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A Bayesian hierarchical occupancy model for track surveys conducted in a series of linear, spatially correlated, sites

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Summary

1. Natural resource agencies often rely on surveys of animal sign (e.g. scat, scent marks, tracks) for population assessment, with repeat surveys required to model and account for uncertain detection. Using river otter *Lontra canadensis* snow-track survey data as a motivating example, we develop a 3-level occupancy model with parameters that describe (i) site-level occupancy probabilities, (ii) otter movement (and thus, track availability) and (iii) recorded presence–absence of tracks (conditional on the availability of tracks for detection).

2. We incorporated several recent developments in occupancy modelling, including the presence of both false negatives and false positives, spatial and temporal correlation and repeated sampling across distinct observers.

3. We investigated optimal allocation of sampling effort (e.g. within and among snowfall events) using simulations. We also compared models that allowed site-level occupancy and track-laying processes to be spatially correlated with models that assumed independence among sites.

4. Both types of models (independence and spatial) performed well across a range of simulated parameter values, but the spatial model resulted in more accurate point estimates for detection parameters and credibility intervals with better coverage rates when data were spatially correlated. When applied to real data, the spatial model resulted in a higher estimate of the occupancy rate ($\hat{\Psi}$) than the baseline model (0·82 vs. 0·59). A minimum of 15–20 helicopter flights, distributed among at least three unique snow events, were needed to meet precision goals (standard error $\hat{\Psi} < 0{\cdot}05$).

5. *Synthesis and applications*. We describe a flexible and robust occupancy modelling framework that accounts for heterogeneous detection rates in surveys of animal sign. The method allows for spatially correlated sites and should have broad relevance to surveys conducted by many natural resource agencies.

Key-words: animal sign, Bayesian occupancy model, *Lontra canadensis*, Markov model, otter, presence–absence, snow-track surveys, simulation, spatial correlation, WinBugs

Introduction

Wildlife populations are notoriously difficult to monitor, owing to the challenges of detecting individuals and the costs of surveying difficult to reach habitat. A variety of approaches have been developed for estimating detection probabilities in wildlife surveys, including double sampling, removal methods, multiple observers, mark–recapture, distance sampling and regression models (Lancia *et al*. 2005).

These methods, however, typically require identifying and possibly marking unique individuals and are therefore difficult to reliably implement in large-scale monitoring efforts or with elusive species (Stanley & Royle 2005; Johnson 2008). As a result, survey designs that record presence or absence of animal sign (e.g. tracks, scent marks, faeces) remain popular among natural resource agencies (Stanley & Royle 2005). In particular, snow-track surveys have been used to monitor a variety of species; recent examples include Eurasian lynx *Lynx lynx* (Linnell *et al*. 2007), white-tailed deer *Odocoileus virginianus* (D'Eon 2001), red fox *Vulpes vulpes* and grey fox *Urocyon cinereoargenteus* (Stanley & Bart 1991), Amur tiger *Panthera tigris*

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altaica (Hayward *et al.* 2002) and wolverine *Gulo gulo* (Magoun *et al.* 2007; Gardner *et al.* 2010). A flurry of recent research has been devoted to developing methods, most often based on a survey design in which sites are repeatedly visited, to correct for uncertain detection in such surveys. The collection of methods for monitoring populations using repeated presence–absence surveys has come to be known as 'occupancy modelling' (MacKenzie *et al.* 2006; Royle & Dorazio 2008).

Wildlife managers in Minnesota (MN), USA, requested a monitoring tool that could be used to assess population status and trends of river otter *Lontra canadensis*. Until recently, targeted harvesting was only allowed in northern MN, but trappers had expressed interest in establishing a season in south-eastern MN in response to perceived increases in abundance (Martin *et al.* 2003). Managers were concerned that otter populations in the south-east might be smaller and more isolated and therefore more prone to overharvest. As a first step in developing a monitoring programme, we collected pilot survey data to determine sources of variation in detection of otter tracks in the snow. In addition, we developed a 3-level occupancy model for track survey data collected in the winter following snowfall events, with parameters that describe (i) site-level occupancy probabilities, (ii) otter movement (and thus, track availability) and (iii) recorded presence–absence of tracks (conditional on the availability of tracks for detection). Biological considerations, together with our survey approach, necessitated that we consider several substantive extensions to the current class of occupancy models, including the prevalence of false detections (Royle & Link 2006), spatial correlation (Magoun *et al.* 2007; Hines *et al.* 2010) and a model for how detection probabilities depend on time since a snowfall event (Stanley & Royle 2005). Together, the data and model provide a useful tool for optimizing survey design and evaluating the ability to detect the effects of management practices (e.g. increased harvest pressure, efforts to reduce wetland drainage and pollution).

