2.4665)	114.701 (20.0379)
V	0.35	0.3612 (1.699×10^{-3})	0.1260 (3.550×10^{-3})	–	–
A_0	0.35	0.3407 (1.155×10^{-3})	0.0808 (1.653×10^{-3})	–	–
σ	2/3	0.6245 (3.219)	0.2390 (4.720×10^{-3})	–	–
P	0.2540	–	–	0.2561 (7.504×10^{-4})	0.054 (4.538×10^{-4})
N	500	486.66 (0.2760)	19.277 (0.3953)	474.84 (0.2635)	18.258 (0.4137)
V	0.35	0.3822 (1.884×10^{-3})	0.1342 (3.480×10^{-3})	–	–
A_0	0.75	0.7428 (1.556×10^{-3})	0.1129 (1.990×10^{-3})	–	–
σ	2/3	0.6473 (2.900×10^{-3})	0.2108 (4.740×10^{-3})	–	–
P	0.4943	–	–	0.5041 (6.801×10^{-4})	0.0488 (3.830×10^{-4})
N	500	495.95 (0.7480)	52.929 (1.2851)	447.56 (0.9486)	63.736 (3.7061)
V	0.75	0.7696 (2.092×10^{-3})	0.1470 (4.341×10^{-3})	–	–
A_0	0.35	0.3524 (1.075×10^{-3})	0.0767 (1.639×10^{-3})	–	–
σ	2/3	0.6194 (3.221×10^{-3})	0.2358 (5.523×10^{-3})	–	–
P	0.3040	–	–	0.2875 (7.524×10^{-4})	0.0546 (4.700×10^{-4})
N	1000	979.49 (1.1402)	81.509 (1.9282)	914.44 (1.413)	92.132 (4.4044)
V	0.35	0.3560 (1.152×10^{-3})	0.0842 (1.624×10^{-3})	–	–
A_0	0.35	0.3519 (7.943×10^{-4})	0.0596 (8.598×10^{-4})	–	–
σ	2/3	0.6294 (2.598×10^{-3})	0.1849 (2.899×10^{-3})	–	–
P	0.2540	–	–	0.2636 (5.325×10^{-4})	0.0379 (3.058×10^{-4})
N	1000	973.28 (0.4063)	27.509 (0.4730)	948.35 (0.3817)	25.484 (0.4043)
V	0.35	0.3576 (1.255×10^{-3})	0.0874 (1.987×10^{-3})	–	–
A_0	0.75	0.7524 (1.219×10^{-3})	0.0863 (8.937×10^{-4})	–	–
σ	2/3	0.6599 (2.193×10^{-3})	0.1649 (2.110×10^{-3})	–	–
P	0.4943	–	–	0.4993 (4.924×10^{-4})	0.0343 (2.327×10^{-4})
N	1000	983.50 (1.0865)	73.911 (1.3121)	869.40 (1.029)	73.451 (2.5544)
V	0.75	0.7506 (1.711×10^{-3})	0.1163 (2.124×10^{-3})	–	–
A_0	0.35	0.3484 (7.821×10^{-4})	0.0565 (9.063×10^{-4})	–	–
σ	2/3	0.6323 (2.534×10^{-3})	0.1882 (3.296×10^{-3})	–	–
P	0.3040	–	–	0.2868 (5.152×10^{-4})	0.0383 (2.836×10^{-4})

as in Equation 3.4.

$$p_d = (1 - e^{-(A_1+V)}) \times \frac{\pi R_1^2}{\pi R_r^2} + \prod_{j=2}^r (1 - e^{-A_j}) \times \frac{\pi R_j^2 - \pi R_{j-1}^2}{\pi R_r^2}$$

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These calculations are carried out for each simulated data set, and from these, we computed the conditional maximum likelihood estimates ($\hat{N}_c, \hat{\theta}_c$) of (N, θ) , the two-step estimators. Then with each 100 bootstrap replications for each of the randomly generated data sets, we computed the estimated standard errors and root mean square errors of \hat{N}_c and of the probability components of $\hat{\theta}_c$.

In Tables 3.3 and 3.4, we report the mean estimates of the population size, N , and the probability of detection, taken over all 10,000 estimates, along with their precision. Also reported are the mean standard error and root mean square error (RMSE) estimates for each component of the models, taken over the 100 bootstrap two-step variance estimation method estimates, along with their precision.

Table 3.3: *Simulation Study of Independent Cues Model Allowing for Aural Cue Rate Decay examining the probability of detection and their estimates compared to pooled time of first detection model for 100 data sets each with 100 bootstrap samples.*

Multiple Cues					
	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
$V = 0.35$	N	500	508.48 (0.9831)	68.943 (3.2570)	90.972 (3.9146)
$A_1 = 0.35$	p_d	0.22	0.2107 (4.700×10^{-4})	0.0331 (4.986×10^{-4})	0.0459 (1.406×10^{-3})
$V = 0.35$	N	500	486.66 (0.2760)	19.277 (0.3953)	29.431 (0.8822)
$A_1 = 0.75$	p_d	0.40	0.3874 (3.855×10^{-4})	0.0278 (2.765×10^{-4})	0.0386 (1.267×10^{-3})
$V = 0.75$	N	500	495.95 (0.7480)	52.929 (1.2851)	71.750 (2.2305)
$A_1 = 0.35$	p_d	0.24	0.2250 (4.042×10^{-4})	0.0284 (4.866×10^{-4})	0.0416 (1.188×10^{-3})

Pooled Cues					
	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
$V = 0.35$	N	500	486.82 (2.4665)	114.701 (20.0379)	143.329 (20.3489)
$A_1 = 0.35$	p_d	0.22	0.2238 (5.809×10^{-4})	0.0418 (3.627×10^{-4})	0.0562 (1.584×10^{-3})
$V = 0.35$	N	500	474.84 (0.2635)	18.258 (0.4137)	34.562 (1.1734)
$A_1 = 0.75$	p_d	0.40	0.3945 (4.110×10^{-4})	0.0297 (2.423×10^{-4})	0.0398 (1.203×10^{-3})
$V = 0.75$	N	500	447.56 (0.9486)	63.736 (3.7061)	102.696 (3.5605)
$A_1 = 0.35$	p_d	0.24	0.2478 (5.644×10^{-4})	0.0410 (3.772×10^{-4})	0.0549 (1.590×10^{-3})

For this group of simulations, it's surprising to see that in this aural cue rate

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Table 3.4: *Simulation Study of Independent Cues Model Allowing for Aural Cue Rate Decay examining the probability of detection and their estimates compared to pooled time of first detection model for 100 data sets each with 100 bootstrap samples.*

Multiple Cues					
	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
$V = 0.35$	N	1000	979.49 (1.1402)	81.509 (1.9282)	111.676 (3.2074)
$A_1 = 0.35$	p_d	0.22	0.2153 (3.219×10^{-4})	0.233 (2.864×10^{-4})	0.0313 (9.311×10^{-4})
$V = 0.35$	N	1000	973.28 (0.4063)	27.509 (0.4730)	46.032 (1.6013)
$A_1 = 0.75$	p_d	0.40	0.3849 (2.822×10^{-4})	0.0199 (1.937×10^{-4})	0.0302 (1.096×10^{-3})
$V = 0.75$	N	1000	983.50 (1.0865)	73.911 (1.3121)	104.977 (3.3537)
$A_1 = 0.35$	p_d	0.24	0.2233 (2.971×10^{-4})	0.0209 (2.616×10^{-4})	0.0324 (1.093×10^{-3})

Pooled Cues					
	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
$V = 0.35$	N	1000	914.44 (1.413)	92.132 (4.4044)	156.551 (5.3828)
$A_1 = 0.35$	p_d	0.22	0.2306 (4.106×10^{-4})	0.0291 (2.445×10^{-4})	0.0405 (1.297×10^{-3})
$V = 0.35$	N	1000	948.35 (0.3817)	25.484 (0.4043)	61.12 (1.9985)
$A_1 = 0.75$	p_d	0.40	0.3923 (2.986×10^{-4})	0.0208 (1.466×10^{-4})	0.0297 (8.764×10^{-4})
$V = 0.75$	N	1000	869.40 (1.029)	73.451 (2.5544)	161.531 (4.0409)
$A_1 = 0.35$	p_d	0.24	0.2484 (3.872×10^{-4})	0.0288 (2.360×10^{-4})	0.0382 (1.099×10^{-3})

decay model setting the multiple competing cue models out perform their pooled cue counterparts. Comparisons are based upon both root mean square error estimates for the population size and for the probability of detection. This favorable outcome may be due to the complex modeling of the cue rates, or perhaps that detection probabilities in these respective cases are moderately low, which may produce poor performance for the pooled cue model.

3.7 Examples

To illustrate the potential of the independent cues model allowing for visual limitations method we use some data collected on one of Jason Riddle’s field experiments. Data

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was collected following roadside survey habitat protocols used by the Breeding Bird Survey, as point counts were along secondary roads randomly selected degree blocks of latitude and longitude. The survey points along a route are 1/2 mile (400 meters) apart and there are 50 point counts in a route. These points counts were broken into four, one and a half-minute intervals, and the observer recorded birds using multi-colored pens to distinguish time intervals. For this illustrative example, we present the results from just one observer and one point count along the survey route.

