Improving distance sampling: accounting for covariates and non-independency between sampled sites

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Summary

1. There is currently much interest in replacing the design-based component of conventional distance sampling methods by a modelling approach where animal densities are related to environmental covariates. These models allow identification of relationships between density and covariates. One of the uses of such models is to assess the effects of some intervention on numbers for species of conservation interest in designed distance sampling experiments.

2. In this context, we use an integrated likelihood approach for modelling sample counts, adopting a Poisson model and allowing imperfect detectability on the sample plots. We use the method of Royle, Dawson & Bates (2004, *Ecology*, **85**, 1591), extended to model heterogeneity in detection probabilities using either multiple covariate distance sampling methods or stratification. Moreover, we include a random effect for site in the plot abundance model to accommodate correlation in repeat counts at a single site.

3. These developments were motivated by a large-scale experimental study to assess the effects of establishing conservation buffers along field margins on indigo buntings in several US states. We analyse the data using an integrated likelihood and include model selection for both the Poisson rate of counts and detection probabilities. We assess model performance by comparing our results with those using a two-stage approach (Buckland *et al.* 2009, *Journal of Agricultural, Biological, and Environmental Statistics*, **14**, 432) which we extended by including a random effect for site in the plot abundance model.

4. The two methods led to the same selected models and gave similar results for parameters, which revealed significant beneficial effects of buffers on indigo bunting densities. Densities on buffered fields were on average 35% higher than on unbuffered fields. Using a detection function stratified by state captured some of the heterogeneity in detection probabilities between the nine states included in the analyses.

5. *Synthesis and applications.* We develop and compare two methods for analysing data from large-scale distance sampling experiments with imbalanced repeat measures. By including a random site effect in the plot abundance model, we relax the assumption of independent sample counts which is generally made for distance sampling methods, and we allow inference to be drawn for the wider region that the sites represent.

Key-words: conservation buffers, designed experiments, habitat model, heterogeneity in detection probabilities, model selection, point transect sampling, Poisson rate adjusted for imperfect detection

Introduction

Distance sampling is a commonly used tool for assessing wildlife populations (e.g. Buckland, Goudie & Borchers 2000; Cañadas & Hammond 2006; Marques *et al.* 2007).

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Traditionally, inference on abundance relies on a model-based component (the estimation of the detection function to account for imperfect detection) and a design-based component (estimation of the encounter rate in the study area based on encounter rate estimates along the transect lines or points, Buckland *et al.* 2001). The design-based component assumes that transect lines or points are randomly distributed within the study area. There is currently much interest in replacing the design-based component of distance sampling analysis methods by a modelling approach, for which random line location is not assumed, and which relates animal density to covariates such as habitat (Hedley, Buckland & Borchers 1999; Buckland *et al.* 2004; Hedley & Buckland 2004; Royle, Dawson & Bates 2004; Johnson, Laake & Ver Hoef 2010; Sillett *et al.* 2012). This allows identification of relationships between animal densities and the covariates retained in the best fitting model which may be of particular interest when the objective of the study lies in establishing the significance of an effect in a designed experiment (Buckland *et al.* 2009). If, for example, the interest lies in establishing whether a habitat restoration project had the desired effect, lines or points can be laid out in restored habitat and paired up with lines or points on nearby unrestored control habitat of similar type. Sample counts are taken at least once at each line or point. A two-level factor covariate, corresponding to samples from treated or untreated habitat, is included in the model, allowing inference on the difference in densities between treatment and control plots.

This paper was motivated by a study in which the effect of establishing conservation buffers along row crop field margins on indigo bunting *Passerina cyanea* L. density was of interest. Over 400 survey sites, each comprising a pair of points (one treatment and one control), were established in farmland in several states in the USA. Treatment points were at the edge of buffered fields, while control points were located at the edge of nearby unbuffered fields. Each site was surveyed between 1–4 times in each of 2 years. Observers recorded the number of detected male birds in predefined distance intervals. A designed distance sampling survey of this magnitude to assess the effect of a conservation measure is unusual if not unique.

