



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

Using Hierarchical Centering to Facilitate a Reversible Jump MCMC Algorithm for Random Effects Models

Citation for published version:

Oedekoven, CS, King, R, Buckland, ST, MacKenzie, ML, Evans, K & Burger Jr., W 2016, 'Using Hierarchical Centering to Facilitate a Reversible Jump MCMC Algorithm for Random Effects Models' Computational statistics & data analysis, vol. 98, pp. 79-90. DOI: 10.1016/j.csda.2015.12.010

Digital Object Identifier (DOI):

[10.1016/j.csda.2015.12.010](https://doi.org/10.1016/j.csda.2015.12.010)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Computational statistics & data analysis

General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.



Using hierarchical centering to facilitate a reversible jump MCMC algorithm for random effects models

C. S. Oedekoven^{a,*}, R. King^b, S. T. Buckland^a, M. L. Mackenzie^a,
K. O. Evans^c and L. W. Burger, Jr.^c

^a*Centre for Research into Ecological and Environmental Modelling,
School of Mathematics and Statistics, University of St Andrews,
The Observatory, Buchanan Gardens, St Andrews, KY16 9LZ, UK Tel.: +44 1334 461826 Fax: +44 1334 461 800*

^b*School of Mathematics, University of Edinburgh,
James Clerk Maxwell Building, The King's Buildings, Peter Guthrie Tait Road, Edinburgh, UK, EH9 3FD*

^c*Department of Wildlife, Fisheries & Aquaculture,
Mississippi State University,
Box 9690, Mississippi State, MS 39762, USA
email: cso2@st-andrews.ac.uk

Abstract

Hierarchical centering has been described as a reparameterisation method applicable to random effects models. It has been shown to improve mixing of models in the context of Markov chain Monte Carlo (MCMC) methods. A hierarchical centering approach is proposed for reversible jump MCMC (RJMCMC) chains which builds upon the hierarchical centering methods for MCMC chains and uses them to reparameterize models in an RJMCMC algorithm. Although these methods may be applicable to models with other error distributions, the case is described for a log-linear Poisson model where the expected value λ includes fixed effect covariates and a random effect for which normality is assumed with a zero-mean and unknown standard deviation. For the proposed RJMCMC algorithm including hierarchical centering, the models are reparameterized by modelling the mean of the random effect coefficients as a function of the intercept of the λ model and one or more of the available fixed effect covariates depending on the model. The method is appropriate when fixed-effect covariates are constant within random effect groups. This has an effect on the dynamics of the RJMCMC algorithm and improves model mixing. The methods are applied to a case study of point transects of indigo buntings where, without hierarchical centering, the RJM-

¹The data and R code for the case study are provided in the annexes of the electronic version of this manuscript.

²* cso2@st-andrews.ac.uk

³* <http://creem2.st-andrews.ac.uk/>

⁴* <http://coedekoven.wix.com/cornelia-oedekoven>

CMC algorithm had poor mixing and the estimated posterior distribution depended on the starting model. With hierarchical centering on the other hand, the chain moved freely over model and parameter space. These results are confirmed with a simulation study. Hence, the proposed methods should be considered as a regular strategy for implementing models with random effects in RJMCMC algorithms; they facilitate convergence of these algorithms and help avoid false inference on model parameters.

Keywords: combined likelihood, “Metropolis Hastings”, point transect sampling, random effects, reparameterisation.

1. Introduction

For Bayesian analyses, for a given model, the posterior distribution of the parameters is formed by combining the likelihood of the data with the prior distributions of the parameters. A Markov chain Monte Carlo (MCMC) algorithm is often used to sample from this posterior distribution to obtain inference on the parameters of interest. In the presence of model uncertainty, the posterior distribution can be extended to be defined jointly over both parameter and model space. This posterior distribution is often explored using the reversible jump Markov chain Monte Carlo (RJMCMC) algorithm (Green, 1995). However, the art of setting up an RJMCMC algorithm can be challenging on multiple levels. The objective is generally to construct a chain that moves freely between models, efficiently exploring model and parameter space simultaneously.

The RJMCMC algorithm entails iteratively updating the parameters conditional on the model (i.e. within-model move) and then updating the model (and corresponding model parameters) conditional on the current parameters (i.e. between-model move). Mixing problems for the within-model moves are often due to high autocorrelation within the constructed Markov chain. Improvements for mixing within a given model have been investigated in the framework of MCMC with the aim of reducing posterior correlations and increasing the effective sample size by reparameterisation. In this context, Browne (2004) and Browne et al. (2009) have shown that hierarchical centering (first described by Gelfand, Sahu, and Carlin, 1995) can significantly reduce the autocorrelation within the MCMC algorithm. The use of hierarchical centering in the presence of random effects refers to exchanging the zero-mean of the random effect component, typically assumed to be of normal form, with a model consisting of an intercept and one or more fixed effect covariates.

22 This will be described in detail in section 2. Papaspiliopoulos, Roberts, and Sköld (2007) investi-
23 gated the circumstances when hierarchical centering performs well in comparison to noncentering
24 for MCMC algorithms.

25 Other methods for improving mixing of an MCMC algorithm include parameter expansion,
26 which refers to augmenting the model with additional parameters to form an expanded model
27 (Browne, 2004). The original model is embedded in the expanded one and parameters from the
28 original model can be constructed with parameters from the expanded model. Vines, Gilks, and
29 Wild (1995) describe a method of reparameterisation for random effects models called *sweeping*
30 which is suitable also for models with multiple sets of random effects in a generalized linear mixed
31 model (*glmm*) framework. The idea consists of adding the mean of the random effect coefficients
32 to the intercept of the fixed effects while subtracting the same quantity from each random effect
33 coefficient.

34 For the between-model move in an RJMCMC algorithm (the RJ step), the current model is
35 updated by proposing to move to an alternative model (with given parameters) and accepting this
36 move with some probability. Mixing problems for these between-model moves may arise for mul-
37 tiple reasons, e.g. due to difficulties in finding proposal distributions and updating procedures that
38 produce suitable acceptance probabilities. Besides careful pilot-tuning of proposal distributions,
39 several methods for improving the acceptance rate for the reversible jump step have been proposed.
40 For example, Green and Mira (2001) proposed delayed rejection, where after initial rejection a sec-
41 ond attempt to jump is made with samples generated from a new distribution that may depend on
42 the rejected proposal. Brooks, Giudici, and Roberts (2003) assumed a family for the proposal dis-
43 tribution, where the proposal parameters are chosen to maximize (in some form) the acceptance
44 probability. Al-Awadhi, Hurn, and Jennison (2004) demonstrated that increasing acceptance prob-
45 abilities may be achieved by using a secondary Markov chain with a fixed number of steps that
46 serves to move the value of an RJMCMC proposal closer to a mode before calculating the accep-
47 tance probability for the proposed move. Papathomas, Dellaportas, and Vasdekis (2011) proposed
48 that model mixing for generalized linear models may be improved by using proposal densities that
49 draw samples from parameter subspaces of competing models. Forster, Gill, and Overstall (2012)
50 used the Laplace approximation to integrate out the random effects and orthogonal projections of
51 the current linear predictor onto the proposed linear predictor to produce effective proposals for

52 *glms*.

