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Research Papers

Separation of Availability and Perception Processes for Aural Detection in Avian Point Counts: a Combined Multiple-Observer and Time-of-Detection Approach

Distinction des composantes (manifestation et détection) de la probabilité de détection aux points d'écoute : approche combinant les méthodes fondées sur les observateurs multiples et le temps de détection

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ABSTRACT. In this study, we review various methods of estimating detection probabilities for avian point counts: distance sampling, multiple observer methods, and recently proposed time-of-detection methods. Both distance and multiple observer methods require the sometimes unrealistic assumption that all birds in the population sing during the count interval. We provide a general model of detection where the total probability of detection is made up of the probability of a bird singing, i.e., availability, and the probability of detecting a bird, conditional on its having sung. We show that the time-of-detection method provides an estimate of the total probability, whereas combining the time-of-detection method with a multiple observer method enables estimation of the two components of the detection process separately. Our approach is shown to be a special case of Pollock's robust capture-recapture design where the probability that a bird does not sing is equivalent to the probability that an animal is a temporary emigrant. We estimate Hooded Warbler and Ovenbird population size, through maximum likelihood estimation, using experimentally simulated field data for which the true population sizes were known. The method performs well when singing rates and detection probabilities are high, and when observers are able to accurately localize individual birds. Population sizes are underestimated when there is heterogeneity of singing rates among individual birds, especially when singing rates are close to zero. Despite the additional expense and the potential for counting and matching errors, we encourage field ornithologists to consider using this combined method in their field studies to better understand the detection process, and to obtain better abundance estimates.

RÉSUMÉ. Dans la présente étude, nous passons en revue diverses méthodes qui tiennent compte de la probabilité de détection au cours de points d'écoute : les méthodes fondées sur la distance et les observateurs multiples, et la méthode récemment proposée qui est fondée sur le temps de détection. Les méthodes fondées sur la distance et les observateurs multiples reposent sur la supposition de base, parfois irréaliste, que tous les oiseaux présents chantent au cours de la période d'écoute. Nous présentons un modèle général de détection dans lequel la probabilité globale de détection est fondée sur la probabilité qu'un oiseau chante (sa manifestation) et la probabilité de détecter un oiseau, qui est conditionnelle à ce que l'oiseau se soit manifesté. Nous montrons que la méthode fondée sur le temps de détection fournit une estimation de la probabilité globale, tandis que la combinaison des méthodes fondées sur le temps de détection et les observateurs multiples permet d'estimer les deux composantes du processus de détection séparément. Notre approche est un cas spécial du dispositif robuste de capture-recapture de Pollock, dans lequel la probabilité

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qu'un oiseau ne chante pas est équivalente à celle qu'un animal soit temporairement émigré. Nous avons estimé la taille de la population de la Paruline à capuchon et celle de la Paruline couronnée au moyen de l'estimation du maximum de vraisemblance, à partir de données simulées expérimentalement et pour lesquelles la taille réelle des populations est connue. La méthode proposée fonctionne bien lorsque les taux de chant et les probabilités de détection sont élevés, et lorsque les observateurs sont capables de localiser précisément les individus. Par contre, la taille des populations est sous-estimée lorsque les taux de chant des individus sont hétérogènes, particulièrement quand ces taux sont près de zéro. Malgré les coûts supplémentaires et le risque d'erreurs de comptage et d'appariement, nous encourageons les ornithologues à prendre en considération cette approche combinée de méthodes dans le cadre de leurs travaux afin de mieux comprendre le processus de détection et d'obtenir de meilleures estimations d'abondance.

Key Words: *availability process; avian point counts; detection probability; multiple observer method; perception process; Pollock's robust capture-recapture design; time-of-detection method*

INTRODUCTION

Point counts are widely used to study the abundance and density of many bird populations (Ralph and Scott 1981, Ralph et al. 1995). The data are easy to collect at larger spatial scales compared to capture-recapture methods that are frequently costly and, therefore, limited to studies on smaller spatial scales. Typically point counts have been viewed as indices of abundance, and standardized protocols are emphasized to reduce variation in detection probability (Ralph et al. 1995). The weaknesses of this approach and the importance of estimating the detection probability have been noted for some time. Three recent overview papers by Thompson (2002), Rosenstock et al. (2002), and Johnson (2008) stress how important the estimation of the detection probability is to sound inference based on point counts.

In this study, we develop a conceptual model for the detection process that includes both availability and detection given availability. Avian sampling literature now contains multiple approaches to estimating detection probability; we briefly review three common sampling methods and show how they contribute to components of the detection model. Though model assumptions are not given here, many references provide them (e.g., see Nichols et al. 2009). We emphasize that detection probability for auditory cues includes the combined probability of a bird singing, i.e., availability, and the probability of detecting a bird, conditional on its having sung. We show how current methods fit into this conceptual framework and show how a combination of methods may lead to much stronger inferences.

