



## TIME-OF-DETECTION METHOD FOR ESTIMATING ABUNDANCE FROM POINT-COUNT SURVEYS

MATHEW W. ALLDREDGE,<sup>1,4</sup> KENNETH H. POLLOCK,<sup>1</sup> THEODORE R. SIMONS,<sup>2</sup>  
JAIME A. COLLAZO,<sup>2</sup> AND SUSAN A. SHRINER<sup>3</sup>

<sup>1</sup>Colorado Division of Wildlife, 317 West Prospect Road, Fort Collins, Colorado 80526, USA;

<sup>2</sup>U.S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit, Department of Zoology,  
Campus Box 7617, North Carolina State University, Raleigh, North Carolina 27695, USA; and

<sup>3</sup>Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523, USA

**ABSTRACT.**—Point-count surveys are often used to collect data on the abundance and distribution of birds, generally as an index of relative abundance. Valid comparison of these indices assumes that the detection process is comparable over space and time. These restrictive assumptions can be eliminated by estimating detection probabilities directly. We generalize a recently proposed removal model for estimating detection probabilities using a time-of-detection approach, which can account for more sources of variation in point-count data. This method is specifically designed to account for variation in detection probabilities associated with singing rates of birds. Our model accounts for both availability bias and detection bias by modeling the combined probability that a bird sings during the count, and the probability that it is detected given that it sings. The model requires dividing the count into several intervals and recording detections of individual birds in each interval. We develop maximum-likelihood estimators for this approach and provide a full suite of models based on capture–recapture models, including covariate models. We present two examples of this method: one for four species of songbirds surveyed in Great Smoky Mountains National Park using three unequal intervals, and one for the Pearly-eyed Thrasher (*Margarops fuscatus*) surveyed in Puerto Rico using four equal intervals. Models incorporating individual heterogeneity were selected for all data sets using information-theoretic model-selection techniques. Detection probabilities varied among count-time intervals, which suggests that birds may be responding to observers. We recommend applying this method to surveys with four or more equal intervals to reduce assumptions and to take full advantage of standard capture–recapture software. The time-of-detection approach provides a better understanding of the detection process, especially when singing rates of individual birds affect detection probabilities. *Received 20 July 2004, accepted 14 June 2006.*

**Key words:** abundance estimation, bird surveys, capture–recapture, detection probability, point counts.

### Estimación de la Abundancia en Puntos de Conteo Mediante el Método del Tiempo de Detección

**RESUMEN.**—Es común usar censos en puntos de conteo para recolectar datos de abundancia y distribución de aves, generalmente como índices de abundancia relativa. Una comparación válida de estos índices supone que el proceso de detección es comparable en el espacio y en el tiempo. Estas restricciones pueden eliminarse mediante la estimación de las probabilidades de detección. Generalizamos un

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<sup>4</sup>E-mail: mat.allredge@state.co.us

modelo de remoción propuesto recientemente para la estimación de probabilidades de detección usando un enfoque basado en el tiempo de detección, el cual considera diversas fuentes de variación en los datos obtenidos de puntos de conteo. Este método fue diseñado específicamente para considerar la variación en las probabilidades de detección asociadas con las tasas de canto de las aves. Nuestro modelo considera tanto el sesgo de disponibilidad como el sesgo de detección mediante el modelado de la probabilidad combinada de que un ave cante durante el conteo, y de que sea detectada dado que canta. El modelo requiere dividir el conteo en varios intervalos y registrar la detección de aves individuales en cada intervalo. Desarrollamos estimadores de máxima verosimilitud para este enfoque y brindamos un paquete completo de modelos basados en modelos de captura-recaptura, incluyendo modelos de covariación. Presentamos dos ejemplos de este modelo: uno para cuatro especies de aves canoras muestreadas en el Parque Nacional Great Smoky Mountains usando tres intervalos desiguales y otro para la especie *Margarops fuscatus*, muestreada en Puerto Rico usando cuatro intervalos iguales. Seleccionamos modelos que incorporan la heterogeneidad individual para todos los datos usando técnicas de la teoría de la información. Las probabilidades de detección variaron entre los intervalos de tiempo, lo que sugiere que las aves podrían estar respondiendo a los observadores. Recomendamos aplicar este método a los muestreos con cuatro o más intervalos iguales para reducir las restricciones y para aprovechar al máximo los programas de computación de captura-recaptura. El enfoque del tiempo de detección brinda un mejor entendimiento del proceso de detección, especialmente cuando las tasas de canto de las aves individuales afectan las probabilidades de detección.

POINT-COUNT SURVEYS are routinely used to determine animal abundance, particularly for breeding birds (Thompson 2002). Nevertheless, statistically valid methods for collecting and analyzing such data are not common practice (Rosenstock et al. 2002). Many studies do not correct for the detection process, relying instead on raw count data as an index of abundance (Ralph et al. 1995, Rosenstock et al. 2002).