53 While these previous approaches describe strategies to improve the acceptance rate for RJ steps
54 in general, they can be quite complex to implement. We propose an approach using hierarchical
55 centering that is relatively straightforward to implement for random/mixed effect models. A par-
56 ticular problem that one may encounter with random effect models is that the random effect coeffi-
57 cients may begin absorbing the effect of one or more fixed effect covariates if these are not present
58 in the model at times during the Markov chain. The inclusion of such effects into the model may
59 then be unlikely as they are already accounted for within the random effects. We will demonstrate
60 below that using hierarchical centering provides a simple way of reparameterising the model that
61 will prevent this problem and improve the between-model mixing.

62 Hierarchical centering was initially described by Gelfand, Sahu, and Carlin (1995) as a method
63 to improve convergence for mixed models using MCMC methods. Here we extend the ideas to im-
64 prove mixing in an RJMCMC algorithm. Although our methods may be applicable to models with
65 other error distributions, we consider the case for a log-linear Poisson model with fixed effects and
66 a normally distributed random effect, where the overall likelihood combines the Poisson likelihood
67 for each observation and the normal density for each random effect coefficient. We demonstrate
68 how the Poisson likelihoods and the normal densities are affected differently during a proposal to
69 add a covariate for a regular RJMCMC algorithm and one including hierarchical centering.

70 We demonstrate the improved model mixing using a case study of point transects of indigo
71 buntings (*Passerina cyanea* L.). Point transects are a form of distance sampling (Buckland et al.,
72 2001) where, in addition to the number of detections during the counts, distance from the point to
73 each detection is collected. This allows estimation of the average detection probabilities at the point
74 and adjustment of counts for imperfect detection. To study the effect of establishing conservation
75 buffers along margins of agricultural fields on density of several species of conservation interest,
76 pairs of points were set up at the edge of fields in a number of states in the USA. These pairs of
77 points consisted of one point on a treatment field and one on a nearby control field without a buffer
78 and these pairs will be referred to as sites in the following. Counts were repeated 1–4 times in
79 each year 2006–2007. We use a combined likelihood including the likelihoods for the detection
80 function and the log-linear Poisson model where counts are adjusted for imperfect detection within
81 the search area around the point (Oedekoven et al., 2014). A random effect for site is included in

82 the Poisson model to accommodate correlated counts between different sites.

83 In the following we describe how to implement hierarchical centering for RJMCMC, describe
84 the effects on the dynamics of the algorithm, and present updating methods for the RJ step using
85 hierarchical centering (section 2). We then apply the methods to our case study (section 3) and
86 confirm our results with a simulation study (section 4) and discuss our findings (section 5).

87 2. Hierarchical Centering

88 The hierarchical centering described in this paper refers to mixed effect models where a normal
89 distribution is assumed for the random effect. Other distributions may be assumed for the random
90 effect (e.g. Komárek and Lesaffre, 2008) to which these methods can be applied but we focus
91 on the normal distribution for simplicity. We describe the case for a *glmm* with a Poisson error
92 structure, suitable e.g. for fitting a model to correlated count data from repeated measurements.
93 In the following we denote the different groups for the random effect with subscript j and the
94 repeated measurements within the individual groups with subscript r . Here, the expected value
95 λ_{jr} is modelled via a log-link function with a common intercept, β_0 and random effect coefficients
96 b_j for groups j are included for which normality is assumed. For a mixed effect model without
97 hierarchical centering, the random effect is incorporated into the model under the assumption of a
98 global zero-mean and unknown standard deviation, σ_b , i.e. $b_j \sim N(0, \sigma_b^2)$ (e.g. Bates, 2009). Let
99 us assume we have a set of K covariates for $k = 1, \dots, K$, x_k (and associated coefficients, β_k) that
100 can be incorporated as fixed effects. The expected value for the full model including all covariates
101 may then be expressed as:

$$\lambda_{jr} = \exp \left(\beta_0 + \sum_{k=1}^K x_{kjr} \beta_k + b_j \right), \quad b_j \sim N(\mu_j = 0, \sigma_b^2), \quad (1)$$

102 where the x_{kjr} are the measured covariate values corresponding to the r th observation of the re-
103 sponse of group j . While all potential models include the intercept and the random effect, different
104 models included in the RJMCMC algorithm correspond to the combinations of covariates present
105 in the model (i.e. non-zero β_k values). During a between-model move (the RJ step) of an RJM-
106 CMC algorithm using this scenario, the proposal to delete or add one (or more) of the covariates
107 alters the formula for λ_{jr} while the distribution for the random effects terms b_j remains the same

108 (see Appendix A for details on the RJ step).

109 Let us now assume that one covariate, say x_1 , was measured at the group level, i.e. values for
110 all repeated measurements for this covariate within a given group were the same, which allows
111 us to use x_1 for hierarchical centering. In hierarchical centering, the mean of the random effect
112 is modelled using a combination of the intercept β_0 and one or more covariates that are “pulled
113 from” the λ_{jr} model from (1) (Gelfand et al., 1995). In the case that the intercept and covariate x_1
114 are used for centering, the full model from (1) becomes:

$$\lambda_{jr} = \exp \left(\sum_{k=2}^K x_{kjr} \beta_k + b_j \right), \quad b_j \sim N \left(\mu_j = \beta_0 + x_{1j} \beta_1, \sigma_b^2 \right). \quad (2)$$

115 Note that we omitted the subscript r for covariate x_1 in (2) since we assume that the measured
116 values for this covariate were the same for all observations in group j . The proposal to delete
117 or add x_1 from the model during the RJ step of the RJMCMC algorithm involves altering the
118 distribution for b_j , while the proposal to delete or add any other covariates remains the same as
119 before in (1) (altering the formula for λ_{jr}).

120 In the case that all k covariates were measured at the group level, all covariates may be included
121 in the centering and the full model from (1) becomes:

$$\lambda_{jr} = \exp(b_j), \quad b_j \sim N \left(\mu_j = \beta_0 + \sum_{k=1}^K x_{kj} \beta_k, \sigma_b^2 \right). \quad (3)$$

122 Again, we omitted the subscript r for the covariates in the model for μ_j in (3). In (3), it could be
123 omitted from λ_{jr} as well, as there are no covariates in the λ_{jr} model (or the μ_j model) that may vary
124 between different observations within the same group. However, we keep it for simplicity in the
125 following equations. In this scenario, the formula for λ_{jr} remains unchanged during the proposals
126 to delete or add any of the covariates, while the distribution for b_j changes for each proposed model
127 move.

128 We note that it is essential that only those covariates are included in the centering (i.e. x_1 in
129 (2) or x_k with $k=1, \dots, K$ in (3)) that have the same measured value for all observations within a
130 group (Browne et al., 2009). We refer to a group in terms of the grouping unit for the random
131 effect where grouping should occur to account for intra-group dependence (Davison, 2003). All

132 observations belonging to the same group j are modelled with the same random effect coefficient
133 b_j in the equations above.

134 The proposed hierarchical centering is only applicable if for at least one covariate, measured
135 values for the respective covariate are the same within a group. If, for example, the grouping unit
136 for a study is *site*, then the covariate *state* (the geographical governed entity) can be included in
137 the centering as each site only belongs to one state and all repeated observations for a site belong
138 to the same state. Conversely, *Julian day* could not be included as values will likely vary between
139 repeated measurements. As long as this condition holds, any combination of covariates may be
140 included.

