



Tools and Technology Article

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

JASON D. RIDDLE,^{1,2} *Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695-7646, USA*

STEPHEN J. STANISLAV, *Department of Statistics, North Carolina State University, Raleigh, NC 27695-8203, USA*

KENNETH H. POLLOCK, *Department of Biology, North Carolina State University, Campus Box 7617, Raleigh, NC 27695-7617, USA*

CHRISTOPHER E. MOORMAN, *Fisheries and Wildlife Sciences Program, Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695-7646, USA*

FERN S. PERKINS, *Department of Biology, Appalachian State University, P.O. Box 32027, 572 Rivers Street, Boone, NC 28608-2027, USA*

ABSTRACT There are various methods of estimating detection probabilities for avian point counts. Distance and multiple-observer methods require the sometimes unlikely 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. We combined the dependent double-observer method with the time-of-detection method and obtained field-based estimates of the components of detection probability for northern bobwhite (*Colinus virginianus*). Our approach was a special case of Pollock's 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 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-minute sampling interval. 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 was precise when availability and detection given availability were substantially lower. Combined methods approaches can provide critical information for researchers and land managers to make decisions regarding survey length and personnel requirements for point-count-based surveys.

KEY WORDS availability process, *Colinus virginianus*, dependent double-observer method, detection probability, North Carolina, northern bobwhite, perception process, point counts, Pollock's Robust Design, time-of-detection method.

Point counts are used widely to study abundance and density of bird populations (Ralph and Scott 1981, Ralph et al. 1995). 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 estimation of detection probability is to sound inference based on point counts.

Detection probability (p) can be thought of as the product of ≥ 3 components: probability that an individual bird associated with the sample area is present during the count (p_p), probability that an individual bird is available (i.e., vocalizing or not visually obscured) given it is present (p_a), and 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 and assume that p_p and p_a are both equal to one 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 $p_a p_d$ and assume that p_p is equal to one or is constant among sites or study areas. Note that p_a and p_d are not separable when time-of-removal and time-of-detection 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 repeated counts 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 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

¹ E-mail: Jason.Riddle@urwp.edu

² Present address: College of Natural Resources, University of Wisconsin–Stevens Point, Stevens Point, WI 54481, USA

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 that account for different components of the detection process. For example, Stanislav (2009) demonstrated that combining the time-of-detection method with 2 independent observers could generate separate estimates of the 2 components p_a and p_d . Stanislav (2009) illustrated this technique with data collected using simulated aural bird detections in the field (Simons et al. 2007). We developed and illustrated a similar model 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 were to 1) present a modified point-count technique that allows one to estimate 2 components (availability and detection given availability) 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 (USA) farms, 3) use our overall likelihood to compare several sub-models of the 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 .

STUDY AREA

We collected data 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 Bladen, Columbus, Duplin, Pender, Sampson, Scotland, and Robeson counties. Treatments were arranged in a balanced 2×2 factorial with field border shape (linear or nonlinear) and landscape context (agriculture- or forest-dominated) as the factors (6 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.

METHODS

Field Methods

The same 2 observers (J. D. Riddle and F. S. Perkins) conducted 2–6 point counts on each farm for northern bobwhite from 15 May to 30 June during each year of the study. Previous analysis suggested bobwhite detectability did not vary by treatment or year, so we combined observations from all treatments (Riddle 2007, Riddle et al. 2008). Also, for the sake of convenience, we only considered data from 2004 and 2005 (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 his or her unique detections with the primary observer while the count is taking place. Observers reverse roles with each new point count. We used a laser range finder and site maps to aid in locating individual birds (Riddle et al. 2008).

With the time-of-detection approach, detections of individual birds are recorded for every interval in which they are perceived. Our point counts were 10 minutes long and divided into 4 intervals of 2.5 minutes each. All point counts had an unlimited radius and were conducted between approximately 15 minutes after sunrise and 1000 hours (Riddle et al. 2008).

