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Line Transect Methods for Plant Surveys

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Summary. Interest in surveys for monitoring plant abundance is increasing, due in part to the need to quantify the rate of loss of biodiversity. Line transect sampling offers an efficient way to monitor many species. However, the method does not work well in some circumstances, for example on small survey plots, when the plant species has a strongly aggregated distribution, or when plants that are on the line are not easily detected. We develop a crossed design, together with methods that exploit the additional information from such a design, to address these problems. The methods are illustrated using data on a colony of cowslips.

Key words: Biodiversity monitoring; Distance sampling; Line transect sampling; Mark–recapture; Sampling immotile objects.

1. Introduction

At the 2002 World Summit on Sustainable Development in Johannesburg, political leaders agreed to strive for "a significant reduction in the current rate of loss of biological diversity" by the year 2010. A natural consequence of this commitment is a demand for survey methods that allow widespread monitoring of biological populations at low cost. As noted by Buckland et al. (2005), the surveys must be carefully designed, to ensure that the monitoring data are spatially representative, and measures of biodiversity should be constructed so that they are not biased when detectability of species within survey plots is imperfect.

Distance sampling (Buckland et al., 2001, 2004) is ideally suited for monitoring a number of species. It provides a rigorous framework for survey design (Buckland et al., 2001, pp. 228–323; Strindberg, Buckland, and Thomas, 2004), and explicitly models detectability. Much of the current research development in distance sampling is to allow reliable application of the methods to a wider range of populations. For example, Laake and Borchers (2004) provide comprehensive methods for populations where detection at the line or point is not certain; Lukacs, Franklin, and Anderson (2004) consider passive distance sampling methods, in which animals record their own distances from the line or point, by entering traps; Buckland et al. (2006) develop point transect methods for when a trap or lure is positioned at each point.

In this article, we consider the problem of estimating the abundance of plants within a colony or site. Currently, there is little biodiversity monitoring of plants, which contrasts with the situation for mammals, birds, reptiles, and amphibians, despite the fact that plants are far more pervasive. Most plant surveys target rare species of conservation interest. Atlas surveys, in which observers record a wide range of species by grid square, are also popular, but these surveys are of little use for monitoring change in abundance; instead, they are designed to identify changes in range of species. Because atlas surveys generally do not have a rigorous survey design, and effort can be very variable, atlas data are of limited value for biodiversity monitoring.

Many plant species spread across the ground, so that individual plants are not readily identifiable. For such species, quadrat sampling of some form is used, in which percent cover of each species is assessed within the sampled quadrats, either by direct estimation or by use of a scale, the values of which increase nonlinearly as percent cover increases. We do not address such surveys here. Rather, we consider the case of species for which individual plants are readily identifiable. For some plants, it may be more appropriate to estimate abundance of individual flower spikes, which may be more visible and identifiable than the rest of the plant. A number of flower spikes may be converted to plant abundance if the mean number of flower spikes per plant is estimated.

In line transect sampling, substantially more ground can be covered in a given time than for quadrat sampling, for which all plants within quadrats must be counted if plant abundance is to be estimated without bias. Because plants often have a very patchy distribution, the ability to cover a large area of ground with modest resources is an important advantage. Further, detectability is modeled in line transect sampling, whereas with quadrat sampling or strip transect

sampling, it is assumed to be certain, and the assumption is seldom tested.

In many circumstances, standard line transect sampling is very effective for plant populations. However, special circumstances often apply, which mean that more sophisticated methods may be needed:

1. The survey site may be very small (although the monitoring program may comprise many such sites within a region). If site-specific abundance or density estimates are required, standard line transect sampling requires that there are of the order of 20 transect lines or more at each site. If these are randomly located (or more usually, a grid of systematically spaced lines is randomly located) in the site, this ensures that plants are uniformly distributed to a good approximation with respect to distance from the nearest line for a single realization of the design. However, a single site or colony may be too small to allow so many lines without overlap of the associated strips. Further, because plants often have very patchy distributions, the assumption of uniformity may be badly violated for a single realization of the design (although it is satisfied when averaged across all possible realizations).
2. For small or cryptic species, plants on the line may pass undetected, violating the assumption of certain detection on the line.

We consider survey design and analysis methods to address both issues. The motivating example relates to herb-rich grassland at Fleecefaulds Meadow in Fife, Scotland, a Scottish Wildlife Trust reserve. We use the methods to estimate abundance of cowslips (*Primula veris*) on a section of the reserve.

2. Methods

2.1 *Survey Design*

We use a "crossed design" comprising two systematic grids of parallel lines perpendicular to each other (Figure 1). We will assume that one of these grids is oriented north to south (N/S), while the other is east to west (E/W). Detections within a distance w of a line are recorded, so that the strips of Figure 1 have width $2w$.

There are two important advantages to this design relative to a conventional design:

1. Locations of detections along one set of lines provide information from which the distribution of plants with respect to distance from the line for the perpendicular set may be estimated. This allows the detection function to be estimated when the distribution of plants with respect to distance from the line is nonuniform.
2. Wherever lines from the two grids intersect, the square of side $2w$ that is centered on the point of intersection (Figure 2) is surveyed twice, providing "double-observer" mark–recapture data, from which probability of detection can be estimated without assuming detection is certain on the line. Moreover, because the square is surveyed from each of its centerlines (one running N/S, and the other E/W), the dependence between detections arising from heterogeneity in the detection probabilities is reduced, making the task of modeling the heterogeneity easier.

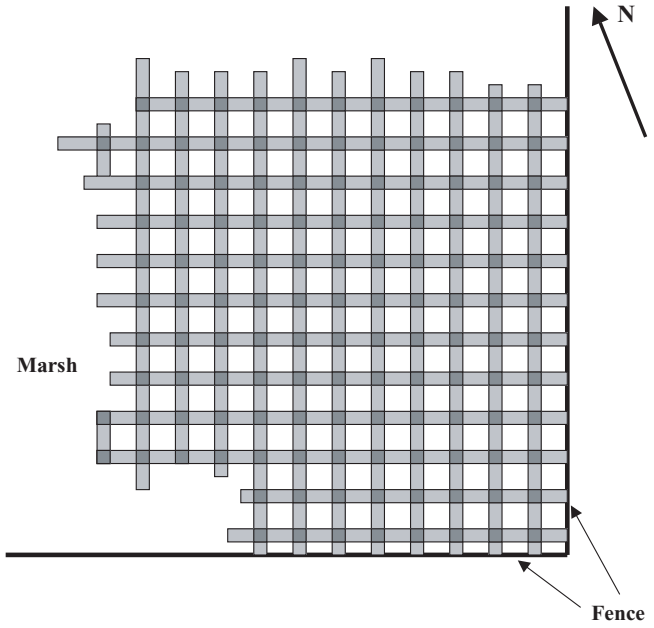

Figure 1. Design of the Fleecefaulds survey, which comprises two systematic grids of strips, one with strips running approximately N/S, and the other with strips running E/W. The strips are of width $2w$, and the transect lines run down the middle of each strip. Each grid is randomly superimposed on the survey region.