Estimating detection probabilities is essential for obtaining reliable estimates of population abundance (Nichols et al. 2000, Farnsworth et al. 2002, Thompson 2002). Farnsworth et al. (2002) and Alldredge (2004) provided descriptions of the two primary components of the detection process on avian point counts: availability and detection given availability. Ignoring either of these components can lead to biased abundance estimates (Marsh and Sinclair 1989). When birds are detected by song or call, availability is a function of singing rate and duration of the count. Farnsworth et al. (2002) advanced a removal model to account for both of these components. The method is based on dividing a count into multiple intervals and recording the interval in which an individual is first detected and uses closed-population removal models to estimate abundance.

Here, we present a time-of-detection approach that uses a closed-population capture-recapture framework (Otis et al. 1978, Williams et al. 2002), which provides a more general alternative to the removal method. The full time-of-detection approach uses both first detections and all subsequent detections of an individual bird to estimate the probability of detection. Seber (1982) showed that capture-recapture models are more efficient (smaller variance) than removal models. Because the time-of-detection method uses information on all detections of an individual bird, there is greater ability to model potential sources of variation in the data. However, capture-recapture models require that observers accurately track individual birds throughout the count. Errors in the capture history will bias the abundance estimates. We first outline the field methods required to collect data suitable for this method and then describe the candidate models and the general form of the model. We present example analyses using data from four equal-interval point counts, and from three unequal-interval point counts, and discuss potential uses and insights, particularly regarding the importance of singing rates in point-count surveys.

## METHODS

*Approach and candidate models.*—Recording data on when individual birds are detected during a point-count survey is useful for constructing a traditional detection history for each bird (a one if it is detected in an interval, a zero if it is not). Shriner (2001) used multi-colored pens to simultaneously map detections and record the time interval of detections. Detections in intervals following initial detection were recorded by underlining previously mapped birds.

The full detection-history data for a time-of-detection survey consist of the number of birds observed with each of the  $2^n - 1$  ( $n$  = number of intervals) possible detection histories. For example, if three periods are used, seven detection histories are possible ( $x_w$ ;  $x_{111}$ ,  $x_{110}$ ,  $x_{101}$ ,  $x_{011}$ ,  $x_{100}$ ,  $x_{010}$  and  $x_{001}$ ), compared with the three possible detection histories for the removal method ( $x_{100}$ ,  $x_{010}$  and  $x_{001}$ ). Zeroes in the detection history represent either individuals that did not sing during a given interval (i.e., were not available) or individuals that sang but were not detected by the observer, which is why this method accounts for both availability and detection probability given availability.

The general assumptions for this method are that (1) there is no change in the population of birds within the sample area during the point count (population is closed); (2) observers accurately track individual birds throughout the count (i.e., there is no double-counting); and (3) if counts are done with a limited radius, observers accurately assign birds to within the radius used. Additional assumptions are made with the various models that account for different sources of variation.

The time-of-detection method provides models that can account for sources of variation associated with the time interval ( $t$ ), changes in detection probability following first detection ( $b$ ; behavior models of Otis et al. 1978), and individual differences in detection probability ( $h$ ; heterogeneity models of Otis et al. 1978). Variation in detection probabilities associated with the interval arises from situations where the probability of detecting a bird changes during the count. For example, time variation might arise in situations where observers affect the singing rates of birds over time (McShea and Rappole 1997). Similarly, differences in

detection probabilities between the first detection of a bird and all subsequent detections may occur when observers key-in on previously detected birds. It is also likely that detection probabilities differ between individual birds of a given species. This may be from observable differences between individuals, such as differences in detection distance, or from unobservable differences, such as topographic differences associated with the location of the bird, differences in singing rates, singing volume, or other factors causing differences in detection probabilities among birds. There are eight general capture–recapture models (Otis et al. 1978, White et al. 1982, Pollock et al. 1990) that incorporate these sources of variation.

Model  $M_0$ : Equal detection probability for all individuals among all periods.

Model  $M_1$ : Equal detection probability for all individuals but different detection probabilities among periods.

Model  $M_b$ : Equal probability of first detection for all individuals among all periods and a unique probability of subsequent detections that is equal for all individuals among all subsequent periods.

Model  $M_{tb}$ : Equal probability of first detection for all individuals but different among periods and a unique probability of subsequent detection that is equal for all individuals but different among subsequent periods.

Model  $M_h$ : Unique probability of detection for each individual that remains constant among all periods.

Model  $M_{th}$ : Unique probability of detection for each individual that differs among periods.

Model  $M_{bh}$ : Unique probability of first capture for each individual that remains constant among periods and a unique probability of subsequent detection that remains constant among periods.

Model  $M_{tbh}$ : Unique probability of first capture for each individual that differs among periods and a unique probability of subsequent detection that differs among periods.

Models  $M_b$  and  $M_{bh}$  are equivalent to the removal models given by Farnsworth et al. (2002). Model  $M_{tbh}$  cannot be fit without several assumptions to constrain the number of parameters (Williams et al. 2002).