Buckland *et al.* (2009) describe a two-stage model-based approach for analysing distance sampling count data from experimental studies. In the first stage, a detection function is fitted to the distance data, from which an offset is estimated to account for imperfect detection within the surveyed plot. In the second stage, the offset is incorporated in a Poisson count model. This two-stage model is similar to the approach described by Hedley & Buckland (2004). However, it focuses on the relationship between animal density and covariates in the context of testing for a treatment effect in a designed distance sampling experiment. By contrast, Hedley & Buckland use these relationships to make density predictions throughout the study area. The shortcoming of this two-stage modelling approach is that the offset, and hence the detection function from the first stage, is assumed known. Nonparametric bootstrapping is then used to quantify precision of parameter estimates, to allow uncertainty from fitting the detection function to propagate into the second stage.

Royle, Dawson & Bates (2004) developed an integrated likelihood for point transect data where distances were measured in intervals. These authors combined the covariate model for the latent variable N_p (true but unknown numbers of animals at the point) with the cell probabilities f_i (derived from the detection function, which was assumed to be half-normal) to model the observed counts n_{pi} in the ith distance interval at the pth point. An advantage of their approach is that all model parameters for both the N_p and the f_i are estimated in one step.

We extend this integrated approach in the following ways. We include covariates in the detection function model, and use a stepwise method to select between models. We also include a random effect for site in the plot abundance model. A site may include multiple lines or points, and may have repeat counts; this approach accommodates any correlation in multiple counts from the same site. By contrast, existing distance sampling methods assume that each count is independent.

In the following we begin by describing our extended version of the integrated likelihood of Royle, Dawson & Bates (2004) for both line and point transects (see *Integrated likelihood approach*), analyse our case study using this integrated likelihood, and contrast results with those using the two-stage approach (*Case study: point transect surveys of indigo buntings*).

Materials and methods

INTEGRATED LIKELIHOOD APPROACH

The likelihood function

Consider a wildlife study carried out at a number of sites, at each of which point or line transects are placed according to some design. Each site is surveyed at least once following a distance sampling protocol (Buckland *et al.* 2001). For line transects, the observer travels down the line and records the perpendicular distances to the line for each detection of the species of interest. For point transects, the observer remains at the point for a fixed amount of time and records the distances from the point to the detections. Distances can be recorded either exactly or in intervals. We assume that animals on the line or point are certain to be detected. If all animals within a distance w of the line or point were detected, then observed counts at the line or point would equal the true number of animals on the plot of half-width (lines) or radius (points) w. These counts could be modelled via a log-link using a generalised linear mixed model (glmm) with a Poisson error structure ($E(N_{jpr}) = \lambda_{jpr}$) where N_{jpr} is the total number of animals present within the plot of size a at visit r to line/point p of site j. The plot size a equals $2wl_{jpr}$ for lines (l_{jpr} = length of the respective line) and πw^2 for points. λ_{jpr} may then be modelled by a linear predictor via a log-link function using:

$$\lambda_{\mathrm{jpr}} = \exp\left(\beta_0 + b_j + \sum_{k=1}^{K} x_{kjpr}\beta_K\right). \qquad \text{eqn 1}$$

Here, β_0 represents the fixed effect intercept, b_j the random effect for site j with $b_j \sim N(0, \sigma_b^2)$, x_{kjpr} the observed values of the $k = 1,...,K$ fixed effects and β_K the associated coefficients. In the following, $\beta_0,...,\beta_K$ may be summarised as $\underline{\beta}$.

As detection is generally not perfect on the plot, we need a formulation to allow for detectability decreasing with distance from the line or point. Here we employ the unconditional probability density function of observed distances $f(y) = \pi(y)g(y)$ (Royle, Dawson & Bates 2004). $\pi(y)$ describes the expected distribution of animals (whether detected or not) with distance from the line or point, and $g(y)$ the probability of detecting an animal given that it is at distance y. $\pi(y)$ is assumed to be known ($1/w$ for lines and $2y/w^2$ for points) and a detection function model is proposed for $g(y)$ (Buckland *et al.* 2001). Detection function parameters are summarised as $\underline{\theta}$. in the following. Our approach assumes that distances from the line or point are recorded by distance interval, or, if distances are recorded exactly, that these are binned into intervals after the survey is completed.