141 Hierarchical centering relies on the fact that the random effect coefficients pick up the effect of
142 the covariates included in the centering (given that they have an effect) as they are updated during
143 the within-model move of each iteration of the RJMCMC. Running separate MCMC algorithms
144 (without between-model moves) on the full models from (1), (2) or (3) should result in nearly
145 identical summary statistics for the covariates if the chain was run long enough (since all Markov
146 chains have the same stationary distribution), although mixing might be different for these different
147 parameterisations. However, when including the between-model moves in an RJMCMC algorithm,
148 mixing problems can become more severe, potentially leading to different summary statistics - due
149 to lack of convergence - and hence potentially to the wrong conclusions. Here, convergence and,
150 hence, obtaining correct results may depend on which scenario and initial starting values were
151 used. If, e.g. under the scenario of (1), the random effect coefficients absorb the effect of covariate
152 x_1 , the chain may get “stuck” in models that do not include x_1 . For the scenarios of (2) and
153 (3), moves to models including covariate x_1 would be favoured if the random effect coefficients
154 absorbed the effect of x_1 as then the coefficients will be closer to their modelled means. We will
155 show below that this is due to the fact that here different parts of the likelihood are affected by a
156 proposed model move compared to (1).

157 2.1. Effects of hierarchical centering on RJMCMC dynamics

158 Using either one of the models for λ_{jr} from above ((1), (2), or (3)), the likelihood of the log-
159 linear Poisson model, $L_n(\beta, \sigma_b)$, with a normally distributed random effect may be formulated as

160 (modified from McCulloch and Searle, 2001):

$$L_n(\boldsymbol{\beta}, \sigma_b) = \prod_{j=1}^J \left(\prod_{r=1}^{R_j} \frac{(\lambda_{jr})^{n_{jr}} \exp(-\lambda_{jr})}{n_{jr}!} \times \frac{1}{\sqrt{2\pi\sigma_j^2}} \exp\left(-\frac{(b_j - \mu_j)^2}{2\sigma_j^2}\right) \right), \quad (4)$$

161 where vector $\boldsymbol{\beta}$ contains the coefficients for covariates included in the models and n_{jr} are the
 162 observed measurements of the response. The indices $j = 1, 2, 3, \dots, J$ represent the groups for the
 163 random effect and $r = 1, 2, 3, \dots, R_j$ indices for the different measurements taken for the j th group.
 164 Hence for each group of observations, j , the probability of observing n_{jr} under the log-linear
 165 Poisson model with expected value of λ_{jr} is multiplied for all observations within that group, which
 166 is then multiplied by the normal density of the random effect coefficient b_j . The only coefficients
 167 that influence both parts of this likelihood, i.e. the Poisson likelihood for the observations and the
 168 normal densities, are the random effect coefficients, regardless of which scenario is used from the
 169 previous section.

170 Consider now, that we use this likelihood as part of calculating the acceptance probabilities for
 171 updating the model as well as the fixed and random effect coefficients in an RJMCMC algorithm
 172 (e.g. Oedekoven et al., 2014). Both the Poisson likelihood and the normal densities are higher if
 173 the observed value of the response or the random effect coefficients are closer to their respective
 174 means (λ_{jr} or μ_j , respectively). Hence, combining what we know from (1) - (4), it is evident that
 175 the Poisson likelihoods will improve if the variation that is not accounted for by the fixed effect
 176 coefficients is picked up by the random effect coefficients (which – as well as the fixed effect
 177 coefficients of the current model – are updated during the within-model move). On the other hand,
 178 the normal densities will return higher values for random effect coefficients close to their mean
 179 values.

180 Intuitively, one may think that a problem arises for a between-model move (using models from
 181 (1)) when a covariate, say x_1 , may have an effect but is not included in the current model. Then,
 182 the random effect coefficients may begin to absorb this effect and in this manner, adjust the value
 183 for λ_{jr} to improve the likelihood. This may result in a “tug-of-war” between the Poisson likeli-
 184 hood trying to adjust the coefficients in such a manner that the effect of x_1 is accounted for and,
 185 on the other hand, the normal densities trying to keep the coefficients close to their mean, i.e. zero
 186 for (1)). This will typically also result in an inflated random effect standard deviation since the

187 random effect coefficients are replacing some unexplained variability attributable to x_1 . If this
188 has indeed occurred, an acceptance of x_1 into the model during a between-model move proposal
189 may become very unlikely as its effect is already accounted for by the random effect coefficients.
190 Hence, during a proposal to add x_1 , the new model with x_1 will create inferior λ_{jr} . These will then
191 return decreased likelihood values even if the randomly drawn value(s) for x_1 would produce a
192 larger likelihood under circumstances before the effect has been absorbed by the random effect co-
193 efficients. In other words, the values of the random effect coefficients are dependent on the model.
194 A strategy to account for this could be to jointly update the coefficient value(s) for covariate x_1
195 and the values for the random effect coefficients. However, this complicates the RJ step involving
196 more complex proposal distributions.

197 Alternatively, this issue may be addressed using hierarchical centering since proposing to add
198 x_1 using either (2) or (3) into the model will not change λ_{jr} (and the Poisson likelihood). Here,
199 the random effect coefficients absorb the effects of the covariates included in the model (given
200 they have an effect) within the mean of the random effect distribution (in addition to the intercept
201 β_0). Using (2) this would be only covariate x_1 ; using (3) this would be covariates x_k with $k =$
202 $1, 2, 3, \dots, K$. The only part of the likelihood that is affected when updating this/these covariate(s)
203 for within-model and between-model moves are the normal densities from (4). It is likely that, on
204 average, the normal densities improve for the individual random effect coefficients as these will
205 on average be closer to their assumed mean. As λ_{jr} remains the same, likelihood values returned
206 by the Poisson part of (4) remain the same (which also increases the speed of calculating the
207 acceptance probability for the RJ step since only the normal densities need to be evaluated).

208 2.2. RJ updating methods using hierarchical centering

209 To demonstrate how to implement hierarchical centering, we use a simple example where
210 during the between-model move of iteration $t + 1$ we propose to include covariate x_1 into an
211 intercept-only model, say model m . Suppose that at iteration t the current state of the chain is
212 model m , where $\lambda_{jr} = \exp(b_j)$ with $b_j \sim N(\mu_j = \beta_0, \sigma_b^2)$ from (3) (although if x_1 is the only
213 covariate available, $K = 1$ and (2) and (3) are equivalent). During iteration $t + 1$ we propose to
214 move to model m' by adding covariate x_1 . Hence, model m' is defined as $\lambda'_{jr} = \exp(b'_j)$ with
215 $b'_j \sim N(\mu'_j = \beta'_0 + x_{1j}\beta'_1, \sigma_b'^2)$. For simplicity, let us assume that covariate x_1 represents a cat-

216 egorical covariate with only two levels where the first level is absorbed in the intercept β'_0 and
 217 the second level has an associated coefficient β'_1 ; hence, x_1 is either 0 for the first level or 1 for
 218 the second level. We note that these methods also apply in the case that the covariate used for
 219 centering has more than two factor levels. Let us further assume that all measurements within a
 220 group j belong to the same level of x_1 and that, for simplicity, we have 200 groups where groups
 221 $j = 1, \dots, 100$ belong to the first level of x_1 and groups $j = 101, \dots, 200$ belong to the second level
 222 of x_1 . We use the identity function as the bijective function (King et al., 2010):

$$u'_0 = \beta_0, \quad \beta'_0 = u_0, \quad \beta'_1 = u_1 \quad (5)$$

223 and draw samples u from the respective proposal distributions for the parameters β'_0 and β'_1 . See
 224 Appendix A for further details.