There are three possible estimators for modeling individual differences in detection probabilities (heterogeneity models) when sources of variation are not observable, but we restricted our analyses to finite mixture models. Finite mixture models may be biologically reasonable for this situation, because the mixtures can be explained by the proportion of the population with a particular singing rate, which corresponds to detection probabilities. Finite mixture models of individual differences are likelihood-based estimators (Norris and Pollock 1996, Pledger 2000) that assume that a population can be subdivided into a finite number of groups with distinct detection probabilities. The advantage of having maximum-likelihood-based estimators is that (1) models can be analyzed with likelihood-ratio tests for evaluating sources of variation and (2) model selection techniques, such as Akaike's Information Criterion (AIC), can be used to select the most parsimonious model (Williams et al. 2002).

Covariates can also be included in all the above models to account for individual differences in detection probabilities among birds. These differences are caused by observable sources of variation (sources that can be measured during the point count), such as detection distance, time of day, time of year, weather conditions, singing rate, etc.

Detection probability is modeled as a function of individual covariates. An intercept ( $\beta_0$ ) and a slope ( $\beta_1$ ) parameter are estimated to model the detection process. If, for example, detection probability is modeled as a function of distance on the logit scale, then, after transforming back to the real parameter estimates, detection probability plotted against distance will appear similar in shape to a half-normal. The original suite of models described can be viewed as intercept-only models. The effect of the covariate term on the slope parameter is modeled as either a constant effect (additive) over time or a variable effect (interaction) over time. Thus, in addition to the original 7 models, an additional 14 models parameterized with either additive or interaction covariate effects are possible, for a total of 21 conceptual models.

*Equal-interval point-count analysis.*—Standard capture–recapture software, such as CAPTURE (White et al. 1982) or MARK (White and Burnham 1999), can provide estimates of detection probabilities and population size

when counts consist of two or more equal intervals. The “Huggins closed captures” data type, which allows for individual covariates, is used in MARK. Model selection is based on AIC. Akaike's Information Criterion is an information-theoretic approach used to select the most parsimonious (best tradeoff between squared bias and variance of parameter estimators) model that explains the variation in the data (Burnham and Anderson 2002). In many situations,  $AIC_c$  should be used, which is a second-order AIC that corrects for small sample size (Burnham and Anderson 2002).

*Unequal-interval point-count analysis.*—Standard capture–recapture programs and their suite of candidate models cannot accommodate point counts divided into unequal intervals, because in this case interval detection probabilities must be modeled as a detection rate. Models that include variation in detection probabilities among intervals could still be examined with a standard model, but not models without time variation. For situations where detection rates are constant, interval detection rates will still vary because of the differing lengths of each interval. Therefore, it is necessary to model interval detection probabilities as a function of time and detection rate. For example, model  $M_0$  would indicate a constant detection rate, but interval detection probabilities would differ because of differences in interval lengths.

One approach to modeling the detection process assumes that singing rates follow a Poisson process and that the probability of detecting all songs of a species is equal. Under these assumptions, the instantaneous detection rate ( $\varphi_i$ ) or the Poisson detectability coefficient is used to model the probability that a bird sings during a specified period. The probability of detecting an individual in time interval  $i$  of length  $t_i$  using an instantaneous rates formulation (Seber 1982) is

$$p_i = 1 - e^{-\varphi_i t_i} \quad (1)$$

This formulation is consistent with that typically used for removal experiments where  $\varphi_i$  corresponds to the “Poisson catchability coefficient” and  $t_i$  corresponds to the effort on the  $i$ th occasion (Otis et al. 1978, Seber 1982). Farnsworth et al. (2002) used an alternative formulation, the discrete rate formulation, which assumes a constant per-minute detection rate

( $\gamma_i$ ), so that the probability of detecting an individual in interval  $i$  of length  $t_i$  was given by

$$p_i = \gamma_i^{t_i} \tag{2}$$

When point counts consist of equal intervals, it is not necessary to use equations (1) or (2), because interval detection probabilities are on the same time scale and, thus, are estimated directly.

Here, we present the likelihoods for the instantaneous rate formulation. For a full development of these models, including discrete rate models, see Allredge (2004). The models that account for differences in subsequent detection probabilities (e.g., model  $M_b$ ) model the change in the detection probability for subsequent detections ( $v$ ) as

$$c_i = 1 - e^{-(\phi_i + v)t_i} \tag{3}$$

where  $c_i$  is the interval detection probability for all subsequent detections. Excluding the models with individual differences in detection probability, model  $M_{tb}$  is the most general model and all other models are constrained forms of this general model. First we present this model, and then we present the models with individual differences.