Royle, Dawson & Bates (2004) showed that when using the unconditional formulation for $f(y)$ for interval distance data, the area under $f(y)$ between the cutpoints of the intervals c_i represent the proportions of N_{jpr} recorded within the ith interval (as opposed to the proportions of n_{jpr} when using the conditional $f(y)$ from Buckland *et al.* 2001) and can be obtained using:

$$f_i = \int_{c_{i-1}}^{c_i} f(y)dy = \int_{c_{i-1}}^{c_i} \pi(y)g(y)dy. \qquad \text{eqn 2}$$

Hence, we divide the observed counts n_{jpr} at the line (point) into the counts made within each distance interval i and consider these counts n_{jpri} as a Poisson random variable, $n_{jpri} \sim Poisson(\lambda_{jpr} f_i)$. The integrated likelihood function, where the Poisson rate λ_{jpr} (equation 1) is adjusted for imperfect detectability using f_i (equation 2), is then defined as (modified from McCulloch & Searle 2001):

$$L_{y,n}(\underline{\beta}, \sigma_b, \underline{\theta}) =$$
$$\prod_{j=1}^{J} \int_{-\infty}^{\infty} \left(\prod_{p=1}^{P_j}\prod_{i=1}^{I_j}\prod_{r=1}^{R_j} \frac{(\lambda_{jpr}f_i)^{n_{jpri}} e^{(-\lambda_{jpr}f_i)}}{n_{jpri}!}\right) \frac{1}{\sqrt{2\pi\sigma_b^2}} e^{-\frac{1}{2\sigma_b^2}b_j^2} db_j \qquad \text{eqn 3}$$

J equals the total number of sites. P_j and R_j refer to the total number of lines (points) and visits to a line (point) for the jth site, respectively and may vary between different sites. The outermost distance interval I_j is generally the same for each site. The component inside the brackets of the right hand side of equation (3) pertains to the Poisson likelihood of the observed counts n_{jpri} and the component to the right of the brackets to the normal densities of the random effect coefficients.

By maximizing this likelihood function, e.g. by using the *optim* or *nlm* function in R, all parameters are estimated simultaneously. Although it is easier to maximize the log-likelihood, the likelihood values inside the integral cannot be converted onto the log scale before integration, so (3) becomes:

$$\ln L_{y,n}(\underline{\beta}, \sigma_b, \underline{\theta}) =$$
$$\sum_{j=1}^{J} \ln\left[\int_{-\infty}^{\infty} \prod_{p=1}^{P_j}\prod_{i=1}^{I_j}\prod_{r=1}^{R_j} \frac{(\lambda_{jpr}f_i)^{n_{jpri}} e^{(-\lambda_{jpr}f_i)}}{n_{jpri}!} \frac{1}{\sqrt{2\pi\sigma_b^2}} e^{-\frac{1}{2\sigma_b^2}b_j^2} db_j\right] \qquad \text{eqn 4}$$

Modelling heterogeneity in detection probabilities

Note that in the formulations above (eqn 3 and 4), detections from all points are pooled to obtain parameter estimates for one common $f(y)$ assuming no heterogeneity in detection probabilities between different lines (points) or different detections. Heterogeneity in detection probabilities can be modelled using stratification or multiple covariate distance sampling (MCDS) (Buckland *et al.* 2001:88-92), replacing the global f_i with stratum-specific or covariate-specific f_{jpri} in (3) and (4). The f_{jpri} may require further breaking down when strata or covariates differ between detections during the same visit to a line or point (e.g. male vs. female birds).