225 In the following, we describe two different ways for implementing the RJ step. The difference
 226 between them lies in the definition of the proposal distributions for the new parameters for the
 227 between-model move, and, hence, should only have an influence on the acceptance probability
 228 of this move. The second approach (Section 2.2.2) uses more information compared to the first
 229 (Section 2.2.1) and should, on average, return higher acceptance rates for this move. Either method
 230 should not have an influence on estimated posterior summary statistics of the parameters in the final
 231 model given that the chain had an adequate burn-in.

232 2.2.1. Hierarchical centering using predefined proposal distributions

233 For this method, we define proposal distributions for the coefficients β_0 , β'_0 and β'_1 . If, for
 234 example, normal proposal distributions are used, we define the proposal distributions for coeffi-
 235 cients β'_1 as $\beta'_1 \sim N(\mu'_1, \sigma'^2_1)$, for some predefined μ'_1 and σ'_1 . Equivalently, the normal proposal
 236 distributions for the intercepts β_0 and β'_0 are defined as $\beta_0 \sim N(\mu_0, \sigma_0^2)$ and $\beta'_0 \sim N(\mu'_0, \sigma'^2_0)$
 237 (for some predefined μ_0 , σ_0 , μ'_0 and σ'_0).

238 2.2.2. Hierarchical centering using updated proposal distributions

239 Here, the mean μ_0 of the proposal distribution for the global intercept β_0 of model m and the
 240 means μ'_0 and μ'_1 of the proposal distributions for the coefficients β'_0 and β'_1 of model m' are updated
 241 before the RJ step during each iteration of the RJMCMC algorithm. To update μ_0 at iteration

242 $t + 1$, we take the overall mean \bar{b}_j^t of the current values of all random effect coefficients b_j^t (i.e.
243 $\beta_0^{t+1} \sim N(\mu_0^{t+1} = \bar{b}_j^t, \sigma_0^2)$ including groups $j = 1, \dots, 200$). To update the μ_1' at iteration $t + 1$, we
244 take the mean \bar{b}_j^t of the random effect coefficients from iteration t belonging to the second level of
245 covariate x_1 . Hence, we have $\beta_1^{t+1} \sim N(\mu_1^{t+1} = \bar{b}_j^t, \sigma_1'^2)$ only including groups $j = 101, \dots, 200$.
246 To update μ_0' at iteration $t + 1$, we take the mean \bar{b}_j^t of all random effect coefficients belonging to
247 the first level of covariate x_1 (i.e. groups $j = 1, \dots, 100$).

248 3. Case study: point transects of indigo buntings

249 3.1. The data

250 To establish the success of planting herbaceous buffers around agricultural fields in several
251 South-eastern and Midwestern US states, point transect surveys were conducted from a large num-
252 ber of randomly selected fields during the breeding season (May–July) of 2006–2007 in each
253 participating state (Fig. Appendix B, Oedekoven et al., 2013). Survey points on control fields
254 of the same agricultural use and located within 1–3km were surveyed concurrently. Each pair
255 of adjacent points from a treated and control field was considered a site. Points were located at
256 the edge of the fields. Observers recorded all male indigo buntings (all singles) detected either
257 visually or aurally during a 10-minute count at each point in one of five predetermined distance
258 intervals (0–25, 25–50, 50–100, 100–250, 250–500 and >500m). It is assumed that indigo
259 buntings distribute themselves evenly within and in the various possible habitats adjacent to the
260 field. Only those sites that were surveyed at least once in each survey year were included in the
261 analysis. These 446 sites were located in nine states: Georgia, Iowa, Illinois, Kentucky, Missouri,
262 Mississippi, Ohio, South Carolina and Tennessee.

263 3.2. Methods

264 As the models from (1) to (3) assume perfect detection on the plot, we needed to supplement
265 these with a model to adjust counts for imperfect detection. We used the methods described in
266 Oedekoven et al. (2014): a detection function was fitted to the frequency of detections in each
267 distance bin. This detection function was used to estimate the effective area, ν (the area beyond
268 which as many birds were seen as were missed within, Fig. Appendix B), which was incorporated
269 into the log-linear Poisson model for the counts as an offset (Buckland et al., 2001). The full model

270 consisted of the likelihood component for the detection function and the likelihood component for
 271 the counts (see Oedekoven et al., 2014 for details). In addition, we extended the count model to
 272 include a subscript p to denote the two points at each site. With the offset included, the full model
 273 without hierarchical centering from (1) became:

$$\lambda_{jpr} = \exp \left(\beta_0 + \mathbf{x}'_{1j} \boldsymbol{\beta}_1 + \sum_{k=2}^K x_{kjpr} \beta_k + b_j + \ln(\nu) \right), \quad b_j \sim N(\mu_j = 0, \sigma_b^2). \quad (6)$$

274 Site was used as the grouping factor for the random effect. Available covariates were *state* (\mathbf{x}_1 , a
 275 factor with nine levels), *year* (x_2 , factor with two levels: 2006 and 2007, corresponding to $x_2 = 0$
 276 and $x_2 = 1$, respectively), *Julian day* (x_3 , discrete with observed integers ranging from 142 to 211)
 277 and *type* (x_4 , factor with two levels: control ($x_4 = 0$) or treatment ($x_4 = 1$) plot). Factor covariate
 278 *state* is represented by a vector \mathbf{x}_{1j} of length 8 either with eight entries zero for observations from
 279 state Georgia – as the coefficient of the baseline state is absorbed in the intercept – or with seven
 280 entries zero, and one 1, indicating which state site j was in, and $\boldsymbol{\beta}_1$ is a column vector of eight
 281 coefficients. Note that similar to (2) we omitted the subscripts r and p for covariate \mathbf{x}_1 since the
 282 values for this covariate were the same for all observations in group j . Furthermore, we did not
 283 include a subscript for the effective area ν as, for simplicity, we only considered global detection
 284 functions, i.e. without stratification or covariates in the detection model. Hence, given a model
 285 and parameter value(s) for the detection function, estimates of the effective area ν were the same
 286 for all counts. As *state* was the only covariate with consistent values for all measurements within
 287 a given site, we were limited to using only one covariate within the hierarchical centering (i.e.
 288 corresponding to (2)). With hierarchical centering using the *state* covariate, \mathbf{x}_1 , the full model
 289 from (2) became:

$$\lambda_{jpr} = \exp \left(\sum_{k=2}^K x_{kjpr} \beta_k + b_j + \ln(\nu) \right), \quad b_j \sim N(\mu_j = \beta_0 + \mathbf{x}'_{1j} \boldsymbol{\beta}_1, \sigma_b^2). \quad (7)$$

290 To estimate parameters of both the detection function ($\boldsymbol{\theta}$) and the count model ($\boldsymbol{\beta}, \sigma_b$) in one step,
 291 we combined the likelihood components pertaining to the respective models using the combined
 292 likelihood, $L_{n,y}(\boldsymbol{\beta}, \sigma_b, \boldsymbol{\theta}) = L_{yG}(\boldsymbol{\theta}) L_n(\boldsymbol{\beta}, \sigma_b | \boldsymbol{\theta})$ described by Oedekoven et al. (2014). In com-
 293 parison to (4), $L_n(\boldsymbol{\beta}, \sigma_b | \boldsymbol{\theta})$ is conditional on detection function parameters $\boldsymbol{\theta}$ when including the

294 effective area as an offset in (6) or (7). The data contained $J = 446$ sites. R_j , the maximum
 295 number of visits to a site, ranged from 2 to 8 between sites as each site was visited 1-4 times in
 296 each of the two survey years. As each site contained two points, we extended (4) accordingly:

