

A Comparison of Methods for Estimating Northern Bobwhite Covey Detection Probabilities

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ABSTRACT We compared the time-of-detection and logistic regression methods of estimating probability of detection for northern bobwhite (*Colinus virginianus*) coveys. Both methods are unusual in that they allow estimation of the total probability of detection (i.e., the product of the probability that a covey is available for detection [i.e., that a covey vocalizes] and detection given availability). The logistic regression method produced an average detection probability of 0.596 (SE = 0.020) and the time-of-detection method produced a detection probability estimate of 0.540 (SE = 0.086), and the 2 estimates were not significantly different. This is the first evaluation of the time-of-detection method with empirical field data. Although the time-of-detection and logistic regression method each have advantages, both can be used under appropriate conditions to improve estimates of bobwhite abundance by allowing for the estimation of detection probabilities. Improved estimates of bobwhite abundance will allow land managers to make more informed management decisions. (JOURNAL OF WILDLIFE MANAGEMENT 72(6):1437–1442; 2008)

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Differences in bird detectability over space and time may bias abundance or density estimates that do not allow for estimation of detection probabilities (Williams et al. 2002). Abundance estimates and detection probabilities are related by the equation:

$$\hat{N}_i = C_i / \hat{p}_i \quad (1)$$

where $\hat{N}$ is the estimate of population abundance, C is the count statistic, $\hat{p}$ is the estimate of detection probability, and i is time or location of the survey. Comparing abundance indices or counts from different times or locations may lead to biased population comparisons and poor management decisions if detection probability is not constant. Nevertheless, Rosenstock et al. (2002) indicated that index methods without corrections for detection probabilities were still used in 95% of the avian studies they reviewed.

Detection probability can be viewed as the product of 2 components: availability and detection given availability (Marsh and Sinclair 1989, Farnsworth et al. 2002, Pollock et al. 2004, Alldredge et al. 2006). In the context of point counts, probability of availability is the probability that a bird sings (or gives some other vocalization) or that it is not visually concealed from the observer. The probability that a bird is detected given availability is simply the probability that a vocalizing bird is heard or that a visible bird is seen (see Alldredge 2004, Pollock et al. 2004, Alldredge et al. 2007a). Therefore, total probability of detection (p) can be written to show its components as:

$$p = p_a p_d \quad (2)$$

where p_a is the probability of a bird being available and p_d is the probability of a bird being detected given that it is available. Distance sampling and multiple-observer methods do not allow estimation of total detection probability (Nichols et al. 2000, Buckland et al. 2001, Alldredge et al. 2006), whereas the time-of-detection and repeated counts methods do (Farnsworth et al. 2002, Royle and Nichols 2003, Alldredge et al. 2007a).

The time-of-detection method proposed by Alldredge et al. (2007a) uses information about whether a bird is detected from separate time intervals within the point count. In other words, the method allows for creation of a detection history that can be viewed in a similar manner to a capture–recapture history in a closed-population model (Alldredge 2004, Alldredge et al. 2007a). The ability of the time-of-detection method to handle variation in bird vocalization rates is one of its strengths (Alldredge et al. 2007a). When ≥ 4 intervals are used and heterogeneity is modeled as a 2-point finite mixture, then it is theoretically possible to model detection by maximum-likelihood estimation using variations of the standard models presented by Otis et al. (1978) for closed-populations (Norris and Pollock 1996, Pledger 2000, Alldredge et al. 2007a; see also Pollock et al. 1990, Williams et al. 2002). Moreover, this makes model selection via information-theoretic approaches possible (e.g., Akaike's Information Criterion [AIC] in Program MARK; White and Burnham 1999, Burnham and Anderson 2002).

Alldredge et al. (2007b) recently evaluated the time-of-detection method with bird song in a realistic but simulated field setting. The method performed reasonably well except under conditions of heterogeneity with low detection probabilities. However, this shortcoming is not unique to the time-of-detection method (Alldredge et al. 2007b). Alldredge et al. (2007b) encouraged other researchers to

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evaluate the method under various field conditions. In particular, Alldredge et al. (2007b) suggest the time-of-detection method may be especially useful with birds that have large territories, high singing rates, and low mobility to minimize localization errors. During autumn, northern bobwhite (*Colinus virginianus*) coveys have large territories, exhibit periods of high singing rates under favorable conditions, and do not move large distances during the time of day when they are most vocal. Therefore, northern bobwhite coveys may be particularly suited for sampling with the time-of-detection method.