For post-stratification, observed distances are divided into different strata based on one of the available covariates. Detection function parameters are estimated for each stratum. Stratifying the detection function by, say, covariate *state*, involves fitting a separate detection function to the detections from each state. A more parsimonious approach is MCDS (Marques & Buckland 2003). Here, the scale parameter of the hazard-rate or half-normal key function $g(y)$ is modelled as a function of fixed effect covariates $\underline{z}$: $\sigma(\underline{z}) = \exp(\beta_0 + \sum_{q=1}^{Q} z_q\beta_q)$. The density of observed distances conditional on the associated covariates $\underline{z}$ becomes $f(y|\underline{z})$. This allows us to model detection probabilities not only as a function of increasing distance from the point or line but also with respect to covariates affecting detection conditions and detectabilities of animals.

Model selection

The function value returned by optimising equation (4) is the log-likelihood (ln$L$) of the model evaluated at the maximum likelihood estimates of the parameters. This can be converted into a model selection criterion, e.g. AIC where $AIC = -2\ln L + 2p$ (p = the number of parameters) (Akaike 1979). In cases where the number of possible models is too large to consider, stepwise model selection may be used where one covariate is added to or removed from the model at a time. To obtain model-averaged estimates for parameters of interest, a weighted average may be taken across the models using AIC weights (Buckland, Burnham & Augustin 1997).

Estimates of precision

Standard errors of parameter estimates are given by the square-root of the diagonal elements of the inverse of the Hessian matrix. The Hessian is calculated by optimisation routines such as the *optim* and *nlm* commands in R.

CASE STUDY: POINT TRANSECT SURVEYS OF INDIGO BUNTINGS

The data

The National CP-33 Monitoring Program coordinated by the Mississippi State University, Department of Wildlife, Fisheries, and Aquaculture was set up to monitor beneficial effects of herbaceous buffers around agricultural fields on bird densities in several Southeastern and Midwestern states (Evans *et al.* 2013). To set up a monitoring scheme, a minimum of 40 CP-33 contracts

per state were randomly selected from all CP-33 contracts. Buffered treatment fields within these contracts were selected for monitoring of several priority species. Here, we analyse data on indigo buntings, a common passerine found throughout the eastern United States in the northern summer where it breeds in brushy borders to deciduous woodland.

During the breeding seasons of 2006–2007, point transect surveys were conducted from one point per field located in the buffer at the edge of the field. Unbuffered control points on the edge of fields of the same agricultural use, located 1–3 km away, were surveyed concurrently to ensure similar conditions. Each pair of adjacent treatment and control points was considered a site, and each site was surveyed between 1–4 times per survey year. The objective was to evaluate whether buffers result in higher bird densities.

The indigo bunting is a sexually dimorphic species; males are bright blue, particularly during breeding, while females are dull brown. Males engage in territorial song during the breeding season, making them easy to detect. Hence, observers recorded all male indigo buntings detected visually or aurally in a 10-minute period in predetermined distance intervals (0–25, 25–50, 50–100, 100–250, 250–500, >500 m). We assume that indigo buntings distribute themselves independently of point locations. Only those sites surveyed at least once in each of the two survey years were included. An additional criterion was that each state included in the analysis contained >50 detections. The 446 sites satisfying these criteria were located in nine states.

Analysis using the integrated likelihood approach

In preliminary modelling of the detection function, estimated detection probabilities dropped below 0·1 beyond 100 m regardless of model choice, and so following recommendations of Buckland *et al.* (2001), we limited the analysis to the three innermost distance intervals (0–25, 25–50 and 50–100 m). With just three intervals, and allowing a degree of freedom for assessing model fit, we considered only one parameter models for the detection function. Hence model selection for the detection function was between the half-normal and hazard-rate models, where for the latter, the shape parameter was fixed. For the same reason, we modelled heterogeneity using three possible stratification factors: *year* (2006 or 2007), *type* (treated or control field) and *state* (9 levels). We used AIC to select appropriate values for the fixed shape parameters for the global or the stratified hazard-rate functions.