297

$$L_n(\boldsymbol{\beta}, \sigma_b | \boldsymbol{\theta}) = \prod_{j=1}^{446} \left(\prod_{p=1}^2 \prod_{r=1}^{R_j} \frac{(\lambda_{jpr})^{n_{jpr}} \exp(-\lambda_{jpr})}{n_{jpr}!} \times \frac{1}{\sqrt{2\pi\sigma_j^2}} \exp\left(-\frac{(b_j - \mu_j)^2}{2\sigma_j^2}\right) \right). \quad (8)$$

298 As distances were recorded in intervals (rather than exact distances), the likelihood for the detection
 299 function component, $L_{yG}(\boldsymbol{\theta})$ was defined as the multinomial likelihood where f_i represents the
 300 probability that a detected animal is in the i th distance interval (for details on calculating the f_i s
 301 see Appendix B):

$$L_{yG}(\boldsymbol{\theta}) = \left(\frac{n!}{\prod_{i=1}^I n_i!} \right) \prod_{i=1}^I f_i^{n_i}. \quad (9)$$

302 Here, n represents the total number of detected animals and n_i the number of animals detected in
 303 the i th distance interval. As detection probabilities generally dropped below 0.1 beyond 100m, we
 304 limited the analysis to the three innermost distance intervals (0–25, 25–50, 50–100m).

305 For the detection models, we considered the half-normal and hazard-rate key functions as the
 306 two (non-nested) model options (Buckland et al., 2001). For the count model, we considered
 307 all possible combinations of the covariates *year*, *type*, *Julian day* and *state*. We ran two different
 308 analyses on the same data. For the first analysis we used “regular” RJMCMC methods with a global
 309 zero-mean random effect (as shown in (6)) which we refer to as the global zero-mean analysis
 310 (GZM).

311 For the second analysis we implemented hierarchical centering by pulling the intercept β_0 and
 312 covariate *state* from the λ_{jpr} model and included them in the model for the random effect mean
 313 (as shown in (7)). This analysis will be referred to as HC in the following. We used predefined
 314 proposal distributions for all parameters. These were the same for both analyses (see Table B.1).

315 Prior model probabilities were equal and the identity function similar to (5) used for the bijec-
 316 tive function of any proposed move. For both analyses, we placed the same set of uniform priors
 317 on the parameters (Table B.1).

318 For each analysis, the chain was started from the most parsimonious models: the half-normal

319 detection function and a count model containing the fixed effect intercept and a random effect for
320 site. We ran 200 000 iterations for each analysis, the first 20 000 were considered as the burn-in
321 phase. The effective sample size was calculated for each parameter in the preferred model using
322 the function *effectiveSize* from the R package *coda*. We express it as the effective sample size per
323 1000 iterations that the chain was in the preferred model to make this quantity comparable between
324 the results of different methods.

325 3.3. Results

326 The preferred detection model was the hazard-rate function with posterior probability of 1.00
327 for both analyses (Table B.2). Estimated probabilities for the count models differed between the
328 methods. For GZM, the preferred count model included the covariates *type* and *Julian day* with
329 probability 0.85. The alternative model included the additional covariate *year* and was selected
330 during the remaining 15% of the iterations. The covariate *state* was never included in any of
331 the models for this method. By contrast, all models included *state* for HC. The preferred model
332 included *type*, *Julian day* and *state* (0.95 probability) and the second most preferred model included
333 *type*, *Julian day*, *year* and *state* (0.05 probability).

334 While the probabilities of being in the model were similar for the covariates *year*, *Julian day*
335 and *type* between the two analyses, the probability of *state* being in the model was 0.00 for GZM
336 and 1.00 for HC. To investigate further, we used a range of different initial starting values and
337 models to assess convergence. In particular, when we initialised the chain so that *state* was in
338 the initial model for the GZM analysis, the posterior probability for *state* was 1.00. Repeated
339 simulations provided the same output with *state* not being updated in GZM. Hence, for GZM
340 the resulting model probabilities were conditional on the model that the chain was started with.
341 In contrast, consistent results were obtained for the HC analysis, irrespective of initial values or
342 initial model choice of the Markov chain.

343 Summary statistics for the parameters resulting from both GZM analyses (started with and
344 without *state*) and the HC analysis are given in Table B.3. Means and 95% credible intervals
345 (CRI) were nearly identical between all methods for the parameters of the hazard-rate detection
346 function. Means and 95% CRIs were also similar for the count model parameters between the three
347 methods, given that the parameters were in the model. Although means for parameter *Julian day*

348 varied, CRIs overlapped between all three methods. The exception was the random effect standard
349 deviation of the count model which was very different for GZM started without *state* compared
350 to the other two analyses. The mean was larger for GZM without *state* and CRIs did not overlap
351 those of the other two methods. This was likely due to the random effects coefficients absorbing
352 the *state* effect.

353 We refrain from including the GZM without *state* analysis in the comparison of effective sam-
354 ple sizes as here, due to non-convergence, the posterior distribution differed from the other two
355 analyses (GZM with *state* and HC). The effective sample sizes for detection function parameters
356 were similar between all the GZM with *state* and HC analyses (Table B.4). Effective sample sizes
357 for count model parameters were generally smaller for HC compared to GZM with *state* except
358 for the random effect standard deviation and the intercept. It was notable that the effective sample
359 sizes for the *state* coefficients were consistently at least two times but up to over 12 times larger for
360 GZM with *state* compared to HC. The only notable increase in effective sample size from GZM
361 with *state* to HC was for the random effects standard deviation with 2.46 for GZM with *state* and
362 8.54 for HC.

363 4. Simulation study

364 The following simulation study was used to investigate whether our proposed methods would
365 consistently improve model mixing. In particular, for a covariate with nested random effects that
366 was part of creating the pattern in the response variable, we investigated whether posterior model
367 probabilities would differ between hierarchical centering and regular RJMCMC methods. Using
368 (2), we simulated 300 data sets of approximately 500 observations each that were similar to our
369 case study. The response variable followed a Poisson distribution for which the expected value λ_{jr}
370 was modelled as a function of a linear term, say *Julian day* x_2 , and random effects coefficients,
371 b_j for the j th site. The b_j were simulated using a factor covariate with five levels, say *state* \mathbf{x}_1
372 (with four associated coefficients β_1 randomly drawn from a uniform distribution, $U(-2.6, 0.8)$,
373 during each simulation and the coefficient of the first level absorbed in the intercept β_0), to model
374 the mean μ_j of their normal distribution, $b_j \sim N(\mu_j = \beta_0 + \mathbf{x}'_{1j}\beta_1, \sigma_b^2)$ and the random effects
375 standard deviation $\sigma_b = 0.7$. Sites were nested within states with 25 – 35 sites per state and repeat
376 observations (2 – 6, subscript r) per site. We also created a dummy variable, a factor covariate

377 with eight levels which was not part of the model for generating the response. Similar to x_1 , this
378 dummy variable had constant levels within each random effect group. However, the levels of the
379 dummy variable to which random effects groups were attributed were chosen at random and did
380 not match the pattern for attributing random effects groups to levels of x_1 .

381 Each data set was analysed using two different approaches equivalent to GZM without *state*
382 and the HC methods above. The former refers to “regular” RJMCMC methods with a global zero-
383 mean random effect (as shown in (1)). The latter refers to hierarchical centering methods where
384 the intercept β_0 , *state* and the dummy variable were included in the model for the random effect
385 mean (as shown in (3)).