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

Statistical Model Development

Dependent double-observers.—We focused on the dependent double-observer method (Nichols et al. 2000) originally applied in an aerial survey context by Cook and Jacobson (1979). The dependent double-observer approach can be viewed as an extension of the removal method (Zippin 1958, Seber 1982). Critical assumptions of this method are as follows: 1) there are equal detection probabilities of all individual birds of each species for each observer; 2) the population is closed to births and deaths and 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) detection probability is the same irrespective of whether an observer is in the primary or secondary role.

We can fit the dependent double-observer method using Program MARK (White and Burnham 1999) or DOBSERV (Nichols et al. 2000). These models allow detection probability to depend on covariates such as species, observer, wind speed, and distance. Programs MARK and DOBSERV use Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to select the simplest model that adequately explains the data. Again, note the estimate of detection probability provided by the dependent double-observer method is simply p_d .

Time-of-detection.—Farnsworth et al. (2002) developed an approach that applied the removal method (Zippin 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 based on full detection histories (i.e., time intervals when a particular bird was detected as well as intervals when that same bird was not detected; Otis et al. 1978, Williams et al. 2002).

Here we can estimate $p_a p_d$, which 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 to births and deaths 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); 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. J. D. Riddle (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 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).

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. Consider t time intervals and 2 dependent observers where 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 fit.) This combined method is equivalent to a robust capture-recapture design with t primary periods (the time intervals) and 2 secondary periods (the observers) within each primary period (Pollock 1982, Williams et al. 2002). In this case, the population is assumed to be closed except for whether 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 in which the probability that a bird sings in an interval is not dependent on whether it sang in the previous interval. 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 our purposes, 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 γ_i does not depend on its value in previous periods. In our context, γ_i may be thought of as the probability that a bird is unavailable for detection in interval i . Thus $p_{ai} = (1 - \gamma_i)$ $i = 1, \dots, t$ is the probability a bird is available in interval i . Conditional detection probabilities for each observer in each period (p_{d1i}, p_{d2i}) $i = 1, \dots, t$ also are included in the model. Unlike the general robust design, we are assuming that all animals survive during the point count so that $\phi_i = 1$. In the random availability model, an estimate of the probability that a bird does not sing during the entire 10-minute count can be obtained as the product of all the $1 - p_{ai}$ s.

To illustrate, consider a detection history for 2 observers over 2 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 the primary observer (and therefore the secondary observer) in interval 1 and detected only by the secondary observer in interval 2. This history has expected cell structure:

$$p_{a1}p_{d11}p_{a2}(1-p_{d12})p_{d22}$$

In this case, the bird has to sing in each interval to be detected by ≥ 1 observer. However, another history (11, 00) has the expected cell structure:

$$p_{a1}p_{d11}[p_{a2}(1-p_{d12})(1-p_{d22}) + (1-p_{a2})].$$

The 00 in the second interval means there were 2 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 detection histories obtained in a study, one can build a likelihood function and obtain parameter estimates and standard errors. Consider t time intervals where birds are tracked throughout the count and there are 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 primary observer, we have

$$\begin{aligned} L(N; \theta) = & \frac{N!}{n_{1,1}! \dots n_{k-1,1}!(N-n)!} \tau \\ & [p_{1,1}(\theta)^{n_{1,1}} \dots p_{k-1,1}(\theta)^{n_{k-1,1}}] \\ & \times \frac{1}{n_{1,2}! \dots n_{k-1,2}!} (1-\tau) \\ & [p_{1,2}(\theta)^{n_{1,2}} \dots p_{k-1,2}(\theta)^{n_{k-1,2}}] p_k(\theta)^{N-n} \end{aligned}$$

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 that are known functions of θ , availability and detection probability parameters [$p_{i,j}(\theta) = f_{i,j}(\theta)$] and $p_k = 1 - \sum_{i=1}^{k-1} \sum_{j=1,2} p_{i,j}$. The model structures we examined here in the dependent double-observer setting follow a similar form of those by Stanislav (2009) 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 1 is the primary observer (often 0.5 by design) and, thus, $1 - \tau$ is for 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 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 $\{[p_a(1 - p_{d11})(1 - p_{d21})] + (1 - p_a)\}\{[p_a(1 - p_{d12})(1 - p_{d22})] + (1 - p_a)\}$. The same is true if the second observer is the primary observer, just with nondetection terms transposed in each time period’s 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

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

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

$$\text{with } q_i(\theta) = \frac{p_i(\theta)}{1 - p_k(\theta)},$$

where $i = 1, 2, \dots, k - 1$.