The expected abundances were modelled using equation (1), with *year*, *type*, continuous *Julian day* and *state* as possible covariates. In these models, the parameter of interest was the covariate *type*. A significant *type* term in the plot abundance model would indicate a difference in expected bird densities between the paired control and treated plots. The random effects term b_j was assumed normal with $b_j \sim N(0, \sigma_b^2)$. Analytical standard errors (ASEs) were obtained from the Hessian matrix.

We used stepwise forward model selection as described in the *Model selection* section. For each contending model, equation (4) was maximized using the *optim* function in R, where the total number of sites was $J = 446$ and the total number of distance intervals was $I_j = 3$. R_j ranged from 2 to 8 visits per site. As each site comprised two points, one control and one treatment, $p = 1$ or 2. The R code is given in Appendix S1 in Supporting Information.

Results

During the two survey years included in this study, 2006–2007, 2924 counts at control or treatment points of the 446 sites were made. During these counts, a total of 3785 indigo buntings were detected in the three innermost distance intervals. The data were analysed using the integrated approach described in the *Integrated likelihood approach* section. For comparison, the same data were analysed with the two-stage approach described by Buckland *et al.* (2009) for which methods are detailed in the Appendix S2 in Supporting Information. In brief, for the two-stage approach the second stage density model conditions on a first stage detection function model by incorporating the effective area (estimated from the detection function) as an offset. To estimate uncertainty of parameter estimates, a nonparametric bootstrap was conducted.

MODEL SELECTION

For the integrated approach, forward stepwise model selection was started with the half-normal model for the detection function and an intercept and random effect for the plot abundance model (Table 1). Considering the global and stratified hazard-rate models next (stratified by

Table 1. Models included in the forward stepwise model selection including the half-normal (HN) and the global and stratified hazard-rate (HR) detection functions for the detection model and the inclusion of four covariates in the abundance model in addition to the intercept β_0 and the random effect b_j. The shape parameter of the HR function was generally fixed at 2 except for the state stratified model where they were fixed at 2, 2·5, 2, 2·5, 2, 2, 2, 3, 2 for the nine states respectively. The column 'Improved?' refers to whether or not the respective model yielded an improved AIC compared to the previous and whether or not this model should be retained

ID	Detection model	Abundance model	Log-likelihood	Parameters	AIC	Improved?
1	HN global	$\beta_0 + b_j$	−7327·74	3	14661·48	NA
2	HR global	$\beta_0 + b_j$	−7296·49	3	14598·97	yes
3	HR by year	$\beta_0 + b_j$	−7295·73	4	14599·47	no
4	HR by type	$\beta_0 + b_j$	−7268·85	4	14545·69	yes
5	HR by state	$\beta_0 + b_j$	−7248·12	11	14518·24	yes
6	HR by state	$\beta_0 + b_j$ + year	−7247·77	12	14519·55	no
7	HR by state	$\beta_0 + b_j$ + type	−7205·50	12	14435·01	yes
8	HR by state	$\beta_0 + b_j$ + type + JD	−7198·99	13	14423·97	yes
9	HR by state	$\beta_0 + b_j$ + type + JD + state	−7121·78	21	14285·56	yes

one of *year*, *type* or *state*) for the detection function indicated that a *state*-stratified hazard-rate model gave the lowest AIC values. With this model for the detection function, covariates were added to the plot abundance model one at a time and retained if inclusion lowered the AIC value. Here, the best model by AIC included the covariates *type, Julian day* and *state*. We did not consider model averaging as the difference in AIC values between the best and the second best model was 138, so that the model-averaged estimates would be the same as the estimates under the best model. The same models were selected for the two-stage approach.