Another sampling method that accounts for total probability of detection and was developed specifically for bobwhite coveys is the logistic regression method of Wellendorf et al. (2004). This method is based on a logistic regression model, which includes the following covariates: number of calling coveys, wind speed, cloud cover, and changes in barometric pressure prior to the count. This model was created from a large sample ($n = 219$) of radiomarked coveys at a large spatial scale from locations throughout the southeastern United States (farms in Tyrrell County, NC; farms in Wilson County, NC; Ames Plantation, TN; a hunting plantation in Leon County, FL; and Tall Timbers Research Station, FL).

We used the same sample of a northern bobwhite covey population to estimate covey detection probabilities using both the time-of-detection method and the logistic regression method. Our objective was to evaluate and compare the time-of-detection with the logistic regression method using empirical field data.

STUDY AREA

We conducted our study on 24 commercial hog farms in Bladen, Columbus, Duplin, Pender, Sampson, Scotland, and Robeson counties in the Coastal Plain of North Carolina, USA. Each hog farm had ≥ 1 hog houses, which were confinement areas for hog production, as well as ≥ 1 row-crop fields. Most farms were on a crop rotation of corn, soybeans, and wheat, although a few farms occasionally grew cotton on some fields. These farms were part of a larger study of the effects of field-border shape and landscape context on bobwhite and early succession songbirds. See Riddle (2007) for additional details regarding experimental design, farm descriptions, and overall project goals. Two of the locations where Wellendorf et al. (2004) developed their method (farms in Wilson and Tyrrell counties) also were located in the Coastal Plain of North Carolina. The close proximity and similar landscapes surrounding farms at these 2 locations to our own 24 study sites further facilitates our ability to make a meaningful comparison of the time-of-detection and logistic regression methods.

METHODS

We sampled autumn coveys on each farm during 2004–2006. We conducted surveys from the first week of October until the second week of November. In general, covey calling behavior is less variable during these 6 weeks than

the rest of autumn in the southeastern United States (Wellendorf et al. 2004). We sampled each farm once per year from one fixed location, which was approximately central to the field borders that we established on each farm (Riddle 2007). Point counts began at 45 minutes before sunrise and lasted 1 hour. We did not conduct surveys during inclement weather. When a covey vocalized, we recorded its location on a digital orthogonal quarter-quadrangle (DOQQ) of the farm to avoid double-counting. In another attempt to avoid double-counting, we considered calls from within 30 m of each other to be from the same covey (Wellendorf et al. 2004), although we rarely had to rely on this rule in practice because of low covey densities at our sites. At sunrise, we recorded wind speed (km/hr) with a handheld anemometer and estimated cloud cover to the nearest 10%. Later, we obtained hourly barometric pressure readings (Hg) for the 6 hours prior to sunrise from the nearest weather stations via the North Carolina State Climate Office. We used these environmental data along with the number of calling coveys from each count to calculate a covey call-rate adjustment according to the following equation adapted from Wellendorf et al. (2004):

$$\text{Logit}(\hat{p}_w) = -0.228 + 0.348x_1 + 3.27x_2 - 0.002x_3 - 0.092x_4 \quad (3)$$

where x_1 is number of coveys heard, x_2 is change in barometric pressure for the 6 hours prior to sunrise, x_3 is cloud cover (%), and x_4 is wind speed. The covey call-rate adjustment is an estimate of detection probability ($\hat{p}_w$). To estimate abundance of coveys in an area, we divided number of coveys heard by the adjustment to correct for environmental variables and the number of calling coveys (Wellendorf et al. 2004).

The time-of-detection method was performed simultaneously with the logistic regression method of Wellendorf et al. (2004) by the same observers. We divided each 1-hour point count into 4 15-minute intervals. We recorded covey calling behavior in each interval separately by circling covey locations on the DOQQs with 4 colors of ink that corresponded to the 4 time intervals. Thus, we created a 4-digit detection history for each covey. For example, a covey that called in intervals 1 and 3, but not in 2 or 4, would have the following detection history: 1010.