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 $\hat{N} = n/1 - \hat{p}_k$, the greatest integer $\leq n/1 - \hat{p}_k$, which maximizes L_1 . This is simpler computationally than maximizing the full likelihood. We can obtain standard errors of the derived estimates based on the second bootstrap method presented by Norris and Pollock (1996), which we also could use to construct confidence intervals.

Through use of the conditional likelihood maximization, an accessible approach for finding estimates of availability and detection probabilities, along with population size, exists. We can find conditional likelihood estimates of parameters directly from likelihood maximization procedures available in any software computing language, such as the `optim` function in R. For some instances, one may require use of constrained optimization to guarantee that probability estimates fall between 0 and 1, and in R the function `constrOptim` handles the task. Akaike’s Information Criterion can be used for model selection (Burnham and Anderson 2002, Williams et al. 2002). The estimated distance to each bird, detected by ≥ 1 observer, can be included as an important covariate influencing detection probability. Laake and Borchers (2004) provide additional details and approaches for modeling distance as a covariate with multiple-observer methods. Any number of observers and time intervals can be accommodated. We follow this approach below and provide examples to illustrate the methodology.

Analysis

For our field data, we fit detection histories for bobwhites 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 one (i.e., all birds are available) and allowed for detection given availability (p_d) to vary or remain constant with time or observer. We also allowed for an observer-based behavioral effect in some models, which is analogous to a trap-response model in classic capture–recapture literature where the animal responds to presence of the trap, except that in this case it is the observer (analogous to the trap) that is responding to the bird. Riddle et al. (2010) discuss observer-based behavioral effects in detail and found these models were heavily favored in point-count methods that 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 was as follows: $p_a(\text{rand}), p_d(.,.,b); p_a(\text{rand}), p_d(.,o,b); p_a(\text{rand}), p_d(.,o,.)$; $p_a(\text{rand}), p_d(.,.,.)$; $p_a(\text{rand}), p_d(t,o,.)$; $p_a(\text{all}), p_d(.,.,b); p_a(\text{all}), p_d(.,o,b); p_a(\text{all}), p_d(.,o,.)$; $p_a(\text{all}), p_d(.,.,.)$; and $p_a(\text{all}), p_d(t,o,.)$. Here, letters t, o, and b represent effects of time, observer differences in detection probability, and an observer-based behavioral response, respectively. The parenthetical terms “rand” and “all” refer to whether availability was random or equal to one, respectively. We fit models in Program R and obtained and used AIC values to select the top model. The R code is available for interested readers upon request.

We also considered an artificial data set with low availability and detection probabilities. We designed the simulated data set 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. We generated our simulated data set from a random multinomial distribution with cell probabilities determined from the constant random availability model, with observer-depen-

Table 1. Akaike's Information Criterion (corrected for small sample size; AIC_c) model selection results for northern bobwhite. Models in the set allow availability (p_a) to be random (rand) or equal to 1 (all; 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 (.). We collected all data on farms in the Coastal Plain of North Carolina, USA, 2004–2005.

Model	AIC_c	ΔAIC_c	AIC_c wt	No. of parameters
p_a (rand), p_d (.,b)	471.76	0.00	0.46	3
p_a (rand), p_d (.,o,b)	472.04	0.28	0.40	5
p_a (rand), p_d (.,o,.)	474.71	2.95	0.11	3
p_a (rand), p_d (.,.,.)	476.53	4.77	0.04	2
p_a (rand), p_d (t,o,.)	487.97	16.21	0	9
p_a (all), p_d (.,b)	702.11	230.35	0	2
p_a (all), p_d (.,o,b)	704.78	233.02	0	4
p_a (all), p_d (.,.,.)	713.24	241.48	0	1
p_a (all), p_d (.,o,.)	714.06	242.3	0	2
p_a (all), p_d (t,o,.)	718.97	247.21	0	8

dent initial detection probabilities constant over time intervals and elevated redetection probabilities. Specifically, $t = 4$ time intervals and 2 dependent observers.