2.2 *Strip Transect Sampling*

In strip transect sampling, we assume that all plants within the strip are detected. Hence this is a form of plot sampling, in which the plots are long and narrow. Estimation equations are given in Web Appendix A. The advantage of the crossed design over a parallel strip design in this case is that the assumption that all plants within the strip are detected can be tested, by determining whether there are plants in the intersection squares that are detected in one of the surveys but not both; if there are many such plants, then more sophisticated methods are needed.

2.3 *Conventional Line Transect Sampling*

We now allow plants to be missed within the covered strips, but we still assume that all plants on the centerline are detected.

In conventional line transect sampling, we fit a detection function to data by specifying a likelihood for the perpendicular distances to detected plants, conditional on sample size. Considering E/W data only, we have

$$L_E(\underline{\theta}_E; \underline{y}) = \prod_{j=1}^{n_E} f_E(y_j) = \frac{\prod_{j=1}^{n_E} g_E(y_j)}{(wP_E)^{n_E}}, \quad (1)$$

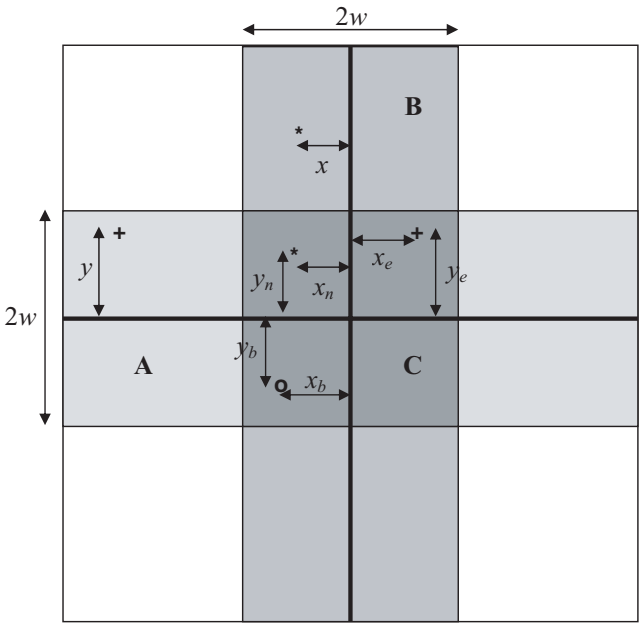

Figure 2. Schematic enlargement of a crossover of perpendicular transects. Detections made from the E/W line only are indicated by +, from the N/S line only by ∗, and from both lines by **o**. Within region **A**, distances y from the E/W line are recorded. Within region **B**, distances x from the N/S line are recorded. Within the intersection square **C**, both y and x are recorded; the subscript $_e$ indicates detected from the E/W line only, $_n$ indicates detected from the N/S line only, and $_b$ detected from both lines. The range for each of x and y is $[0, w]$; that is, we record absolute distance from each line, and we truncate observations at distance w.

where y_j is distance from the line of the jth detected plant, $j = 1, \ldots, n_E$; $f_E(y_j)$ is the probability density function $f_E(y)$ of distances y evaluated at $y = y_j$; $\underline{\theta}_E$ is the vector of parameters used to specify $f_E(y)$; $g_E(y_j)$ is the probability that a plant at distance y_j from the line is detected; and $P_E = \frac{1}{w}\int_0^w g_E(y)\,dy$ is the probability that a plant is detected, given that it is somewhere within the surveyed strip of half-width w.

Note that $f_E(y) = g_E(y)/(wP_E)$ for all y in $[0, w]$. For a given set of distances y_j, $j = 1, \ldots, n_E$, we maximize the above likelihood to obtain the maximum likelihood estimator $\hat{\underline{\theta}}_E$ of $\underline{\theta}_E$, and hence $\hat{P}_E = \frac{1}{w}\int_0^w \hat{g}_E(y)\,dy$. We can now estimate plant abundance as $\hat{N}_E = \frac{An_E}{a_E\hat{P}_E}$ where A is the size of the survey region and $a_E = 2wL_E$ is the covered area corresponding to the E/W lines, with L_E defined as the total length of E/W lines (Buckland et al., 2001). It is assumed that plants available for detection are uniformly distributed with respect to distance from the line, a requirement that is achieved on average by appropriate randomization of the survey design. We can obtain a second estimate $\hat{N}_N$ from the data from the N/S lines. In this case, the likelihood is

$$\mathsf{L}_N(\underline{\theta}_N; \underline{x}) = \frac{\prod_{i=1}^{n_N} g_N(x_i)}{(wP_N)^{n_N}},$$

where $P_N = \frac{1}{w}\int_0^w g_N(x)\,dx$, x_i is the distance of the ith detected plant from the N/S lines ($i = 1, \ldots, n_N$), and $g_N(x)$ is the probability that a plant at distance x from a N/S line is detected.

The optimal way to pool the data from the two sets of transects is to form a joint (conditional) likelihood. A possible strategy is to form a likelihood for data from the intersection squares based on the probability that a plant is detected from at least one of the lines passing through a square. However, this forces the assumption that whether a plant is detected from the E/W line is independent of whether it is detected from the N/S line. We prefer to avoid this assumption, as abundance estimation is sensitive to failures of it. We can replace this assumption by the weaker assumption that probability of detection of a plant from one line is independent of its distance from the other line, by taking as the joint likelihood

$$\mathsf{L}(\underline{\theta}_E, \underline{\theta}_N; \underline{y}, \underline{x}) = \mathsf{L}_E(\underline{\theta}_E; \underline{y}) \times \mathsf{L}_N(\underline{\theta}_N; \underline{x}). \tag{2}$$

We consider this issue in greater detail in the next section.

We maximize the likelihood in (2) to give $\hat{\underline{\theta}}_E$ and $\hat{\underline{\theta}}_N$, and hence $\hat{P}_N$ and $\hat{P}_E$. Software `Distance` (Thomas et al., 2005) may be used for this purpose, by conducting independent analyses of the E/W data and the N/S data. If field methods are identical for the N/S and the E/W lines, it is reasonable to assume that $g_N(y) \equiv g_E(y) = g(y)$ say, so that $\underline{\theta}_N \equiv \underline{\theta}_E = \underline{\theta}$ say. This analysis may be achieved in distance by entering the E/W data as one stratum and the N/S data as a second stratum, and fitting a pooled detection function across the two strata. Stratum-specific abundance estimates should then be averaged, not summed.

A Horvitz–Thompson-like estimator (Borchers, Buckland, and Zucchini, 2002, p. 143) now provides our estimate of abundance:

$$\hat{N}_1 = \frac{A}{a}\left(\frac{n_E}{\hat{P}_E} + \frac{n_N}{\hat{P}_N}\right), \tag{3}$$

with $a = a_E + a_N = 2w(L_E + L_N)$. Note that each intersection square has been surveyed twice, and its size is included in a twice.