In addition to developing new methods of estimating detection probability, our research group has carried out field tests using simulated populations of birds to evaluate the combined multiple-observer and time-of-detection methods, along with many others, based on a systematic computer generation of auditory cues (see Simons et al. 2007 for details). The system can realistically simulate a known population of songbirds under a range of factors that affect the detection probabilities. This experimental system is unique because it allows us to evaluate the performance of various sampling methods with populations of known size. Simulated field test examples are presented, followed by a general discussion and suggestions for future research.

MODELING OVERALL DETECTION PROBABILITY

Components of detection probability

The overall probability of detection for an individual bird is comprised of an availability process, i.e., the probability a bird is available for detection, and a detection process, i.e., the probability a bird is detected, given that it is available for detection. Thus $p = p_a p_d$ where p, is the overall probability of detecting a bird that is present in the sampled area during the sampling period, p_a is the probability that such a bird is available for detection, and p_d is the conditional detection probability given availability.

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

Estimates of population size and density

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

$$\hat{N} = n / \hat{p}, \quad (1)$$

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

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

where n is the number of birds detected, w is the radius of the circle around the point, and the area surveyed is $k\pi w^2$ if k points are surveyed.

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

$$\hat{N} = \sum_{i=1}^{n} 1 / \hat{p}_i \ , \quad (3)$$

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

MULTIPLE-OBSERVER METHODS

Two independent observers

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

The notation is as follows:
– p_{d1} (p_{d2}) is the probability of detection, given available, by the first, or second, observer;
– x_{11} is the number detected by both observers; x_{10} is the number detected by the first observer only; x_{01} is the number detected by the second observer only; and
– n_1 (n_2) is the number detected by the first, or second, observer.

The probability of detection by each observer is estimated by:

$$\hat{p}_{d1} = x_{11} / n_2 \text{ and } \hat{p}_{d2} = x_{11} / n_1 . \quad (4)$$

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

$$\hat{p}_d = 1 - (1 - \hat{p}_{d1})(1 - \hat{p}_{d2}) . \quad (5)$$

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

The double-observer method only estimates the probability of detection given that the animal is available. The estimator for p_1 has the approximate expected value:

$$E(\hat{p}_1) = E(x_{11}) / E(n_2) = \frac{Np_a p_{d1} p_{d2}}{Np_a p_{d2}} = p_{d1}. \qquad (6)$$

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

TIME-OF-DETECTION APPROACHES

Temporal capture-recapture approach

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

To illustrate, consider two equal-length time intervals and assume that it is possible to track individual birds and accurately record detections as occurring in period one and/or period two. We then denote x_{11}, x_{10}, and x_{01} as the number of birds detected in both time intervals, in time interval one only, and in time interval two only. For more than two samples we would have a more general set of capture histories ω and a vector of counts for each history $\{x_\omega\}$. The probability of detection for each time interval could again be estimated by the Lincoln Petersen equations (Seber 1982).

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

$$E(\hat{p}_1) = E(x_{11})/E(n_2) = \frac{Np_{a1} p_{d1} p_{a2} p_{d2}}{Np_{a2} p_{d2}} = p_{a1} p_{d1} = p_1 \qquad (7)$$

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

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

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

Animals with detection probabilities near zero may be of special importance in time-of-detection applications. Alldredge (2004) and Brewster (2007) emphasize that avian singing rates may vary among individuals of the same species because of pairing status and other factors related to nesting phenology. Some individuals had exceedingly low singing rates, which made them almost impossible to detect.

COMBINING MULTIPLE-OBSERVERS AND TIME-OF-DETECTION METHODS

Here, we combine multiple-observer and time-of-detection methods into one design, which allows separate estimation of the components of the detection process. Consider *t* time intervals and two independent observers where the birds are tracked throughout the count. We suggest that in practice *t* = 3–5 time intervals be used so that heterogeneity models could possibly be used.

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

Under the classic random temporary emigration model, γ_i, is the probability that an animal is a temporary emigrant in time interval i, and this parameter does not depend on its value in previous periods. In the context of our paper, γ_i may be thought of as the probability that a bird is unavailable for detection in time interval i. Thus the probability a bird is available may be written as $p_{ai} = (1-\gamma_i)$ for $i = 1, ..., t$ time intervals. The conditional detection probabilities for the first and second observer in each time period may be written as (p_{d1i}, p_{d2i}) for $i = 1, ..., t$ time intervals. Unlike the general robust design, we are assuming that all animals survive during the point count ($\phi_i = 1$) due to its short duration.