Although we report on a detailed case study motivated by the need to develop a monitoring programme for river otter, we expect that our modelling approach will have widespread applicability to natural resource surveys for which the presence or absence of animal sign is recorded, as well as occupancy studies that rely on cluster sampling designs for selecting sites. Cluster designs, in particular, are popular for wildlife surveys because they provide a cost-effective means of sampling large areas (Giudice *et al.* 2010), but model-based inferences are often challenging because of spatial dependencies in the data. Our approach builds on recent applications of spatial occupancy models to track surveys (Magoun *et al.* 2007; Gardner *et al.* 2010; Hines *et al.* 2010), by incorporating a model component that accounts for the process by which tracks are laid down. Because the presence of tracks will depend on survey timing relative to the last snowfall, this approach has the potential to account for an important source of heterogeneity in the detection process.

The data we consider were collected by the Minnesota Department of Natural Resources (MNDNR) in 2003 using helicopter surveys with multiple observers, multiple sampling intervals (representing unique snowfall events) and multiple days within each sampling interval (days since the last snowfall event). Flight paths followed the main channels of river systems, which were later divided into a series of spatially contiguous quadrats (hereafter, we will refer to these quadrats as 'sites' or 'plots'). Owing to the potential for clustering of individual home ranges in space and movement across site boundaries, we expected the response, presence or absence of a recorded track, to be spatially correlated among sites. In addition, sites were more likely to contain tracks if they were sampled several days after a snowfall event. Lastly, observer-to-observer variability was significant, probably owing to measurement error associated with the post hoc creation of site boundaries (which may have resulted in tracks being assigned to the wrong site) and the difficulty of correctly identifying otter tracks (Evans *et al.* 2009). Thus, these data serve as a useful case study to illustrate methods for handling several complications that may be present in repeated presence–absence survey applications.

In addition to fitting models to the Minnesota otter data, we use extensive simulations to evaluate the robustness and precision of model-based estimates of occupancy probabilities under this sampling design. To promote learning and to facilitate adaption to other applications, we implement our approach using open source software, Program R (R Development Core Team 2009) and WinBUGS (Lunn *et al.* 2001), with the R package BRugs (Thomas *et al.* 2006) to communicate between the two software platforms. Lastly, we show how simulations can be used to compare different sampling designs, and we make recommendations regarding allocation of sampling effort in future surveys.

Materials and methods

OTTER SURVEY DATA COLLECTION

Details of the survey are given in Martin *et al.* (2003) and Martin (2007), but generally, aerial snow-track surveys were conducted using a Bell OH-58A + helicopter following snowfalls of > 2·5 cm in depth. The data discussed in this paper were collected in 2003 from the Mississippi River (Fig. 1). There were five unique snowfall events. Flights occurred 1, 2 or 3 days after each unique snowfall event, although they did not occur on every day. There were three observers, and in some cases, multiple observers flew over the river in different flights on the same day.

Surveys followed a near-linear flight path up the river (from Southeast to North-west). A total of 56·3 km of the river was flown, although seven of 20 flights only surveyed the lower half of the route. Observers collected a Global Positioning System waypoint upon encountering a track and continued to log waypoints every 5 s thereafter if a track remained present. In cases where a track was difficult to identify with certainty, the pilot circled the general area containing the track until the observer felt comfortable deciding track presence or absence. The pilot then returned to the original flight path.

After all data had been collected, the section of the Mississippi River that was flown was divided into 140 402-m segments, and the presence (1) or absence (0) of a waypoint in each segment on a given flight was determined and recorded. No attempt was made to measure effective strip widths or to determine whether detection decreased

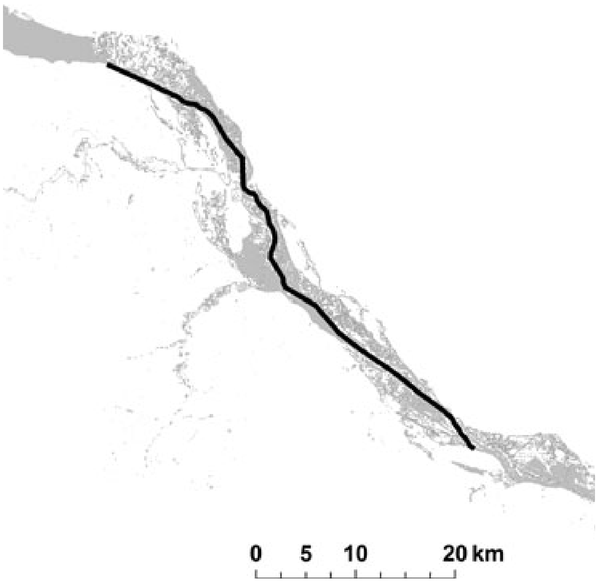

Fig. 1. Mississippi River and survey route (black line).

with distance from the flight path, although this information could easily be collected in future surveys.

