Point-Based Mark-Recapture Distance Sampling

J. L. LAAKE, B. A. COLLIER, M. L. MORRISON, and R. N. WILKINS

Avian surveys using point sampling for abundance estimation have either focused on distance sampling or more commonly mark-recapture to correct for detection bias. Combining mark-recapture and distance sampling (MRDS) has become an effective tool for line transects, but it has been largely ignored in point sampling literature. We describe MRDS and show that the previously published methods for point sampling are special cases. Using simulated data and golden-cheeked warbler (*Dendroica chrysoparia*) survey data from Texas, we demonstrate large differences in abundance estimates resulting from different independence assumptions. Data and code are provided in supplementary materials.

Key Words: Avian surveys; Detection bias; Distance sampling; Double-observer methods; Golden-cheeked warbler; Mark-recapture; Point independence; Unmodeled heterogeneity.

1. INTRODUCTION

Bias from incomplete detection in wildlife surveys has typically been addressed using mark-recapture (Cook and Jacobson 1979; Graham and Bell 1989) or distance sampling (Gates 1968; Eberhardt 1968; Buckland et al. 2001). Both methods have been used with line transect (Eberhardt 1968; Graham and Bell 1989) and point sampling (Ramsey and Scott 1979; Nichols et al. 2000). However, mark-recapture has been used primarily for point sampling (Nichols et al. 2000; Farnsworth et al. 2002; Alldredge et al. 2006; Nichols, Thomas, and Conn 2009) and distance sampling has been the primary focus for line transect sampling (Eberhardt 1968; Gates 1968; Buckland et al. 2001).

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For mark-recapture applications, concurrent dual-observer sampling can be conducted with two independent observers (Graham and Bell 1989) or with a primary independent observer and a dependent secondary observer who can detect anything the primary observer misses (Cook and Jacobson 1979). We will refer to the former as the independent observer (IO) configuration and the latter as the removal configuration because it is equivalent to a removal capture-recapture model. Nichols et al. (2000) referred to these alternatives as independent and dependent observers. Detection probability is estimated using the number of animals seen by each observer and by both observers. For example, with an IO survey, if n_1, n_2, m_2 are the number seen by observers 1 and 2 and the number seen by both observers, respectively, we can estimate detection probability for observer 2 by $\widehat{p}_2 = m_2/n_1$ and observer 1 by $\widehat{p}_1 = m_2/n_2$. The well-known Lincoln–Petersen estimator $n_1 n_2/m_2 = n_2/\widehat{p}_2 = n_1/\widehat{p}_1$ provides an estimate of the complete count. However, it is well-known that if animal detection probability is heterogeneous (e.g., vocalizing versus quiet birds), the abundance estimator will be negatively biased (Otis et al. 1978) because the observations contain a disproportionate number of animals with higher detection probabilities. Identifiable covariates for detection probability can be used to model the variation and remove bias (Huggins 1989); however, bias will remain if any heterogeneity remains. We hereafter refer to this problem as bias due to unmodeled heterogeneity.

Unmodeled heterogeneity is less problematic for conventional distance sampling because detection probability is measured differently. Conceptually, detection probability at distance y ($p(y)$) is estimated by the ratio of the density of detections at distance $y > 0$ to the density of detections at $y = 0$. The estimate of detection probability is valid as long as animals do not move prior to detection and a proper sampling design is used to achieve an expected uniform density of animals relative to the point or line and $p(0) = 1$ (Buckland et al. 2001). Thus, in the context of a mark-recapture sample the probability is measured relative to a sample ($y = 0$) where there is no heterogeneity because detection is perfect (or assumed to be so). It does not matter that only highly visible or vocal birds are detected at larger distances as long as all birds are detected at $y = 0$. However, it was the assumption that $p(0) = 1$ that led Pollock and Kendall (1987) to question the utility of distance sampling for aerial surveys and to recommend dual-observer methods instead.

Pollock and Kendall (1987) suggested future research on "the intriguing prospect of combining the line transect method with a method which uses the Petersen estimate". In fact, such research had already begun in the literature of the International Whaling Commission (Butterworth, Best, and Basson 1982) where the assumption that $p(0) = 1$ was clearly untenable with submerged whales. This apparently simple idea which we call mark-recapture distance sampling (MRDS) has been further explored and developed by various authors (Alpizar-Jara and Pollock 1996; Manly, McDonald, and Garner 1996; Borchers 1996; Laake 1999; Chen 2000; Buckland 2006; Buckland, Laake, and Borchers 2010). However, the manner in which the authors "combined" mark-recapture and distance sampling have differed and the resulting abundance estimates can be widely different (Laake 1999; Laake and Borchers 2004).

With the exception of Kissling, Garton, and Handel (2006), avian point sampling literature (Farnsworth et al. 2002; Moore et al. 2004; Alldredge et al. 2006; Nichols et al. 2000)

has not considered MRDS developments in the line transect sampling literature. Thus, we have titled and focused this paper on MRDS for point sampling to make it clear that the line transect MRDS developments are useful for point sampling as well. To demonstrate the fundamental problem of unmodeled heterogeneity, we first provide a field based example using golden-cheeked warbler (*Dendroica chrysoparia*) survey data to show how abundance predictions can differ significantly dependent upon the analytical method applied. Next, we outline the concepts of unmodeled heterogeneity and the full independence (FI) and point independence (PI) assumptions (Borchers et al. 2006) and show how unmodeled heterogeneity can be quantified. We then introduce a likelihood and modeling framework for line and point-based MRDS that follows the development of Buckland, Laake, and Borchers (2010). We also provide the appropriate MRDS likelihood and modeling framework for binned (interval) distances which has not been addressed previously for PI. We analyze a simulated example and revisit the golden-cheeked warbler data to show how MRDS analysis based on the PI assumption is an improvement over mark-recapture or distance sampling alone.

2. DEMONSTRATING THE PROBLEM

We applied mark-recapture and distance sampling to avian point sampling data collected during surveys of woodland warblers in Texas. The golden-cheeked warbler is a federally endangered neotropical migrant with a breeding range existing only in central Texas (Pulich 1976). During March–June 2008, random point count locations were distributed within patches of oak-juniper (*Quercus-Juniperus*) woodland across the warblers breeding range. Point count stations were separated by ≥ 400 m and were ≥ 25 m from patch edges. At each station, a randomly selected primary observer recorded locations of golden-cheeked warblers during a 5 minute survey period and reported those locations to the secondary observer who recorded data for the first observer and also recorded any birds they detected that were missed by the first observer (removal configuration). We categorized all detected warblers regardless of observer into two distance bins (0–50, >50–100 m).