The estimate $n_E/\hat{P}_E$ corresponds to estimated abundance in the E/W strips, and similarly $n_N/\hat{P}_N$ is estimated abundance in the N/S strips. Overall abundance is estimated by dividing their sum by the ratio of size of the covered region to the size of the whole survey region (Borchers et al., 2002, p. 56). If plants are markedly nonuniform through the survey region and the number of lines in the design is small, the following estimator might be preferred:

$$\hat{N}_2 = 0.5\left(\frac{n_E}{q_E\hat{P}_E} + \frac{n_N}{q_N\hat{P}_N}\right), \tag{4}$$

where q_E is the proportion of plants detected from the N/S lines that fall within the intersection squares (and hence within the E/W strips), and conversely for q_N. Thus q_E estimates the proportion of objects in the survey region that fall within the E/W strips, and q_N the proportion that fall within the N/S strips. If by chance there are proportionally more plants in the surveyed strips than in the gaps between them for a given realization of the design, estimator $\hat{N}_1$ will tend to overestimate abundance, whereas estimator $\hat{N}_2$ essentially

uses two ratio estimators to adjust for the unevenness in distribution.

The detection function may be modeled as a function of covariates in addition to distance from the line, using the conditional likelihood methods of Borchers et al. (1998) and Marques and Buckland (2003). If the covariates for detection j are denoted by the vector $\underline{z}_j$, then $\hat{P}_E(\underline{z}_j) = \frac{1}{w}\int_0^w \hat{g_E}(y, \underline{z}_j)\, dy$ and $\hat{N}_E = \sum_{j=1}^{n_E} \frac{1}{\hat{P}_E(\underline{z}_j)}$, and similarly for $\hat{N}_N$. In practice, a single model for the detection function is likely to prove adequate: $g_E(y, \underline{z}) \equiv g_N(y, \underline{z}) = g(y, \underline{z})$ say.

If $\hat{P}_E$, $\hat{P}_N$, n_E, and n_N are assumed to be independent, the delta method may be used to estimate an approximate variance of $\hat{N}_1$:

$$\hat{\text{var}}(\hat{N}_1) = \left(\frac{A}{a}\right)^2 \left[\hat{\text{var}}\left(\frac{n_E}{\hat{P}_E}\right) + \hat{\text{var}}\left(\frac{n_N}{\hat{P}_N}\right)\right], \qquad (5)$$

where $\hat{\text{var}}(\frac{n_E}{\hat{P}_E}) \approx (\frac{n_E}{\hat{P}_E})^2[\{cv(n_E)\}^2(1 - \frac{a_E\hat{P}_E}{A}) + \{cv(\hat{P}_E)\}^2]$ and similarly for $\hat{\text{var}}(\frac{n_N}{\hat{P}_N})$. The coefficients of variation $cv(n_E)$ and $cv(\hat{P}_E)$ may be estimated for example using the software `Distance` (Thomas et al., 2005). Note the use of the finite population correction, as outlined by Buckland et al. (2001, p. 87). In most applications, $a \ll A$ and the correction is negligible, but this may not be true in surveys of small populations of plants, where the covered area a may be a substantial proportion of the survey region A. Similarly, estimator $\hat{N}_2$ has approximate variance:

$$\hat{\text{var}}(\hat{N}_2) = 0.25\left[\hat{\text{var}}\left(\frac{n_E}{q_E\hat{P}_E}\right) + \hat{\text{var}}\left(\frac{n_N}{q_N\hat{P}_N}\right)\right], \qquad (6)$$

where $\hat{\text{var}}(\frac{n_E}{q_E\hat{P}_E}) \approx (\frac{n_E}{q_E\hat{P}_E})^2[\{cv(n_E)\}^2(1 - \frac{a_E\hat{P}_E}{A}) + \{cv(\hat{P}_E)\}^2 + \{cv(q_E)\}^2]$ and similarly for $\hat{\text{var}}(\frac{n_N}{q_N\hat{P}_N})$, where $cv(q_E)$ may be estimated from the between-line sample variance in q_E, weighted by the number of observations contributing to the estimate of q_E from each line. If the number of lines is small, the bootstrap segments based around the intersection squares, as defined below, may be used, so that the cv is estimated from the between-segment sample variance. This method may also be used to estimate $cv(n_E)$.

The nonparametric bootstrap provides a simple yet robust method of estimating variance, without having to assume independence between $\hat{P}_E$ and $\hat{P}_N$. Usually in line transect sampling, the lines would be resampled (Buckland et al., 2001, p. 83). However, there are two problems with that approach here: first, the data within each intersection square need to be kept intact for some of the methods of this article, for which it would be unclear how to proceed if one of the two lines forming an intersection appeared in a resample but the other did not and second, if the number of lines is small, as it sometimes is for surveys of plants, bootstrap resampling of lines yields poor estimates of variance. An advantage of the crossed design is that we can divide the covered region up into small segments that are systematically spaced through the survey region, with one intersection square per segment. For example if there are just five E/W lines and five N/S lines, this yields 25 units, which is sufficient for the nonparametric bootstrap to provide reliable estimates of variance. We show in Figure 3 two ways of superimposing a grid of squares over a crossed survey design so that bootstrap resamples can be generated by sampling the squares (and their associated data) with replacement.

Having generated a large number of resamples, the data from each resample are analyzed using the same procedures as for the real sample. The sample variance of the bootstrap estimates of a given parameter of interest (such as N) provides an estimated variance of the corresponding estimate. A simple but robust method of estimating confidence limits is to order the bootstrap estimates of the parameter, and extract the appropriate percentiles from the ordered list as approximate limits (Buckland, 1984). If bootstrap resamples are constrained so that each resample has the correct number of edge squares of each type (see Figure 3), then total effort will not vary across resamples. However, this strategy may give poor estimates of variance when the number of edge squares of each configuration is small (Web Appendix A).

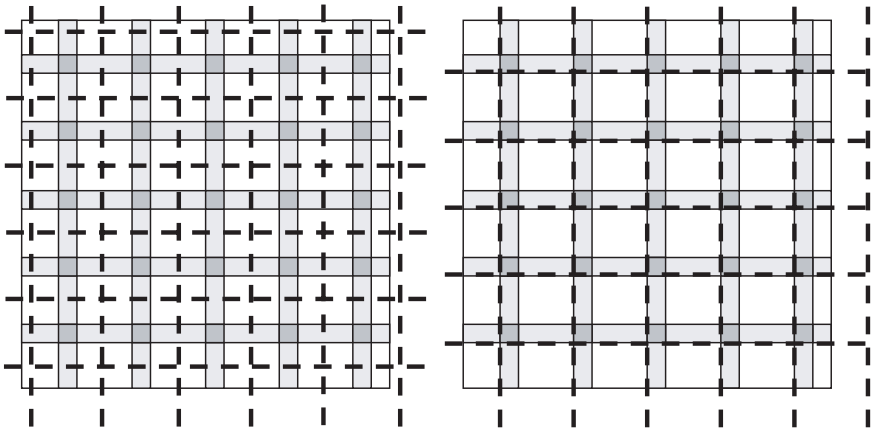

Figure 3. Two examples of a square grid (dashed lines) superimposed over a crossed design so that covered regions within grid squares are systematically spaced through the survey region. Nonparametric bootstrap resampling is implemented by resampling squares, together with the associated data, from the grid. In the left-hand scheme, the covered regions resampled by this procedure are crosses, while in the right-hand scheme, they are L's.