We focus first on the Northern Cardinal (*Cardinalis cardinalis*), which with previous population size estimate techniques estimated a population of around 115 birds, with a 50 meter inner radius region, and we approximate an outer ring radius of 200 meters. We also present results for the Northern Mockingbird (*Mimus polyglottos*), with previous population size estimates near 80 birds, with a 50 meter inner radius region, and again we approximate an outer ring radius of 200 meters. This outer ring distances are approximate for use in our method, as no outer region radius had been recorded upon data collection. Parameter estimates for the independent cues model allowing for visual limitations are presented in Table 3.5.

Parameter estimates for the Northern Cardinal and Northern Mockingbird population sizes are shown to be in the vicinity of those estimates previously attained. However, these parameter estimates might not be viewed as very precise, this may be due to in part by an unknown outer region radius. Ideally one would set the outer band limit, however this was not done for the real data example presented here. Careful planning and training by observers can lead to more precise estimation of population parameters. In this illustration, as point counts were conducted 1/2 mile (400 meters

Table 3.5: *A comparison of the Northern Cardinal and Northern Mockingbird parameter estimates (standard errors) for an Independent Cues Model Allowing for Visual Limitations (2-ring model). Estimates and standard errors found with $B = 500$ bootstrap samples.*

Parameter	Parameter Estimates	
	Northern Cardinal	Northern Mockingbird
N	119.37 (8.75)	85.85 (16.72)
A_1	0.6582 (0.329)	0.1652 (0.083)
A_2	0.7291 (0.106)	0.6967 (0.252)
V	0.1678 (0.119)	0.6286 (0.155)

apart), we chose a limiting outer region radius to be 200 meters to avoid potential double counting of individuals. This outer radius may be in fact much less, which would increase precision and accuracy of estimates.

3.8 Discussion

The multiple competing cue model framework presented here allows more insight into estimation of heterogeneity features of animal populations. We do not claim that the results in other studies will be as promising as those based on our data. However, through our simulation studies we know the true values of the parameters of interest and are encouraged in their results. We focused mainly on the aural cue rate decay model because of possible implications to adding a distance covariate to the modeling process. However, while using a distance covariate may perhaps be a useful in gaining additional information about the population, in practice it may become difficult in this complex model setting. Extensions to joint species analyses may also be possible. One can think of an observer being bombarded with competing cues from several species

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at once so one could possibly build in competition between species cues especially for sound cues.

While we did not examine initial model incarnations in the multiple cue, we believe there may be use to these simpler models, which in turn may be more accommodating to a distance covariate. Future work may investigate these models as well as expanding the number of cases for simulation to encompass higher detection probability values. However, despite its additional expense and the potential for complex and yet to be studied errors, we encourage field ornithologists to consider use of these multiple cue methods for at least a sub-sample of their points to better understand the detection process in their field studies and potentially obtain better estimates of population abundance and a better understanding of the population make up.

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Appendix

APPENDIX A

Additional Tables

Here we provide additional tables showing the adverse effect of reconciliation time on the combined time-of-detection independent double-observer method.

Table A.1: *Simulation Study of Combined Multiple-Observer and Time-of-Detection Approach allowing for Reconciliation time for M_b model for 100 data sets each with 100 bootstrap samples. For the moderately difficult to detect setting for a population of $N = 500$ birds.*

	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
DDO	N	500	502.03 (0.1584)	10.789 (0.1822)	15.066 (0.542)
	p_a	0.60	0.6000 (2.841×10^{-4})	0.0202 (2.405×10^{-4})	0.0274 (7.636×10^{-4})
	p_d	0.50	0.4984 (5.146×10^{-4})	0.0361 (4.044×10^{-4})	0.0492 (1.553×10^{-3})
	c_d	0.70	0.6984 (4.581×10^{-4})	0.0303 (3.625×10^{-4})	0.0438 (1.404×10^{-3})
IDO (100%)	N	500	500.63 (0.1284)	9.125 (0.1102)	12.330 (0.377)
	p_a	0.60	0.6043 (2.522×10^{-4})	0.0173 (1.349×10^{-4})	0.0243 (8.103×10^{-4})
	p_d	0.50	0.4978 (3.193×10^{-4})	0.0222 (1.977×10^{-4})	0.0308 (9.032×10^{-4})
	c_d	0.70	0.6966 (2.468×10^{-4})	0.0176 (1.270×10^{-4})	0.0238 (7.585×10^{-4})
IDO (90%)	N	500	500.20 (0.1403)	9.678 (0.1232)	13.411 (0.4275)
	p_a	0.60	0.6026 (2.673×10^{-4})	0.0179 (1.485×10^{-4})	0.0257 (8.206×10^{-4})
	p_d	0.50	0.499 (3.355×10^{-4})	0.0232 (1.692×10^{-4})	0.0322 (9.646×10^{-4})
	c_d	0.70	0.6998 (2.566×10^{-4})	0.0188 (1.686×10^{-4})	0.0248 (7.032×10^{-4})
IDO (75%)	N	500	500.870 (0.1413)	10.837 (0.1513)	13.818 (0.3262)
	p_a	0.60	0.6001 (2.622×10^{-4})	0.0196 (1.516×10^{-4})	0.0253 (7.019×10^{-4})
	p_d	0.50	0.5002 (3.706×10^{-4})	0.2057 (2.055×10^{-4})	0.0356 (1.069×10^{-3})
	c_d	0.70	0.7029 (3.086×10^{-4})	0.0205 (2.097×10^{-4})	0.0295 (9.834×10^{-4})
IDO (50%)	N	500	501.12 (0.1701)	13.433 (0.2029)	16.537 (0.4363)
	p_a	0.60	0.6001 (3.567×10^{-4})	0.242 (2.167×10^{-4})	0.0340 (1.115×10^{-3})
	p_d	0.50	0.4993 (4.284×10^{-4})	0.0313 (3.108×10^{-4})	0.0415 (1.124×10^{-3})
	c_d	0.70	0.7025 (3.653×10^{-4})	0.0253 (2.578×10^{-4})	0.0348 (1.172×10^{-3})

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Table A.2: *Simulation Study of Combined Multiple-Observer and Time-of-Detection Approach allowing for Reconciliation time for M_b model for 100 data sets each with 100 bootstrap samples. For the moderately easy to detect setting for a population of $N = 500$ birds.*

	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
DDO	N	500	499.39 (0.0352)	2.387 (0.0306)	3.373 (0.1212)
	p_a	0.75	0.7499 (1.644×10^{-4})	0.0119 (9.492×10^{-5})	0.0158 (4.603×10^{-4})
	p_d	0.70	0.6992 (3.959×10^{-4})	0.0273 (2.736×10^{-4})	0.0380 (1.152×10^{-3})
	c_d	0.85	0.8492 (2.030×10^{-4})	0.0144 (1.294×10^{-4})	0.0194 (6.382×10^{-4})
IDO (100%)	N	500	499.59 (0.0335)	2.278 (0.0287)	3.190 (0.112)
	p_a	0.75	0.7496 (1.552×10^{-4})	0.0111 (8.782×10^{-5})	0.0150 (4.328×10^{-4})
	p_d	0.70	0.7019 (2.827×10^{-4})	0.0177 (1.466×10^{-4})	0.0267 (9.811×10^{-4})
IDO (90%)	N	500	498.90 (0.0352)	2.363 (0.0312)	3.468 (0.1294)
	p_a	0.75	0.7522 (1.715×10^{-4})	0.0118 (9.116×10^{-5})	0.0163 (6.013×10^{-4})
	p_d	0.70	0.7004 (2.524×10^{-4})	0.0186 (1.519×10^{-4})	0.0245 (6.532×10^{-4})
	c_d	0.85	0.8492 (1.321×10^{-4})	0.0100 (7.883×10^{-5})	0.0128 (3.487×10^{-4})
IDO (75%)	N	500	499.072 (0.0370)	2.665 (0.0356)	3.640 (0.1175)
	p_a	0.75	0.7489 (1.908×10^{-4})	0.0129 (8.698×10^{-5})	0.0184 (5.504×10^{-4})
	p_d	0.70	0.6997 (2.827×10^{-4})	0.0204 (1.644×10^{-4})	0.0272 (7.993×10^{-4})
	c_d	0.85	0.8502 (1.512×10^{-4})	0.0108 (9.478×10^{-5})	0.0145 (4.388×10^{-4})
IDO (50%)	N	500	498.934 (0.0417)	3.181 (0.0554)	4.167 (0.1147)
	p_a	0.75	0.7475 (2.275×10^{-4})	0.0159 (1.425×10^{-4})	0.0221 (6.383×10^{-4})
	p_d	0.70	0.7002 (3.584×10^{-4})	0.0248 (2.131×10^{-4})	0.0341 (1.136×10^{-3})
	c_d	0.85	0.8529 (1.804×10^{-4})	0.0133 (1.352×10^{-4})	0.0178 (4.451×10^{-4})