MODEL DEVELOPMENT AND LIKELIHOOD FORMULATION

Fundamentally, the otter survey data consist of a set of correlated binary responses, $y_{i,j,k,l}$, arising from a set of biological (occupancy, movement) and observational (detection) processes:

$$y_{i,j,k,l} = \begin{cases} 1, & \text{if the } l\text{th observer records a track in site } i \\ & \text{on the } k\text{th day of the } j\text{th snowfall event} \\ 0, & \text{otherwise.} \end{cases}$$

We define $\psi_i = P(\text{site } i \text{ is 'occupied'})$, for $i = 1,\ldots,N$, where we consider a site to be occupied if it falls within the home range of at least one otter. Further, let z_i be an indicator of site-level occupancy status, with $z_i \sim \text{Bernoulli}(\psi_i)$. In addition, we define survey periods as consisting of the first t days after a snowfall event, but prior to a subsequent snowfall event (or other event that might erase tracks, e.g. wind or melting).

In our application, otter tracks, when present, were readily observable from the air. However, observations made by different observers on the same day were often inconsistent, and it was not uncommon for observers to record a track one day and not record a track a day later (within the same site and survey period). In addition to potential problems related to locating and correctly identifying otter sign, we suspect tracks observed near boundaries of the plots were occasionally assigned to the wrong unit. Thus, we felt it important to allow for false positives as well as false absences in our approach (Royle & Link 2006).

In developing our approach, we make the following assumptions: (i) We assume site-level occupancies, $(z_1,\ldots,z_N)$, that do not change during the course of the study. (ii) Conditional on $z_i = 1$, a track is laid down with probability θ_i on any given day following a snowfall event. (iii) Tracks remain present until the end of the survey period. (iv) Detection probabilities do not depend on how many tracks are laid down. That is, the probability of detecting a track is the same if tracks are laid down on a single day or on multiple days within a survey period. We revisit this assumption in the discussion. (v) Conditional on the presence or absence of a track, correct detection and false detection probabilities (p_l and e_l, respectively) vary by observer, but they are constant across sites and sampling instances. (vi) Conditional on true presence or absence of a track, observations made by different observers are independent. (vii) Conditional on true presence or absence of a track, observations made by the same observer (on different sampling dates) are independent. In other words, observers are not influenced by having flown the river on a prior date.

Construction of the likelihood of the data is difficult because of the dependencies arising from the latent occupancy and track-laying processes. For example, consider one site (i), surveyed by a single observer during each of the first 3 days of a survey period. Suppose the observer records a track the first and third days but no track the second day. We denote this outcome as 1-0-1. There are five possible events that could have produced this data vector, as seen by conditioning on the occupancy of the site and whether or not a track was laid down on a particular day. Thus, the probability for outcome 1-0-1 is the sum of the following five terms:

1. $\psi_i\theta_i p(1-p)p$ (site is occupied, track was laid on first day, and correctly recorded on the first and third days, and not recorded on the second day).
2. $\psi_i(1-\theta_i)\theta_i e(1-p)p$ (site is occupied, track was first laid on second day, and falsely recorded on first day, not recorded on the second day, and correctly recorded on third day).
3. $\psi_i(1-\theta_i)^2\theta_i e(1-e)p$ (site is occupied, track was first laid on third day, and falsely recorded on first day, not falsely recorded on second day, and correctly recorded on the third day).
4. $\psi_i(1-\theta_i)^3 e(1-e)e$ (site is occupied, no track was laid, and falsely recorded on first and third days, and not falsely recorded on second day).
5. $(1-\psi_i)e(1-e)e$ (site is not occupied, and track was falsely recorded on first and third days, and not falsely recorded on second day).

To extend this approach to additional observers and survey periods again requires that one consider all surveys at a particular site simultaneously (although track-laying processes are assumed to be independent among survey periods, occupancy status induces correlation among observations from the same site).