We surveyed 590 point sampling stations in 118 patches and detected warblers at 315 point sampling locations in 95 patches of woodlands across Texas. During the survey period, 551 warblers were detected with 473 birds detected by the primary observer and 78 detected by the secondary observer. Within the two distance intervals, the proportion (relative to the total number of birds detected) of birds detected by primary observers was (0.88, 0.85) with secondary observers detecting the remainder. We first fit a Huggins removal model with MARK (White and Burnham 1999) using distance as a covariate to estimate detection probabilities for each distance bin. Estimated detection probabilities were high for each distance bin (0.87, 0.82) and as expected were higher when observers were combined (0.98, 0.97). Estimated abundance was 567 (SE 4); which is simply the binned counts (187, 364) divided by the combined observer detection probabilities for each bin (0.98, 0.97), respectively. Note that all of our standard errors for abundance were computed as shown in Section 3.3.

Next, we analyzed the warbler data using conventional distance sampling methods, assuming $p(0) = 1$, a half-normal detection function, and distance intervals of 0–50 and >50–100 m. We conducted two analyses, one using birds seen by the primary observer, and the second using birds seen by both observers. As expected, detection probability declined as distance increased (0.89, 0.55) giving an abundance estimate for observations based on the primary observer of 745 (SE 69) . When we incorporated data collected by the secondary observers, we found a slight increase in bin-specific detection probability (0.90, 0.58) and an increase in estimated abundance 835 (SE 72). The distance sampling analysis showed a moderate decline in detection probability with distance, whereas the decline was weak for the mark-recapture analysis and a model without the distance covariate was favored slightly ($\triangle$AICc = 0.6).

Based on the mark-recapture abundance estimate (567), one would assume that the raw count underestimated the actual population size by 16 individuals. But, using the abundance estimate from distance sampling with both observers, raw counts underestimated population size by 284. This is counter-intuitive because we would expect estimates from distance sampling to be less than mark-recapture estimates when $p(0) < 1$. This same paradox confronted Walter and Hone (2003) who also noticed that the abundance estimates from mark-recapture increased when they excluded data at larger distances. What they unknowingly observed was bias due to unmodeled heterogeneity inflating estimates of detection probability and as distance increased, the effect of heterogeneity increased (e.g., only more noticeable individuals are detected as distance increases). Excluding data with larger distances removed the more extreme heterogeneity and improved consistency of the estimates for Walter and Hone (2003) and the same would occur for the warbler data. However, the solution is not truncation but a combination that uses the strengths of each method while avoiding unmodeled heterogeneity and the dependence that it creates.

2.1. Independence and Unmodeled Heterogeneity

One of the more confusing aspects of this paradox is the link between independence and unmodeled heterogeneity and why it causes bias with mark-recapture and MRDS in some cases. The assumption of independence for mark-recapture sampling is mistakenly thought to be satisfied if the observers act independently (e.g. do not cue each other); however, that is only part of the picture. Consider an independent observer (IO) point survey with observer-specific detection probabilities p_1 and p_2. If detections by the observers are statistically independent, then the probability that both observers detect an animal (duplicate detection) is the product of the probabilities ($p_1 p_2$). Also, if we define $p_{1|2}$ to be the conditional probability that observer 1 detects an animal that observer 2 has detected and vice versa for $p_{2|1}$, then independence also implies that $p_{1|2} = p_1$ and $p_{2|1} = p_2$. Observer dependence can be demonstrated by considering a situation in which observer 1 was cued to each detection by observer 2. The probability of a duplicate would be p_2 and not $p_1 p_2$ because observer 1 would detect anything detected by observer 2, and thus $p_{1|2} = 1$ which is not equal to p_1 unless observer 1 had perfect detection. However, observer independence does not guarantee statistical independence because any unmodeled

heterogeneity induces positive covariance (Borchers et al. 2006) resulting in dependence because $p_{1|2} > p_1$, $p_{2|1} > p_2$, and $p_{1|2}p_2 = p_{2|1}p_1 > p_1 p_2$. Consider a simple example in which 50% of 200 birds are active and vocalizing and the other 50% are quiet and sedentary. Let's assume that their detection probabilities for each observer are 0.8 and 0.1, respectively. Then the expected proportion of the birds detected by one observer would be the average ($p_1 = p_2 = 0.45$). Using the expectations, observer 1 will detect 80 active birds and 10 sedentary birds. The average detection probability for their sample is 0.72. Detection probability for observer 2 is measured from the sample detected by observer 1, so $p_{2|1} = 0.72$ because we would expect observer 2 to detect 64 of the active and one of the sedentary birds detected by observer 1 ($65/90 = 0.72$). The same would occur if we reversed observer roles. If we estimated separate detection probabilities for active and sedentary birds, the heterogeneity would be included in the model removing the dependence and resulting bias. Unfortunately, it may not be possible to identify or measure all of the covariates that affect detection probability and any remaining unmodeled heterogeneity will introduce bias (Southwell et al. 2007).

Distance (y) from the observer to an animal is one potential source of heterogeneity in detection probability that is modeled with the detection function $p(y)$. In the initial attempts to combine mark-recapture and distance sampling (Alpizar-Jara and Pollock 1996; Manly, McDonald, and Garner 1996; Borchers, Zucchini, and Fewster 1998), independence was assumed to hold at each value of y and probabilities for the detection histories (e.g., $\omega = (1, 0)$, $(0, 1)$, or $(1, 1)$ seen by primary observer only, secondary only and by both observers) were specified as $p_1(y)(1 - p_2(y))$, $p_2(y)(1 - p_1(y))$, and $p_1(y)p_2(y)$, respectively, with observer-specific detection functions ($p_j(y)$, $j = 1, 2$). Laake (1999) called this assumption "full conditional independence" because observer detections were assumed to be independent conditional on their values of y. Using that assumption, it was common for an abundance estimate based on MRDS to yield estimates that were lower than estimates from conventional distance sampling even though the resulting estimated $p(0)$ was less than 1 (Laake 1999). Additional sources of heterogeneity other than distance can create dependence and positive bias at larger distances which offsets the decrease from $p(0) < 1$ (Laake 1999). Borchers, Zucchini, and Fewster (1998) specifically recognized that all covariates that affect detection needed to be included in the model to ensure validity of the independence assumption. Laake (1999) argued that it was unlikely that all covariates could be identified and appropriately measured and showed that it was only necessary to assume independence for $y = 0$ because data from both mark-recapture and distance sampling provide information about $p(y)$. Essentially, $p(0)$ (i.e., the intercept) was estimated from the mark-recapture data and the shape of $p(y)$ (i.e., how it decreases with distance) was estimated from distance sampling which assumes $p(0) = 1$. Further developed by Borchers et al. (2006), the more restrictive assumption was renamed "full independence" (FI) in comparison to the weaker "point independence" (PI) assumption (Laake and Borchers 2004). Point independence allows the shape of $p(y)$ from distance sampling to differ from the shape of $p(y)$ from the mark-recapture data; whereas FI forces identical detection function shapes and any unmodeled heterogeneity thus distorts the shape of the mark-recapture detection function which can result in bias.