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Table A.3: *Simulation Study of Combined Multiple-Observer and Time-of-Detection Approach allowing for Reconciliation time for M_b model for 100 data sets each with 100 bootstrap samples. For the difficult to detect setting for a population of $N = 1000$ birds.*

	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
DDO	N	1000	1002.09 (0.7996)	54.885 (0.894)	75.843 (2.615)
	p_a	0.30	0.3045 (2.857×10^{-4})	0.0197 (3.235×10^{-4})	0.0275 (9.177×10^{-4})
	p_d	0.50	0.4971 (5.470×10^{-4})	0.0396 (4.027×10^{-4})	0.0531 (1.408×10^{-3})
	c_d	0.60	0.5989 (6.526×10^{-4})	0.0488 (6.672×10^{-4})	0.0627 (1.881×10^{-3})
IDO (100%)	N	1000	1008.84 (0.6434)	44.449 (0.470)	61.391 (2.177)
	p_a	0.30	0.3010 (2.161×10^{-4})	0.0157 (1.611×10^{-4})	0.0208 (6.054×10^{-4})
	p_d	0.50	0.4951 (2.794×10^{-4})	0.0208 (1.610×10^{-4})	0.0275 (7.465×10^{-4})
	c_d	0.60	0.5961 (4.185×10^{-4})	0.0282 (2.663×10^{-4})	0.0403 (1.225×10^{-3})
IDO (90%)	N	1000	999.81 (0.7102)	47.854 (0.6531)	64.877 (2.282)
	p_a	0.30	0.3009 (3.003×10^{-4})	0.0164 (2.716×10^{-4})	0.0263 (7.912×10^{-4})
	p_d	0.50	0.4997 (3.317×10^{-4})	0.0278 (2.997×10^{-4})	0.0332 (9.431×10^{-4})
	c_d	0.60	0.6023 (5.681×10^{-4})	0.0320 (3.305×10^{-4})	0.0467 (1.289×10^{-3})
IDO (75%)	N	1000	1006.28 (0.7344)	49.533 (0.7688)	70.112 (2.763)
	p_a	0.30	0.2993 (3.126×10^{-4})	0.0179 (3.145×10^{-4})	0.0279 (8.705×10^{-4})
	p_d	0.50	0.5019 (4.114×10^{-4})	0.0310 (3.219×10^{-4})	0.0399 (1.091×10^{-3})
	c_d	0.60	0.5968 (6.224×10^{-4})	0.0376 (4.786×10^{-4})	0.0573 (1.672×10^{-3})
IDO (50%)	N	1000	1000.77 (0.7822)	57.892 (0.8437)	79.981(3.282)
	p_a	0.30	0.3011 (3.764×10^{-4})	0.0218 (4.251×10^{-4})	0.0325 (1.127×10^{-3})
	p_d	0.50	0.5036 (6.553×10^{-4})	0.0458 (3.219×10^{-4})	0.0626 (1.091×10^{-3})
	c_d	0.60	0.5952 (7.114×10^{-4})	0.0443 (6.129×10^{-4})	0.0598 (2.012×10^{-3})

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Table A.4: *Simulation Study of Combined Multiple-Observer and Time-of-Detection Approach allowing for Reconciliation time for M_b model for 100 data sets each with 100 bootstrap samples. For the moderately difficult to detect setting for a population of $N = 1000$ birds.*

	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
DDO	N	1000	998.66 (0.2508)	15.932 (0.1818)	20.005 (0.627)
	p_a	0.60	0.5954 (1.979×10^{-4})	0.0132 (1.229×10^{-4})	0.0194 (6.154×10^{-4})
	p_d	0.50	0.5030 (3.809×10^{-4})	0.0264 (2.458×10^{-4})	0.0338 (8.168×10^{-4})
	c_d	0.70	0.6997 (3.414×10^{-4})	0.0234 (2.456×10^{-4})	0.0297 (1.007×10^{-3})
IDO (100%)	N	1000	1001.382 (0.1912)	13.073 (0.1352)	18.338 (0.577)
	p_a	0.60	0.6011 (1.694×10^{-4})	0.0121 (9.130×10^{-5})	0.0163 (5.004×10^{-4})
	p_d	0.50	0.4993 (2.354×10^{-4})	0.0158 (1.273×10^{-4})	0.0222 (8.094×10^{-4})
IDO (90%)	c_d	0.70	0.7005 (1.783×10^{-4})	0.0125 (1.028×10^{-4})	0.0171 (5.266×10^{-4})
	N	1000	999.860 (0.1908)	13.837 (0.1255)	18.390 (0.5290)
	p_a	0.60	0.5999 (1.829×10^{-4})	0.0128 (8.278×10^{-5})	0.0176 (5.211×10^{-4})
IDO (75%)	p_d	0.50	0.5026 (2.308×10^{-4})	0.0167 (1.217×10^{-4})	0.0233 (6.815×10^{-4})
	c_d	0.70	0.7006 (1.883×10^{-4})	0.0132 (1.036×10^{-4})	0.0181 (5.508×10^{-4})
	N	1000	1000.311 (0.2008)	15.113 (0.1582)	19.288 (0.5823)
IDO (50%)	p_a	0.60	0.6019 (1.940×10^{-4})	0.0140 (1.159×10^{-4})	0.0189 (5.076×10^{-4})
	p_d	0.50	0.4991 (2.362×10^{-4})	0.0181 (1.338×10^{-4})	0.0229 (6.080×10^{-4})
	c_d	0.70	0.6990 (1.995×10^{-4})	0.0144 (9.037×10^{-5})	0.0193 (5.492×10^{-4})
IDO (50%)	N	1000	1000.627 (0.2469)	18.519 (0.2424)	23.833 (0.6785)
	p_a	0.60	0.6023 (2.409×10^{-4})	0.0172 (1.277×10^{-4})	0.0234 (6.407×10^{-4})
	p_d	0.50	0.4993 (3.351×10^{-4})	0.0222 (1.4785×10^{-4})	0.0315 (1.184×10^{-3})
	c_d	0.70	0.6957 (2.653×10^{-4})	0.0177 (1.484×10^{-4})	0.0255 (8.741×10^{-4})

Appendix A. Additional Tables

Table A.5: *Simulation Study of Combined Multiple-Observer and Time-of-Detection Approach allowing for Reconciliation time for M_b model for 100 data sets each with 100 bootstrap samples. For the moderately easy to detect setting for a population of $N = 1000$ birds.*

	Parameter	True Value	Mean of Estimates	Mean of Std. Error Estimates	Mean of RMSE Estimates
DDO	N	1000	999.16 (0.0528)	3.375 (0.0383)	5.052 (0.179)
	p_a	0.75	0.7505 (1.173×10^{-4})	0.0083 (6.478×10^{-5})	0.0113 (3.290×10^{-4})
	p_d	0.70	0.7015 (2.798×10^{-4})	0.0193 (1.499×10^{-4})	0.0267 (8.896×10^{-4})
	c_d	0.85	0.8502 (1.382×10^{-4})	0.0103 (8.939×10^{-5})	0.0134 (3.401×10^{-4})
IDO (100%)	N	1000	999.59 (0.0469)	3.309 (0.0320)	4.443 (0.1606)
	p_a	0.75	0.7492 (1.207×10^{-4})	0.0080 (5.762×10^{-5})	0.0115 (3.983×10^{-4})
	p_d	0.70	0.7007 (1.886×10^{-4})	0.0127 (8.944×10^{-5})	0.0181 (5.401×10^{-4})
	c_d	0.85	0.8493 (9.253×10^{-5})	0.0068 (5.499×10^{-5})	0.0089 (2.565×10^{-4})
IDO (90%)	N	1000	999.017 (0.0485)	3.521 (0.0336)	4.655 (0.1741)
	p_a	0.75	0.7500 (1.222×10^{-4})	0.0085 (6.431×10^{-5})	0.0116 (3.831×10^{-4})
	p_d	0.70	0.6990 (1.840×10^{-4})	0.0132 (9.793×10^{-5})	0.0178 (4.947×10^{-4})
	c_d	0.85	0.8493 (9.237×10^{-5})	0.0071 (5.387×10^{-5})	0.0091 (2.370×10^{-4})
IDO (75%)	N	1000	998.935 (0.0527)	3.824 (0.0348)	5.109 (0.1739)
	p_a	0.75	0.7510 (1.313×10^{-4})	0.0092 (6.110×10^{-5})	0.127 (3.587×10^{-4})
	p_d	0.70	0.6987 (2.122×10^{-4})	0.0145 (1.138×10^{-4})	0.0203 (6.528×10^{-4})
	c_d	0.85	0.8498 (1.064×10^{-4})	0.0077 (5.386×10^{-5})	0.0102 (2.989×10^{-4})
IDO (50%)	N	1000	998.456 (0.0572)	4.612 (0.0561)	5.716 (0.1636)
	p_a	0.75	0.7514 (1.618×10^{-4})	0.0114 (9.746×10^{-5})	0.0158 (4.083×10^{-4})
	p_d	0.70	0.6993 (2.496×10^{-4})	0.0177 (1.369×10^{-4})	0.0240 (6.981×10^{-4})
	c_d	0.85	0.8506 (1.310×10^{-4})	0.0095 (8.407×10^{-5})	0.0127 (3.491×10^{-4})

APPENDIX B

Technical Details

Here we provide proof of the asymptotic equivalent distributions of \hat{N}_u and \hat{N}_c used in the thesis.