A count consisting of four intervals has 15 possible observable detection histories ( $x_w: x_{1111}, x_{1110}, \dots, x_{0001}$ ). The set of possible detection probabilities for the observable capture histories is denoted by  $\pi_w$ . The expected values of the counts for each detection history of the general model can be written as

$$\begin{aligned} E(x_{1111}) &= N(1 - e^{-\phi_1 t_1})(1 - e^{-(\phi_2 + v)t_2}) \\ &(1 - e^{-(\phi_3 + v)t_3})(1 - e^{-(\phi_4 + v)t_4}) = N\pi_{1111} \\ E(x_{1110}) &= N(1 - e^{-\phi_1 t_1})(1 - e^{-(\phi_2 + v)t_2}) \\ &(1 - e^{-(\phi_3 + v)t_3})(e^{-(\phi_4 + v)t_4}) = N\pi_{1110} \\ &\vdots \\ E(x_{1010}) &= N(1 - e^{-\phi_1 t_1})(e^{-(\phi_2 + v)t_2}) \\ &(1 - e^{-(\phi_3 + v)t_3})(e^{-(\phi_4 + v)t_4}) = N\pi_{1010} \\ &\vdots \\ E(x_{0001}) &= N(e^{-\phi_1 t_1})(e^{-\phi_2 t_2})(e^{-\phi_3 t_3}) \\ &(1 - e^{-\phi_4 t_4}) = N\pi_{0001} \end{aligned} \tag{4}$$

The full multinomial likelihood can be written as

$$L(N, \phi_i, v_i, | x_w) = \frac{N!}{\prod_w x_w! \left(N - \sum_w x_w\right)!} \prod_w \pi_w^{x_w} \left(1 - \sum_w \pi_w\right)^{N - \sum_w x_w} \tag{5}$$

Where  $x_w$  is the number of observations for each possible detection history, excluding the history for the individuals never detected and  $\pi_w$  (equation 4) is the probability of observing each capture history, excluding the probability of never seeing an individual.

Because  $N$  cannot be directly observed, we condition on the total number of birds counted ( $x_T$ ) to make the problem more amenable to numerical methods. This is necessary when using SURVIV (White 1983) but may not be necessary when using other software packages. To do this, the likelihood is decomposed into a marginal distribution  $L_1$  and a conditional distribution  $L_2$ . Then, the detection probabilities can be estimated from the conditional distribution, and abundance can be estimated from the marginal distribution. The relationship between these likelihoods is  $L = L_1 \times L_2$ . Marginal likelihood  $L_1$  can be written as

$$L_1(N | x_T) = \binom{N}{x_T} (\pi_\bullet)^{x_T} (1 - \pi_\bullet)^{N - x_T} \tag{6}$$

where  $\pi_\bullet$  is the sum of the  $\pi_w$ . The likelihood  $L_2$  is conditional on the observed capture histories, given by

$$L_2(\phi_i, v_i | x_w) = \binom{x_T}{x_{1111} \dots x_{0001}} \prod_w \left(\frac{\pi_w}{\pi_\bullet}\right)^{x_w} \tag{7}$$

From equation (7), the  $\phi_i$ 's and  $v$ 's can be estimated by maximizing the likelihood for the observed data. The probability that an individual is detected at least once during the count ( $\hat{p}_T$ ) can be calculated by

$$\hat{p}_T = 1 - e^{-\hat{\phi}_1 t_1} e^{-\hat{\phi}_2 t_2} e^{-\hat{\phi}_3 t_3} e^{-\hat{\phi}_4 t_4} = \hat{\pi}_\bullet \tag{8}$$

The variance of  $\hat{p}_T$  is obtained for each estimator by reparameterizing to estimate  $\hat{p}_T$  directly. This can be done by solving one of the equations of

$p_T$  for the last interval parameter and using this in the likelihood. For example, if we solve equation (8) for  $\varphi_4$  we get

$$\varphi_4 = \frac{1}{t_4} \ln \left( \frac{1 - p_T}{e^{\varphi_1 t_1} e^{\varphi_2 t_2} e^{\varphi_3 t_3}} \right) \tag{9}$$

Replacing the final interval parameter with this equation will allow for direct estimation of the probability that an individual is detected at least once and the associated variance. An alternative approach is to use the delta method (Seber 1982) and obtain estimators for the approximate variances. Abundance is estimated from the likelihood  $L_1$  as

$$\hat{N} = \frac{x_T}{\hat{p}_T} \tag{10}$$

The observed count ( $x_T$ ) is one realization of a random variable and, thus, has a variance associated with it. Assuming that the observed count ( $x_T$ ) is from a binomial distribution and that  $x_T$  and  $\hat{p}_T$  are independent, an estimate of the variance of abundance is (Nichols et al. 2000, Williams et al. 2002)

$$\widehat{Var}(\hat{N}) = \frac{x_T^2 \widehat{Var}(\hat{p}_T)}{\hat{p}_T^4} + \frac{x_T(1 - \hat{p}_T)}{\hat{p}_T^2} \tag{11}$$

In general, four or more intervals are required to parameterize heterogeneity models, unless very strong assumptions are made, as in Farnsworth et al. (2002). We developed heterogeneity models based on  $\geq 4$  intervals. The assumptions required for the restricted heterogeneity models are given with the presentation of the three interval examples.