The ratio of the mark-recapture and distance sampling detection function shapes at each value of y, we define as $\delta(y)$. Full independence implies that $\delta(y) = 1$ because the shapes are identical; whereas PI only requires $\delta(0) = 1$ and typically $\delta(y) > 1$ because the mark-recapture detection function declines more slowly with distance because of unmodeled heterogeneity. The function $\delta(y)$ is conceptually similar to the species interaction factor (φ) in occupancy modeling (MacKenzie et al. 2006):

$$\varphi = \frac{\psi_{AB}}{\psi_A \psi_B}$$

where ψ_A and ψ_B are occupancy rates of species A and B and ψ_{AB} is proportion of sites occupied by both species. In comparison, we can express the MRDS $\delta(y)$ as

$$\delta(y) = \frac{\Pr\{\omega = (1, 1) \mid y\}}{p_1(y) p_2(y)}.$$

Both $\delta(y)$ and φ represent the ratio of the proportion of duplicates to its expected value under independence. If the ratio is greater than 1 there is a positive association (dependence) between observer detections and if less than 1, a negative dependence.

3. MARK-RECAPTURE DISTANCE SAMPLING

3.1. LIKELIHOOD STRUCTURE AND LEVELS OF INDEPENDENCE

Mark-recapture distance sampling combines mark-recapture and distance sampling into a single analysis. The data are the distance y_i and "capture history" ω_i of each of the $i = 1, \ldots, n$ detected animals (or groups of animals). If observer 1 detects n_1 animals ($\omega = (1, 0)$ and $(1, 1)$), observer 2 detects n_2 ($\omega = (0, 1)$ and $(1, 1)$) and m_2 ($\omega = (1, 1)$) is the number that they saw in common, then the number of unique detections is $n = n_1 + n_2 - m_2$. For the removal configuration with observer 2 knowing what observer 1 detects, the history $\omega = (1, 0)$ is not possible and $m_2 = n_1$ and $n = n_2$. Time intervals have also been used in place of observer roles (Farnsworth et al. 2002, 2005).

The MRDS likelihood can be expressed as the product of a mark-recapture likelihood ($\mathcal{L}_\omega$) and a distance sampling ($\mathcal{L}_y$) likelihood (Laake and Borchers 2004; Borchers, Zuc-chini, and Fewster 1998). The mark-recapture likelihood is a product of the probabilities of the observed capture histories conditional on having been seen by at least one observer at their distances from the line or point $p.(y_i)$:

$$\mathcal{L}_\omega = \prod_{i=1}^{n} \frac{\Pr(\omega_i \mid y_i)}{p.(y_i)}. \tag{3.1}$$

The capture history probabilities can be expressed in terms of the observer-specific detection functions ($p_j(y)$ $j = 1, 2$) and the dependence function ($\delta(y)$). For the IO configuration:

$$\Pr\{\omega_i = (1, 0) \mid y_i\} = p_1(y_i)\{1 - \delta(y_i) p_2(y_i)\},$$

$$\Pr\{\omega_i = (0, 1) \mid y_i\} = p_2(y_i)\{1 - \delta(y_i) p_1(y_i)\},$$

$$\Pr\{\omega_i = (1, 1) \mid y_i\} = \delta(y_i) p_1(y_i) p_2(y_i)$$

and for the removal configuration,

$$\Pr\{\omega_i = (0, 1) \mid y_i\} = p_2(y_i)\{1 - \delta(y_i)p_1(y_i)\},$$
$$\Pr\{\omega_i = (1, 1) \mid y_i\} = p_1(y_i).$$

In general, for removal models you must assume that $p_1 = p_2$ (Otis et al. 1978); however, if personnel are rotated among primary and secondary observer roles, it is possible to estimate an observer effect (Cook and Jacobson 1979) so we have used a separate $p_2(y)$ above rather than specifying $\Pr\{\omega_i = (0, 1) \mid y_i\} = p_1(y_i)\{1 - \delta(y_i)p_1(y_i)\}$. For both configurations

$$p.(y_i) = p_1(y_i) + p_2(y_i) - \delta(y_i)p_1(y_i)p_2(y_i).$$

The detection functions $p_j(y)$ can include covariates other than distance y, such as time of day, weather, canopy cover, etc., but we have not included explicit notation for additional covariates.

Distance sampling makes the assumption of constant density around the line or point. For lines, this implies a uniform probability distribution for distances $\pi(y) = \frac{1}{W}$ where $2W$ is the transect width. For points, area increases linearly with distance, so a constant density implies the probability distribution for distances is $\pi(y) = \frac{2y}{W^2}$ where W is the radius. The distance sampling likelihood is the product of the probability densities for the observed detections:

$$\mathcal{L}_y = \prod_{i=1}^{n} f(y_i) = \prod_{i=1}^{n} \frac{p.(y_i)\pi(y_i)}{\int_0^W p.(y)\pi(y)\,dy}. \tag{3.2}$$

Distance sampling alone cannot provide an estimate of $p.(0)$ because it cancels in the above likelihood. Mark-recapture alone (Alpizar-Jara and Pollock 1996; Nichols et al. 2000; Farnsworth et al. 2002; Moore et al. 2004; Alldredge et al. 2006) must assume $\delta(y) = 1$ (FI) and thus is likely biased from unmodeled heterogeneity. Using the product of the two likelihoods ($\mathcal{L}_y\mathcal{L}_\omega$), some authors (Manly, McDonald, and Garner 1996; Borchers, Zucchini, and Fewster 1998; Farnsworth et al. 2005) have assumed FI and maximized over the parameters contained in $p_1(y)$ and $p_2(y)$. However, with the PI assumption, Borchers et al. (2006) showed that $\mathcal{L}_y$ and $\mathcal{L}_\omega$ can be maximized separately. If you replace $p_1(y)$ and $p_2(y)$ with $p_{1|2}(y)/\delta(y)$ and $p_{2|1}(y)/\delta(y)$ in $\mathcal{L}_\omega$, it only contains the conditional probability functions $p_{2|1}$ and $p_{1|2}$ which demonstrates that mark-recapture only provides estimates of the conditional detection functions. They are used to estimate $p.(0)$ based on the assumption of independence at $y = 0$. The detection function $p.(y)$ for all observations can be fitted separately by maximizing $\mathcal{L}_y$ to estimate relative (i.e., assumes $p(0) = 1$) detection probability as a function of distance. The dependence function $\delta(y)$ was never specified but can be computed as $\delta(y) = [p_{1|2}(y) + p_{2|1}(y) - p_{1|2}(y)p_{2|1}(y)]/p.(y)$.