For the logistic regression method, we obtained an average covey call-rate adjustment for the entire study by averaging all of the covey call-rate adjustments from each farm. For the time-of-detection method, we entered detection histories from all farms and years into Program MARK and compared the following models in a Huggins closed-capture framework: M_0 , M_t , M_b , M_{th} , M_{bh} , M_h , where the subscripts 0, t, b, and h represent constant detection probability, temporal variation in detection probability, behavioral response in detection probability, and heterogeneity of detection probabilities among individual coveys, respectively (Huggins 1989, 1991; see Williams et al. 2002). All heterogeneity models were 2-point mixtures (Pledger 2000). We evaluated models using AIC_c (AIC corrected for

Table 1. Akaike's Information Criterion (AIC)^a for closed-capture models used with the time-of-detection method for sampling bobwhite coveys. We collected all data from commercial hog farms, North Carolina, USA (2004–2006).

Model ^b	AIC _c	ΔAIC _c	AIC _c wt	Model likelihood	Model parameters	Estimable parameters	Deviance
M _t	177.079	0.00	0.947	1.000	4	4	416.523
M _{th}	182.864	5.79	0.053	0.055	9	5	411.736
M _b	226.340	49.26	0.000	0.000	2	2	469.896
M _{bh}	228.388	51.31	0.000	0.000	3	3	469.896
M ₀	257.108	80.03	0.000	0.000	1	1	502.695
M _h	259.139	82.06	0.000	0.000	2	2	502.695

^a AIC_c, AIC corrected for small sample size; ΔAIC_c, difference in AIC_c values between respective model and best model; AIC_c wt, relative likelihood of the respective model given the data and other models in the model set (Burnham and Anderson 2002).

^b The model subscripts 0, t, b, and h represent constant detection probability, temporal variation in detection probability, behavioral response in detection probability, and heterogeneity of detection probabilities among individual coveys, respectively (see Williams et al. 2002).

small sample size) and we chose the model with the largest AIC_c weight (relative likelihood of the respective model given the data and other models in the model set) to calculate a detection probability (Burnham and Anderson 2002). Combining detection histories from all years and farms was necessary to perform this analysis because of small sample sizes (no. of calling coveys on each farm in this case). However, our work with summer bobwhite calls indicated that combining the data in this way was reasonable (Riddle 2007).

To make the 2 estimates comparable, we had to convert the probability of detection at least once in 15 minutes to the probability of detection at least once in an hour for the time-of-detection method using the following equation:

$$\hat{p}_t = 1 - \prod_{i=1}^4 (1 - \hat{p}_i), \quad (4)$$

with

$$Var(\hat{p}_t) = \sum_{i=1}^4 [Var(\hat{p}_i) \prod_{j \neq i} (1 - \hat{p}_j)], \quad (5)$$

based on the Delta or Taylor Series method (Williams et al. 2002).

We used the detection estimate from the logistic regression method ($\hat{p}_w$) and the time-of-detection method ($\hat{p}_t$) to test the following hypothesis: H₀: $\hat{p}_w = \hat{p}_t$ versus H_a: $\hat{p}_w \neq \hat{p}_t$. We used the normal Z-statistic for comparing 2 different proportions (e.g., Williams et al. 2002). A failure to reject H₀ implies that the time-of-detection method produced a similar probability of detection to that of the logistic regression method.

RESULTS

We could not use data from 4 covey counts in 2004 because of logistical reasons. Of the other 68 covey count surveys performed ($n = 20$ in 2004; $n = 24$ in 2005; $n = 24$ in 2006), only 31 resulted in detections (i.e., we could use only 31 to estimate the average covey call-rate adjustment for the logistic regression method). The average covey call-rate adjustment was 0.596 (SE = 0.020).