Asymptotic Equivalent Distributions of \hat{N}_u and \hat{N}_c

The following assumptions are made throughout.

- I. At every admissible value of θ , the functions $p_i(\theta)$ admit continuous first-order partial derivatives.
- II. Given a $\delta > 0$, it is possible to find an $\epsilon > 0$ such that

$$\inf_{|\theta_* - \theta_0| > \delta} \sum_{i=1}^{l-1} q_i(\theta_0) \log(q_i(\theta_0)/q_i(\theta_*)) > \epsilon$$

where $q_i(\theta) = p_i(\theta)/(1 - p_l(\theta))$, $i = 1, 2, \dots, l - 1$.

We let $p_i(\theta)$, $L(N; \theta)$ and $L_2(\theta)$ be denoted by p_i^0 , L^0 , and L_2^0 respectively when $(N, \theta) = (N_0, \theta_0)$ and by \hat{p}_i , \hat{L} , and \hat{L}_2 respectively when $(N, \theta) = (\hat{N}, \hat{\theta})$. Similarly let the partial derivatives of $p_i(\theta)$, $\log L(N; \theta)$ and $\log L_2(\theta)$ with respect to θ_j , the j^{th} component of θ , be denoted by $p_{i,j}$, L_j^0 and $L_{2,j}^0$ respectively when $(N, \theta) = (N_0, \theta_0)$ and by $\hat{p}_{i,j}$, \hat{L}_j , and $\hat{L}_{2,j}$ respectively when $(N, \theta) = (\hat{N}, \hat{\theta})$. Throughout this appendix,

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unless otherwise specified, the subscript i will range from 1 to l and the subscripts j and m from 1 to r .

Theorem 1. *Let N_0 be the true value of N and $\theta_0 = (\theta_{01}, \dots, \theta_{0r})$ be the true value of θ . Let \hat{N} and $\hat{\theta} = (\hat{\theta}_1, \dots, \hat{\theta}_r)$ be estimates of N_0 and θ_0 respectively, such that as $N_0 \rightarrow \infty$.*

$$(i) \hat{\theta} \xrightarrow[a.s.]{} \theta_0;$$

$$(ii) N_0^{-1/2}(\hat{N} - n/(1 - \hat{p}_l)) \xrightarrow[a.s.]{} 0;$$

$$(iii) N_0^{-1/2} \hat{L}_j \xrightarrow[a.s.]{} 0, \quad j = 1, \dots, r.$$

Let Σ^{-1} be the $(r+1) \times (r+1)$ matrix given by

$$\Sigma^{-1} = \begin{bmatrix} \mathbf{A} & \mathbf{a}'_0 \\ \mathbf{a}_0 & a_{00} \end{bmatrix}$$

where $\mathbf{A} = (a_{ij})$ defined by $a_{ij} = \sum_{s=1}^l (p_s)^{-1} p_{s,i}^0 p_{s,j}^0$, $i, j = 1, \dots, r$; $\mathbf{a}_0 = (a_{10}, \dots, a_{r0})$ defined by $a_{i0} = -(p_l)^{-1} p_{l,i}^0$, $i = 1, \dots, r$, and $a_{00} = (1 - p_l^0)/p_l^0$.

Then, $(N_0^{-1/2}(\hat{\theta} - \theta_0), N_0^{-1/2}(\hat{N} - N_0))$ is asymptotically $\mathcal{N}(0, \Sigma)$.

\mathbf{A} is the usual information matrix for the multinomial distribution $M(N; p_1(\theta_0), \dots, p_{l-1}(\theta_0))$ when N is known. Σ is implicitly assumed to be nonsingular in the theorem.

Proof. Let n_l denote $N_0 - n$. We then have

$$N_0^{-1/2} \sum_i (\hat{p}_i)^{-1} n_i \hat{p}_{i,j} = -N_0 (\hat{p}_l)^{-1} (\hat{N} - N_0) \hat{p}_{l,j} + N_0^{-1/2} \hat{L}_j$$

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Since $\sum_i p_{i,j} = 0$, it follows that

$$\begin{aligned} N_0^{-1/2} \sum_i (\hat{p}_i)^{-1} (n_i - N_0 p_i^0) \hat{p}_{i,j} &= N_0^{-1/2} \sum_i (\hat{p}_i)^{-1} (\hat{p}_i - p_i^0) \hat{p}_{i,j} \\ &\quad - N_0^{-1/2} (\hat{p}_i)^{-1} (\hat{N} - N_0) \hat{p}_{i,j} + N_0 \hat{L}_j \end{aligned} \quad (\text{B.1})$$

If we use the mean value representation

$$\hat{p}_i - p_i^0 = \sum_m (\hat{\theta}_m - \theta_{0m}) p_{i,m}(\theta_m^i), \quad \theta_m^i \in (\hat{\theta}_m, \theta_{0m})$$

So then B.1 can be written as

$$\sum_m b_{j,m} N_0^{-1/2} (\hat{\theta}_m - \theta_{0m}) + b_{j,r+1} N_0^{-1/2} (\hat{N} - N_0) = N_0^{-1/2} \sum_i d_{i,j} y_i - N_0^{-1/2} \hat{L}_j \quad (\text{B.2})$$

where for $j = 1, \dots, r$ and $m = 1, \dots, r+1$, $b_{j,m} \xrightarrow{a.s.} \sigma_{j,m}$, as $\sigma_{j,m}$ is the $(j, m)^{th}$ element of Σ^{-1} ,

$$d_{i,j} \xrightarrow{a.s.} (p_i^0)^{-1} p_{i,j}^0 \quad (\text{B.3})$$

and

$$y_i = n_i - N_0 p_i^0$$

Since $N_0^{-1/2} y_i$ has a limiting distribution

$$N_0^{-1/2} \sum_i d_{i,j} y_i - z_j \xrightarrow{p} 0 \quad (\text{B.4})$$

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where

$$z_j = N_0^{-1/2} \sum_i (p_i^0)^{-1} p_{i,j}^0 y_i = N_0^{-1/2} \sum_i (p_i^0)^{-1} p_{i,j}^0 n_i \quad (\text{B.5})$$

Thus by using (iii) in the statement of the theorem,

$$\sum_m b_{j,m} N_0^{-1/2} (\hat{\theta}_m - \theta_{0m}) + b_{j,r+1} N_0^{-1/2} (\hat{N} - N_0) - z_j \xrightarrow[p]{} 0 \quad (\text{B.6})$$

Now consider the following equation

$$\begin{aligned} N_0^{-1/2} (\hat{N}(1 - \hat{p}_l) - n) &= N_0^{-1/2} (\hat{N} - N_0)(1 - \hat{p}_l) \\ &\quad - N_0^{-1/2} (\hat{p}_l - p_l^0) - N_0^{-1/2} (n - N_0(1 - p_l^0)) \end{aligned} \quad (\text{B.7})$$

Using the mean value representation for $\hat{p}_l - p_l^0$, dividing (B.7) by p_l^0 and using condition (ii) of the theorem, we have

$$\sum_m b_{r+1,m} N_0^{-1/2} (\hat{\theta}_m - \theta_{0m}) + b_{r+1,r+1} N_0^{-1/2} (\hat{N} - N_0) - z_{r+1} \xrightarrow[p]{} 0 \quad (\text{B.8})$$

where $b_{r+1,m} \xrightarrow[a.s.]{} \sigma_{r+1,m}$, $m = 1, \dots, r+1$ and $z_{r+1} = N_0^{-1/2} (p_l^0)^{-1} (n - N_0(1 - p_l^0))$.

Let $\mathbf{U}' = (N_0^{-1/2}(\hat{\theta} - \theta_0), N_0^{-1/2}(\hat{N} - N_0))$ and $\mathbf{Z}' = (z_1, \dots, z_{r+1})$. Then by inverting the relations (B.6) and (B.8), we have

$$\mathbf{U} - \Sigma \mathbf{Z} \xrightarrow[p]{} \mathbf{0} \quad (\text{B.9})$$

Next, we will show that $\mathbf{Z} \xrightarrow[d]{} \mathcal{N}(\mathbf{0}, \Sigma^{-1})$.

For $m = 1, \dots, N_0$ let $\mathbf{V}_m = (V_{m,1}, \dots, V_{m,r+1})$ be a random vector such that

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- (i) when the m^{th} trial results in the i^{th} category, i ranging from 1 to $l-1$, $V_{m,j}$ takes the value $(p_i^0)^{-1}p_{i,j}^0, j = 1, \dots, r$ and $V_{m,r+1}$ takes the value 1.
- (ii) when the m^{th} trial results in the l^{th} category, $V_{m,j}$ takes the value $(p_l^0)^{-1}p_{l,j}^0, j = 1, \dots, r$ and $V_{m,r+1}$ takes the value $-(p_l^0)^{-1}(1 - p_l^0)$.