On the other hand, the likelihood is relatively easy to construct using a series of hierarchical, conditionally independent latent variables that together determine occupancy and presence or absence of tracks. Specifically, let

$$x_{i,j,k} = \begin{cases} 1, & \text{if a track is laid in site } i \text{ on the } k\text{th day of} \\ & \text{the } j\text{th snowfall event} \\ 0, & \text{otherwise} \end{cases}.$$

From assumption (2), we have $x_{i,j,k}|z_i \sim \text{Bernoulli}(\theta_i)$. Let

$$w_{i,j,k} = \begin{cases} 1, & \text{if a track is present in site } i \text{ on the } k\text{th day} \\ & \text{of the } j\text{th snowfall event} \\ 0, & \text{otherwise} \end{cases}.$$

The vector of w's for each survey period is constructed directly from the x's. For $k = 1$,

$$w_{i,j,1} = x_{i,j,1};$$

and for $k > 1$,

$$w_{i,j,k} = \begin{cases} 1, & \text{if} w_{i,j,k-1} = 1 \\ x_{i,j,k}, & \text{otherwise.} \end{cases}$$

Finally, from assumptions (4–7), we have that $y_{i,j,k,l}|w_{i,j,k}$ are mutually independent, and

$$y_{i,j,k,l}|w_{i,j,k} \sim \text{Bernoulli}(w_{i,j,k}p_l + (1 - w_{i,j,k})e_l).$$

In summary, our model consists of three levels with parameters describing (i) occupancy $\{\psi_i\}$, (ii) availability of tracks for detection (due to movement), conditional on occupancy $\{\theta_i\}$ and (iii) recorded presence–absence of tracks, conditional on their availability for detection $\{e_l,p_l\}$.

In most occupancy modelling applications, site-level processes are assumed to be independent and identically distributed (possibly after conditioning on measured covariates). Thus, one would typically replace ψ_i and θ_i with constants ψ and θ (or model these parameters as functions of covariates). We refer to the model with these independence assumptions as the baseline, uncorrelated model.

Rather than determine the marginal likelihood for $y_{i,j,k,l}$ by integrating over the latent variables, we will use Markov chain Monte Carlo (MCMC) to numerically integrate over the latent variables using a Bayesian formulation of the problem. For an introduction to the use of MCMC in occupancy models see MacKenzie *et al.* (2006). Alternatively, a Frequentist approach to the problem could be implemented using the EM algorithm to maximize the likelihood (Dempster, Laird & Rubin 1977).

SPATIAL CORRELATION

While it is reasonable, we believe, to assume independence between observers, there is ample evidence to suggest that sites are not mutually independent. Otters tend to travel long distances (Evans *et al.* 2009), which suggests that a track at site i is positively correlated with a track at site $i + 1$. We applied a run test (Conover 1980) to our otter track data and rejected the hypothesis that sites were independent.

To account for the spatial dependence in the data, we developed a second model that incorporated spatial dependence in both the occupancy and track-laying processes. In contrast to the baseline model in which we assumed the latent occupancy vector $(z_1,\ldots,z_N)$ consisted of i.i.d. Bernoulli random variables with constant ψ, in our spatial model we assumed $z_i \sim \text{Bernoulli}(\psi_i)$, with $\text{logit}(\psi_i) = \alpha_0 + \alpha_i$. Spatial dependence in the occupancy process was obtained by defining contiguous sites as neighbours and placing an intrinsic conditional autoregressive (CAR) prior distribution on the α_i's:

$$\alpha_i|\alpha_{-\mathbf{i}} \sim \begin{cases} N\left(\alpha_{i+1}, \tau^2\right), & \text{if } i = 1 \\ N\left(\frac{\alpha_{i-1}+\alpha_{i+1}}{2}, \frac{\tau^2}{2}\right), & \text{for } i = 2,\ldots,N-1 \\ N\left(\alpha_{i-1}, \tau^2\right), & \text{if } i = N \end{cases}$$

where α_{-i} denotes the full α vector except for the ith site, and τ^2 is the conditional variance of the CAR process (note: WinBugs parameterizes normal distributions using a precision parameter $= 1/\tau^2$). The use of CAR models in ecological studies has been growing in popularity in recent years (Lichstein *et al.* 2002). Magoun *et al.* (2007) describe an application using aerial surveys of wolverine tracks that shares some similarities to our work.

Together with the correlated occupancy process, the track-laying process was modelled as a stationary, two-state Markov chain with parameter β introduced to quantify the additional likelihood that a site contained a track given that there was a track in a neighbouring site. Specifically, we define θ^* as the probability of a track being laid down in site i, given site i is occupied and no track was laid down in site $i-1$, and $\theta^* + \beta$ as the probability of a track being laid down in site i, given site i is occupied and there was a track laid down in site $i-1$.