A difficulty of the above implementation of the bootstrap is that there is no finite population correction. If the covered area a is a substantial proportion of the survey region A (say 10% or more), then the bootstrap can be used to estimate $cv(n_E)$, $cv(n_N)$, $cv(\hat{P}_E)$, and $cv(\hat{P}_N)$, and these estimates are then substituted into equation (5), if estimator $\hat{N}_1$ is used. For estimator $\hat{N}_2$, we also need to obtain bootstrap estimates of $cv(q_E)$ and $cv(q_N)$, so that we can use equation (6). However, this strategy has the disadvantage that the estimates n_E, n_N, $\hat{P}_E$, $\hat{P}_N$ and, where relevant, q_E and q_N are all assumed to be independent. If for example we wish to allow in equation (5) for covariance between n_E and n_N, and between $\hat{P}_E$ and $\hat{P}_N$, these covariances may be estimated by the sample covariances of the bootstrap estimates, and the covariance terms can be added to (5) to give

$$\hat{\text{var}}(\hat{N}_1) = \left(\frac{A}{a}\right)^2\left[\hat{\text{var}}\left(\frac{n_E}{\hat{P}_E}\right) + \hat{\text{var}}\left(\frac{n_N}{\hat{P}_N}\right) + 2\hat{\text{cov}}\left(\frac{n_E}{\hat{P}_E}, \frac{n_N}{\hat{P}_N}\right)\right] \tag{7}$$

where $\hat{\text{var}}(\frac{n_E}{\hat{P}_E})$ and $\hat{\text{var}}(\frac{n_N}{\hat{P}_N})$ are as before, and

$$\hat{\text{cov}}\left(\frac{n_E}{\hat{P}_E}, \frac{n_N}{\hat{P}_N}\right) \approx \left(\frac{n_E}{\hat{P}_E}\right)\left(\frac{n_N}{\hat{P}_N}\right) \times \left[\frac{\hat{\text{cov}}(n_E, n_N)}{n_E n_N}\sqrt{\left(1 - \frac{a_E\hat{P}_E}{A}\right)\left(1 - \frac{a_N\hat{P}_N}{A}\right)} + \frac{\hat{\text{cov}}(\hat{P}_E, \hat{P}_N)}{\hat{P}_E\hat{P}_N}\right].$$

The above implementation of the bootstrap assumes that the resampling units are randomly distributed, when in reality they are systematically distributed. Fewster, Buckland et al. (2005) consider possible solutions to reduce any bias in the resulting variance estimates.

2.4 *Line Transect Sampling with Nonuniform Distribution of Objects*

Consider first the E/W lines. Define $\pi_E(y)$ to be the pdf of distances from the line of all objects within the covered strips, whether or not they are detected, with $0 \le y \le w$, and suppose the parameters of $\pi_E(y)$ are $\underline{\phi}_E$. Note that $\pi_E(y)$ is the distribution of distances from the line after pooling data across all the E/W lines. Similarly we define $\pi_N(x)$ parameterized by $\underline{\phi}_N$ for distances x of plants from the nearest N/S line.

If we were to consider data from the E/W lines only, then the likelihood of the observed y, conditional on sample size n_E, is:

$$\mathsf{L}_E(\underline{\theta}_E, \underline{\phi}_E; \underline{y}) = \prod_{j=1}^{n_E} f_E(y_j) = \frac{\prod_{j=1}^{n_E} g_E(y_j)\pi_E(y_j)}{P_E^{n_E}}, \tag{8}$$

where $P_E = \int_0^w g_E(y)\pi_E(y)\,dy$ (Borchers and Burnham, 2004). If objects are uniformly distributed with respect to distance from the line, then $\pi_E(y) = 1/w$ and (8) simplifies to (1). When $\pi_E(y)$ and $g_E(y)$ must both be estimated, the above likelihood is not sufficient, as the two functions always appear as a product. The intersection squares provide us with the data we need to estimate $\pi_E(y)$; if we consider plants detected from the N/S lines, their distances from the E/W lines are a representative sample from $\pi_E(y)$, provided probability of detection from the N/S line is independent of distance *along* the N/S line and hence independent of distance *from* the E/W line.

The likelihood we need will now comprise six components: one for detections in regions of type A (Figure 2), another for those in regions of type B, and four for those from intersection squares (type C). Consider the first two components. Suppose we have perpendicular distances y_j, $j = 1, \ldots, n_A$ for detections in regions of type A, and distances x_i, $i = 1, \ldots, n_B$, for detections in regions of type B. Applying (8) to these regions, we have

$$\mathsf{L}_A(\underline{\theta}_E; \underline{y}) = \frac{\prod_{j=1}^{n_A} g_E(y_j)\pi_E(y_j)}{P_E^{n_A}}$$

$$\mathsf{L}_B(\underline{\theta}_N; \underline{x}) = \frac{\prod_{i=1}^{n_B} g_N(x_i)\pi_N(x_i)}{P_N^{n_B}},$$

where $P_E = \int_0^w g_E(y)\pi_E(y)\,dy$ and $P_N = \int_0^w g_N(x)\pi_N(x)\,dx$.

Now consider the n_C detections in the intersection squares, together with the distances (x_j, y_j), $j = 1, \ldots, n_C$. We need to consider the three types of detection: n_e plants detected from an E/W line only, and their distances $(x_{e,j}, y_{e,j})$ from the nearest N/S line and E/W line respectively, $j = 1, \ldots, n_e$; n_n plants detected from a N/S line only, and corresponding distances $(x_{n,j}, y_{n,j})$, $j = 1, \ldots, n_n$; and n_b detected from both an E/W and a N/S line, with distances $(x_{b,j}, y_{b,j})$, $j = 1, \ldots, n_b$. Thus $n_C = n_e + n_n + n_b$.

Formulation of an appropriate likelihood for observations in intersection squares requires some care. In particular, within an intersection square, we need to avoid the assumption that detection from the E/W line is independent of being recorded from the N/S line. A large, clearly visible plant is likely to be detected from both lines, so that an analysis that assumes independence without modeling such heterogeneity will yield biased estimates of abundance. Our notation implicitly assumes that $g_E(y)$ is independent of x, and $g_N(x)$ is independent of y, which seems very reasonable. This assumption ensures that $y_{n,j}$, $j = 1, \ldots, n_n$, taken with $y_{b,j}$, $j = 1, \ldots, n_b$, are jointly a random sample of size $n_n + n_b$ from $\pi_E(y)$. Similarly, $x_{e,j}$, $j = 1, \ldots, n_e$ and $x_{b,j}$, $j = 1, \ldots, n_b$ are together a random sample of size $n_e + n_b$ from $\pi_N(x)$. These therefore contribute $\mathsf{L}_C(\underline{\phi}_E; \underline{y}_n, \underline{y}_b) = \prod_{j=1}^{n_n}\pi_E(y_{n,j})\prod_{j=1}^{n_b}\pi_E(y_{b,j})$ and $\mathsf{L}_C(\underline{\phi}_N; \underline{x}_e, \underline{x}_b) = \prod_{j=1}^{n_e}\pi_N(x_{e,j})\prod_{j=1}^{n_b}\pi_N(x_{b,j})$ to the likelihood.