COMPARING CONTENDING MODELS FROM THE INTEGRATED APPROACH

Parameter estimates with standard errors for each contending model for the integrated approach from Table 1 are shown in Appendix S3 in Supporting Information. Substantial differences in parameter estimates between models were obtained by including *state* in the plot abundance model (model 9). This resulted in an increase in detection function parameters for seven states and a decrease for the remaining two. Given the same truncation distance and fixed shape parameters, larger scale parameters of a hazard-rate detection function translate into larger estimates of f_{jpri} (i.e. proportions of the true number of birds N_{jpr} that were detected) for the respective strata. Including *state* in the plot abundance model also led to a decrease in the random effect standard deviation. The change in detection function parameters was probably because with *state* in the abundance model, the state-specific f_{jpri} represent proportions of the estimates of the expected N_{jpr} that are modelled as a function of *state* (as well as of *type* and *Julian day*), while before they represented proportions of estimates of the expected N_{jpr} that were not modelled as a function of *state*. In addition to a change in point estimates for parameters, the standard errors increased for all detection function parameters after including *state* in the abundance model (model 9 compared to models 5–8).

The decrease in the random effect standard deviation for model 9 indicated that the *state* covariate modelled part of the variation absorbed by the random effects coefficients in the plot abundance models 1–8 (Appendix S3).

COMPARING BEST MODELS FROM THE INTEGRATED AND TWO-STAGE APPROACH

For the best fitting model, estimates of the scale parameters of the hazard-rate detection function from the integrated approach ranged between 26·11 for Tennessee (ASE = 0·04, fixed shape = 2·0, Table 2) and 57·79 for South Carolina (ASE = 4·40, fixed shape = 3·0). They were generally larger for the integrated approach except for Mississippi where the estimate was slightly smaller. The discrepancy between parameter estimates was less

than 10% in five states and up to 24% in the remaining four.

In the following we refer to baseline expected number of male indigo buntings within the plot area *a* for the values returned by the model after setting the covariates to *type* = Control, *Julian day* = 174 (the mid-point of all days surveyed), *state* = GA and incorporating a contribution of the random effects term using the mean of $logN(0, \hat{\sigma}_b^2)$. To compare these baselines for the two approaches, we applied the following transformation: exp (intercept + *Julian day* coefficient × 174 + 0·5 × $\hat{\sigma}_b^2$) using the coefficient values from Table 2 for the respective approaches (see equations (1) and (6) for details). For the two-stage approach the resulting value was also multiplied by the search area of the plot ($a = \pi w^2 = 31416$ m^2), as the intercept represents birds m^{-2} (as opposed to birds per search area of the plot for the integrated approach). The baseline expected numbers of male indigo buntings per plot were 1·05 (ASE = 0·29) and 1·43 (BSE = 0·59) (or 33·52 (ASE = 9·12) and 43·51 (BSE = 18·91) birds km^{-2}) for the integrated and two-stage approach, respectively.

The remaining fixed effects represent proportional changes compared to this baseline. The *type* coefficient was the same for the two approaches (0·30, Table 2) with ASE = 0·02 for the integrated approach and ASE = 0·03 and bootstrap standard error (BSE) = 0·04 for the two-stage approach. This indicated a 35·0% increase in density or abundance on the treated fields (exp (0·30) = 1·35). For the remaining fixed effect coefficients in the plot abundance model, parameter estimates were again larger for the integrated approach. The coefficient for the continuous covariate *Julian day* was 0·0053 (ASE = 0·0005) for the integrated likelihood approach and 0·0046 (ASE = 0·0017, BSE=0·0018) for the two-stage approach. Discrepancies in estimates for the *state* coefficients between the two approaches were more pronounced than for detection function parameters, ranging between 1 and 111%. Larger coefficients again translate into proportionately larger increases in abundances or densities for the respective factor levels compared to the baseline expected number of birds. The random effect standard deviation was slightly larger for the integrated likelihood approach (0·50, ASE = 0·02 vs. 0·49, BSE = 0·04).

Comparing ASEs between the two approaches, those corresponding to detection function parameters were smaller for the integrated approach for three states and larger for the remaining six, whereas ASEs from the integrated approach were smaller than BSEs from the two-stage approach in five states and larger in four.

ASEs for the intercept and the coefficients for *type* and *Julian day* in the plot abundance models were smaller for the integrated approach than ASEs and BSEs for the two-stage approach. For the *state* coefficients, ASEs from the integrated approach were always larger than ASEs from the two-stage approach but always smaller than BSEs.