We used a two-point finite mixture model because a maximum-likelihood approach allowed us to use information-theoretic model-selection procedures. Pledger (2000) found that two-point mixtures generally provide the most parsimonious models and best estimators. Our approach is easily extended to more mixtures if appropriate. The model is presented using four sampling intervals.

Data from four interval point counts are summarized using the counts for the 15 observable detection histories  $x_w$ . Assuming that the population comprises only two groups (two mixtures), the probabilities for each capture history are calculated by summing the products of

the proportion of animals in each group times the group-specific capture and recapture probabilities. For example, the expected value of the count for the four-interval detection history for individuals detected in all intervals is

$$E(x_{1111}) = N(\lambda(1 - e^{-\varphi_{11}t_1})(1 - e^{-(\varphi_{21} + v_1)t_2})(1 - e^{-(\varphi_{31} + v_1)t_3})(1 - e^{-(\varphi_{41} + v_1)t_4}) + (1 - \lambda)(1 - e^{-\varphi_{12}t_2})(1 - e^{-(\varphi_{22} + v_2)t_2})(1 - e^{-(\varphi_{32} + v_2)t_3})(1 - e^{-(\varphi_{42} + v_2)t_4}) \tag{12}$$

where  $\lambda$  is the proportion of animals in detection group one, and the proportion of animals in detection group two is  $1 - \lambda$  as they must occur in one of the groups, and the  $\varphi_{ij}$ 's and  $v_j$ 's are the probabilities of first detection and subsequent detection in the  $i$ th interval for individuals in the  $j$ th group. There are similar expressions for the other  $x_w$ . The conditional likelihood  $L(\varphi_{ij}, v_j, \lambda | x_w)$  is similar to equation (7):

$$L_2(\varphi_{ij}, v_j, \lambda | x_w) = \binom{x_T}{x_{1111} \dots x_{0001}} \prod_{w} \left( \frac{\pi_{w1} + \pi_{w2}}{\pi_*} \right)^{x_w} \tag{13}$$

where  $\pi_*$  is the probability of being detected at least once during the entire count,  $\pi_{w1}$  is the probability of being in the first group and having capture history  $w$ , and  $\pi_{w2}$  is the probability of being in the other group and having capture history  $w$ . Using this likelihood, the  $\varphi_{ij}$ 's and  $v_j$ 's can be estimated by maximizing the likelihood for the observed data.

The probability that an individual is detected at least once during the count ( $\hat{p}_T$ ) is calculated using the estimated detection coefficients:

$$\hat{p}_T = 1 - \left[ \frac{\hat{\lambda}(e^{-\varphi_{11}t_1} e^{-\varphi_{21}t_2} e^{-\varphi_{31}t_3} e^{-\varphi_{41}t_4}) + (1 - \hat{\lambda})(e^{-\varphi_{12}t_1} e^{-\varphi_{22}t_2} e^{-\varphi_{32}t_3} e^{-\varphi_{42}t_4})}{\hat{\lambda}(e^{-\varphi_{11}t_1} e^{-\varphi_{21}t_2} e^{-\varphi_{31}t_3} e^{-\varphi_{41}t_4}) + (1 - \hat{\lambda})(e^{-\varphi_{12}t_1} e^{-\varphi_{22}t_2} e^{-\varphi_{32}t_3} e^{-\varphi_{42}t_4})} \right] \tag{14}$$

for the equal interval formulation. The variance for  $\hat{p}_T$  can again be calculated by reparameterizing the model estimators to directly estimate  $\hat{p}_T$ . Equations (10) and (11) are then used to estimate abundance and the corresponding variance.

Parameter estimation for unequal interval data is done by maximizing the likelihood for the observed data. This can be done in SURVIV (White 1983). Model selection is based on AIC<sub>c</sub>.

## FIELD TRIALS

We present examples from two different field studies, one using point counts using four equal intervals and the other from point counts using three unequal intervals. The first example, for the Pearly-eyed Thrasher (*Margarops fuscatus*), is based on point counts conducted in the karst belt of north-central Puerto Rico in 2003. Data were collected during the breeding season (mid-February through May). Surveys were conducted using three teams of two experienced and trained observers each. Forty-nine routes of 1–29 (average 9.7) point counts each were sampled, for a total of 477 points. Point-count routes were located away from human habitation along “low use” trails. The first point was located 500 m from the start of the trail and subsequent points were located 200 m from the previous.

Point counts were conducted from 0400 to 0800 hours on days with suitable weather. Each count was conducted for 10 min. Counts were divided into four equal intervals, and the complete detection history was recorded for each individual by using different colored pens for each interval. Point counts were fixed 100-m radius plots, and detection distance within this plot was recorded for all detections. During the previous year, distances at each plot were flagged at 10-m intervals to give observers visual references to help verify distance estimates during a count.