For this model, we defined the true population size (N) to be 500, true probability that such a bird is available for detection, p_a , to be 0.3, probability of first detection, p_{d1} , to be 0.5, and for subsequent detections, the detection probability, c_{d2} , was 0.6.

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 60.48% (SE = 2.01) of the population was available during any given 2.5-minute 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_c 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 (279.18 and 279.08, respectively).

In our simulated data set, 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)

Table 2. Northern bobwhite parameter estimates and standard errors for model p_a (rand), p_d (.,b) (i.e., random availability with an observer-based behavioral effect). N is abundance, p_a is the probability of availability, p_d is the probability of detection given availability, and c_d is conditional redetection probability. We calculated estimates and standard errors with $B = 100$ bootstrap samples. We collected all data on farms in the Coastal Plain of North Carolina, USA, 2004–2005.

Parameters	Parameter estimates	SE
N	279.18	3.46
p_a	0.605	0.020
p_d	0.799	0.040
c_d	0.902	0.021

Table 3. Northern bobwhite parameter estimates and standard errors for model p_a (rand), p_d (.,o,b) (i.e., random availability with observer differences and an observer-based behavioral effect). N is abundance; p_a is the probability of availability; p_{d1} and p_{d2} are the probabilities of detection given availability for observers 1 and 2, respectively; and c_{d1} and c_{d2} are conditional redetection probabilities for observers 1 and 2, respectively. We calculated estimates and standard errors with $B = 100$ bootstrap samples. We collected all data on farms in the Coastal Plain of North Carolina, USA, 2004–2005.

Parameters	Parameter estimates	SE
N	279.08	3.51
p_a	0.606	0.023
p_{d1}	0.782	0.046
p_{d2}	0.840	0.041
c_{d1}	0.884	0.032
c_{d2}	0.922	0.023

for subsequent detections. The total population was estimated at 525.31 (SE = 45.22) birds (Table 4).

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, ours 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 within a certain span of time (2.5 min in our case) was a more limiting factor than ability of observers to detect calling bobwhites. These results could help 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-minute count (Fig. 1).

Similarly, one could compare probability estimates that an observer would detect an individual bobwhite at least once given that it was available in ≥ 1 interval from the double-observer method and time-of-detection method (Fig. 2). For example, our top model suggests that if one visit of 2.5 minutes was made, then the probability of ≥ 1 observer detecting an individual bobwhite is higher with the dependent double-observer method than with one observer on their own. However, if one observer of similar skill to

Table 4. Parameter estimates and standard errors for the simulated data set with random availability and an observer-based behavioral effect. N is abundance, p_a is the probability of availability, p_d is the probability of detection given availability, and c_d is conditional redetection probability. We calculated estimates and standard errors with $B = 100$ bootstrap samples.

Parameters	True value	Parameter estimates	SE
N	500	525.31	45.22
p_a	0.30	0.291	0.028
p_d	0.50	0.460	0.050
c_d	0.60	0.607	0.063

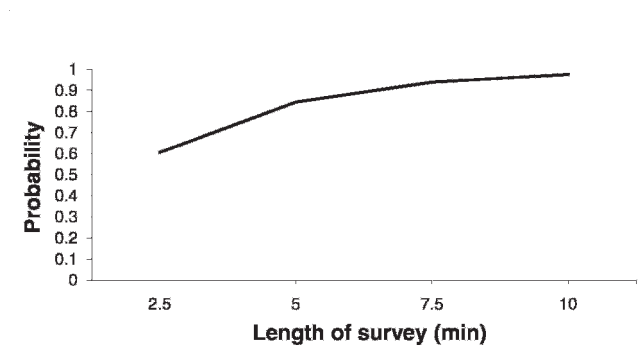


Figure 1. Probability that an individual bobwhite will be available (vocalize) at least once over surveys of various lengths on farms in the Coastal Plain of North Carolina, USA, 2004–2005.

those in our study used the time-of-detection method for ≥ 2 2.5-minute intervals, then they would be expected to detect individual birds with a higher probability than one 2.5-minute visit by 2 observers. Furthermore, 2 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 one 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 (2009) provided examples of combining time-of-detection and independent double-observer approaches. 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). 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 few vocal cues are available to be mapped (Alldredge 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 (Stanislav 2009).