As an alternative modeling framework Buckland, Laake, and Borchers (2010) suggested specifying models for $p_1(y)$, $p_2(y)$ and $\delta(y)$ and maximizing $\mathcal{L}_y\mathcal{L}_\omega$ jointly to provide a consistent framework for FI and PI models. With their approach each detection function is observer-specific rather than a mix of conditional observer-specific detection functions (e.g., $p_{1|2}(y)$) and a detection function ($p.(y)$) that combines observers. The only challenge

was to develop a model for $\delta(y)$ that could represent FI and PI and which provided valid probabilities for computed quantities like $p_.(y)$. They used the following representation for $\delta(y)$:

$$\delta(y) = L(y) + [U(y) - L(y)]\delta_0(y) \tag{3.3}$$

where

$$\log_e\left\{\frac{\delta_0(y)}{1 - \delta_0(y)}\right\} = \gamma y + \log_e\left\{\frac{1 - L(y)}{U(y) - 1}\right\}.$$

The lower bound $L(y)$ on $\delta(y)$ ensures probabilities do not exceed 1 and the upper bound $U(y)$ ensures non-negative probabilities:

$$U(y) = \min\{1/p_1(y), 1/p_2(y)\},$$

$$L(y) = \max\left\{0, \frac{p_1(y) + p_2(y) - 1}{p_1(y)p_2(y)}\right\}.$$

This formulation ensures $\delta(0) = 1$ and FI is achieved with $\gamma = 0$. In most cases, only positive dependence is likely because the observers are affected in a similar manner by detection probability heterogeneity. By setting $L(y)$ to zero and restricting $\gamma > 0$ by using e^γ for γ, positive dependence ($\delta(y) \geq 1$) is enforced. Enforcing positive dependence ensures that the conditional detection probability function $\delta(y)p_j(y)$ is monotone; whereas non-monotone functions are possible without the restriction. With positive dependence, $\delta(y)$ is

$$\delta(y) = \frac{U(y)}{1 + \exp[-\exp(\gamma)y - \ln(1/(U(y) - 1))]}. \tag{3.4}$$

Various functional forms could be used to represent $p(y)$ but we will use the logistic form used by Buckland, Laake, and Borchers (2010):

$$p_j(y) = \frac{1}{1 + \exp(-\beta_{0j} - \beta_{1j}y)} \quad \text{for } j = 1, 2. \tag{3.5}$$

The functional forms of both $\delta(y)$ and $p(y)$ can easily incorporate additional covariates other than distance y. If covariates are added to $\delta(y)$ they must be an interaction with distance to ensure $\delta(0) = 1$. Alternate forms for $p_j(y)$ (Innes et al. 2002) such as

$$p_j(y) = \frac{1}{1 + \exp(-\beta_{0j})} \exp\left(-\frac{y^2}{2\exp(\beta_{1j})^2}\right) \quad \text{for } j = 1, 2,$$

may be useful to maintain strict monotonicity with distance when covariates are added to either the intercept or scale; however, defining models becomes slightly more complex because covariates can be used in $p(0)$ or for the scale function for distance or both. The removal-distance sampling model of Farnsworth et al. (2005) used this alternate form where they specified $p(y) = P_a \exp[-y^2/(2\sigma^2)]$. A similar logistic model could be specified using (3.5) where $\beta_{0j} = \ln([P_a/(1 - P_a)]$.

3.2. LIKELIHOOD STRUCTURE AND BINNED DISTANCES

Laake, Dawson, and Hone (2008) analyzed double-observer line transect data from aerial surveys of wild horses (*Equus ferus)* with binned distances where each observation was assigned to one of a set of distance intervals $\{(c_0, c_1), (c_1, c_2), \ldots, (c_{k-1}, c_k)\}$ where $c_k = W$ and $c_0 = 0$. They presumed that $\mathcal{L}_\omega$ and $\mathcal{L}_y$ could be maximized separately with the PI assumption even though distances were binned. They used mid-point of the distance bins for the mark-recapture analysis and used a binned distance analysis with DISTANCE. Kissling, Garton, and Handel (2006) took a similar approach except that they limited the mark-recapture analysis to distances in an interval from 0 to $y*$ such that $p(y)$ was relatively constant in the interval. Here we will outline a better approach that enables use of all the data.

For the ith observation we will use $(c_{j(i)-1}, c_{j(i)})$ to represent its distance interval. For the set of binned distances, the likelihood is the product of the binned likelihoods for mark-recapture and distance sampling data (Borchers, Zucchini, and Fewster 1998):

$$
\begin{aligned}
\mathcal{L}_y &= \prod_{i=1}^{n} \frac{\int_{c_{j(i)-1}}^{c_{j(i)}} p.(y)\pi(y)\,dy}{\int_0^W p.(y)\pi(y)\,dy}, \\
\mathcal{L}_\omega &= \prod_{i=1}^{n} \frac{\int_{c_{j(i)-1}}^{c_{j(i)}} \mathrm{Pr}(\omega_i|y)\pi(y)\,dy}{\int_{c_{j(i)-1}}^{c_{j(i)}} p.(y)\pi(y)\,dy}.
\end{aligned}
\tag{3.6}
$$

Each component is a ratio of integrals over a range of y and unless $\delta(y)$ is constant within each distance interval, the likelihood components are not separable and the approach of Laake, Dawson, and Hone (2008) was at best approximately correct. However, by specifying models for $p_1(y)$, $p_2(y)$ and $\delta(y)$ as described above, the extension to binned data is easily accomplished by maximizing $\mathcal{L}_y\mathcal{L}_\omega$ (Equation (3.6)) over the model parameters.