Detection probability illustrative example

To illustrate potential detection histories, first consider a detection history for two observers over two time intervals. Here we assume a model which models both time and observer effects. The history – 11,01 – denotes a bird detected by both observers in time interval one and detected only by the second observer in time interval two. This history has expected cell structure:

$$p_{11,01} = p_{a1}\, p_{d11}\, p_{d21}\, \{ p_{a2}\, (1 - p_{d12})\, p_{d22} \}. \quad (8)$$

Notice here the birds have sung in each time interval and were detected by at least one observer.

We illustrate another potential history – 10,00 – which has the expected cell structure:

$$p_{10,00} = \quad (9)$$
$$p_{a1}\, p_{d11} (1 - p_{d21})\, \{ p_{a2}\, (1 - p_{d12})(1 - p_{d22}) + (1 - p_{a2}) \}$$

The 00 in the second time interval created the need for two components in the second time interval probability; the first component where we account for the possibility that the bird is available but is missed by both observers, and the second where the bird is not available.

For each of the observable detection histories ($x_{00,01}$, $x_{00,11}$, ... $x_{11,11}$) and paired detection probabilities ($p_{00,01}$, $p_{00,11}$, ... $p_{11,11}$), we then have the following multinomial likelihood:

$$L(N,p|x) = \frac{N!}{x_{00,01}! \cdots x_{11,11}! (N-n)!} p_{00,01}^{x_{00,01}} \cdots p_{11,11}^{x_{11,11}} p_{00,00}^{N-n} \quad (10)$$

where:

$$n = \sum_{\omega} x_{\omega} \quad (11)$$

denotes the total number of birds detected, p_{ω} represents the multinomial probability associated with the ω detection history, and the probability a bird goes undetected is:

$$p_{00,00} = 1 - \sum_{\omega} p_{\omega}. \quad (12)$$

The assumptions for the combined multiple-observer and time-of-detection approach are (1) that observations among observers are independent, (2) observers match their detections accurately, (3) the detection probabilities of each species are equal for each observer, (4) there is no undetected movement out of the sampled area, and (5) observers accurately assign birds to within or beyond the radius used for the fixed-radius circle.

We computed estimates directly through use of the traditional conditional likelihood estimation proposed by Sanathanan (1972), which writes the likelihood above as:

$$L(N,p|x) = L_1\,(N|p_{00,00}) \times L_2\,(p_{\omega}) \quad (13)$$

where:

$$L_1(N|p_{00,00}) = \frac{N!}{n!(N-n)!}\,(1-p_{00,00})^n\, p_{00,00}^{N-n}$$

$$L_2(p_\omega) = \frac{n!}{x_{00,01}!\,\ldots\,x_{11,11}!}\, q_{00,01}^{x_{00,01}} \cdots q_{11,11}^{x_{11,11}} \tag{14}$$

with:

$$q_\omega = \frac{p_\omega}{1 - p_{00,00}}\,. \tag{15}$$

Following this approach we first maximize the conditional likelihood function, L_2, to obtain estimates of the availability and detection probability components, so that $p_{00,00}$ may be estimated. It then follows from the work of Sanathanan (1972) that the estimate of the population size is:

$$\hat{N} = [\, n \,/\, 1 - \hat{p}_{00,00} \,] \tag{16}$$

which maximizes L_1, and consequently L.

The standard errors of all the populations estimates can be obtained based on the bootstrap methods presented by Norris and Pollock (1996), and could also be used to construct confidence intervals. AIC can be used for model selection (Burnham and Anderson 2002, Williams et al. 2002). Any number of observers and time intervals can be accommodated. In addition, estimated distance to each detected bird could be incorporated as an important covariate influencing the detection probability, thus combining a distance sampling type procedure into this methodology. In the following section we provide examples to illustrate the methodology.

EXAMPLES

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

A total of 60 8-minute point counts were simulated over two days in early March 2006. Point counts were broken into four 2-minute intervals, and observers recorded birds using multicolored pens to distinguish time intervals. Detection of a previously recorded bird in subsequent time intervals was recorded by circling the previous detection in the color designated for the interval. For this illustrative example, we present the results from just two observers. Here we know which ones the two observers saw in common whereas in standard point counts they would have had to use a matching rule.

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

For HOWA, the AIC criteria selected a model with random temporary emigration constant over time

Table 1. Model selection for the Hooded Warbler using the AIC Criteria. The model set includes temporary emigration process being none or random. Conditional detection probability is interval varying (t), observer varying (o), and or constant (.).