We also know that $y_{e,j}$, $j = 1, \ldots, n_e$, and $y_{b,j}$, $j = 1, \ldots, n_b$, are jointly a random sample of size $n_e + n_b$ from $g_E(y)\pi_E(y)/P_E$. Similarly, $x_{n,j}$, $j = 1, \ldots, n_n$, and $x_{b,j}$, $j = 1, \ldots, n_b$, are jointly a random sample of size $n_n + n_b$ from $g_N(x)\pi_N(x)/P_N$. Thus these contribute the following components to the likelihood.

$$\mathsf{L}_C(\underline{\theta}_E, \underline{\phi}_E; \underline{y}_e, \underline{y}_b) = \frac{\prod_{j=1}^{n_e} g_E(y_{e,j})\pi_E(y_{e,j})\prod_{j=1}^{n_b} g_E(y_{b,j})\pi_E(y_{b,j})}{P_E^{n_e+n_b}},$$

$$\mathsf{L}_C(\underline{\theta}_N, \underline{\phi}_N; \underline{x}_n, \underline{x}_b) = \frac{\prod_{j=1}^{n_n} g_N(x_{n,j})\pi_N(x_{n,j}) \prod_{j=1}^{n_b} g_N(x_{b,j})\pi_N(x_{b,j})}{P_N^{n_n+n_b}}.$$

The overall conditional likelihood for detections in intersection squares (conditional on the observed sample sizes n_e, n_n, and n_b) is then the product of these four components.

Note that the distances for duplicate detections have each been used twice, but each of these distances is observed twice: once from an E/W line, and once from a N/S line. Consider a plant at $[x_{b,j}, y_{b,j}]$, detected from both lines. Then $x_{b,j}$ as observed from the E/W line is a random draw from $\pi_N(x)$, whereas $x_{b,j}$ as observed from the N/S line is a random draw from $g_N(x)\pi_N(x)/P_N$. The above product of likelihood components gives the appropriate likelihood provided these draws are independent of each other, and of the corresponding draws of $y_{b,j}$. We know $x_{b,j}$ is observed from the E/W line with probability $g_E(y_{b,j})$, and from the N/S line with probability $g_N(x_{b,j})$. The first probability is a function of y alone, and the second of x alone. Thus if we assume that the joint density of plant locations (whether detected or not) $\pi(x, y) = \pi_N(x)\pi_E(y)$, then the draws are independent. This assumption also ensures that $y_{b,j}$ is drawn independently of $x_{b,j}$.

As before, in most surveys it would be reasonable to assume that $g_N(y) \equiv g_E(y) = g(y)$, and given that the number of intersection squares is likely to be quite large even when the number of transects in each direction is small, and they are systematically spaced throughout the region, independence of the x and y locations ($\pi(x, y) = \pi_E(y)\pi_N(x)$ for all x and y in $[0, w]$) is likely to be quite a mild assumption. Under these simplifying assumptions, the combined likelihood for all three region types (A, B, and C) is:

$$\begin{aligned}\mathsf{L}(\underline{\theta}, \underline{\phi}_N, \underline{\phi}_E; \underline{x}, \underline{y}) &= \frac{1}{P_E^{n_A+n_e+n_b} P_N^{n_B+n_n+n_b}} \prod_{j=1}^{n_A} g(y_j)\pi_E(y_j) \prod_{j=1}^{n_B} g(x_j)\pi_N(x_j) \\ &\times \prod_{j=1}^{n_n} \pi_E(y_{n,j}) \prod_{j=1}^{n_b} \pi_E(y_{b,j}) \prod_{j=1}^{n_e} \pi_N(x_{e,j}) \prod_{j=1}^{n_b} \pi_N(x_{b,j}) \\ &\times \prod_{j=1}^{n_e} g(y_{e,j})\pi_E(y_{e,j}) \prod_{j=1}^{n_b} g(y_{b,j})\pi_E(y_{b,j}) \\ &\times \prod_{j=1}^{n_n} g(x_{n,j})\pi_N(x_{n,j}) \prod_{j=1}^{n_b} g(x_{b,j})\pi_N(x_{b,j}). \qquad (9)\end{aligned}$$

(Although we have used the same index j for each expression, the sample to which it refers is indicated by the upper limit of the range of j.) When $\pi_E(y)$ and $\pi_N(x)$ are both uniform on $[0, w]$, (9) is equivalent to (2) with the added assumption that $g_N(y) \equiv g_E(y) = g(y)$.

We maximize the likelihood in (9) to give $\hat{\underline{\theta}}$, $\hat{\underline{\phi}}_N$ and $\hat{\underline{\phi}}_E$, and hence $\hat{P}_N$ and $\hat{P}_E$. A Horvitz–Thompson-like estimator (Borchers et al., 2002, p. 143) provides our estimate of abundance, which we can separate out into estimates of abundance in regions of type A, B, and C (Figure 2):

$$\hat{N}_A = \frac{n_A}{\hat{P}_E} \quad \hat{N}_B = \frac{n_B}{\hat{P}_N} \quad \hat{N}_{C,E} = \frac{n_e + n_b}{\hat{P}_E} \quad \hat{N}_{C,N} = \frac{n_n + n_b}{\hat{P}_N},$$

from which overall abundance is estimated as

$$\hat{N}_3 = \frac{A}{a}\left(\hat{N}_A + \hat{N}_B + \hat{N}_{C,E} + \hat{N}_{C,N}\right), \qquad (10)$$

with $a = 2w(L_N + L_E)$.

The estimates $\hat{N}_A$, $\hat{N}_B$, $\hat{N}_{C,E}$, and $\hat{N}_{C,N}$ correspond to estimates of abundance in sections of the covered region. Also, $\hat{N}_A + \hat{N}_{C,E}$ is an estimate of the total number of plants in the E/W strips, based on distances of detected plants from the E/W lines, and $\hat{N}_B + \hat{N}_{C,N}$ is the corresponding estimate for the N/S strips. In (10), we divide their sum by a/A. If plants are markedly nonuniform through the survey region and the number of lines in the design is small, we could again use q_E and q_N in place of this ratio:

$$\hat{N}_4 = 0.5\left(\frac{\hat{N}_A + \hat{N}_{C,E}}{q_E} + \frac{\hat{N}_B + \hat{N}_{C,N}}{q_N}\right). \qquad (11)$$

The bootstrap may be implemented as before, to quantify the precision of these estimates. Note that, because $\hat{N}_{C,E}$ and $\hat{N}_{C,N}$ both estimate the same quantity, we could calculate the difference $\hat{N}_{C,E} - \hat{N}_{C,N}$ in each bootstrap resample, and hence obtain a bootstrap confidence interval for the true difference. If this interval does not include zero, this may indicate that we have an inappropriate model for our data.