Then

$$\mathbf{Z}' = N_0^{-1/2} \sum_{m=1}^{N_0} \mathbf{V}_m \quad (\text{B.10})$$

From the definition of \mathbf{V}_m , it may be easily deduced that each \mathbf{V}_m has $\mathbf{0}$ as its mean vector and Σ^{-1} as its covariance matrix. Also the \mathbf{V}_m 's are identically distributed. Therefore by Central Limit Theorem

$$\mathbf{Z} \xrightarrow[d]{} \mathcal{N}(\mathbf{0}, \Sigma^{-1}) \quad (\text{B.11})$$

Thus by (B.9) $\mathbf{U} \xrightarrow[d]{} \mathcal{N}(\mathbf{0}, \Sigma)$.

□

Theorem 2. *Assume I and II then*

- (i) $(\hat{N}_c/N_0, \hat{\theta}_c, \hat{p}_c) \xrightarrow[a.s.]{} (1, \theta_0, p_l^0)$ as $N_0 \rightarrow \infty$.
- (ii) $(\hat{N}_u/N_0, \hat{\theta}_u, \hat{p}_u) \xrightarrow[a.s.]{} (1, \theta_0, p_l^0)$ as $N_0 \rightarrow \infty$.
- (iii) $(N_0^{1/2}(\hat{\theta}_c - \theta_0), N_0^{1/2}(\hat{N}_c - N_0))$ and $(N_0^{1/2}(\hat{\theta}_u - \theta_0), N_0^{1/2}(\hat{N}_u - N_0))$ are both asymptotically $N(0, \Sigma)$.

Proof. Statement *i* can be proved as follows:

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By the law of large numbers,

$$n/N_0 \xrightarrow[a.s.]{} 1 - p_l^0 \quad \text{as} \quad N_0 \longrightarrow \infty \quad (\text{B.12})$$

and so $n \xrightarrow[a.s.]{} \infty$ as $N_0 \longrightarrow \infty$.

But $\hat{\theta}_c$ is the maximum likelihood estimate of θ_0 based on an observation from $M(n; q_1(\theta_0), \dots, q_{l-1}(\theta_0))$ and so by II, $\hat{\theta}_c \xrightarrow[a.s.]{} \theta_0$ as $n \rightarrow \infty$ and hence by B.12

$$\hat{\theta}_c \xrightarrow[a.s.]{} \theta_0 \quad \text{as} \quad N_0 \longrightarrow \infty \quad (\text{B.13})$$

We also have $\hat{p}_c \rightarrow p_l^0$ as $N_0 \rightarrow \infty$ by the continuity of $p_l(\theta)$. $\hat{N}_c = [n/(1 - \hat{p}_c)]$ implies $(1/N_0)\{\hat{N}_c - n/(1 - \hat{p}_c)\} \xrightarrow[a.s.]{} 0$ as $N_0 \rightarrow \infty$ and so $\hat{N}_c/N_0 \xrightarrow[a.s.]{} 1$ as $N_0 \rightarrow \infty$.

Thus statement *i* of the theorem is true.

Statement *ii* can be proved as follows:

It is enough to prove that $\sum_{i=1}^{l-1} (n_i/n) \log(q_i(\hat{\theta}_u)/(n_i/n)) \xrightarrow[a.s.]{} 0$ since this together with II would imply $\hat{\theta}_u \xrightarrow[a.s.]{} \theta_0$.

Consider L_1 and L_2 as defined in 2.5 and 2.6. $\log L_1 = 0$ at the point $(N, p_l) = (n, 0)$ and is less than or equal to zero at all other points. Since $\hat{\theta}$ maximizes $\log[L(\hat{N}_u; \theta)]/n$, we have

$$\begin{aligned} & \sum_{i=1}^{l-1} (n_i/n) \log q_i(\hat{\theta}_u) + \text{a negative number} \\ & \geq \sup_{\theta} \left\{ \sum_{i=1}^{l-1} (n_i/n) \log q_i(\theta) + \log[L_1(N; p_l(\theta))]/n \right\} \\ & \geq \sum_{i=1}^{l-1} (n_i/n) \log q_i(\theta_0) + \log[L_1(N_0; p_l(\theta_0))]/n \end{aligned}$$

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Also, by an inequality in information theory

$$\sum_{i=1}^{l-1} (n_i/n) \log(q_i(\hat{\theta}_u)) \leq \sum_{i=1}^{l-1} (n_i/n) \log(n_i/n)$$

Combining the two inequalities above we have

$$\begin{aligned} 0 &\geq \sum_{i=1}^{l-1} (n_i/n) \log q_i(\hat{\theta}_u) \\ &\geq \sum_{i=1}^{l-1} (n_i/n) \log q_i(\theta_0) + \log[L_1(N_0; p_l(\theta_0))]/n \end{aligned}$$

As $N_0 \rightarrow \infty$, and $n_i/n \xrightarrow{a.s.} q_i(\theta_0)$. Also, using the normal approximation to the binomial probability $L_1(N_0; p_l(\theta_0))$ and (B.12) it is seen that $\log[L_1(N_0; p_l(\theta_0))]/n \xrightarrow{a.s.} 0$. Hence the result.

We will now show that both $(\hat{N}_c, \hat{\theta}_c)$ and $(\hat{N}_u, \hat{\theta}_u)$ satisfy conditions (ii) and (iii) of Theorem 1. $\hat{N}_c = \lceil n/(1 - \hat{p}_c) \rceil$ implies that $|\hat{N}_c - n/(1 - \hat{p}_c)| < 1$ and therefore condition (ii) of Theorem 1 is satisfied by $(\hat{N}_c, \hat{\theta}_c)$ and similarly by $(\hat{N}_u, \hat{\theta}_u)$. Having condition (iii) of Theorem 1 being satisfied by $(\hat{N}_u, \hat{\theta}_u)$ is clear from the definition of $(\hat{N}_u, \hat{\theta}_u)$. For $(\hat{N}_c, \hat{\theta}_c)$, by definition $\theta = \hat{\theta}_c$ maximizes $L_2(\theta)$ and since the partial derivatives are assumed to exist, we have

$$L_{2,j}(\hat{\theta}_c) = 0, \quad j = 1, \dots, r.$$

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Therefore

$$\begin{aligned} N_0^{-1/2} L_j(\hat{N}_c; \hat{\theta}_c) &= N_0^{-1/2} L_{1,j}(\hat{N}_c; \hat{p}_c) \\ &= N_0^{-1/2} p_{l,j}(\hat{\theta}_c) ((\hat{N}_c - n)/\hat{p}_c - n/(1 - \hat{p}_c)), \quad i = 1, \dots, r. \end{aligned}$$

By B.13 and I, $p_{l,j}(\hat{\theta}_c) \xrightarrow[a.s.]{} p_{l,j}^0$ as $N_0 \rightarrow \infty$. Also since $\hat{p}_c \xrightarrow[a.s.]{} p_l^0$, $(\hat{N}_c - n)/\hat{p}_c - n/(1 - \hat{p}_c)$ is almost surely bounded in the limit. Therefore $N_0^{-1/2} L_j(\hat{N}_c; \hat{\theta}_c) \xrightarrow[a.s.]{} 0$. Thus condition (iii) of Theorem 1 is satisfied by $(\hat{N}_c; \hat{\theta}_c)$ and this completes the proof of Theorem 2. □

**Separating Components of the Detection
Process with Combined Methods: An
Example with Northern Bobwhite**

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Christopher E. Moorman, and Fern S. Perkins**

Abstract. There are various methods of estimating detection probabilities for avian point counts. The distance and multiple observer methods require the sometimes unrealistic assumption that all birds in the population are available (i.e., sing or are visible) during a count, but the time-of detection method allows for the possibility that some birds are unavailable during the count. Here we combine the dependent double-observer method with the time-of-detection method and obtain the first field-based estimates of the components of detection probability for Northern Bobwhite (*Colinus virginianus*). Our approach is a special case of Pollocks robust capture-recapture design where the probability that a bird does not sing is analogous to the probability that an animal is a temporary emigrant. Top models indicated that observers detection probabilities were relatively similar (0.78-0.84) if bobwhite were available, but bobwhite only had an approximately 0.61 probability of being available during a 2.5-min sampling in-

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terval. Additionally, observers detection probabilities increased substantially after the initial encounter with an individual bobwhite (analogous to a trap happy response on the part of the observer). A simulated data set revealed that the combined method also performed well in terms of precision when availability and detection given availability were substantially lower. Combined methods approaches can provide critical information for decisions regarding survey length and personnel requirements.

Key Words: availability process, detection probability, dependent double-observer method, perception process, point counts, Pollocks Robust Design, North Carolina, Northern Bobwhite, time-of-detection method.