For simplicity, and to make connections between track-laying parameters in the spatial (θ^*,β) and baseline (θ) models, assume temporarily that $\psi_i = \psi$ is constant over sites. In this case, the probability that a track is laid down in site i, conditional on no track in site $i-1$, is equal to $\theta^*\psi$. Similarly, the probability that a track is laid down in site i, conditional on there being a track in site $i-1$, is $(\theta^* + \beta)\psi$. The Markov transition matrix for the track-laying process is thus

$$\begin{array}{cc} & \begin{array}{cc} 0 & 1 \end{array} \\ \begin{array}{c} 0 \\ 1 \end{array} & \begin{pmatrix} 1 - \theta * \psi & \theta * \psi \\ 1 - (\theta * + \beta)\psi & (\theta * + \beta)\psi \end{pmatrix} \end{array}. \qquad \text{eqn 1}$$

Note that spatial independence in the track-laying process is equivalent to $\beta = 0$, in which case $\theta^* = \theta$, and the transition matrix reduces to that of the baseline model.

The stationary distribution of the Markov chain (i.e. if iterated on an infinite spatial lattice) is given by:

$$\left(1 - \frac{\theta * \psi}{1 - \psi\beta}, \frac{\theta * \psi}{1 - \psi\beta}\right).$$

That is, the stationary probability that a site contains a track one day after a snowfall event is $\theta^*\psi/(1-\psi\beta)$. It follows that the conditional probability (in stationarity) that a site contains a track one day after a snowfall event, given that the site is occupied, is

$$\tilde{\theta} = \frac{\theta *}{1 - \psi\beta}. \qquad \text{eqn 2}$$

Thus, we expect θ in the baseline model to behave like $\tilde{\theta}$ in equation 2 when the model is fit to data generated using the Markov model. This equivalence will be exploited in our simulation work (e.g. to determine reasonable values of θ^* for generating data and also to determine a reasonable reference value when summarizing the distribution of $\hat{\theta}$s when fitting the baseline model to data simulated with spatial correlation).

BAYESIAN IMPLEMENTATION

The conditional nature of the biological and observational data processes naturally lends itself to a Bayesian hierarchical model specification, with parameter estimation accomplished via MCMC using R, WinBUGS and BRugs. For more background on Bayesian hierarchical modelling and MCMC, we refer the reader to Royle & Dorazio (2008) and Ntzoufras (2009).

The early occupancy models presented in MacKenzie *et al.* (2006) assumed no false positives. As described in Royle & Link (2006), one difficulty in incorporating false positives into the occupancy model is the 'dual role' of the false-positive rate e and the true detection rate p. Without other contextual information, the model cannot discern whether a 1 denotes an occupied site that was correctly detected or an unoccupied site that was falsely detected. In particular, if $\theta = 1$, then the likelihood function has the symmetrical property that $L(\psi,\theta,p,e) = L(1-\psi,\theta,e,p)$. This gives rise to bimodal posterior distributions. The inclusion of the track-laying parameter θ complicates the picture even more because of the different ways that a 1 in the data can be interpreted. Thus, we expected issues of nonidentifiability and bimodality to be highly relevant to our approach.

A suggestion made by Royle & Link (2006), which we pursued in our models, was to restrict the parameter space so that $p >> e$. In particular, we restricted the support of p and e to the intervals (0·6,1) and (0,0·3), respectively. This seemed to correspond well with our intuition and understanding of the actual detection process (e.g. we expected detection of tracks, once present, to be high). In addition, we placed Beta(a, b) and Beta(c, b) prior distributions on each p_l and e_l, respectively, with hyperparameters a,b,c assigned diffuse Gamma(1, 0·1) distributions. This specification is akin to a fixed effects specification in Frequentist models (i.e. as each observer was given a separate prior, there was no shrinkage to an overall 'observer-mean as would be accomplished in a hierarchical specification in which all three observer parameters were drawn from the same distribution).

For the spatial model, we assigned a uniform(−0·1,1) prior distribution for β, restricting the support of $\theta + \beta$ to (0,1). We used a Gamma(0·5, 0·0005) prior distribution for the inverse variance parameter of the CAR model as suggested by Kelsall & Wakefield (1999). For the intercept term, we chose a normal(0, 0·1) prior distribution. In all other cases, we chose vague uniform priors.

Following specification of the likelihood and priors, the MCMC approach generates a Markov chain to characterize the posterior distribution empirically. We conducted an extensive simulation study to evaluate the statistical properties of the baseline and spatial models and also fit both models to survey data collected on the Mississippi River. To assess convergence, we ran three independent chains and inspected the Gelman–Rubin statistic (Brooks & Gelman 1998). This statistic compares 'between chain' and 'within chain' variation, with values close to one suggesting convergence. We also visually inspected (i) the full trajectory of the Markov chain simulations to see whether the independent chains had 'settled down' to a similar range of values and (ii) the estimated posterior distributions for signs of bimodality.