2.5 *Line Transect Sampling with Uncertain Detection on the Trackline*

The data from the intersection squares can be regarded as two-sample mark–recapture data; the observer marks the plants detected while transiting the first line through a square, and recaptures occur during the second transit. So far, we have ignored this information, because its use comes at the cost of strong independence assumptions about the probability of detection in each sample, and estimation is not robust to failure of these assumptions. When detection on the trackline is certain, this fact need only be supplemented by an estimate of the shape of the detection function, to yield an estimate of the function itself; the pooling robustness property (Buckland et al., 2004, pp. 389–392) shows that this is achievable when variation in detection probability due to factors other than distance from the line are ignored. When detection on the trackline is uncertain, we must rely on the mark–recapture data to help estimate the detection function, and hence we must consider the effects of heterogeneity in the capture probabilities. This heterogeneity can be modeled over all distances (Laake and Borchers, 2004), or we can assume "point independence" (Laake, 1999; Laake and Borchers, 2004), or both (Borchers et al., 2006).

We first consider the case without additional covariates for modeling heterogeneity. We follow the convention of Laake and Borchers (2004) that $g(y)$ represents the shape of the detection function, but scaled so that $g(0) = 1$, whereas $p(y)$ represents the detection function itself. Thus if detection on the line is certain, the two functions are equivalent.

For regions A and B of Figure 2, we have the same likelihoods as before. Replacing g by p:

$$\mathsf{L}_A(\underline{\theta}_E;\underline{y}) = \frac{\prod_{j=1}^{n_A} p_E(y_j)\pi_E(y_j)}{P_E^{n_A}}$$

$$\mathsf{L}_B(\underline{\theta}_N;\underline{x}) = \frac{\prod_{i=1}^{n_B} p_N(x_i)\pi_N(x_i)}{P_N^{n_B}},$$

where $P_E = \int_0^w p_E(y)\pi_E(y)\,dy$ and $P_N = \int_0^w p_N(x)\pi_N(x)\,dx$.

(We could if we wished divide top and bottom of the first likelihood by $[p(0)]^{n_A}$, in which case the likelihood is again in terms of g rather than p; the two forms are equivalent, which is why we can use this likelihood to infer only the shape of $p_E(y)$.) For region C, following the development of Laake and Borchers (2004) and Borchers et al. (2006), we have:

$$\mathsf{L}_C(\underline{\theta}_E,\underline{\phi}_E;\underline{y}_e,\underline{y}_b) = \frac{\prod_{j=1}^{n_e} p_E(y_{e,j})\pi_E(y_{e,j})\prod_{j=1}^{n_b} p_E(y_{b,j})\pi_E(y_{b,j})}{P_E^{n_e+n_b}},$$

$$\mathsf{L}_C(\underline{\theta}_N,\underline{\phi}_N;\underline{x}_n,\underline{x}_b) = \frac{\prod_{j=1}^{n_n} p_N(x_{n,j})\pi_N(x_{n,j})\prod_{j=1}^{n_b} p_N(x_{b,j})\pi_N(x_{b,j})}{P_N^{n_n+n_b}}.$$

In addition, we have from the previous section

$$\mathsf{L}_C(\underline{\phi}_E;\underline{y}_n,\underline{y}_b) = \prod_{j=1}^{n_n}\pi_E(y_{n,j})\prod_{j=1}^{n_b}\pi_E(y_{b,j})$$

and

$$\mathsf{L}_C(\underline{\phi}_N;\underline{x}_e,\underline{x}_b) = \prod_{j=1}^{n_e}\pi_N(x_{e,j})\prod_{j=1}^{n_b}\pi_N(x_{b,j}).$$

We now need the mark–recapture component of the likelihood corresponding to the intersection squares. Let $\underline{\omega}_j$ be the capture history of the jth detected plant in region C. Then

$$\mathsf{L}_C(\underline{\theta}_N,\underline{\theta}_E;\boldsymbol{\omega}) = \prod_{j=1}^{n_C}\frac{\Pr\{\underline{\omega}_j \mid x_j, y_j\}}{p_N(x_j)+p_E(y_j)-p_N(x_j)p_{E|N}(y_j)},$$

where $p_{E|N}(y_j)$ is the probability that a plant at distance y_j from an E/W line is detected, given that it was detected from a N/S line, and $\boldsymbol{\omega}$ is the full set of observed capture histories. The conditional likelihood is thus

$$\begin{aligned}\mathsf{L}(\underline{\theta}_N,\underline{\theta}_E,\underline{\phi}_N,\underline{\phi}_E;\underline{x},\underline{y},\boldsymbol{\omega}) &= \mathsf{L}_A(\underline{\theta}_E;\underline{y})\times\mathsf{L}_B(\underline{\theta}_N;\underline{x})\times\mathsf{L}_C(\underline{\theta}_E,\underline{\phi}_E;\underline{y}_e,\underline{y}_b)\\ &\quad\times\mathsf{L}_C(\underline{\theta}_N,\underline{\phi}_N;\underline{x}_n,\underline{x}_b)\times\mathsf{L}_C(\underline{\phi}_E;\underline{y}_n,\underline{y}_b)\\ &\quad\times\mathsf{L}_C(\underline{\phi}_N;\underline{x}_e,\underline{x}_b)\times\mathsf{L}_C(\underline{\theta}_N,\underline{\theta}_E;\boldsymbol{\omega}).\end{aligned}$$

We have

$$\Pr\{\underline{\omega}_j = (1,0)\mid x_j,y_j\} = p_E(y_j)[1-p_{N|E}(x_j)],$$

$$\Pr\{\underline{\omega}_j = (0,1)\mid x_j,y_j\} = p_N(x_j)[1-p_{E|N}(y_j)],$$

$$\Pr\{\underline{\omega}_j = (1,1)\mid x_j,y_j\} = p_E(y_j)p_{N|E}(x_j) = p_N(x_j)p_{E|N}(y_j).$$

If we assume independence, then $p_{N|E}(x_j) = p_N(x_j)$ and $p_{E|N}(y_j) = p_E(y_j)$. In this case, bias in the abundance estimate may be reduced by modeling the detection functions (and hence the capture history probability distribution) as functions of additional covariates (Laake and Borchers, 2004). In the presence of additional covariates $\underline{z}_j$, but with the simplifying assumptions of independence, with $\pi_N(x_j)$ and $\pi_E(y_j)$ both uniform on $[0, w]$, and $p_N(y_j,z_j) \equiv p_E(y_j,z_j) = p(y_j,z_j)$ say, the likelihood reduces to

$$\mathsf{L}(\underline{\theta};\underline{x},\underline{y},\boldsymbol{\omega}) = \prod_{j=1}^{n_E}\frac{p(y_j,z_j)}{P_E(z_j)}\times\prod_{j=1}^{n_N}\frac{p(x_j,z_j)}{P_N(z_j)} \times\prod_{j=1}^{n_C}\frac{\Pr\{\underline{\omega}_j\mid x_j,y_j,z_j)}{p(x_j,z_j)+p(y_j,z_j)-p(x_j,z_j)p(y_j,z_j)},$$

where

$$\Pr\{\underline{\omega}_j = (1,0)\mid x_j,y_j,z_j\} = p(y_j,z_j)[1-p(x_j,z_j)],$$

$$\Pr\{\underline{\omega}_j = (0,1)\mid x_j,y_j,z_j\} = p(x_j,z_j)[1-p(y_j,z_j)],$$

$$\Pr\{\underline{\omega}_j = (1,1)\mid x_j,y_j,z_j\} = p(y_j,z_j)p(x_j,z_j).$$

In most surveys, it will be reasonable to assume that $\pi_N(x_j)$ and $\pi_E(y_j)$ are both uniform on $[0, w]$ (and the crossed design provides data to test this assumption).