Table 2. Maximum likelihood estimates (MLE), analytic (ASE) and bootstrap (BSE, two-stage approach only) standard errors for detection function and abundance/count model parameters obtained by the integrated likelihood and the two-stage approach for the respective best models. Shape parameters for the one-parameter hazard-rate detection function were fixed (see *Analysis using the integrated likelihood approach*). States included are Georgia (GA), Illinois (IL), Indiana (IN), Kentucky (KY), Missouri (MO), Mississippi (MS), Ohio (OH), South Carolina (SC) and Tennessee (TN)

	Integrated likelihood		Two-stage			
	MLE	ASE	MLE	ASE	BSE	Fixed shape
Detection model parameters						
Scale State GA	45·85	9·33	37·27	7·72	8·12	2
Scale State IL	36·03	3·21	34·42	2·86	3·17	2·5
Scale State IN	27·31	2·66	24·34	2·35	4·92	2
Scale State KY	29·63	1·23	27·75	1·13	1·52	2·5
Scale State MO	41·31	3·03	37·78	3·14	2·86	2
Scale State MS	38·50	3·31	38·73	3·33	4·21	2
Scale State OH	27·15	2·16	24·59	1·97	1·94	2
Scale State SC	57·79	4·40	56·30	4·13	6·85	3
Scale State TN	26·11	0·04	21·08	1·74	3·51	2
Abundance model parameters						
Random effects						
Standard deviation	0·50	0·02	0·49	NA	0·04	
Fixed effects						
Intercept N_{jpri}	−0·99	0·28				
Intercept D_{jpr}			−10·91	0·29	0·43	
Type Treated	0·30	0·02	0·30	0·03	0·04	
Julian Day	0·0053	0·0005	0·0046	0·0017	0·0018	
State IL	1·46	0·32	1·20	0·18	0·38	
State IN	1·50	0·32	1·34	0·18	0·49	
State KY	2·00	0·29	1·79	0·17	0·36	
State MO	0·53	0·29	0·32	0·16	0·36	
State MS	1·25	0·31	0·91	0·17	0·37	
State OH	1·11	0·30	0·92	0·17	0·37	
State SC	0·59	0·31	0·28	0·18	0·39	
State TN	2·14	0·28	2·12	0·17	0·44	

Discussion

Designed experimental studies generally have an advantage over purely observational studies in that they allow inference on cause and effect of a treatment. Designed experiments allow attribution of the change in animal abundances directly to the treatment, while purely observational studies do not.

For the CP-33 Monitoring Program, the experimental design comprised sites, each with a pair of survey points, one in a buffered treatment field and one in a nearby unbuffered control field; repeat surveys were conducted concurrently at both points of each site. This study is possibly unique due to its scale (over 400 sites with repeat surveys each year at each site). Analysis of such data is complex and it is critical to attribute the causes for variations in observed counts to the correct sources by appropriate model specification together with objective model selection criteria.

The aim of our case study was to determine whether buffers improved habitat for birds which would be indicated by higher abundances near buffered compared to unbuffered fields. As detection on the plot was not perfect, one source of differences in observed abundances between buffered and unbuffered fields could have been different detection probabilities between these two strata. Hence, we selected the best of a range of competing detection models.

Further, it was necessary to rule out that variations in abundances could be best explained by other covariates in the abundance model. Hence, we also included a selection routine for the contending abundance models to objectively arrive at the best fitting model. The significant *type* term with a positive coefficient of 0·30 for level Treated in the best fitting abundance model demonstrated that implementation of buffers resulted in an increase of indigo bunting densities by 35%. Previous studies have shown beneficial effects of such buffers for birds (e.g. Evans *et al.* 2013). Conover, Burger & Lindner (2011) showed that field buffers increased nesting activities along field margins for a range of birds, including indigo buntings. In contrast, Riddle & Moorman (2010) showed that implementing field borders had no beneficial effect on nesting success of indigo buntings. However, their effort was limited to 12 hog farms and his inference limited to breeding success. Besides the potential for additional breeding habitat, buffers may also provide new habitat for foraging and escape cover. While our results give evi-

dence of larger densities of indigo buntings on buffered fields, behavioural data would be necessary to make inference on how these birds make use of this habitat.