Model	AICc	ΔAICc	AICc Weights	Num. Par
γ (rand), p (.,o)	213.22	0	0.865	3
γ (rand), p (.,.)	218.08	4.86	0.076	2
γ (rand), p (t,.)	218.67	5.45	0.057	5
γ (rand), p (t,o)	225.12	11.9	0.002	9
γ (none), p (.,o)	291.11	77.89	0	2
γ (none), p (.,.)	292.18	78.96	0	1
γ (none), p (t,.)	296.18	82.96	0	4
γ (none), p (t,o)	304.15	90.93	0	8

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

Parameter estimates for the Ovenbird using the same model, constant random temporary emigration and observer dependent detection probabilities constant over time intervals, are illustrated (Table 2). Notice that here the probability that an Ovenbird sings in a 2-minute interval is 0.74, much lower than for the HOWA. The conditional detection probabilities are high for observer 1 (0.84) and observer 2 (0.91) but not as high as for the HOWA estimates presented in Table 2. The total available population is estimated to be 93.769, which is close to the number of birds that actually sang (100). However, the estimate substantially underestimates the overall population of 127 birds.

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

For this model we define the true population size (N) to be 100, the true probability that such a bird is available for detection, p_a, to be 0.45, the probability of detection by the first observer, p_{d1}, is defined to be 0.5 and for the second observer (p_{d2}) is 0.65.

Parameter estimates for this simulated data set of the same model are provided (Table 3). It is

Table 2. A comparison of the Hooded Warbler and Ovenbird parameter estimates (standard errors) for a random singing model – constant random temporary emigration model, with observer dependent detection probabilities constant over time intervals. The population of birds that sing at least once in eight minutes is N = 100. Estimates and standard errors found with B = 500 bootstrap samples.

Parameters	Parameter Estimates	
	Hooded Warbler	Ovenbird
N	101.12 (3.98)	93.769 (3.84)
p_a	0.9109 (0.0147)	0.7416 (0.0150)
p_{d1}	0.8909 (0.0104)	0.8436 (0.0109)
p_{d2}	0.9451 (0.0081)	0.9113 (0.0088)

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

DISCUSSION

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

When using the time-of-detection method we recommend that the capture-recapture version, which uses all times of detection, be used and that the point counts should be sufficiently long, 10 minutes might be reasonable. We recommend the use of at least four time intervals and that they always be of equal length, perhaps five intervals of two minutes each. The key assumption of the method is that the observer can keep track of individual birds without error. We believe that the method has great promise for species that have larger territories and that move little during a point count so that localization errors can be kept to a minimum. This will then mean that individuals can be tracked more accurately. For many point counts a large number of species may be detected and in those cases it may be necessary to focus on a subset of the species that have lower localization errors. Our applications of the time-of-detection method have assumed that detection is by ear. In this case birds sing in discrete bouts and we have found it is possible to record in exactly which intervals birds sing and then are detected.

The combination of time-of-detection and multiple-observer methods allows for estimation of both components of the detection process. We have

Table 3. A comparison of the simulated dataset parameter estimates (standard errors) for a random singing model – constant random temporary emigration model, with observer dependent detection probabilities constant over time intervals. The population of birds that sing at least once in eight minutes is N = 100. Estimates and standard errors found with B = 500 bootstrap samples.

Parameters	True Value	Parameter Estimates	Relative Bias (%)	RMSE
N	100	102.27 (6.41)	2.2196	6.8001
p_a	0.45	0.4253 (0.0448)	-5.8077	0.0512
p_{d1}	0.5	0.4952 (0.0424)	-0.9693	0.0427
p_{d2}	0.65	0.6494 (0.0496)	-0.0924	0.0496

shown estimates for illustration for some simulated field data from our bird radio project. Here we focused on the random temporary emigration model because they are simpler to interpret, more precise, and allow for easier computation of the total population of birds, including those not available in an interval. More study of Markovian models might be of great interest for this combined approach because we know that birds may sing in nonrandom bouts (Collins 2004). However the complexity of such models is likely to make them of limited usefulness in practice. Nevertheless, it is likely this methodology may accommodate heterogeneity in detection probabilities, once extensions to Markovian modeling are undertaken. In doing so, this may address the points of Efford and Dawson (2009) with respect to distance heterogeneity, by more advanced modeling of availability and/or detection. We do not claim that the results in other studies will be as promising as those based on our data. The data from our "bird radio" study is unique in that we know exactly which birds each observer saw in each interval. In "real" point counts there could be additional matching errors between observers. One advantage, however, of our system is that we know the true numbers and we are encouraged by the accuracy of the estimates we obtained, especially for the HOWA. There is a need for more research on species that have heterogeneous singing rates and this was exemplified by our Ovenbird estimates, which were negatively biased.

Despite its additional expense and the potential for some counting and matching errors, we encourage field ornithologists to consider use of this combined time-of-detection method for at least a subsample of their points to better understand the detection process in their field studies and potentially obtain better estimates of population abundance. Finally, we note that it is possible to develop similar results for dependent observers combined with the time-of-detection method. We have explored that idea in collaboration with Jason Riddle of North Carolina State University (*personal communication*). He has implemented the design for some point count surveys on bobwhite quail and a manuscript on that work is in preparation.

Responses to this article can be read online at:
http://www.ace-eco.org/vol5/iss1/art3/responses/

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