Adapting the point independence method of Laake and Borchers (2004) to the crossed design, we assume independence of detection between the E/W and N/S lines only at distance zero. In this case, the detection function for the E/W lines is modeled as $p_{E|N}(0)g_E(y)$. Here $p_{E|N}(0)$ is the conditional detection function $p_{E|N}(y)$, given detection from the N/S lines, evaluated at $y = 0$, which is equal to the unconditional probability at distance zero: $p_{E|N}(0) = p_E(0)$ by assumption. Detection probabilities for the N/S lines are modeled similarly. The conditional detection functions $p_{E|N}(y)$ and $p_{N|E}(x)$ are estimated from the likelihood component $\mathsf{L}_C(\underline{\theta}_N,\underline{\theta}_E;\boldsymbol{\omega})$ alone. This is equivalent to using binary regression, treating detections in areas of type C from the N/S lines as trials, and detection/nondetection of these from the E/W lines as the binary response. The detection probability for the N/S lines is estimated similarly, using detections in areas of type C from the E/W lines as trials, and detection/nondetection of these from the N/S lines as the binary response. As in the previous section, overall abundance may be estimated using either equation (10) or equation (11).

2.6 *A Full Likelihood Approach*

We could add a further component to our likelihoods, corresponding to inference about population size N, given the data in our survey strips (Web Appendix A).

3. Fleecefaulds Meadow

Fleecefaulds Meadow is a Scottish Wildlife Trust (SWT) reserve near Ceres in Fife, Scotland. An SSSI (Site of Special Scientific Interest) since 1983, the field contains scrub and herb-rich grassland, approximately 1 ha of which was used for the survey (Figure 1). Data were collected in June 2005 on several species, and the cowslip was selected for testing the methods.

Parallel line transects were systematically spaced at 9 m intervals with a random start, with 12 running approximately N/S, and another 12 E/W. A strip half-width of $w = 1.5$ m was used. The 24 transects gave 129 intersection squares, that is, areas of 9 m^2 where plants were potentially detectable from both transects (Figure 1).

Each transect was surveyed by one of two observers, who walked along the E/W transects first, concentrating their search effort on and close to the transect line. Detected plants were only recorded once the observer had carefully searched for other nearby plants. Distances of detected plants from the line were then measured with a 1.5 m rule; any plants further than 1.5 m from the line were not recorded. The transect line had marks every meter, allowing distances along the line to be easily measured. A 30 cm rule was used for smaller scale measurements on the plant itself. All detected plants from the E/W transects were marked by writing a unique number on the underside of a leaf, to ensure that if the plant was seen from one of the N/S lines, it could be identified. For each detected plant, in addition to distances along and from the line, the following variables were recorded: its size, defined as the length of the plant multiplied by its width (cm^2); the number of individual flower heads on the plant; and a visibility code, taking values from one to four, one corresponding to a plant standing above the surrounding vegetation, through to four for a plant surrounded by much taller vegetation.

Data collected from the E/W lines indicated that cowslips could be assumed to be uniformly distributed with respect to distance from the N/S lines (Kolmogorov–Smirnov, Cramér-von Mises and χ^2 tests, $p > 0.2$ in each case), and similarly for the converse (Kolmogorov–Smirnov, Cramér-von Mises and χ^2 tests, $p > 0.1$ in each case). Despite the very clustered distribution of cowslips (resulting in wide confidence intervals in Table 1), 12 lines in each direction were sufficient to ensure that the assumption that plants were uniformly distributed with respect to distance from the line, once the distance data were pooled across parallel strips, was reasonable. A half-normal model for the detection function was found to fit well for both sets of lines, and AIC was marginally smaller when the model was fitted separately to the two data sets, rather than to the pooled data. Resulting estimates are shown in Table 1. Estimators $\hat{N}_1$ and $\hat{N}_2$ gave similar precision (as estimated from equations (5) and (6), respectively), but estimated abundance was rather lower using estimator $\hat{N}_2$.

The effect of covariates on detectability was explored. In the case of analyses with $p(0) = 1$, AIC selected a model with an observer effect (a factor covariate with two levels) for E/W lines, and a model with effects of observer, plant size and visibility code for the N/S lines. The number of flower heads was not selected in either model. Resulting abundance estimates are shown in Table 1.

We allowed for $p(0) \leq 1$ by assuming logistic forms for $p_{E|N}(y)$ and $p_{N|E}(x)$, while initially retaining the assumption of uniform distribution of plants with respect to lines. Selecting variables on the basis of AIC led to a model for $p_{E|N}(y)$ and $p_{N|E}(x)$ which included distances but not line orientation (E/W or N/S) as explanatory variables. This model gave an estimated $p(0)$ of 0.694, with 95% confidence interval (0.452, 0.839). This implies that about 30% of plants on the lines are missed; if we assume $p(0) = 1$, abundance estimates are around 30% lower than if we relax this assumption. Using equation (11), abundance is estimated to be 1258 plants, while using equation (10), it is estimated to be 1507 plants (Table 1).

Table 1
Estimates of density (plants/ha) of cowslips at Fleecefaulds Meadow (95% confidence limits in brackets)

	Transects	Abundance estimate	95% C.I.
Conventional distance sampling	N/S lines	980	(466, 2059)
	E/W lines	1113	(670, 1849)
	Both, $\hat{N}_1$	1048	(689, 1593)
	Both, $\hat{N}_2$	873	(568, 1342)
Conventional distance sampling with covariates	N/S lines	978	(468, 2045)
	E/W lines	1124	(680, 1857)
	Both, $\hat{N}_1$	1052	(696, 1591)
	Both, $\hat{N}_2$	877	(574, 1341)
Allowing for $p(0) < 1$	Both, $\hat{N}_3$	1507	(1105, 2256)
	Both, $\hat{N}_4$	1258	(929, 1920)
Allowing for nonuniform $\pi(y)$ and $p(0) < 1$	Both, $\hat{N}_3$	1758	(1219, 2710)
	Both, $\hat{N}_4$	1467	(1032, 2278)

In the case of the analyses with $p(0) \leq 1$ and estimated $\pi_N(\cdot)$ and $\pi_E(\cdot)$, AIC indicated a detection function model with effects for E/W vs. N/S and distance, together with a single model for $\pi_N(\cdot)$ and $\pi_E(\cdot)$ (which we refer to as $\pi(\cdot)$). This was modeled using a left- and right-truncated normal distribution. The estimate of $\pi(\cdot)$ is shown in Figure 4a. While this distribution is not significantly different from uniform at the 5% level, a nonuniform model for $\pi(\cdot)$ is preferable on the basis of AIC (953.3 vs. 955.7). The fit from the $p(0) \leq 1$ analyses is shown in Figure 4b. In this case, abundance is estimated to be 1467 plants using equation (11), while using equation (10), it is estimated to be 1758 plants (Table 1). These estimates are slightly higher than those obtained when assuming uniform $\pi_N(\cdot)$ and $\pi_E(\cdot)$ because a higher proportion of plants are estimated to be at greater distances, where detection probability is lower (see Figure 4).