To facilitate the use of these methods, we have written R code (R Development Core Team 2009) to maximize the joint likelihood for line and point sampling data with binned or unbinned distances and either IO or removal configuration. We have provided the code as an R Package which is available as a Supplement to this manuscript or from the authors (J.L. Laake or B.A. Collier). Models can be fitted with either $\delta(y) = 1$ (FI) or with $\delta(0) = 1$ (PI) and model assessment can be done using AICc (Burnham and Anderson 2002).

3.3. ABUNDANCE ESTIMATION

The abundance estimator for MRDS is essentially the same as for any analysis with distance sampling because the only difference is the estimation of detection probability. Here we will focus on abundance within the covered survey region (e.g., set of circles) which Buckland, Laake, and Borchers (2010) denote as $\hat{N}_c$. If there are no covariates other than distance, then the estimator is

$$
\hat{N}_c = \frac{n}{\int_0^W \hat{p}.(y)\pi(y)\,dy} = \frac{n}{\hat{E}(p.)}
$$

where $\hat{p}_.(y)$ implies that it depends on estimated parameters. The variance estimator (Borchers et al. 1998) is

$$\hat{\text{var}}(\hat{N}_c) = \frac{\hat{N}_c[1 - \hat{E}(p_.)]}{\hat{E}(p_.)} + \underline{\hat{d}}^T \hat{\mathbf{I}}^{-1} \underline{\hat{d}}$$

where $\underline{\hat{d}}$ is a vector of first derivatives of $\hat{N}_c$ with respect to the parameters in $p(y)$ and $\delta(y)$ and $-\hat{\mathbf{I}}$ is the matrix of second derivatives of the parameters with respect to the likelihood function. When additional covariates are used for $p(y)$ then the abundance and variance estimators are

$$\hat{N}_c = \sum_{i=1}^{n} \frac{1}{\hat{E}(p_{i.})},$$

$$\hat{\text{var}}(\hat{N}_c) = \sum_{i=1}^{n} \left[\frac{[1 - \hat{E}(p_{i.})]}{\hat{E}(p_{i.})^2} \right] + \underline{\hat{d}}^T \hat{\mathbf{I}}^{-1} \underline{\hat{d}}$$

where $\hat{E}(p_{i.})$ is computed with the covariates for the ith observation. For a description of abundance and variance estimation for the entire survey region refer to Buckland, Laake, and Borchers (2010).

4. EXAMPLE USING SIMULATED DATA

Here we provide an analysis of simulated MRDS data for point sampling with a removal configuration of two observers. Our goal is not to provide a complete simulation study as suggested by Efford and Dawson (2009). Instead, our interest is solely to demonstrate the impacts of unmodeled heterogeneity and why the concept of point independence can be important and that is easier to do with a known population albeit simulated. See Buckland, Laake, and Borchers (2010) for a simulation comparison of estimators.

Because we are only interested in inference about estimated detection probability, we simulated bird locations for a single point of radius 100 with an expected uniform density rather than sampling from a larger area with multiple points. For each bird, we simulated its capture history (00, 01, 11) by first simulating whether the primary observer saw the bird using a Bernoulli random variable with probability

$$p(y) = p_1(y) = p_2(y) = \frac{1}{1 + \exp(-\ln[p_0/(1 - p_0)] + 0.04y)}$$

where $p_0 = p(0) = 0.8$ and then for birds missed by the primary observer, simulating whether the secondary observer saw the bird with another Bernoulli random variable with probability $p(y)[1 - \delta(y)p(y)]$, where

$$\delta(y) = \frac{1}{p(y)} \frac{1}{1 + \exp[-0.02y - \ln[p(y)/(1 - p(y))]]}.$$

For our simulated data, we categorized each location into distance bins using intervals of 0–25, 25–50, 50–75, and 75–100 m.
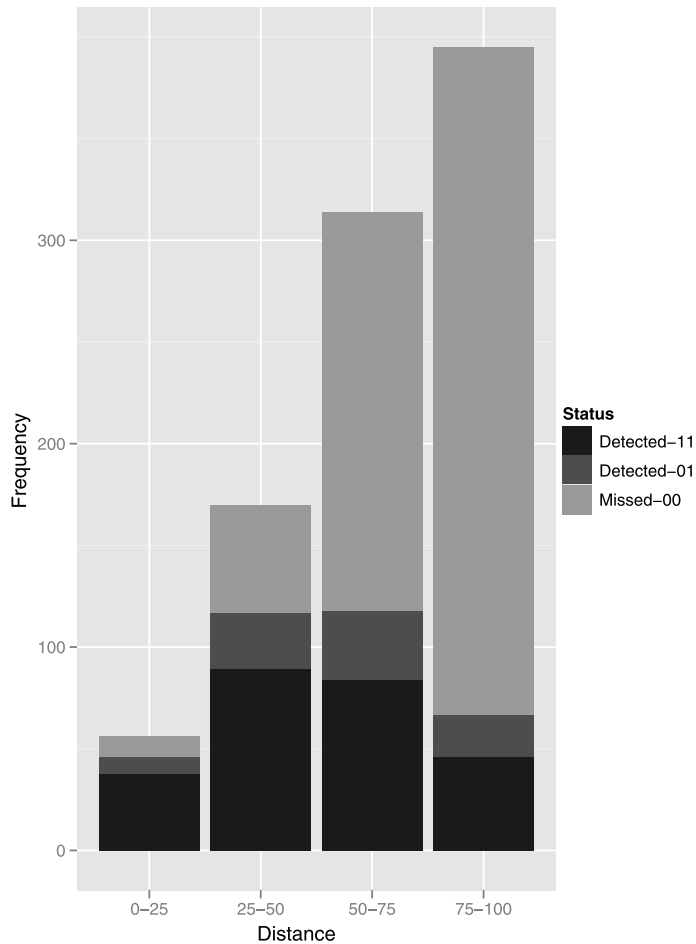
Figure 1.   Distribution of simulated birds with capture histories 11, seen by first observer, 01, missed by first observer but detected by second, and 00 missed by both observers.

Of the 935 simulated birds in the population, 257 were detected by the primary observer and 91 were detected by the secondary observer that were missed by the primary observer. The proportion of birds observed in the four distance intervals were 0.68, 0.52, 0.27, 0.12 for the primary observer and 0.82, 0.69, 0.38, 0.17 for both observers together (Figure 1).