C.1 Introduction

Point counts are used widely to study the abundance and density of bird populations (Ralph and Scott 1981, Ralph et al. 1995). The data are easy to collect at larger spatial scales compared to mark and recapture methods that are frequently costly and, therefore, limited to studies on smaller spatial scales. Typically, point counts have been viewed as indices of abundance and standardized protocols are emphasized to reduce variation in detection probability (Ralph et al. 1995). The weaknesses of this view and the importance of estimating detection probability have been noted for some time (e.g., Burnham 1981). Two recent overview papers by Thompson (2002) and Rosenstock et al. (2002) stress how important the estimation of detection probability is to sound inference based on point counts.

Detection probability (p) can be thought of as the product of at least three com-

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ponents: the probability that an individual bird associated with the sample area is present during the count (p_p), the probability that an individual bird is available (i.e., vocalizing or not visually obscured) given it is present (p_a), and the probability that an individual bird is detected given it is present and available (p_d) (See recent review by Nichols et al. 2009). In other words, the detection process can be represented mathematically as:

$$p = p_p p_a p_d$$

Different methods of accounting for the detection process provide different estimates of p . For example, distance sampling (Buckland et al. 2001) and multiple-observer methods (e.g., Nichols et al. 2000, Alldredge et al. 2006) only provide estimates of p_d . They assume that p_p and p_a are both equal to 1 and/or are constant among sites or study areas. Time-of-removal (Farnsworth et al. 2002) and time-of-detection (Alldredge et al. 2007) methods provide an estimate of $p_a p_d$. They assume that p_p is equal to 1 and/or is constant among sites or study areas. Note that p_a and p_d are not separable when these methods are used alone. Repeated counts methods provide the full estimate of $p_p p_a p_d$ (Royle 2004, Nichols et al. 2009). None of the components of the detection process are separable when this method is used alone. Additionally, the abundance estimate (N) provided by this method is actually a superpopulation estimate that may be difficult to translate or relate to habitat area or bird density in many instances (Royle and Dorazio 2008). In other words, the population sampled with this method includes all birds that have territories that overlap the survey area even if some birds were not present in the survey area on each visit.

Separating components of the detection process allows one to determine the relative

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importance or contribution of each component to the overall detection process, which in turn could be used to inform survey design decisions such as the optimal number of visits or length of time that should be spent at a site. For example, consider a situation in which p_p was essentially equal to 1, but p_a was very low (e.g., a species with low mobility and low singing rates). With this knowledge, a practitioner might decide that available resources should be directed at spending more time at each point count location than making many multiple visits of short duration. Separating components of the detection process requires combining methods. Stanislav et al. (North Carolina State University, unpublished data) demonstrated that combining the time-of-detection method with two independent observers could generate separate estimates of the two components p_a and p_d . They illustrated this technique with data collected using simulated aural bird detections in the field (Simons et al. 2007). Here, we develop and then illustrate a similar model, but with real Northern Bobwhite (*Colinus virginianus*) detections collected using a combination of the dependent double-observer method and the time-of-detection method.

Our objectives are to:

1. present a modified point count technique that allows one to estimate two components (availability and perception) of the detection process using a combined dependent double-observer and time-of-detection approach;
2. illustrate our approach with point count data collected on bobwhites from eastern North Carolina farms;
3. use our overall likelihood to compare a number of different submodels of the

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detection process; and

4. demonstrate that the combined approach also gives precise estimates for a simulated scenario with lower values of p_a and p_d .

Our paper contains an extended statistical methods section and a description of the field methods used in the Northern Bobwhite study. We then present the quail detection probability estimates, discuss the method, and make suggestions for future research.

C.2 Study Area

Data for this study were collected on 24 commercial swine farms in the Coastal Plain of North Carolina as part of a study on bird use of field borders in different landscape contexts. Specifically, farms were located in the following counties: Bladen, Columbus, Duplin, Pender, Sampson, Scotland, and Robeson. Treatments were arranged in a balanced 2 x 2 factorial with field border shape (linear or nonlinear) and landscape context (agriculture- or forest-dominated) as the factors (six replicates in each treatment). Most farms were on a crop rotation of corn, soybeans, and wheat. Riddle (2007) and Riddle et al. (2008) provided detailed descriptions of field border, farm, and landscape characteristics.

C.3 Methods

C.3.1 Field Methods

The same two observers (JDR and FSP) conducted 2-6 point counts on each farm for Northern Bobwhite from May 15 - June 30 during each year of the study. Previous analysis suggested quail detectability did not vary by treatment or year (see Riddle 2007, Riddle et al. 2008). Therefore, we combined observations from all treatments. Also, for the sake of convenience, we only considered data from 2004 and 2005 (a total of 236 point count surveys). We combined the dependent double-observer approach (Nichols et al. 2000) and the time-of-detection approach (Alldredge et al. 2007). In the dependent double-observer approach, the primary observer records all birds seen or heard. The secondary observer records all birds detected by the primary, but also records birds he or she detects that the primary does not. The secondary observer does not share their unique detections with the primary observer while the count is taking place. Observers reverse roles with each new point count. With the time-of-detection approach, detections of individual birds are recorded for every interval in which they were perceived. Our point counts were 10 minutes in overall length, and divided into 4 equal intervals of 2.5 minutes each. All point counts had an unlimited radius.

An example of a detection history for an individual bobwhite sampled with our method might be 11, 01, 00, 11. This detection history would indicate that the primary observer detected the bird in the first 2.5 minute interval (and therefore the secondary must also record it as detected), only the secondary observer detected the bird in the second interval, the bird was unavailable or was available and not detected by either

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observer in the third interval, and the primary observer detected the bird in the final interval.

C.3.2 Statistical Model Development

Dependent double-observers

We focus on the dependent double-observer method (Nichols et al. 2000) originally applied in an aerial survey context by Cook and Jacobsen (1979). The dependent double-observer approach can be viewed as an extension of the removal method (Zippin 1958, Seber 1982, p.309). Critical assumptions of this method are:

1. there are equal detection probabilities of all individual birds of each species for each observer;
2. the population is closed in that there is no undetected movement out of the sampled area;
3. observers accurately assign birds to within the radius used for the fixed radius circle if fixed radius counts are used; and
4. the detection probability is the same irrespective of whether an observer is in the primary or secondary role.

The method can be fit using program MARK (White and Burnham 1999) or DOBSERV (Nichols et al. 2000). These models allow the detection probability to depend on covariates such as species, observer, wind speed, and distance. MARK and DOBSERV use Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) to select the

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simplest model that adequately explains the data. Again, note the estimate of detection probability provided by this method is simply p_d .

Time-of-detection

Farnsworth et al. (2002) developed a method which applied the removal method (Zip-pin 1958, Seber 1982) to the time when birds were first detected. A more efficient approach has been developed by Alldredge (2004) and Alldredge et al. (2007), which uses t -sample closed capture-recapture models (Otis et al. 1978, Williams et al. 2002) based on full detection histories (i.e., the time intervals when a particular bird was detected as well as intervals when that same bird was not detected). Here we are able to estimate $p_a p_d$. This is a special feature of the time-of-detection method because the multiple observer and distance methods cannot account for unavailable birds. The ability to incorporate availability in the estimation of p for time-of-detection models emerges directly from the separation of individual detections by time intervals. It accounts for the possibility that a bird is available in one time interval but not in another.

Model assumptions are as follows:

1. there is no undetected change in the population of birds within the detection radius during the point count (i.e., the population is closed and birds do not move in or out without being detected);
2. there are no identification errors (i.e., observers are able to accurately identify and track individual birds with no double-counting or lumping of individuals);

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3. all individual birds of a species have a constant per minute probability of being detected in each interval; and
4. observers accurately assign birds to within the fixed radius circle (when fixed radius plots are used).

If the probability of detection changes after the first detection (analogous to trap response in a true capture-recapture setting), then assumption 3 can be weakened. “Trap response models may be useful and in this application recapture probabilities are likely greater than first capture probabilities because an observer will be anticipating that an individual bird of a species may call again and thus be more likely to be detected if it does call. Riddle et al. (North Carolina State University, unpublished data) found that trap response models often were chosen with time-of-detection data.

If the probability of detection varies among individual birds, then heterogeneity models may be used. Much has been written about these models in the capture-recapture literature (Burnham and Overton 1978, Otis et al. 1978, Pollock et al. 1990, Williams et al. 2002). Link (2003) noted model identifiability problems when these models are used. Modeling heterogeneity in detection probability using covariates can reduce problems associated with identifiability (Huggins 1989, 1991, Alho 1990).

C.3.3 Modeling Availability by Combining Dependent-Observers and Time-of-Detection Methods

We combined dependent double-observer and time-of-detection methods into one overall design which allows separate estimation of the components of the detection process.

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Consider t time intervals and two dependent observers where the birds are tracked throughout the count. (We suggest that in practice $t = 3 - 5$ time intervals be used so that heterogeneity models could possibly be used.) This combined method is equivalent to a robust capture-recapture design (Pollock 1982, Williams et al. 2002) with t primary periods (the time intervals) and two secondary periods (the observers) within each primary period. In this case, the population is assumed to be closed except for whether or not a bird is available (sings or is visible) in an interval. In the more general robust design, births and deaths in addition to lack of availability (commonly referred to as temporary emigration) are allowed. Modeling approaches already developed to account for temporary emigration can be adapted for our application (Kendall and Nichols 1995, Kendall et al. 1997). The simplest model assumes that the temporal pattern of bird song follows a random process. An alternative approach assumes a Markovian process where the probability that a bird sings in an interval depends on whether it sang in the previous interval. For the purposes of this paper, we only consider availability as a random process.