We detected 64 coveys and entered the detection histories

into Program MARK for use with the time-of-detection method. The best model was M_t (AIC_c wt = 0.947; Table 1). The M_t model assumes that every covey has an equal probability of being detected within each sampling period, but detection probability can vary among sampling periods (Williams et al. 2002). M_{th} was the only other model with an AIC_c weight > 0. However, only 5 of 9 parameters were estimable for this model. If we removed M_{th} from the group of compared models because of lack of convergence, then M_t would have received all of the weight (i.e., AIC_c wt = 1). Detection estimates for each of the 4 time periods were $\hat{p}_1 = 0.236$ (SE = 0.060), $\hat{p}_2 = 0.371$ (SE = 0.084), $\hat{p}_3 = 0.008$ (SE = 0.009), $\hat{p}_4 = 0.034$ (SE = 0.018). Therefore, average detection probability, calculated by equation 4, was 0.540 (SE = 0.086). The 2 estimates were not statistically different [$P(|z_{0.05/2}| \geq 0.64) = 0.522$].

DISCUSSION

The time-of-detection method provided an estimate of detection probability that was similar to that of the logistic regression method. Moreover, the selected model, M_t, is consistent with what is known about covey calling behavior. Hamrick (2002) determined that coveys were most likely to give their first call at 27.36 (SE = 0.21) minutes before sunrise. Similarly, Wellendorf et al. (2004) reported coveys are most likely to give their first call at 23.4 (SE = 0.5) minutes before sunrise, with 87% of calls occurring prior to 15 minutes before sunrise, which corresponds with the higher detection probability estimates for time intervals 1 and 2, which were 0.236 and 0.371, respectively. Detection probabilities for periods 3 and 4 were only slightly > 0.0, which again is consistent with known covey calling behavior. Extremely low probabilities of detecting coveys during periods 3 and 4 limited our ability to detect heterogeneity, if it was present. If we had focused the first 30 minutes of sampling with multiple short intervals, it is possible we could have fit model M_{th}. Nevertheless, the time-of-detection method allowed for the selection of a model that was able to identify and capitalize on a key aspect of covey behavior, as well as call-rate variability, and produce a reliable detection estimate. This is the first evaluation of the time-of-detection method with empirical field data. The

time-of-detection method appears to perform very well in the context of northern bobwhite covey sampling.

The time-of-detection method produced a similar detection estimate to the logistic regression method but did not require the collection of additional data on wind speed, cloud cover, or barometric pressure. In this regard, the time-of-detection method is more convenient and less expensive. Handheld anemometers can be costly and may range from \$74 to \$245 (United States currency; J. D. Riddle, North Carolina State University, personal observation). We were able to obtain barometric pressure readings from the North Carolina State Climate Office without charge because of our affiliation with North Carolina State University. However, if we had been required to pay for these data, the cost would have been \$25/request or \$25/hour of data retrieval (United States currency). The time-of-detection method also allows for study-specific estimation of detection probability, which makes it sensitive to unidentified or unmeasured factors that could influence covey call variability. Additional factors that could influence covey call variability or detection probabilities could easily be included as covariates in Program MARK. However, the time-of-detection method will not perform well when only a few coveys are detected in a study.

The primary advantage of the logistic regression method is that it allows for adjustments on a count-by-count basis. Therefore, it is especially useful for smaller scale studies with few replicates, or with larger scale studies on sites with few coveys or logistical constraints that prohibit repeated visits within a season to increase precision (e.g., Riddle 2007). The logistic regression method was developed on 5 study sites located across the southeastern United States and used similarities in covey call rates across sites (Wellendorf et al. 2004). Wellendorf et al. (2004) were interested in making sampling recommendations that most researchers could use, or improve upon, at most sites. Nevertheless, there are many site-specific factors, such as landscape differences and timing of recruitment and covey formation, which could be important and were not included in their model (Wellendorf et al. 2004).

The logistic regression method and the time-of-detection method share several assumptions. Both assume that the population of coveys within the sampled area is closed during the point count, which is likely to hold in most cases. For example, it is possible that entire coveys (especially small ones) are depredated within the course of one hour at any particular site, but we believe this is unlikely to happen very often. Both methods assume that individual coveys are accurately identified (i.e., no double-counting of single coveys and no mistaking multiple coveys as a single covey). Using DOQQs to map covey locations and the 30-m rule help to avoid double-counting. However, the ability of observers to determine if birds giving covey calls are within 30 m of one another probably will decrease with increasing distance from the observer, which is not a major concern when covey densities are moderate to low (as in our study) but could be problematic in areas of high covey density (Roseberry 1982, DeMaso et al. 1992). The time-of-