With the simulated data we fit a Huggins mark-recapture model (White and Burnham 1999) using the distance interval mid-point as a covariate (Moore et al. 2004; Alldredge et al. 2006). The resulting detection probability estimates for each distance bin were 0.77, 0.70, 0.61, 0.51 for the primary observer and 0.95, 0.91, 0.85, 0.76 for both observers combined. Obviously these are much higher than the true values and the differences (0.13, 0.22, 0.47, 0.59) increase with distance. As expected, this translates to an estimate of abundance 405 (SE 11) that is much lower than the true abundance with abundance only differing by 7 in the first distance bin but by a substantially greater difference of 307 in the last bin. From these simulated data this was not a surprise because they were generated

with this behavior such that heterogeneity (dependence) increased with distance and no dependence at $y = 0$.

We also analyzed the simulated data with distance sampling using a half-normal detection function and the same distance intervals. Here we have assumed that $p(0) = 1$, even though we knew that was a bad assumption. We analyzed the data from the primary observer and also the data from both observers. With the primary observer data, the estimated detection probabilities for the four distance intervals were 0.93, 0.69, 0.38, 0.16 and the estimated abundance was 683 (SE 65) which is low because $p(0)$ is truly less than 1. Note that the abundance estimator for distance sampling is not $38/0.93 + 89/0.69 + 84/0.38 + 46/0.16 = 679.9$. Instead, it is computed as $257/0.38$ which uses an average probability integrated across distance. In this case, they were close but that is not always true. The analysis of all observed distances yielded similar but obviously less biased estimates because $p(0)$ was closer to 1 by incorporating observations of the secondary observer missed by the primary observer. The distance interval-specific estimates of detection probabilities were 0.93, 0.71, 0.42, 0.19 and the resulting abundance estimate was 861 (SE 72).

Finally, we fitted MRDS models to the data using the binned data likelihood (3.6) with $p(y)$ specified by (3.5) for a single observer and $\delta(y)$ specified by (3.4) for the PI model and $\delta(y) = 1$ for the FI model. As expected, the FI model was inferior to the PI model (ΔAICc = 9.3). This was evident in the lack of fit for the FI model (Figure 2) in comparison to the PI model (Figure 3). The PI model was able to fit the flatter detection function from the mark-recapture data (Figure 3d) and the steeper declining detection from the distance data (Figure 3c); whereas the FI model was constrained to fit the same detection function to both sources of data (Figure 2c–d). The estimated abundance from the FI model 690 (SE 53) was higher than the Huggins estimate 405 (SE 11), which treated distance as a covariate in mark-recapture. In this case, with the FI assumption there was a gain by including $\mathcal{L}_y$ but that is not always the case, as we show later. Regardless, the estimates from both the Huggins and FI models were much lower than estimates derived from distance sampling which assumed that $p(0) = 1$ because bias in detection probabilities at distance from unmodeled heterogeneity offset the gain from letting $p(0) < 1$. The abundance estimate from the PI model 932 (SE 124) was much closer to the true abundance of 935 in the simulated population.

5. REVISITING THE WARBLER SURVEY DATA

Here, we re-evaluate our warbler data using MRDS under both FI and PI assumptions. Remember from above we had modeled warbler abundance using mark-recapture with distance as a covariate and estimated abundance (567) whereas distance sampling estimates with data from the primary (745) or both (835) observers were significantly higher. Here, we fit an additional set of MRDS models following the simulated example above to the warbler survey data using the binned data likelihood (3.6) with $p(y)$ specified by (3.5) containing various combinations of covariates and either $\delta(y) = 1$ for FI model or $\delta(y)$
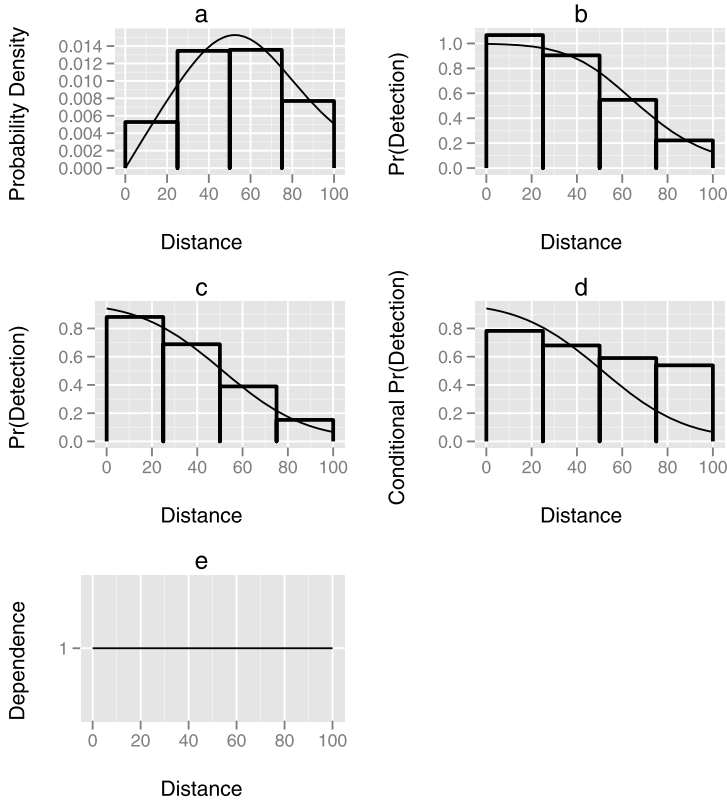
Figure 2. Fitted MRDS model to simulated data with full independence assumption. (a) fitted probability density $f(y) = p_.(y)\pi(y) / \int_0^w p_.(u)\pi(u)\,du$ and scaled histogram of the observed distances, (b) fitted detection function $p_.(y)$ and scaled histogram of the observed distances, (c) fitted detection function $p(y)$ and scaled histogram of the observed distances for the primary observer, (d) fitted conditional detection function $p(y)\delta(y)$ and histogram representation of interval-specific probabilities derived from Huggins removal model from MARK, (e) assumed dependence function $\delta(y) = 1$.

specified by (3.4) for the PI model. Because we also have the ability to incorporate explanatory covariates on the detection function, for this example analysis, we used the number of days from the estimated peak time (DaysFromPeak) for warbler territorial activities (20 April) to model the potential effect of changes in warbler reproductive phenology on detection. We also evaluated an effect of date (Date) as an additional option for explaining temporal variation in detection (Collier et al. 2010). We also considered a covariate with two levels for lighter ($\leq 66\%$) and heavier ($>66\%$) canopy cover (CC). Canopy cover could attenuate calls and reduce visual detections because golden-cheeked warblers nest in the canopy. Finally, we grouped observers into experienced (graduate students) and inexperienced (technicians) observers (experience) as we expected that observer experience would influence detection rates.