Furthermore, it is essential to avoid false inference due to random variation in observed counts (in contrast e.g. to variation in observed counts due to a response to the treatment), which is more likely to occur if sites are surveyed only once. Hence, Buckland *et al.* (2009) recommended that repeat surveys be made on plots. This, however, possibly introduces correlation between counts at the same site which we accommodated by including a random effect for site in the abundance model. This is a new technique in the context of distance sampling analysis methods where covariate models for abundance have generally been limited to fixed effects. If sites are few and budget limitations allow for multiple repeats of counts at each site, site may indeed be included as a fixed effect in the abundance model, although inference is then restricted to the sites surveyed. For large-scale studies, such as our case study, this strategy would require the estimation of too many parameters. In any case, we wish to draw inference on the effects of field buffers generally, and not just on those field buffers in the survey, and inclusion of a random effect for site in the abundance model allows us to do this.

Potential correlations between counts at the same site may be accommodated by expanding the two-stage approach of Buckland *et al.* (2009) by including a random effect for site in the count model (see Appendix S2). However, the two-stage approach conditions on the first-stage detection model for the second-stage density model and uncertainty from the first stage does not propagate into the second stage. For our case study, this was evident in artificially small analytical standard errors for *state* in the count model obtained with the two-stage approach. Underestimation of standard errors may result in retaining the wrong covariates in the final model. This issue may generally be avoided using the integrated likelihood approach where all parameters are estimated simultaneously. Hence, the integrated approach with the random effect in the plot abundance model has this additional benefit over the two-stage approach.

We considered a collection of abundance models and models for the detection function. One may argue that modelling raw counts (i.e. not adjusted for imperfect detection on the plot) in a glmm without an offset might have been sufficient for inference on the parameter of interest. For our case study, inference on the parameter of interest, the *type* coefficient, would have remained the same regardless of choice of model (those including *type* in the plot abundance model, models 7–9, Appendix S3) or approach (Table 2). As the best detection function did not include the *type* covariate and *state* and *type* were not correlated (absolute correlation between *type* and any *state* coefficients was <0·01), inference on this parameter would have also remained the same if modelling raw counts in a glmm without any offset. However, inference on parameter estimates for a covariate that is in both the detection function and the abundance model may differ substantially between the integrated and the two-stage approach (or when comparing either of these approaches to modelling raw counts). Dissimilarities between estimates for *state* both in the detection function and the abundance model likely resulted from estimating all parameters in one step for the integrated approach as opposed to two steps for the two-stage approach. Hence, we emphasise again the importance of modelling heterogeneity in detection probabilities and obtaining parameter estimates for both models in one step. Conceptually the difference between the approaches is that for the integrated approach, we assume that the patterns by which animals distribute themselves in the study area (and resulting densities) and the observation process influence each other, while they are considered as separate processes for the two-stage approach. We argue – along the lines of Royle, Dawson & Bates (2004) and Johnson, Laake & Ver Hoef (2010) – that the former case is the more realistic assumption.

We expect designed distance sampling experiments to become widely used for assessing effectiveness of conservation measures, and for environmental impact studies. The use of random effects as described here allows correlations in multiple counts from a single sampling unit to be accommodated, and allows inference to be extended to a wider area for which the sites are a representative sample, thus strengthening the ability of wildlife and natural resource managers to evaluate the implications of changes in the environment. We demonstrated that modelling heterogeneity in detection probabilities may have a strong influence on parameters in the plot abundance model and that using a model selection routine is necessary to determine which parameters should be retained in the final models.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. R code for the analysis of the indigo bunting data using the integrated and the two-stage approach.

Appendix S2. The two-stage approach.

Appendix S3. Contending models using the integrated approach.

Table S3. Parameter estimates and standard errors for contending models using the integrated approach.