The Pearly-eyed Thrasher data were analyzed using the full suite of models, including heterogeneity and detection-distance covariate models. Both additive and interaction effects between detection distance and time were used. All analyses were done using MARK. Data were not truncated, because a fixed radius plot was used. Model selection was based on  $AIC_c$  (Burnham and Anderson 2002).

The other example is based on point-count data collected in Great Smoky Mountains National Park in 1998. Analyses were restricted to data from a single year and a single observer to avoid temporal and observer effects. Point counts were conducted along pre-established survey routes along trails (Shriner 2001). Counts were conducted in May and June between dawn and 1000 hours under acceptable environmental conditions. Counts were divided into 3-, 2-, and 5-min intervals, and the complete detection history was recorded for each individual by using

different colored pens for each interval. Point counts were unlimited radius plots, and detection distance was recorded for all detections.

Example analyses are presented for Red-eyed Vireo (*Vireo olivaceus*), Black-throated Green Warbler (*Dendroica virens*), Ovenbird (*Seiurus aurocapilla*), and Hooded Warbler (*Wilsonia citrina*), all of which have relatively loud songs and high singing rates. All models (except the covariate models) were evaluated using SURVIV. We truncated 10% of the data by omitting observations with the largest detection distances to omit outliers. Truncation would also serve to define a detection radius for each species if density estimates were required. Model selection was based on  $AIC_c$  (Burnham and Anderson 2002).

We modeled heterogeneity using constrained forms of the two-point mixture models. These models must be constrained so that all parameters are identifiable. Like Farnsworth et al. (2002), we constrained our models by fixing the detection probabilities for one of the groups in the mixture to 1. This parameterization makes the very strong assumption that all individuals in the fixed detection group are detected in every interval of the survey.

## RESULTS

*Four-interval data set.*—Sixteen of the 21 conceptual models for the four-interval Pearly-eyed Thrasher data set gave reasonable results. The other five models had parameters that were not identifiable. The most parsimonious model selected for this data set was model  $M_{th}$  ( $\Delta AIC_c$  weight = 0.70), with the remaining support for model  $M_{th}$  (additive distance effect) ( $\Delta AIC_c$  weight = 0.30) (Table 1). For all models, the general form of the model and its two covariate formulations were always ordered together according to  $AIC_c$  model selection. Heterogeneity models were always “better” than models not accounting for heterogeneity. Of the models that did not account for unobservable heterogeneity, models incorporating detection distance always had lower  $AIC_c$  values.

Under the selected model, 29% of the population had low detection probabilities, whereas the remaining portion had high detection probabilities (Table 2). Low detection probabilities ranged from 0.09 to 0.56, and high detection probabilities ranged from 0.70 to ~1.00. Because the

TABLE 1. Values of  $\Delta\text{AIC}_c$  for the four-interval Pearly-eyed Thrasher data set. A value of 0.0 indicates the most parsimonious model that adequately fits the data. When  $\Delta\text{AIC}_c$  weight  $> 0$ ,  $\Delta\text{AIC}_c$  weight is given in parentheses. Distance is modeled as either an additive effect with time or an interaction effect with time.

Model	No distance	Additive distance	Interaction distance
$M_0$	170.2	165.2	164.2
$M_t$	148.1	143.1	139.7
$M_b$	102.3	99.5	97.4
$M_{tb}$	– <sup>a</sup>	– <sup>a</sup>	
$M_h$	72.2	70.3	53.4
$M_{bh}$	23.3	13.7	– <sup>a</sup>
$M_{th}$	0.0 (0.7)	1.7 (0.3)	– <sup>a</sup>

<sup>a</sup> Models not included because of unreasonable parameter estimates.

TABLE 2. Estimated detection probabilities  $p_{ij}$ , probability of group occurrence  $\lambda_j$ , and standard errors (SE) for interval  $i$  and group  $j$  of the four-interval Pearly-eyed Thrasher data set based on model  $M_{th}$ . Standard error for group two and interval two is not estimable.

Parameter	Group 1		Group 2	
	Estimate ( $\hat{p}_{ij}$ )	SE ( $\hat{p}_{ij}$ )	Estimate ( $\hat{p}_{ij}$ )	SE ( $\hat{p}_{ij}$ )
$p_{1j}$	0.21	0.036	0.78	0.030
$p_{2j}$	0.09	0.090	~1.0	– <sup>a</sup>
$p_{3j}$	0.47	0.050	0.84	0.023
$p_{4j}$	0.56	0.055	0.70	0.026
$\lambda_j$	0.29	0.037	0.71	0.037

<sup>a</sup> Models not included because of unreasonable parameter estimates.

detection probability was essentially 1 for one of the heterogeneity groups during the second interval, abundance for this group is equivalent to the count. Note that the standard error (SE) is not estimable for parameter estimates near the boundary. The total number of observations for this data set was 520, and the estimated abundance for the sampled area was 547 (SE = 8.6), which is 5% higher than the observed count.