Under the classic random temporary emigration model, γ_i is the probability that an animal is a temporary emigrant in period i and this parameter does not depend on its value in previous periods. In the context of our paper, γ_i may be thought of as the probability that a bird is unavailable for detection in interval i . Thus $p_{a_i} = 1 - \gamma_i$ $i = 1, \dots, t$ is the probability a bird is available in interval i . The conditional detection probabilities for each observer in each period $(p_{d_{1i}}, p_{d_{2i}})$ $i = 1, \dots, t$ also are included in the model. Unlike the general robust design, we are assuming that all animals survive during the point count so that In the random availability model, an estimate of the

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probability that a bird does not sing during the entire 10 minute count can be obtained as the product of all the $1 - p_{a_i}$ terms.

To illustrate, consider a detection history for two observers over two time periods, where the first observer is the primary observer for a model with both time and observer effects. The history 11, 01 denotes a bird detected by both primary and secondary observers in interval 1 and detected only by the secondary observer in interval 2. This history has expected cell structure:

$$p_{a_1}p_{d_{11}} \times p_{a_2}(1 - p_{d_{12}})p_{d_{22}}$$

In this case, the birds have to sing in each interval to be detected by at least one observer. However, another history 11, 00 has the expected cell structure:

$$p_{a_1}p_{d_{11}} \times \{p_{a_2}(1 - p_{d_{11}})(1 - p_{d_{22}}) + (1 - p_{a_2})\}$$

The 00 in the second interval means there were two components for the probability, the first where the bird sings but is missed by both observers and the second where the bird does not sing.

Based on all the detection histories obtained in a study, one can build a likelihood function and obtain parameter estimates and standard errors. Consider t time intervals where the birds are tracked throughout the count, and 2 observers per time period, then based on the information obtained from the $k = 3^t$ detection histories (i.e., 11, 01, and 00) for each primary observer case where $n_{i,j}, i = 1, 2, \dots, k - 1$ represents the number of birds that have the i^{th} detection history detected when observer j is the

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primary observer, we have

$$L(N; \theta) = \frac{N!}{n_{1,1}! \dots n_{k-1,1}!(N-n)!} \tau \{p_{1,1}(\theta)^{n_{1,1}} \dots p_{k-1,1}(\theta)^{n_{k-1,1}}\} \\ \times \frac{1}{n_{1,2}! \dots n_{k-1,2}!} (1-\tau) \{p_{1,2}(\theta)^{n_{1,2}} \dots p_{k-1,2}(\theta)^{n_{k-1,2}}\} p_k(\theta)^{N-n} \quad (\text{C.1})$$

where $n = \sum_{i=1}^{k-1} \sum_{j=1,2} n_{i,j}$ denotes the total number of detected birds, $p_{i,j}$ represents the multinomial cell probabilities which are known functions of θ , the availability and detection probability parameters ($p_{i,j}(\theta) = f_{i,j}(\theta)$) and $p_k = \sum_{i=1}^{k-1} \sum_{j=1,2} p_{i,j}$. The model structures examined here in the dependent double-observer setting follow a similar form of those by Stanislav et al. (North Carolina State University, unpublished data) although there is one major difference: there is no detection history where the primary observer detects the bird and the secondary observer does not, because the secondary observer role is only to add information (bird detections) that the primary observer may miss. Also for this dependent double-observer method, a known parameter enters into the multinomial likelihood. This parameter τ is the fraction of the detection histories where observer one is the primary observer (often 0.5 by design) and thus $1 - \tau$ is for the detection histories where the roles are reversed.

For notation, we assume that the k^{th} detection history is the undetected history when either observer 1 or 2 is the primary observer, which is why the multinomial probability is not scaled. We can do this because in any time period when you have no detection, the probability is the same regardless of which observer is the primary observer. Without loss of generality, we assumed model M_{ot} structure where the “o” subscript indicates that detection probably is allowed to vary with each observer and

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with $t = 2$ time periods. If the first observer is the primary observer, the probability of not being detected during the whole point-count is $\{p_{a_2}(1 - p_{d_{11}})(1 - p_{d_{21}}) + (1 - p_{a_2})\}\{p_{a_2}(1 - p_{d_{12}})(1 - p_{d_{22}}) + (1 - p_{a_2})\}$. The same is true if the second observer is the primary observer, just with non-detection terms transposed in each time periods probability.

Due to the structure of the undetected detection history, we may use the conditional likelihood approach proposed by Sanathanan (1972) for estimation of the population size, N , which writes the likelihood above as $L(N; \theta) = L_1(N; p_k(\theta)) \times L_2(\theta)$ where

$$L_1(N; p_k(\theta)) = \frac{N!}{n!(N - n)!} (1 - p_k(\theta))^n p_k(\theta)^{N-n} \quad (\text{C.2})$$

$$L_2(\theta) = \frac{n!}{n_1! \dots n_{k-1}!} q_1(\theta)^{n_1} \dots q_{k-1}(\theta)^{n_{k-1}} \quad (\text{C.3})$$

with $q_i(\theta) = \frac{p_i(\theta)}{1 - p_k(\theta)}$, with $i = 1, 2, \dots, k - 1$.

We optimized the conditional likelihood function, L_2 , to obtain estimates of the availability and detection probabilities. Then, it follows from the work of Sanathanan (1972) that for any given \hat{p} that the estimate of the population size is $\hat{N} = \left\lfloor \frac{n}{1 - \hat{p}_k} \right\rfloor$, the greatest integer $\leq \frac{n}{1 - \hat{p}_k}$, which maximizes L_1 . This is simpler computationally than maximizing the full likelihood. The standard errors of the derived estimates can be obtained based on the second bootstrap method presented by Norris and Pollock (1996) which also could be used to construct confidence intervals.

Through use of the conditional likelihood maximization, an accessible approach for finding estimates of the availability and detection probabilities, along with the

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population size, exists. Conditional likelihood estimates of parameters can be found directly from likelihood maximization procedures available in any software computing language, such as the *optim* function in *R*. For some instances one may require the use of constrained optimization to guarantee that probability estimates fall between 0 and 1, and in *R* the function *constrOptim* handles the task. AIC can be used for model selection (Burnham and Anderson 2002, Williams et al. 2002). The estimated distance to each bird, detected by at least one observer, could be incorporated as an important covariate influencing the detection probability. Any number of observers and time intervals can be accommodated. This is the approach that we followed in the next section where we provide examples to illustrate the methodology.

C.3.4 Analysis

Field data

We fit detection histories for the bobwhite data with modifications of the general likelihood we introduced previously to compare a suite of models that allowed availability (p_a) to be a random process or equal to 1 (i.e., all birds are available) and allowed for detection given availability (p_d) to vary or remain constant with time and/or observer. We also allowed for an observer-based behavioral effect in some models. This is analogous to a trap response model in classic capture-recapture literature where the animal responds to the presence of the trap, except that in this case it is the observer (analogous to the trap) which is responding to the bird. Riddle et al. (North Carolina State University, unpublished data) discuss observer-based behavioral effects in detail. They found these models were heavily favored in point count methods that

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produced detection histories (e.g., time-of-detection) or site histories (e.g., repeated counts or repeated presence/absence methods). The complete set of models we considered were: $p_a(rand) p_d(., ., b)$; $p_a(rand) p_d(., o, b)$; $p_a(rand) p_d(., o, .)$; $p_a(rand) p_d(., ., .)$; $p_a(rand) p_d(t, o, .)$; $p_a(all) p_d(., ., b)$; $p_a(all) p_d(., o, b)$; $p_a(all) p_d(., o, .)$; $p_a(all) p_d(., ., .)$; and $p_a(all) p_d(t, o, .)$. Here, the subscripts t, o, and b represent the effects of time, observer differences in detection probability, and an observer-based behavioral response, respectively. Models were fit in R and AIC values were obtained and used to select the top model.

Simulated data set

We also considered an artificial dataset with relatively low availability and detection probabilities. The simulated dataset was designed to evaluate the relative performance of our method for populations or species that might not be as available or detectable given availability as breeding season bobwhites were on farms in eastern North Carolina. Our simulated dataset was generated from a random multinomial distribution with cell probabilities determined from the constant random availability model, with observer dependent initial detection probabilities constant over time intervals and elevated redetection probabilities. Specifically, $t = 4$ time intervals and two dependent observers.

For this model, we defined the true population size (N) to be 500, the true probability that such a bird is available for detection, p_a , to be 0.3, the probability of first detection, p_d , to be 0.5 and for the subsequent detections, the detection probability, c_d , was 0.6.