SIMULATION STUDY

To test the reliability, accuracy and precision of our estimators, we conducted an extensive simulation study. Data were simulated based on a complete, four-way, three-level factorial design with variables: (i) occupancy correlation (levels: 0, medium and high), (ii) track-laying correlation (levels: 0, medium and high corresponding to $\beta = 0$, 0·4 and 0·6, respectively), (iii) occupancy probability ($E[\psi_i] = 0{\cdot}3$, 0·55 and 0·8) and (iv) track-laying parameter, $\tilde{\theta}$ (equation 2) = (0·1, 0·3 and 0·5).

To generate correlated occupancy probabilities, we let logit(ψ_i) = $\gamma + \epsilon_i$, with ϵ_i given by a mean 0, ar(1) process. In contrast to the intrinsic CAR model, which uses a single conditional variance parameter to capture both heterogeneity and spatial correlation, the ar(1) process is defined using an unconditional variance parameter (σ^2) and autocorrelation parameter (ρ). Thus, our data generating model differed slightly from our spatial estimation model. We set $(\sigma,\rho) = (0,0)$, (1, 0·35) and (4, 0·8) for the (0, medium and high) correlation scenarios, respectively. In each case, we generated values of ϵ_i using the arima.sim function in Program R (R Development Core Team 2009).

Conditional on a site being occupied, a track was laid down with either constant probability $\tilde{\theta}$ (independence model) or using the Markov transition matrix (equation 1) (spatial model); tracks were always kept on successive days of the same snow event. To use the Markov matrix for simulation, we first determined an appropriate value of θ^* by plugging in prespecified values of $\tilde{\theta}$, ψ and β into equation 2, replacing ψ with the mean of the occupancy vector (i.e. the proportion of occupied sites):

$$\Psi = \frac{1}{N}\sum_{i=1}^{N} z_i, \qquad \text{eqn 3}$$

when ψ was not constant. Finally, conditional on there being a track, it was either recorded with probability p_l or not, and conditional on there not being a track, it was either incorrectly recorded with probability e_l or not.

Data were generated for 100 sites with five unique snow events, three observations after each snow event and three observers. Thus, in each case, our data consist of a 100×45 array of 0s and 1s. We set $p = (p_1,p_2,p_3) = (0{\cdot}65,0{\cdot}70,0{\cdot}80)$ and $e = (e_1,e_2,e_3) = (0{\cdot}05,0{\cdot}10,$ $0{\cdot}15)$, to allow for reasonable values of the detection and false-positive probabilities. Our primary interest in developing the occupancy model was a desire to estimate otter population-level occupancy rates (i.e. Ψ in equation 3). For this purpose, we used:

$$\hat{\Psi} = \frac{1}{N}\sum_{i=1}^{N} \hat{z}_i.$$

All simulations were run so that the Markov chain standard error estimates were an order of magnitude smaller than the standard deviation estimates, typically of order 10^{-4}. We also monitored the Gelman–Rubin statistic as a diagnostic for determining whether or not the MCMC algorithm was converging. The MCMC algorithm for the base model required 3000 iterations after an initial burn-in of 3000 iterations. The spatial model required 6000 iterations after a burn-in of 10 000 iterations. The base model took about 5 min to run on a laptop PC, and the spatial model took about 20 min.

SIMULATION WORK TO LOOK AT STUDY DESIGN

We also used simulations to help determine efficient sampling practices. Specifically, we aimed to help clarify what types of flights were most useful and how many flights were necessary for a desired level of accuracy. Based in part on the results of fitting our model to the Mississippi River data (see below), we generated samples with parameter values of $E[\psi_i] = 0{\cdot}76$, $\tilde{\theta} = 0{\cdot}20, \beta = 0{\cdot}4, p = 0{\cdot}65, e = 0{\cdot}05$ and with moderate correlation in the occupancy process ($\sigma = 1$ and $\rho = 0{\cdot}35$). We varied the number of snow events (1–5), days flown after a snow event (1–3) and number of observers (1–3) using a complete factorial design to determine the combination of these parameters that resulted in the fewest flights, with the requirement that the standard error for $\hat{\Psi} < 0{\cdot}05$. We simulated these 45 scenarios twice, both times using the same set of parameters, to make sure our conclusions were robust to Monte Carlo error. In each case, we used a burn-in period of 10 000 iterations, followed by a tracking period of 10 000 iterations.

Results

SIMULATION STUDY

Estimates of Ψ and $\tilde{\theta}$ from the 81 simulation runs are summarized in Figs 2 and 3, respectively. Each panel depicts nine simulation runs, with the degree of spatial correlation held constant and Ψ and $\tilde{\theta}$ varied within each panel.