*Three-interval data set.*—Heterogeneity models were the most parsimonious for the three unequal-interval data sets from Great Smoky Mountains National Park (Table 3). The  $\Delta\text{AIC}_c$  weights for all models without heterogeneity were always negligible, indicating no evidence supporting these models. Model  $M_{th}$  was selected as the most parsimonious for three of the species, whereas Model  $M_h$  was selected for the Ovenbird. All species except the Ovenbird showed evidence for time variation in instantaneous rates of detection, indicating that detection probabilities do not remain constant for the duration of counts. There was little support

for models incorporating both heterogeneity and behavior, which indicates that detection probabilities for birds did not change after first detection.

Interval-detection probabilities showed a consistent pattern; the shortest intervals had the smallest detection probabilities, and the longest intervals had the highest detection probabilities (Table 4). This was not true for the Red-eyed Vireo, which had a detection probability of 0.41 for the 3-min interval and 0.48 for the 2-min interval. This may indicate an observer effect that made this species less detectable during the first interval. The overall probability of detecting an individual at least once during a 10-min count was 0.92 (SE = 0.006) for the Ovenbird, 0.79 (SE = 0.021) for the Black-throated Green Warbler, 0.71 (SE = 0.031) for the Red-eyed Vireo, and 0.65 (SE = 0.037) for the Hooded Warbler. Comparing the observed counts to the estimated abundance in the sample area showed differences of 5% (Ovenbird) to 16% (Hooded Warbler).

TABLE 3. Values of  $\Delta AIC_c$  for the 11 time-of-detection models fit to the Great Smoky Mountains National Park data sets. For the most parsimonious model for each data set,  $\Delta AIC_c = 0.0$ .  $\Delta AIC_c$  weights (in parentheses) indicate the strength of the evidence for a given model compared with the other models (the larger the number, the more evidence for that model).

Species	$M_0$	$M_t$	$M_b$	$M_{tb}$ <sup>a</sup>	$M_h$	$M_{bh}$	$M_{th}$
Red-eyed Vireo	75.3 (0.00)	55.5 (0.00)	75.0 (0.00)	–	7.7 (0.02)	9.7 (0.01)	0.0 (0.97)
Black-throated Green Warbler	41.7 (0.00)	38.9 (0.00)	43.7 (0.00)	–	0.3 (0.40)	2.3 (0.14)	0.0 (0.46)
Ovenbird	44.3 (0.00)	28.5 (0.00)	46.3 (0.00)	–	0.0 (0.62)	2.0 (0.22)	2.7 (0.16)
Hooded Warbler	51.8 (0.00)	40.7 (0.00)	53.9 (0.00)	–	10.1 (0.01)	12.2 (0.00)	0.0 (0.99)

<sup>a</sup>Parameter estimates for model  $M_{tb}$  were not reasonable (SE > 1).

TABLE 4. Parameter estimates from the selected model for the three-interval Great Smoky Mountains National Park point-count data sets.  $\lambda_1$  is the proportion of the population that is in group 1. Detection probability ( $p_{ij}$ ) is the probability of detecting an individual from group  $j$  in interval  $i$ . Detection probabilities for group 2 ( $p_{t2}$ ) were fixed to 1. Standard errors (SE) are in parentheses.

Species	Observed	$\hat{\lambda}_1$	$\hat{p}_{11}$	$\hat{p}_{21}$	$\hat{p}_{31}$	$\hat{p}_{t2}$	$\hat{N}$
Red-eyed Vireo	397	0.66 (0.033)	0.41 (0.039)	0.48 (0.040)	0.55 (0.040)	1.0	457 (15.9)
Black-throated Green Warbler	377	0.71 (0.032)	0.52 (0.040)	0.40 (0.040)	0.63 (0.039)	1.0	409 (8.83)
Ovenbird	444	0.72 (0.036)	0.56 (0.042)	0.43 (0.044)	0.75 (0.038)	1.0	468 (7.03)
Hooded Warbler	274	0.72 (0.035)	0.45 (0.045)	0.35 (0.043)	0.46 (0.046)	1.0	318 (11.50)

DISCUSSION

The time-of-detection method of modeling point-count data collected from consecutive intervals is a less restrictive approach for estimating detection probabilities than the removal method of Farnsworth et al. (2002). Recording the complete detection history of birds during a point count provides a much larger suite of models that can incorporate more sources of variation, such as time variation, than the removal model. With the exception of behavior models that are equivalent to removal models (Seber 1982), this approach is more efficient (smaller variance) than the removal approach.

Heterogeneity models accounting for unobservable differences in detection probabilities among birds were selected as the best models for all data sets. The AIC model-selection techniques tend to select the fuller models, such as the heterogeneity models; therefore, the

simpler models should not be ignored. Clearly, heterogeneity exists in these data, as evidenced by the large differences in AIC among models; however, heterogeneity models should be interpreted with caution. Link (2003) demonstrated that there are difficulties or inconsistencies in distinguishing among alternative heterogeneity models. We are confident that variation from individual differences in detection probability is a component of these data and must be modeled, but we acknowledge that the estimates from heterogeneity models may also be biased.