386 The RJMCMC analyses for each data set were initiated with the models for λ_{jr} and μ_j that
387 only contained the intercept and random effects coefficients between the two models combined
388 and the chains for both analysis methods had the same initial coefficient values. Both approaches
389 used the same proposal distributions for new parameter values, the same mechanism for updating
390 the model, i.e. proposing to add or delete covariates depending on whether it was currently in the
391 model (including the dummy variable), and the same MH algorithm for updating parameter values.
392 Each analysis included 100 000 iterations where the first 10 000 were considered burn-in.

393 For the GZM without *state* analysis, posterior probabilities of *state* being in the model were 0
394 for all 300 data sets. By contrast, posterior probabilities of *state* being in the model for the HC anal-
395 ysis were on average 0.94 (95% CRI = {0.62,1.00}) across all 300 data sets. The random effects
396 standard deviation was generally overestimated for those models without *state*, i.e. those iterations
397 of the HC analysis where *state* was not in the model (posterior distribution mean 0.92, 95% CRI
398 = {0.69,1.24}) and for all models from the GZM analysis (0.96, {0.71,1.32}). By contrast, for
399 those models with *state* from the HC analysis, the posterior distribution of this parameter (0.66,
400 {0.49,0.88}) was more accurate with a mean closer to the known true value 0.7. The marginal
401 posterior probability that the dummy variable was included in the model was zero for all 300 data
402 sets and both analysis methods.

403 5. Discussion

404 The purpose of incorporating random effects in count models is generally to model variation
405 that is otherwise unaccounted for. When using RJMCMC methods, the danger exists that the

406 random effect coefficients account for too much of the variation and prevent the inclusion of a
407 fixed effect covariate into the model – a problem that is not limited to the linear predictor for the
408 Poisson distribution. We demonstrated this case with our GZM analysis that was initiated without
409 *state* in the model. Due to poor mixing (between models) leading to lack of convergence, the
410 covariate *state* was never selected. This would have led to incorrect inference as the sampled
411 values are not from the posterior distribution due to poor mixing. In addition, for this analysis
412 the resulting random effect standard deviation was much larger compared to the HC analysis of
413 the same data. Both these findings, the poor model mixing and inflated random effects standard
414 deviation for the GZM analysis, were confirmed by our simulation study.

415 For the HC analysis of the case study, the model was also initiated without *state* but revealed
416 posterior probabilities of *state* being in the model of 1.00. Furthermore, the mean and 95% CRI of
417 the random effects standard deviation were smaller compared to the GZM without *state* analysis.
418 Both these findings were again confirmed by our simulation study. For both analyses of the case
419 study that were initiated without *state* in the model, GZM and HC, the random effect coefficients
420 absorbed the effect of the *state* covariate. For GZM, this prevented the inclusion of this parameter
421 into the model. For HC, this favoured the inclusion of *state* into the model as here this covariate
422 was part of the model for the random effect mean. Here, the chain was able to explore models with
423 *state* as a covariate due to improved mixing between models.

424 Unsurprisingly, implementing hierarchical centering had little effect on the remaining covari-
425 ates in the model as these were not involved in the centering. However, we could not confirm
426 the findings of Browne (2004), that implementing hierarchical centering would improve the ef-
427 fective sample size for the covariate involved in the centering. He compared the effective sample
428 sizes for the same covariate in two different MCMC chains, one with hierarchical centering and
429 one without. For our case study, effective sample sizes for coefficients involved in the centering
430 were mostly larger for GZM with *state* compared to HC except for the intercept and the random
431 effect standard deviation where, using hierarchical centering, the effective sample size increased
432 3.47-fold.

433 Overall we showed that implementing hierarchical centering in the context of RJMCMC algo-
434 rithms improves mixing between models and, hence, improves the inference on model parameters.
435 For our case study, summary statistics for covariates not involved in the centering were nearly

436 identical between the GZM and the HC analyses. However, inference on the *state* covariate using
437 the GZM analysis could potentially have led us to believe falsely that this covariate had no effect
438 on densities of indigo buntings.

439 **Acknowledgements**

440 The National CP-33 Monitoring Program was funded by the Multistate Conservation Grant
441 Program (Grant MS M-1-T), which is supported by the Wildlife and Sport Fish Restoration Pro-
442 gram and managed by the Association of Fish and Wildlife Agencies and US Fish and Wildlife
443 Service. Further support was provided by the US Department of Agriculture (USDA) Farm Ser-
444 vice Agency and USDA Natural Resources Conservation Service Conservation Effects Assessment
445 Project. Collaborators included the AR Game and Fish Commission, GA Department of Natural
446 Resources (DNR), IL DNR/Ballard Nature Center, IN DNR, IA DNR, KY Department of Fish and
447 Wildlife Resources/KY Chapter of The Wildlife Society, MS Department of Wildlife, Fisheries
448 and Parks, MO Department of Conservation, NE Game and Parks Commission, NC Wildlife Re-
449 sources Commission, OH DNR, SC DNR, TN Wildlife Resources Agency, TX Parks and Wildlife
450 Department, Southeast Quail Study Group and Southeast Partners In Flight. The first author was
451 supported by a studentship jointly funded by the University of St Andrews and EPSRC, through
452 the National Centre for Statistical Ecology (EPSRC grant EP/C522702/1), with subsequent funding
453 from EPSRC/NERC grant EP/1000917/1. We thank Prof. William Browne, University of Bristol,
454 for inspiring the presented methods and for commenting on a draft manuscript.

455 **Appendix A. RJMCMC algorithm**

456 In general, the posterior distribution $\pi(\delta_m, m|x)$ is given as the distribution encompassing the
457 joint posterior distribution of models and parameters (Green, 1995; King et al., 2010) with:

$$\pi(\delta_m, m|x) \propto L(x|\delta_m, m)p(\delta_m|m)p(m). \quad (\text{A.1})$$

458 Here, $L(x|\delta_m, m)$ is the probability density function of the data x conditional on model m with
459 current parameter values δ_m , $p(\delta_m|m)$ is the prior probability for model parameters δ_m conditional
460 on the chain being in model m , and $p(m)$ is the prior probability of model m .

461 Suppose that we propose to move from model m with parameters δ_m to model m' with param-
 462 eters $\delta'_{m'}$ during the between-model move (RJ step) of an RJMCMC algorithm. We define u and
 463 u' as random samples from some proposal distribution for the respective parameters. To transform
 464 parameters δ_m into $\delta'_{m'}$ we use a bijective function which may have the form $(\delta'_{m'}, u') = g(\delta_m, u)$.
 465 Then, the acceptance probability is given by $\min(1, A)$ where A can be expressed as:

$$A = \frac{\pi(\delta'_{m'}, m'|x)P(m|m')q'(u')}{\pi(\delta_m, m|x)P(m'|m)q(u)} \left| \frac{\partial g(\delta_m, u)}{\partial(\delta_m, u)} \right|. \quad (\text{A.2})$$

466 $P(m'|m)$ is the probability of proposing to move to model m' given that the chain is in model m ,
 467 $q(u)$ and $q'(u')$ are the proposal densities of u and u' . $\left| \frac{\partial g(\delta_m, u)}{\partial(\delta_m, u)} \right|$ is the Jacobian.

468 For the within-model move (the MH step) of the RJMCMC algorithm we use a random walk
 469 single-update Metropolis-Hastings algorithm (Hastings, 1970; Metropolis et al., 1953).