detection method has additional assumptions associated with the specific model(s) that best fits the data. M_t was the best model for our data, and this adds the additional assumption that each covey has an equal detection probability within each sampling interval. This assumption might be violated if, for example, call rates of some coveys were elevated within a particular sampling interval because they had been disturbed and scattered during the night or if covey density differed dramatically at different survey locations within a study area because of density-dependent behavior in calling rates (Wellendorf et al. 2004). However, Wellendorf et al. (2004) estimated that nocturnal disturbance had not occurred for >95% of the coveys surveyed. In future studies, more intervals of shorter length (especially during the first 30 min of sampling) might allow one to account for this as a form of heterogeneity. Heterogeneity models could also account for the effect of differences in covey densities on covey calling behavior at different survey locations as well. The logistic regression method has the additional assumption that wind speed, cloud cover, and barometric pressure changes are recorded accurately. The logistic regression method was developed at specific sites from an observed range of values used to estimate each of the betas (regression coeff.) used in equation 3. Technically, use of the logistic regression method at sites and under conditions outside the range of those from which it was developed is a form of extrapolation, which may not be as large of a concern in situations where the method is used in close proximity to where it was developed (e.g., this study). However, it could be more problematic when used at locations far from where it was developed. Similarly, another potential issue with the logistic regression method is that adjustments made to individual counts are not totally independent because the estimated betas in the logistic regression used to adjust each count are based on the same prior data set of Wellendorf et al. (2004).

We acknowledge that other studies have suggested covey call surveys provide poor density estimates when compared to line-transect methods that flush coveys (DeMaso et al. 1992, Rusk et al. 2007). Line-transect methods typically perform best when coveys are at high densities in relatively homogeneous habitat, such as some rangelands in Texas, USA (Guthery 1998). However, these conditions are not typical for most bobwhite populations. Line-transects may perform poorly when densities are low and habitats are heterogeneous (e.g., interspersed fields and forests; Kuvlesky et al. 1989). Furthermore, on 2 sites with a variety of woodland, grassland, shrubland, and cropland habitats, Janvrin et al. (1991) determined that some northern bobwhite did not flush, even when observers stepped over them, and that 40% of coveys moved away from observers upon approach. Thus, 2 major assumptions of line-transect sampling were violated: 1) detection probability on the line is 1.0 and 2) birds do not move towards or away from an observer prior to detection (Guthery 1988). DeMaso et al. (1992) suggested that the poor performance of covey call methods as an index of covey density in their study may have

resulted in part from violations of the assumptions that the proportion of coveys calling is constant over space and time. Indeed, Wellendorf et al. (2004) demonstrated that covey calling behavior is not constant over biweekly periods or over space (i.e., because covey calling behavior is density-dependent and each survey location may have different densities). At a smaller temporal scale, our results indicate that detection probabilities changed significantly over a short amount of time (i.e., over the course of an hr). Compared to traditional covey call surveys, surveys conducted with the time-of-detection method or the logistic regression method may produce density estimates that are more comparable to estimates from line-transect methods in environments where line-transect methods are appropriate. However, line-transect methods, or other methods that rely on distance data alone, will still be biased by their lack of ability to account for both components (availability and detection given availability) of the detection process.

Management Implications

Attempts to evaluate the effectiveness of bobwhite management activities only will be as reliable as the survey methods used in the evaluations. We recommend that researchers simultaneously use both the time-of-detection and logistic regression methods when possible. The time-of-detection method adds little extra effort to the logistic regression method. It would be informative if other researchers were able to assess the performance of both methods for covey counts at other study sites to determine if our results are repeatable. When it is not possible to use both methods, we recommend the logistic regression method for smaller scale studies where replication or multiple independent counts may not be feasible or in situations where number of detections is likely to be low. We recommend the time-of-detection method for larger scale studies where number of detections may be high and gathering wind speed and climatic data may be prohibitive because of logistics or costs. However, even in this case, it still may be informative to double-sample with the logistic regression method on a subset of points to allow for comparisons where possible (Bart and Earnst 2002). We also note that both methods could be combined intuitively within a Bayesian framework.

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