Many factors cause unobservable individual heterogeneity in detection probabilities. These factors are often related to variation in the behavior of individual birds (Burnham 1981, Johnson et al. 1986), such as age and breeding status (mated, unmated, incubating, etc.). Other factors affecting detection probabilities include habitat differences associated with topography and vegetation, weather, time of day, time of

year, and the presence of predators or competitors. Although stratification by habitat type and standardization of the conditions under which point counts are conducted can eliminate some differences among points (Buckland et al. 1993, Nichols et al. 2000), unobservable heterogeneity exists in all data (Burnham 1981).

A particularly important source of heterogeneity in auditory point counts is individual variation in singing rate. Singing rates change during the breeding season as birds form pairs, begin incubation, and begin caring for nestlings (Wasserman 1977, Lein 1981). Therefore, asynchronous breeding inevitably results in temporal heterogeneity in detection probabilities. Singing rates are also affected by habitat, local abundance, and the proximity of observers (McShea and Rappole 1997).

Evidence for a time effect was found in four of the five data sets presented here. Therefore, it appears that the assumption of constant detection rates under the removal model may not be valid. McShea and Rappole (1997) found that singing rates were affected by the presence of an observer. Movement of an individual during the count would also affect the detection process, because as birds move away from observers they are less likely to be detected. This assumption is not necessary with our method, because there is sufficient information to model time variation from the full detection history.

The time-of-detection approach also reduces the number of assumptions required to estimate abundance. The removal method for three intervals had five assumptions (Farnsworth et al. 2002), which could be relaxed to four if more than three intervals were used. The time-of-detection approach has only three assumptions for counts conducted with more than three intervals.

Assumption (1): there is no change in the population within the detection radius during the point count (closed population). Violations of the closure assumptions are more likely to occur for longer-duration point counts and for wide-ranging species. This method may not be applicable for wide-ranging species, such as woodpeckers (Picidae) or crows (*Corvus* spp.), where movement during the count may be significant. Violations of the closure assumption are probably less of a problem for many small breeding songbirds that have relatively small, fixed territories during the breeding season (Farnsworth et al. 2002).

Short-duration counts reduce violations of the closure assumption. The probability that birds move into or out of the sample area increases with the duration of the count. This does not imply that all point counts should be arbitrarily short, because there is a tradeoff associated with count duration and the need for four intervals to fit the full heterogeneity models. If intervals are too short, interval detection probabilities will be small and the variance on abundance or density estimates will be large. Careful consideration must be given to the appropriate length of point counts for the species surveyed. This may imply different survey protocols for different species groups.

Assumption (2): Individuals can be accurately tracked throughout the count (i.e., no double-counting). Double-counting results in abundance estimates that are too large. Problems with double-counting are likely to increase as the length of the count increases because of undetected movement of birds. Infrequent singing by individuals may also lead to double-counting, because of limited ability of observers to track these birds throughout the survey. Our method requires observers to track individuals during the count, which should reduce double counting. However, violations of this assumption related to bird movement are more likely as count durations increase.

Assumption (3): Distance estimates are accurate. Although observers are often trained to estimate detection distance or assign birds to fixed-radius plots, the accuracy and precision of distance estimation on auditory point counts has not been rigorously assessed. We suspect that, even with training, observers tend to overcount individuals within fixed-radius plots, especially for louder species, and that the ability of observers to estimate detection distances for singing birds may be poor.

As with other point-count methods that allow for abundance estimation, this method requires collection of additional information during the point count. This extra demand on observers may make the method impractical in some situations. For example, if the number of birds and the number of species at a point are large, it is unlikely that observers can accurately record the detection history of every bird. In such cases, other methods, or limiting the collection of time-of-detection data to a subset of species, might be more appropriate.

Our findings suggest that singing rates have a strong influence on detection probabilities, but further work is needed in this area. The time-of-detection approach we have described should prove useful in this effort. We recommend implementing this method with four or more equal intervals, because it permits the use of standard capture–recapture software and allows for the application of full two-point mixture models.

Farnsworth et al. (2002) recommended combining the removal approach with the distance-sampling approach to provide better estimates. We have done this by incorporating detection distance as a model covariate. Further development is needed to incorporate alternative forms of the detection function.

Finally, because point-count data usually consist of multiple species, we recommend using a multiple-species modeling approach (Allredge 2004, Allredge et al. 2007). Modeling multiple species with similar detection probabilities may provide more parsimonious models. This is especially useful for rare or hard-to-detect species. However, it would also require additional work to determine which factors are affecting the detection process to appropriately group species.

#### ACKNOWLEDGMENTS

This project was funded by the U.S. Geological Survey, the National Park Service, and the Puerto Rico Department of Natural and Environmental Resources. We appreciate the suggestions by two anonymous reviewers and D. Johnson.

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*Associate Editor: D. H. Johnson*