470

471 Appendix B. The detection function component

472 To calculate the offset for (6) and (7), we used the probability density function of observed
 473 distances, $f(y) = \pi(y)g(y) / \int_0^w \pi(y)g(y)dy$, where w is the truncation distance (Buckland et al.,
 474 2001). The function describing the distribution of birds is given for points by $\pi(y) = 2y/w^2$ and
 475 the detection function is given by $g(y)$. We included two detection functions as model options in
 476 the RJMCMC algorithm, the half-normal ($g(y) = \exp(-y^2/2\sigma^2)$) and the hazard-rate ($g(y) = 1 -$
 477 $\exp(-(y/\sigma)^{-\tau})$). When using interval distance data (as opposed to exact distance measurements),
 478 f_i is defined as the probability that a detected animal is in the i th interval which is delineated by
 479 the cutpoints c_{i-1} and c_i and is given by:

$$f_i = \frac{\int_{c_{i-1}}^{c_i} f(y) dy}{\int_0^w f(y) dy}, \quad (\text{B.1})$$

480 where the truncation distance, w corresponds to the outermost cutpoint. The f_i feed into the like-
 481 lihood component given in (9). $g(y)$ is also used to calculate the effective area, which for points is
 482 given by $\nu = 2\pi \int_0^w yg(y)dy$.

483 **Literature cited**

- 484 Al-Awadhi, F., Hurn, M., Jennison, C., 2004. Improving the acceptance rate of reversible jump
485 MCMC proposals. *Statistics & Probability Letters* 69, 189–198.
- 486 Bates, D., 2009. Computational methods for mixed models. R package version 0.999375-31. Tech.
487 rep., <http://lme4.r-forge.r-project.org/>.
- 488 Brooks, S. P., Giudici, P., Roberts, G. O., 2003. Efficient construction of reversible jump Markov
489 chain Monte Carlo proposal distributions. *Journal of the Royal Statistical Society B* 65(1), 3–55.
- 490 Browne, W. J., 2004. An illustration of the use of reparameterisation methods for improving
491 MCMC efficiency in crossed random effect models. *Multilevel Modelling Newsletter* 16, 13–25.
- 492 Browne, W. J., Steele, F., Golalizadeh, M., Green, M. J., 2009. The use of simple reparameteriza-
493 tions to improve the efficiency of Markov chain Monte Carlo estimation for multilevel models
494 with applications to discrete time survival models. *Journal of the Royal Statistical Society A* 172
495 (3), 579–598.
- 496 Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., Thomas, L., 2001.
497 *Introduction to Distance Sampling*. Oxford University Press.
- 498 Davison, A. C., 2003. *Statistical Models*. Cambridge University Press.
- 499 Forster, J. J., Gill, R. C., Overstall, A. M., 2012. Reversible jump methods for generalised linear
500 models and generalised linear mixed models. *Statistics and Computing* 22 (1), 107–120.
- 501 Gelfand, A. E., Sahu, S. K., Carlin, B. P., 1995. Efficient parametrisations for normal linear mixed
502 models. *Biometrika* 82 (3), 479–488.
- 503 Green, P. J., 1995. Reversible Jump Markov chain Monte Carlo computation and Bayesian model
504 determination. *Biometrika* 82(4), 711–732.
- 505 Green, P. J., Mira, A., 2001. Delayed rejection in reversible jump Metropolis-Hastings. *Biometrika*
506 88(4), 1035–1053.

- 507 Hastings, W. K., 1970. Monte Carlo sampling methods using Markov Chains and their applica-
508 tions. *Biometrika* 57(1), 97–109.
- 509 King, R., Morgan, J., Gimenez, O., Brooks, S., 2010. *Bayesian Analysis for Population Ecology*.
510 CRC Press.
- 511 Komárek, A., Lesaffre, E., 2008. Generalized linear mixed model with a penalized Gaussian mix-
512 ture as a random effects distribution. *Computational Statistics and Data Analysis* 52, 3441–3458.
- 513 McCulloch, E. C., Searle, S. R., 2001. *Generalized, Linear, and Mixed Models*. John Wiley &
514 Sons, Inc.
- 515 Metropolis, N., Rosenbluth, A. W., Rosenbluth, M. N., Teller, A. H., Teller, E., 1953. Equations of
516 state calculations by fast computing machines. *Journal of Chemical Physics* 21, 1087–1091.
- 517 Oedekoven, C. S., Buckland, S. T., Mackenzie, M. L., Evans, K. O., Burger, L. W., 2013. Improv-
518 ing distance sampling: accounting for covariates and non-independency between sampled sites.
519 *Journal of Applied Ecology* 50(3), 786–793.
- 520 Oedekoven, C. S., Buckland, S. T., Mackenzie, M. L., King, R., Evans, K. O., Burger, L. W.,
521 2014. Bayesian methods for hierarchical distance sampling models. *Journal of Agricultural,*
522 *Biological, and Environmental Statistics* 19 (2), 219–239.
523 URL <http://dx.doi.org/10.1007/s13253-014-0167-0>
- 524 Papaspiliopoulos, O., Roberts, G. O., Sköld, M., 2007. A general framework for the parametriza-
525 tion of hierarchical models. *Statistical Science* 22 (1), 5973.
- 526 Papathomas, M., Dellaportas, P., Vasdekis, V. G. S., 2011. A novel reversible jump algorithm for
527 generalized linear models. *Biometrika* 98 (1), 231–236.
- 528 Vines, S. K., Gilks, W. R., Wild, P., 1995. Fitting multiple random effects models. Tech. rep., MRC
529 Biostatistics Unit, Cambridge.

530 **List of Figures**

531 B.1 Left: Distribution of surveys conducted as part of the CP-33 Monitoring Program
532 between 2006-20011 (source: <http://www.fwrc.msstate.edu/bobwhite/monitoring/index.asp>).
533 Right: frequency of detections in the three distance bins (0–25, 25–50, 50–100m)
534 as rescaled blue histogram bars; probability density of observed distances (PDF)
535 using means from the posterior distribution of parameters of the hazard-rate detec-
536 tion function (see Table B.3, black line); the slope of the red line is the slope of
537 the PDF at distance zero; ρ is the radius of the effective area ν ; the red polygon
538 represents the proportion of birds missed within ρ and is equal in size to the
539 green polygon which represents the proportion of birds detected between ρ and
540 the truncation distance w of 100m (Buckland et al., 2001). See Appendix B for
541 more details. 23