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 (Stanislav 2009).

MANAGEMENT IMPLICATIONS

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

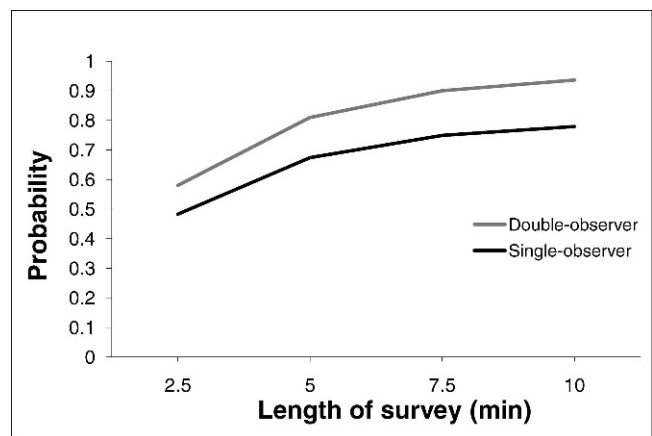


Figure 2. Probability of detecting a bobwhite once by one observer in a single-observer survey and by ≥ 1 observer in a double-observer survey given availability in ≥ 1 interval for surveys of various durations on farms in the Coastal Plain of North Carolina, USA, 2004–2005.

subsample of their points to better understand the detection process in field studies and potentially obtain better estimates of population abundance. This approach should lead to more informed decisions regarding the best use of personnel and time thereby reducing expenses over time. We think this is especially critical for species like northern bobwhite, which appear 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).

ACKNOWLEDGMENTS

We thank M. W. Alldredge for his thoughts and suggestions on early versions of this manuscript. We also thank K. Westerbeak, D. Williams, and all of the Murphy-Brown, LLC staff for allowing us to conduct the field border study on their farms, which resulted in this data set. J. D. Riddle thanks M. Krachey, K. Pacifici, and R. Mordecai for numerous stimulating conversations on detection probability and sampling issues.

LITERATURE CITED

- Alho, J. M. 1990. Logistic regression in capture–recapture models. *Biometrics* 46:623–635.
- Alldredge, M. W. 2004. Avian point-count surveys: estimating components of the detection process. Dissertation, North Carolina State University, Raleigh, USA.
- Alldredge, M. W., K. Pacifici, T. R. Simons, and K. H. Pollock. 2008. A novel field evaluation of the effectiveness of distance and independent observer sampling to estimate aural avian detection probabilities. *Journal of Applied Ecology* 45:1349–1356.
- Alldredge, M. W., K. H. Pollock, and T. R. Simons. 2006. Estimating detection probabilities from multiple-observer point counts. *Auk* 123:1172–1182.
- Alldredge, M. W., K. H. Pollock, T. R. Simons, J. A. Collazo, and S. A. Shriner. 2007. Time-of-detection method for estimating abundance from point-count surveys. *Auk* 124:653–664.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling. Oxford University Press, Oxford, United Kingdom.