In all cases, we found FI models were inferior to PI models (see Table 1). The lowest ranking (based on AICc) PI model was ΔAICc = 12.9 units higher than the highest ranked FI model. As found in the simulated data, the PI model fit the flatter detection function from
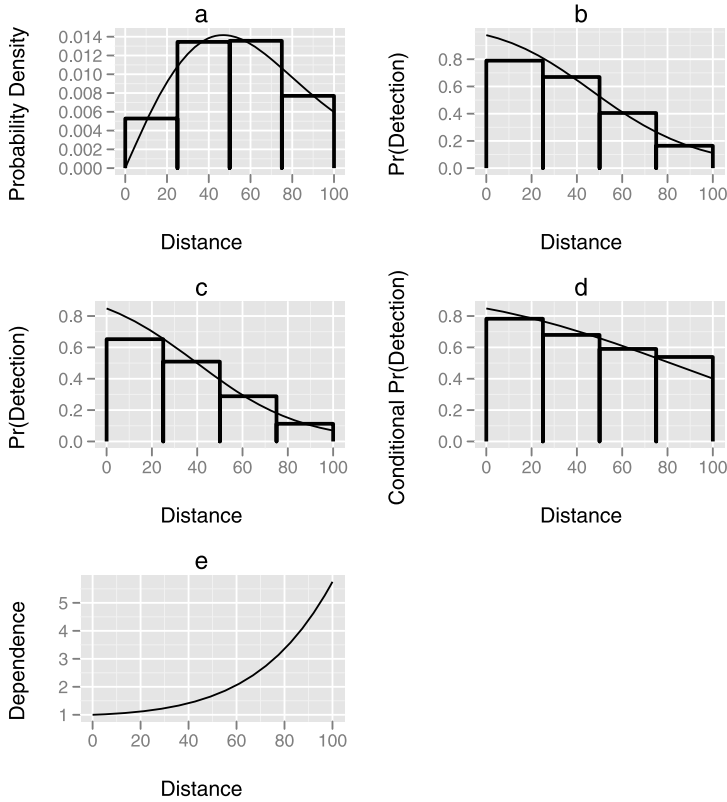
Figure 3. Fitted MRDS model to simulated data with point independence assumption. (a) fitted probability density $f(y) = p_.(y)\pi(y)/\int_0^w p_.(u)\pi(u)\,du$ and scaled histogram of the observed distances, (b) fitted detection function $p_.(y)$ and scaled histogram of the observed distances, (c) fitted detection function $p(y)$ and scaled histogram of the observed distances for the primary observer, (d) fitted conditional detection function $p(y)\delta(y)$ and histogram representation of interval-specific probabilities derived from Huggins removal model from MARK, (e) fitted dependence function $\delta(y)$ with $\delta(0) = 1$.

Table 1. Model selection table and abundance estimates for models fitted to 2008 double-observer point sampling of golden-cheeked warblers in Texas.

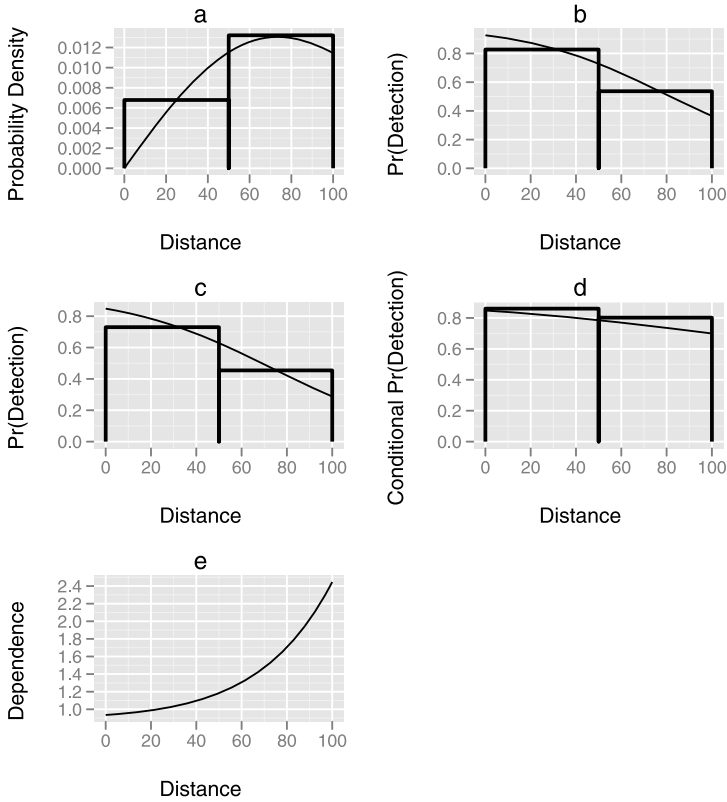| Model	Full Independence		Point Independence	
	ΔAICc	$\widehat{N}$	ΔAICc	$\widehat{N}$
~distance	31.1	570.4	13.2	868.0
~distance + CC	31.2	572.7	11.9	870.4
~distance + Date	32.9	571.9	14.6	873.6
~distance + DaysFromPeak	28.2	575.2	8.4	877.1
~distance + experience	30.4	570.3	9.0	876.1
~distance + CC + Date	31.2	576.0	11.8	880.3
~distance + CC + DaysFromPeak	26.1	585.1	4.7	883.3
~distance + CC + Date + experience	31.0	575.2	7.7	932.6
~distance + CC + DaysFromPeak + experience	26.3	582.5	0.0	904.0

Figure 4. Point independence MRDS model fitted to the golden-cheeked warbler survey data with formula ~distance + CC + DaysFromPeak + experience for $p(y)$ using Equation (3.5). (a) fitted probability density $f(y) = p.(y)\pi(y)/\int_0^w p.(u)\pi(u)\,du$ and scaled histogram of the observed distances, (b) fitted detection function $p.(y)$ and scaled histogram of the observed distances, (c) fitted detection function $p(y)$ and scaled histogram of the observed distances for the primary observer, (d) fitted conditional detection function $p(y)\delta(y)$ and histogram representation of interval-specific probabilities derived from Huggins removal model from MARK, (e) fitted dependence function $\delta(y)$ with $\delta(0) = 1$.