In general, both models resulted in precise estimates of model parameters with little bias (Figs 2 and 3). When data were simulated without spatial correlation (in the occupancy and track-laying processes), β in the spatial model was estimated to be close to 0, and the two models (baseline and spatial) gave similar estimates of Ψ and $\tilde{\theta}$ (Figs 2g and 3g). Estimates of Ψ from the baseline model had a lower mean-squared error (MSE) = 0·0032 (baseline model) vs. 0·0064 (spatial model), whereas mean absolute deviations (MADs) were more similar, 0·030 (baseline model) vs. 0·031 (spatial model). On the other hand, the spatial model outperformed the baseline model with respect to estimating $\tilde{\theta}$, with MSE = 0·0057 (baseline model) vs. 0·0012 (spatial model) and MAD = 0·032 (baseline model) vs. 0·024 (spatial model). In particular, the baseline model tended to overestimate $\tilde{\theta}$ when occupancy and track-laying process were spatially correlated (e.g. Fig. 3c).

Across the 81 simulated scenarios, 95% credibility intervals for Ψ included the true value 91% of the time for the baseline model and 95% of the time for the spatial model (Table 1). Coverage rates for $\tilde{\theta}$ were higher for the spatial model (93% vs. 78%; Table 1). Coverage rates for correct and false detection probabilities (p_l and e_l, respectively) were near nominal values for both models, as was the coverage rate for β in the spatial model (Table 1).

For both models, estimates of Ψ became more precise as $\tilde{\theta}$ increased (i.e. as tracks became more prevalent). When $\tilde{\theta} = 0{\cdot}5$, 95% credibility intervals for Ψ were on the order of 0·01 in width. Thus, we can expect 'good' estimates of population occupancy rates when track-laying probabilities are high.

ANALYSIS OF MINNESOTA OTTER DATA

The sampling effort for the Mississippi River data was irregular both with respect to the number of observers and the number of days sampled for each snow event. Our formulation of the problem in WinBugs treated these irregularities as if non-surveyed dates were missing data (as a result, WinBugs drew values for these response data at each MCMC iteration). Although this approach was easier to code in WinBugs, it resulted in longer run times and more iterations to obtain convergence.

The estimated occupancy rate was higher for the spatial model ($\hat{\Psi} = 0{\cdot}82$ vs. 0·59; Table 2). This result is consistent with the findings of Hines *et al.* (2010), where an independence model gave lower occupancy rates than their spatial model. The spatial model estimated lower track-laying rates, with significant positive correlation among sites ($\hat{\beta} = 0{\cdot}53$; Table 2). Thus, the spatial model suggests that tracks were less likely to be laid down than indicated by the baseline model parameters, but when they were laid down, they were likely to cross site boundaries.

OPTIMAL STUDY DESIGN

In our study design analysis, we were interested in the number and character of flights, which would result in a maximum standard error of 0·05 for $\hat{\Psi}$. The optimal designs under these criterion included (i) a total of 18 flights distributed among three snow events, with 3 days surveyed per snow event and by two observers each and (ii) a total of 15 flights distributed among five snow events, with 3 days surveyed per snow event and by one observer. The first scenario resulted in parameter estimates (with standard errors) of $\hat{\Psi} = 0{\cdot}74(0{\cdot}05)$, $\hat{\tilde{\theta}} = 0{\cdot}22(0{\cdot}03)$ and $\hat{\beta} = 0{\cdot}44(0{\cdot}07)$. The second scenario estimates were $\hat{\Psi} = 0{\cdot}75(0{\cdot}05)$, $\hat{\tilde{\theta}} = 0{\cdot}18(0{\cdot}02)$ and $\hat{\beta} = 0{\cdot}42(0{\cdot}08)$. The true parameters, by comparison, were given by $\Psi = 0{\cdot}76$, $\tilde{\theta} = 0{\cdot}20$ and $\beta = 0{\cdot}40$.

There were different survey designs with similar numbers of flights (for instance, two snow events, 3 days surveyed, and three observers each, or five snow events, one day surveyed, and three observers each) that resulted in less accurate estimates and larger standard errors. The number of days per snow event appeared to be the most important of the three control variables (number of snow events, observations per snow event and number of observers). In almost all cases, three observations after each snow event on consecutive days were required for the model to converge and for $\hat{\Psi}$ to meet our precision requirement. The number of snow events appeared to be of intermediate importance; precision requirements could be met with at least three unique snow events, and with only two snow events, the standard errors increased rapidly. Finally, the number of observers appeared to be the least important of the variables. Accurate estimates of Ψ were obtained for all number of observers, as long as there were sufficient number of snow events and observations after each snow event.