C.4 Results

The top model for the bobwhite field data was random availability with an observer-based behavioral effect on detection given availability (Table 1). Parameters from this model indicated that about 60% of the population was available during any given 2.5 min period. Initial detection probabilities were approximately 0.80 (SE = 0.04). Once either observer had detected a bobwhite, their probability of detecting that individual during subsequent intervals increased to approximately 0.90 (SE = 0.02; Table 2). The second most competitive model, according to AIC weights, allowed for each observer to have a unique probability of initial detection and redetection (Table 3). However, estimates of N from each model were almost identical.

For our simulated data, availability was estimated at 0.29 (SE = 0.03) and detection given availability was estimated at 0.46 (SE = 0.05) for first detections and 0.61 (SE = 0.06) for subsequent detections. The total available population was estimated at 525.31 (SE = 45.22) birds (Table 4).

C.5 Discussion

We were able to successfully estimate components of the detection process because we combined time-of-detection and dependent double-observer methods. To our knowledge these are the first estimates of availability for detection for Northern bobwhite. Our models provided reasonable estimates of availability and detection given availability for both initial and subsequent detections of bobwhites.

Separating the components of the detection process demonstrated that availability

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within a certain span of time (2.5 minutes in our case) was a more limiting factor than the ability of observers to detect calling bobwhites. These results could help to inform decisions about survey length. For example, one could plot the probability that a bobwhite present in the survey area is available at least once for surveys of varying duration. Based on our top model, just over half of all individuals are available after 2.5 minutes. but nearly all individuals should have vocalized at least once over the course of a 10 minutes count (Figure 1).

Similarly, one could compare probability estimates that an observer would detect an individual bobwhite at least once given that it was available in at least one interval from the double-observer method and time-of-detection method (Figure 2). For example, our top model suggests that if a single visit of 2.5 minute were made, then the probability of at least one observer detecting an individual bobwhite is higher with the dependent double-observer method than with a single observer on their own. However, if a single observer of similar skill to those in our study used the time-of-detection method for at least two 2.5-minute intervals, then they would be expected to detect individual birds with a higher probability than a single 2.5 minute visit by two observers. Furthermore, two observers using the dependent-double observer method combined with time-of-detection with only two 2.5-minute intervals would be expected to detect individual birds more often than a single observer who used time-of-detection for up to four 2.5-minute intervals. Such comparisons could inform decisions about tradeoffs involving personnel requirements and survey duration.

Stanislav et al. (North Carolina State University, unpublished data) provided examples of combining time-of-detection and independent double-observer approaches.

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Allredge et al. (2006) showed that the independent double-observer approach is more efficient than the dependent approach, because capture-recapture methods generally are more efficient than removal methods (Seber 1982, p.324). However, the independent double-observer approach requires observers to match observations which can consume valuable time in the field. Furthermore, matching errors can be substantial even when relatively few vocal cues are available to be mapped (Allredge et al. 2008). In contrast, the dependent double-observer approach does not require matching. If the time saved by not matching (i.e., using the dependent observer approach) is spent conducting more samples, then gains through increased sample size may be substantial enough to make the dependent double-observer approach more efficient than the independent double-observer approach in some cases (S. J. Stanislav, North Carolina State University, unpublished data).

One critical assumption of the dependent double-observer method is that an observer's detection probability does not change when they switch roles from primary to secondary. For example, the secondary observer may tend to cue in on individual birds that are more difficult to detect because their role as secondary observer is specifically designed to detect individuals that the primary is missing. However, preliminary simulations suggest that this assumption may be relaxed without affecting estimates of abundance (S. J. Stanislav, North Carolina State University, unpublished data).

Despite its additional expense, we encourage field ornithologists and managers to consider use of this combined double-observer time-of-detection method for at least a sub-sample of their points to better understand the detection process in their field studies and potentially obtain better estimates of population abundance. We think

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this is especially critical for species like Northern Bobwhite, which appears to have experienced substantial declines in recent decades. We also encourage future work with combined methods that consider the possibility of Markovian rather than random availability. These models could be especially useful because birds often sing in nonrandom bouts (Collins 2004).

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Table C.1: *AICc model selection results for Northern Bobwhite. Models in the set allow availability (p_a) to be random or equal to 1 (i.e., all birds are always available). Conditional detection probability (p_d) is allowed to vary with time (t), observer (o), to be different for initial and subsequent detections (b), or to be constant (.).*

Model	AICc	Δ AICc	AICc Weights	Parameters
$p_a(\text{random}) p_d(., ., b)$	471.76	0	0.456	3
$p_a(\text{random}) p_d(., o, b)$	472.04	0.28	0.397	5
$p_a(\text{random}) p_d(., o, .)$	474.71	2.95	0.105	3
$p_a(\text{random}) p_d(., ., .)$	476.53	4.77	0.042	2
$p_a(\text{random}) p_d(t, o, .)$	487.97	16.21	0	9
$p_a(\text{all}) p_d(., ., b)$	702.11	230.35	0	2
$p_a(\text{all}) p_d(., o, b)$	704.78	233.02	0	4
$p_a(\text{all}) p_d(., ., .)$	713.24	241.21	0	1
$p_a(\text{all}) p_d(., o, .)$	714.06	242.30	0	2
$p_a(\text{all}) p_d(t, o, .)$	718.97	247.21	0	8

Table C.2: *Northern Bobwhite parameter estimates (standard errors) for model $p_a(\text{rand}) p_d(., ., b)$ (i.e., random availability with an observer-based behavioral effect), c_d is the conditional redetection probability. Estimates and standard errors found with $B = 100$ bootstrap samples.*

Parameters	Parameter Estimates
N	279.18 (3.46)
p_a	0.6048 (0.0201)
p_d	0.7985 (0.0400)
c_d	0.9016 (0.0211)

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Table C.3: *Northern Bobwhite parameter estimates (standard errors) for model $p_a(\text{rand}) p_d(\cdot, o, b)$ (i.e., random availability with observer differences and an observer-based behavioral effect), c_{d1} and c_{d2} are the conditional redetection probabilities for observers 1 and 2, respectively. Estimates and standard errors found with $B = 100$ bootstrap samples.*

Parameters	Parameter Estimates
N	279.08 (3.51)
p_a	0.6056 (0.0225)
p_{d1}	0.7821 (0.0463)
p_{d2}	0.8397 (0.0411)
c_{d1}	0.8842 (0.0315)
c_{d2}	0.9218 (0.0226)

Table C.4: *A comparison of the simulated dataset parameter estimates (standard errors) for a random availability model constant random temporary emigration model, with observer-based behavioral effect. The population of birds that sing at least once in 8 minutes is $N = 500$. Estimates and standard errors found with $B = 100$ bootstrap samples.*

Parameters	True Value	Parameter Estimates	Relative Bias (%)	RMSE
N	500	525.31 (45.22)	4.8181	51.8213
p_a	0.30	0.2908 (0.0276)	-3.1637	0.0291
p_d	0.50	0.4603 (0.0500)	-8.6248	0.0638
c_d	0.60	0.6069 (0.0625)	1.1369	0.0629

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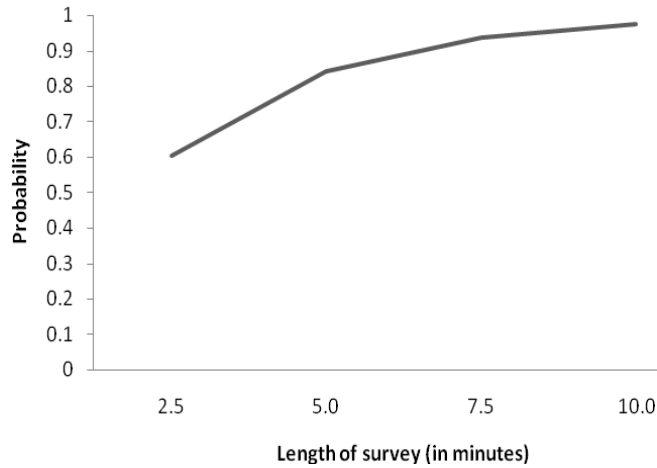


Figure C.1: *The probability that an individual Bobwhite will be available (vocalize) at least once over surveys of varying length.*

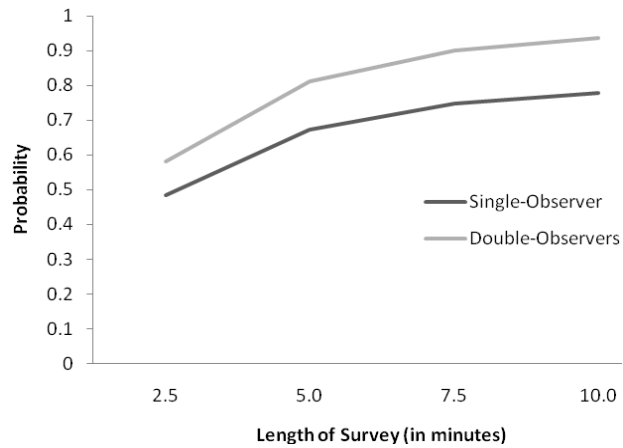


Figure C.2: *The probability of detecting a Bobwhite once by one observer in a single-observer survey and by at least one observer in a double-observer survey given availability in at least one interval for surveys of various durations.*