the mark-recapture data (Figure 4d) and the steeper declining detection function from the distance data (Figure 4c); whereas the FI model was constrained to fit the same detection function to both sources of data (Figure 5c–d). Estimated abundance 904 (SE 88) from the best PI model (~distance + CC + DaysFromPeak + experience) was substantially greater than estimated abundance 585 (SE 18) from the best ranked FI model (~distance + CC + DaysFromPeak). The bias due to unmodeled heterogeneity inherent in fitting the same detection function to both data sources is clear. With the best model, FI estimated abundance exceeded the mark-recapture abundance estimate by approximately 18. However, when allowing for different detection functions, addressing unmodeled heterogeneity, the estimated abundance was substantially greater than the mark-recapture abundance estimate (337) and likely represents a more accurate estimate.
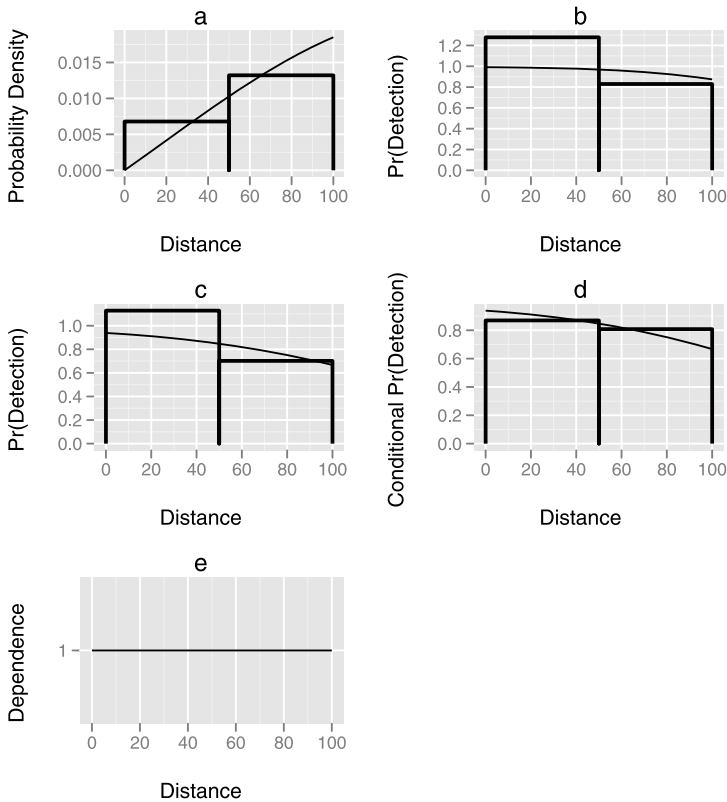
Figure 5. Full independence MRDS model fitted to the golden-cheeked warbler survey data with formula ~distance + CC + DaysFromPeak for $p(y)$ using Equation (3.5). (a) fitted probability density $f(y) = p.(y)\pi(y)/\int_0^w p.(u)\pi(u)\,du$ and scaled histogram of the observed distances, (b) fitted detection function $p.(y)$ and scaled histogram of the observed distances, (c) fitted detection function $p(y)$ and scaled histogram of the observed distances for the primary observer, (d) fitted conditional detection function $p(y)\delta(y)$ and histogram representation of interval-specific probabilities derived from Huggins removal model from MARK, (e) fitted dependence function assuming $\delta(y) = 1$.

6. DISCUSSION

We demonstrated that unmodeled heterogeneity will bias detection probabilities and cause abundance estimates derived from mark-recapture methods for avian point sampling to be negatively biased. Additionally, we have shown how the often used distance sampling assumption of $p(0) = 1$ can also result in negatively biased abundance estimates. Mark-recapture distance sampling provides a robust form of estimation that improves on the weaknesses of both methods. However, while the FI and PI assumptions provide alternative modeling options, we have shown that the PI model guarantees a reasonable expectation that estimates from the combined approach will be as large as the estimate based on distance sampling assuming $p(0) = 1$.

Even though we can model heterogeneity using covariates or develop non-specific models for heterogeneity (Pledger 2000), they cannot cope with extreme heterogeneity where some animals are essentially undetectable. Point-based surveys of birds will likely have

extreme heterogeneity due to forest cover. Detection heterogeneity due to variation in vocalizations or visual cues is difficult to model and mark-recapture data will likely be dominated by the most detectable birds that were detected by both observers. This heterogeneity effect will typically increase with distance and models using only mark-recapture are likely to conclude that detection probability does not decrease with distance (Alldredge et al. 2006; Butler et al. 2007).

While PI models were clearly better in our example, that assessment was based on distance sampling assumptions. The lack of fit associated with FI could also result from failures of the assumptions. First, the observed pattern could appear if birds were truly at higher density near the point center because point locations were not selected at random relative to bird distribution. Second, if observers routinely underestimated distance, more birds could be recorded near the point center that were really farther away. Finally, attractive or random movement prior to detection would inflate the number of birds near the point center. All distance sampling assumptions, other than $p(0) = 1$ must hold for MRDS. We believe all of the MRDS assumptions are quite reasonable for our golden-cheeked warbler example. Points were selected randomly from within patches of woodland habitat, observers were trained in distance estimation and only needed to assign distances to one of two bins and the effect of any movement was reduced by restricting the counts to a 5 minute interval. If the MRDS assumptions are likely to fail for a particular application, one alternative is using mark-recapture with distance as a covariate. If that is the only viable option, we recommend collecting as many relevant detection covariates as possible with the knowledge that abundance estimates may be negatively biased due to unmodeled heterogeneity.

Mark-recapture distance sampling with PI does require the assumption that $\delta(0) = 1$; however, it is a far less restrictive assumption than $\delta(y) = 1$ or $p(0) = 1$. Inclusion of covariates for detection probability may help to ensure that $\delta(0) = 1$ but any unmodeled heterogeneity at $y = 0$ will also bias PI methods (Buckland, Laake, and Borchers 2010). Alternatively, limiting independence (Buckland, Laake, and Borchers 2010) may be useful if $\delta(0) > 1$ but it can generate implausible estimates in some cases.

Avian ecologists have generally accepted that methods such as mark-recapture or distance sampling, when appropriately used, will provide unbiased estimates of population size via their accounting for imperfect detection. Nichols, Thomas, and Conn (2009) provided a recent review of point sampling methods and included a brief description of MRDS. However, they did not provide guidance on the reliability of the various methods. We have shown that unmodeled heterogeneity can bias estimates of detection and hence population size. Obviously, it is not possible to address all potential factors influencing detection heterogeneity. Thus, population estimates based on mark-recapture alone are likely to exhibit substantial negative bias, even if distance is included as a covariate. We hope that this paper will serve as a catalyst for greater understanding and future discussion on the limitations of mark-recapture and benefits of MRDS in point sampling.

SUPPLEMENTARY MATERIALS

R-Package mr (mark-recapture point transect) includes all code and data used in the paper (mrpt.zip file).

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