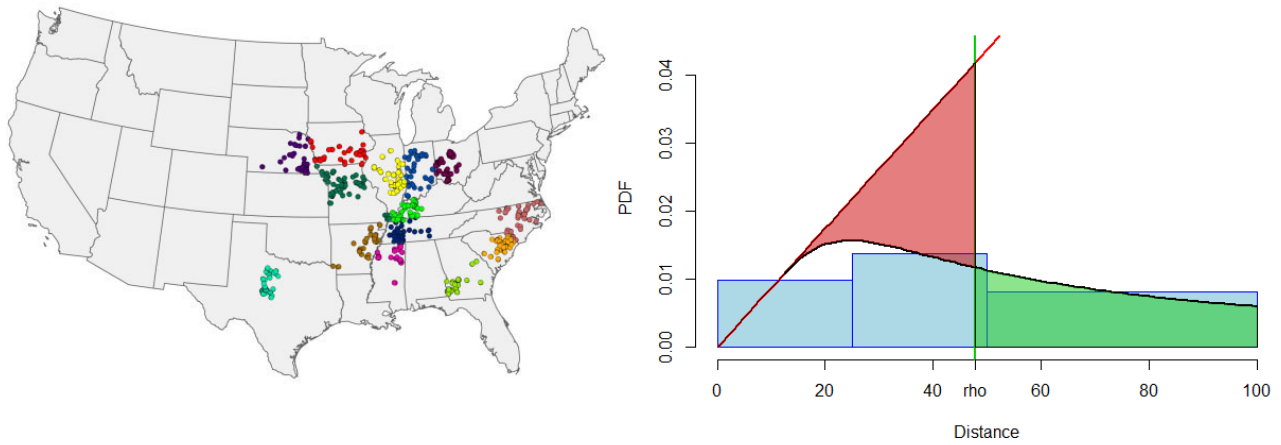


Figure B.1: Left: Distribution of surveys conducted as part of the CP-33 Monitoring Program between 2006-2011 (source: <http://www.fwrc.msstate.edu/bobwhite/monitoring/index.asp>). Right: frequency of detections in the three distance bins (0–25, 25–50, 50–100m) as rescaled blue histogram bars; probability density of observed distances (PDF) using means from the posterior distribution of parameters of the hazard-rate detection function (see Table B.3, black line); the slope of the red line is the slope of the PDF at distance zero; ρ is the radius of the effective area ν ; the red polygon represents the proportion of birds missed within ρ and is equal in size to the green polygon which represents the proportion of birds detected between ρ and the truncation distance w of 100m (Buckland et al., 2001). See Appendix B for more details.

542 **List of Tables**

543 B.1 Means and standard deviations (SD) of normal proposal distributions for model
544 parameters as well as lower and upper boundaries for uniform prior distributions
545 for model parameters. HN and HR refer to the half-normal and the hazard-rate
546 detection functions respectively. We note that the random effect standard deviation
547 and the intercept for the count model were always in the model. 25

548 B.2 Posterior model probabilities for the analyses of the indigo bunting data. Shown
549 are results from the GZM analysis (global zero-mean for the random effect) and
550 results from the HC (hierarchical centering) analysis. Both analyses were started
551 without *state* in the initial model. 26

552 B.3 Mean and 95% credible intervals for models with highest posterior support from
553 the analyses of the indigo bunting data. Results are from the analyses GZM (global
554 zero-mean) started without *state*, GZM started with *state* and HC (hierarchical cen-
555 tering) started without *state*. For models with *state*, the *state* level GA is absorbed
556 in the intercept. 27

557 B.4 Effective sample sizes per 1000 iterations that the chain was in the respective pre-
558 ferred model for model parameters from the analyses of the indigo bunting data:
559 GZM (global zero-mean) with *state* in the initial model and HC (hierarchical cen-
560 tering). 28

Table B.1: Means and standard deviations (SD) of normal proposal distributions for model parameters as well as lower and upper boundaries for uniform prior distributions for model parameters. HN and HR refer to the half-normal and the hazard-rate detection functions respectively. We note that the random effect standard deviation and the intercept for the count model were always in the model.

Parameters	Mean	SD	Lower	Upper
Detection Function Parameters				
Scale HN:	37	2	10	99
Scale HR:	28	2	10	99
Shape HR:	2	1	1	10
Count Model Parameters				
Random effect standard deviation	–	–	0	1
Intercept:	–	–	-20	-7
Year level: 2007	0.05	0.2	-1	1
Type level: Treated	0.3	0.1	0	1
Julian Day:	0.0055	0.003	-0.1	0.1
State level: IL	0.4	0.5	-2.5	2.5
State level: IN	0.3	0.5	-2.5	2.5
State level: KY	0.7	0.5	-2.5	2.5
State level: MO	0	0.5	-2.5	2.5
State level: MS	0.5	0.5	-2.5	2.5
State level: OH	0	0.5	-2.5	2.5
State level: SC	0.2	0.5	-2.5	2.5
State level: TN	0.8	0.5	-2.5	2.5

Table B.2: Posterior model probabilities for the analyses of the indigo bunting data. Shown are results from the GZM analysis (global zero-mean for the random effect) and results from the HC (hierarchical centering) analysis. Both analyses were started without *state* in the initial model.

Analysis	GZM	HC
Detection Model		
CDS: Hazard-rate key	1.000	1.000
Count Model		
Type + JD	0.851	0.000
Year + Type + JD	0.149	0.000
Type + JD + State	–	0.946
Year + Type + JD + State	–	0.054

Table B.3: Mean and 95% credible intervals for models with highest posterior support from the analyses of the indigo bunting data. Results are from the analyses GZM (global zero-mean) started without *state*, GZM started with *state* and HC (hierarchical centering) started without *state*. For models with *state*, the *state* level GA is absorbed in the intercept.

Analysis	GZM without <i>state</i>	GZM with <i>state</i>	HC
Detection Model Parameters			
Scale HR σ	28.20 (25.03,31.25)	28.21 (24.77,31.23)	28.05 (25.00,31.04)
Shape τ	2.08 (1.92,2.26)	2.08 (1.91,2.26)	2.08 (1.92,2.25)
Count Model Parameters			
Random effect standard deviation σ_b	0.77 (0.65,0.91)	0.58 (0.49,0.68)	0.51 (0.45,0.57)
Intercept β_0	-10.62 (-11.21,-10.13)	-10.76 (-11.25,-10.29)	-10.44 (-10.97,-10.01)
Type level: Treated β_4	0.31 (0.24,0.37)	0.31 (0.24,0.37)	0.30 (0.24,0.37)
Julian Day β_3	0.008 (0.006,0.012)	0.006 (0.003,0.009)	0.004 (0.002,0.007)
State level: IL $\beta_{1_{IL}}$	-	0.88 (0.54,1.23)	0.97 (0.63,1.32)
State level: IN $\beta_{1_{IN}}$	-	0.70 (0.36,1.06)	0.79 (0.45,1.14)
State level: KY $\beta_{1_{KY}}$	-	1.16 (0.84,1.50)	1.24 (0.90,1.57)
State level: MO $\beta_{1_{MO}}$	-	0.27 (-0.02,0.58)	0.35 (0.04,0.67)
State level: MS $\beta_{1_{MS}}$	-	1.12 (0.76,1.49)	0.97 (0.64,1.31)
State level: OH $\beta_{1_{OH}}$	-	0.40 (0.08,0.71)	0.39 (0.07,0.72)
State level: SC $\beta_{1_{SC}}$	-	0.66 (0.31,1.02)	0.68 (0.32,1.04)
State level: TN $\beta_{1_{TN}}$	-	1.31 (0.98, 1.65)	1.38 (1.04,1.72)

Table B.4: Effective sample sizes per 1000 iterations that the chain was in the respective preferred model for model parameters from the analyses of the indigo bunting data: GZM (global zero-mean) with *state* in the initial model and HC (hierarchical centering).

Parameter	GZM with <i>state</i>	HC
Detection Model		
Scale HR	5.04	4.99
Shape	6.18	5.92
Count Model		
Random effect standard deviation	2.46	8.54
Intercept	0.57	1.06
Type Treatment	71.15	64.07
Julian Day	0.58	0.26
State IL	4.15	0.64
State IN	3.63	0.69
State KY	2.58	0.42
State MO	3.38	0.28
State MS	3.30	0.57
State OH	3.54	0.39
State SC	4.41	0.69
State TN	3.74	0.52