In this example, truth is unknown. To further assess the methods, a population of known size was established, and analyses of a survey conducted on the population are given in web Appendix A and Web Figure 1.

4. Discussion

In many circumstances, quadrat (or plot) sampling is likely to prove adequate for plant surveys. We believe however that the more complex methods of this article are potentially useful in the following circumstances.

First, if individual plants are easily overlooked, quadrat sampling may require painstaking searching on hands and knees, severely limiting the amount of ground that can be covered. The methods of this article in which detection on the transect line is allowed to be uncertain may prove a more cost-effective option. In the case of cowslips above, we estimate that approximately 30% of the cowslips at distance zero

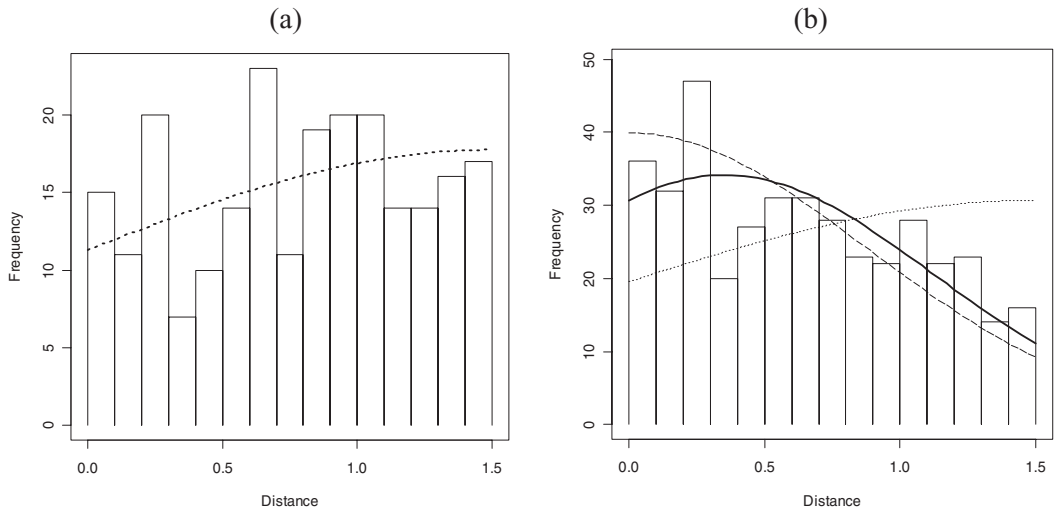

Figure 4. (a) Histogram of the combined distances from the N/S lines of plants detected from the E/W lines, and distances from the E/W lines of plants detected from the N/S lines for cowslip data. The dotted line is the estimate of $\pi(\cdot)$ (assumed to be the same for both platforms), scaled to have the same area as the histogram. (b) Plot of scaled estimated detection probability (dashed line), estimated $\pi(\cdot)$ (dotted line), and estimated probability density function for observed distances (solid line) for cowslip data. The histogram shows number of detections by distance from the line from which they were detected. All functions have been scaled to have the same area as the histogram.

were missed in the thick vegetation present in June, despite very careful searching along the transects by the observers.

Second, if plant distribution in the survey region is very clumped, or if plants are sparsely distributed, quadrat sampling may give poor precision. For similar resources, it is possible to cover a substantially higher proportion of the survey region with line transect sampling than with quadrat sampling, because it is not necessary to detect all plants within the covered strips. This provides better spatial coverage of survey effort, and hence higher precision. Potential problems due to insufficient lines coupled with a markedly nonuniform distribution of plants are avoided using our methods. The solution to the problem of nonuniformity advocated by Melville and Welsh (2001), to locate all plants within a subset of strips so that the detection function may be estimated without assuming uniformity (because we know for each plant whether or not it was detected from the transect line), is unsatisfactory for two reasons: substantial resources may be required to ensure complete enumeration within the subset; and when the number of strips in the subset is very small (either one or two strips in the cases presented by Melville and Welsh), the resulting estimated detection function may be unrepresentative of the detection function for the remaining strips, due to variation in vegetation height and color, light, or other factors. Our design avoids both problems; complete enumeration is not required anywhere, and the intersection squares are sufficiently numerous, and are systematically spread through the survey region, so that representativeness is assured.

If performance of the method is in doubt, a strategy suggested by the associate editor is to select a random sample of intersection squares, and attempt complete enumeration of these. Relative to complete enumeration of whole strips, this has the advantage that intersection squares are small, so that a reasonable number of squares can be surveyed by this means, and calibration will then be more robust to variation in detectability across the survey region.

Note that inference related to the counts of plants in strips is design-based, and the sampling frame is the set of strips of half-width w (in each direction) that fully span the survey region. The finite population correction is then taken as one minus the proportion of the survey region that is effectively covered; that proportion is the area of sampled strips, with half-width taken as the effective strip half-width $\mu = \int_0^w g(y)\,dy$, divided by A, the size of the survey region. If the grid of strips is fixed, then a uniform distribution of objects with respect to distance from the line within $(0, w)$ is not assured. Randomization of the grid location ensures that this assumption is met, in the sense that the average distribution of objects' distances from the line over the infinity of possible randomizations is uniform (Fewster, Laake, and Buckland, 2005; Fewster, Buckland et al., 2005). However, for a single realization of the design, especially if the number of strips sampled is small or if the objects' spatial pattern is markedly aggregated, it may prove beneficial to model any nonuniformity observed for that realization. In most studies, we would expect that the added variance from modeling nonuniformity would outweigh the reduction in bias, resulting in an increased mean square error.

The proposed bootstrap method was assessed for the case of conventional distance sampling (Section 2.3) by simulation (Web Appendix A). The simulations were based on the Fleecefaulds study, for which the finite population correction was sufficiently large to be needed. With this correction, the method was found to work well for uniformly distributed populations (as would be expected), for clustered populations and for populations exhibiting a linear trend in density through the region (Web Table 1; see Web Figure 2 for a

single realization of each type of population). When bootstrap resamples were constrained so that each resample has the correct number of edge squares of each type, the performance of the bootstrap was relatively poor, which might be expected given that for example each corner unit was of a unique type in these simulations, and so each appeared exactly once in each resample. Estimator $\hat{N}_2$ had higher variance than $\hat{N}_1$ in all simulations except when clustering was extreme, and in that case, the bootstrap estimate of the variance showed upward bias, so that the improved precision was not reflected in the estimated variance (Web Table 1). Hence we recommend use of estimator $\hat{N}_1$.

5. Supplementary Materials

Web Appendix A, Web Table 1 and Web Figures 1 and 2 referenced in Sections 2.2, 2.3, 2.6, 3, and 4 are available under the Paper Information link at the *Biometrics* website `http://www.tibs.org/biometrics`.

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