- Burnham, K. P. 1981. Summarizing remarks: environmental influences. Pages 324–325 in C. J. Ralph and J. M. Scott, editors. Estimating numbers of terrestrial birds. Studies in Avian Biology 6. Cooper Ornithological Society, Lawrence, Kansas, USA.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Burnham, K. P., and W. S. Overton. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65:625–633.
- Collins, S. 2004. Vocal fighting and flirting: the functions of birdsong. Pages 39–79 in P. Marler and H. Slabbekoorn, editors. *Nature's music: the science of birdsong*. Elsevier Academic Press, San Diego, California, USA.
- Cook, R. D., and J. O. Jacobson. 1979. A design for estimating visibility bias in aerial surveys. *Biometrics* 35:735–742.
- Farnsworth, G. L., K. H. Pollock, J. D. Nichols, T. R. Simons, J. E. Hines, and J. R. Sauer. 2002. A removal model for estimating detection probabilities from point-count surveys. *Auk* 119:414–425.
- Huggins, R. M. 1989. On the statistical analysis of capture experiments. *Biometrika* 76:133–140.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725–732.
- Kendall, W. L., and J. D. Nichols. 1995. On the use of secondary capture–recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* 22:751–762.
- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's Robust Design. *Ecology* 78:563–578.
- Laake, J. L., and D. L. Borchers. 2004. Methods for incomplete detection at distance zero. Pages 108–189 in S. T. Buckland, D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas, editors. *Advanced distance sampling: estimating abundance of biological populations*. Oxford University Press, Oxford, United Kingdom.
- Link, W. A. 2003. Nonidentifiability of population size from capture–recapture data with heterogeneous detection probabilities. *Biometrics* 59:1123–1130.
- Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *Auk* 117:393–408.
- Nichols, J. D., L. Thomas, and P. B. Conn. 2009. Inferences about landbird abundance from count data: recent advances and future directions. Pages 201–235 in D. L. Thompson, E. G. Cooch, and M. J. Conroy, editors. *Environmental and ecological statistics. Volume 3: modeling demographic processes in marked populations*. Springer, New York, New York, USA.
- Norris, III, J. L., and K. H. Pollock. 1996. Nonparametric MLE under two closed capture–recapture models with heterogeneity. *Biometrics* 52:639–649.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62.
- Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs* 107.
- Ralph, C. J., J. R. Sauer, and S. Droege, editors. 1995. *Monitoring bird populations by point counts*. U.S. Department of Agriculture, Forest Service General Technical Report PSW-149, Albany, California, USA.
- Ralph, C. J., and J. M. Scott, editors. 1981. *Estimating numbers of terrestrial birds*. Studies in Avian Biology 6. Cooper Ornithological Society, Lawrence, Kansas, USA.
- Riddle, J. D. 2007. Maximizing the impact of field borders for quail and early-succession songbirds: what's the best design for implementation? Dissertation, North Carolina State University, Raleigh, USA.
- Riddle, J. D., C. E. Moorman, and K. H. Pollock. 2008. The importance of habitat shape and landscape context to northern bobwhite populations. *Journal of Wildlife Management* 72:1376–1382.
- Riddle, J. D., R. S. Mordecai, K. H. Pollock, and T. R. Simons. 2010. Effects of prior detections on estimates of detection probability, abundance, and occupancy. *Auk* 127:94–99.
- Rosenstock, S. S., D. R. Anderson, K. M. Giesen, T. Leukering, and M. F. Carter. 2002. Landbird counting techniques: current practices and an alternative. *Auk* 119:46–53.
- Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60:108–115.
- Royle, J. A., and R. M. Dorazio. 2008. *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations, and communities*. Academic Press, San Diego, California, USA.
- Sanathanan, L. 1972. Estimating the size of a multinomial population. *The Annals of Mathematical Statistics* 43:142–152.
- Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*. Second edition. Charles W. Griffin, London, United Kingdom.
- Simons, T. R., M. W. Alldredge, K. H. Pollock, and J. M. Wettröth. 2007. Experimental analysis of the auditory detection process on avian point counts. *Auk* 124:986–999.
- Stanislav, S. J. 2009. Developments and applications of a closed capture–recapture robust design model to avian point count data. Dissertation, North Carolina State University, Raleigh, USA.
- Thompson, W. L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. *Auk* 119:18–25.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, Supplement:120–138.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations: modeling, estimation, and decision making*. Academic Press, San Diego, California, USA.
- Zippin, C. 1958. The removal method of population estimation. *Journal of Wildlife Management* 22:82–90.

Associate Editor: Collier.