Discussion

Efficient and cost-effective monitoring tools are needed to understand ecological systems, and these tools must be able to separate signal (e.g. population trends) from noise (e.g. owing to changes in detection probabilities). We were successfully able to incorporate false detection, spatial data correlation and the dependence of detection probabilities on time since snowfall events into a model, despite the complex and sparse nature of the data analysed. While others have had success incorporating one of these processes into occupancy models (Magoun *et al.* 2007; Royle & Link 2006; Stanley & Royle 2005), we are not aware of any studies that have incorporated all three.

Although our models were complex, they were relatively easy to implement and test using WinBugs. Bayesian methods excel at problems such as these, where the marginal likelihood is either analytically or numerically intractable, but it is relatively easy to construct in terms of a series of conditionally independent latent random variables. WinBugs has built in tools that make it easy to adapt models to allow for spatial correlation. Lastly, large sample theory is not needed to derive measures of uncertainty. Bayesian credibility intervals contained true values ≈95% of the time in our simulation study, despite the small number of sites (100) and despite differences between the simulation and estimation models [i.e. a proper CAR process was used to simulate spatial occupancy data, but models were estimated under an independence assumption (baseline model) or using an intrinsic CAR model (spatial model)].

Sampling designs that allow for spatial clustering are appealing for wildlife surveys because they allow large areas to be

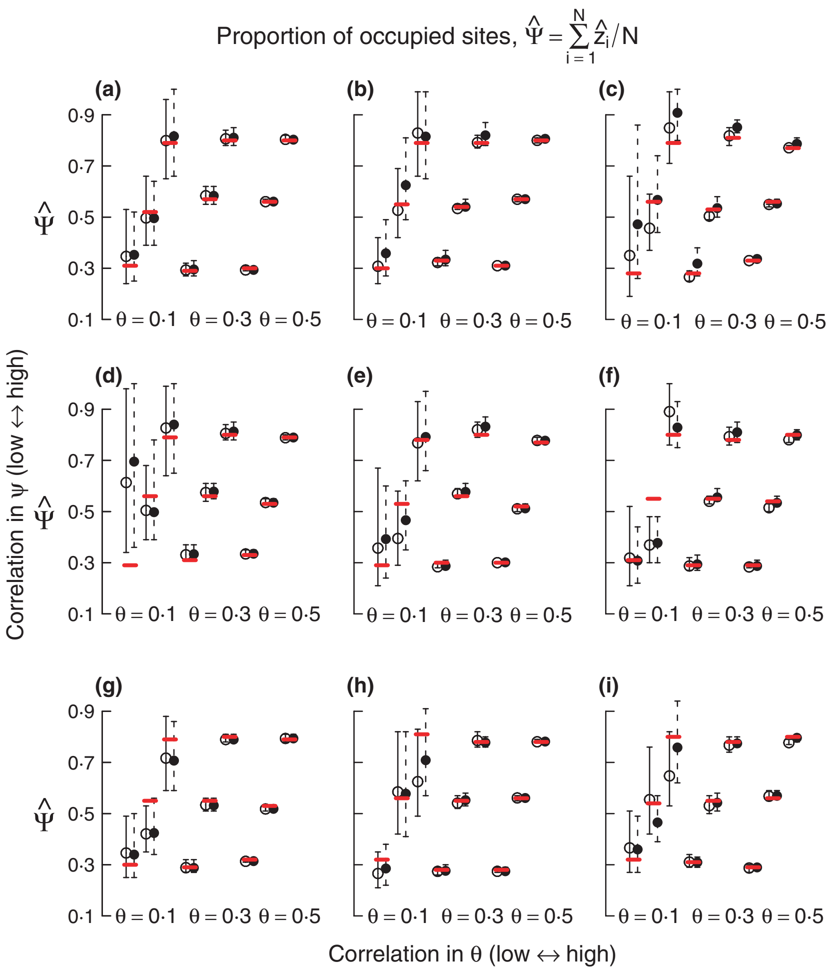

Fig. 2. Posterior means and 95% credibility intervals for $\hat{\Psi} = \sum_{i=1}^{N} \hat{z}_i/N$, the population occupancy rate, from fitting the baseline model (open circle, solid lines) and the spatial model (solid circles, dashed lines) to simulated data. True parameter values are given by horizontal red lines. Data were simulated based on a complete, four-way, three-level factorial design with variables: (i) occupancy correlation [levels: 0 (g–i), medium (d–f) and high (a–c), represented by separate rows in the figure], (ii) track-laying correlation [levels: 0 (a, d, g), medium (b, e, h) and high (c, f, i), represented by separate columns in the figure], (iii) occupancy probability ($E[\psi_i] = 0{\cdot}3$, 0·55 and 0·8) and (iv) track-laying parameter $\tilde{\theta}$ (equation 2) = (0·1, 0·3 and 0·5). The latter two factors are varied within each panel.

sampled efficiently. Although the effective sample size can usually be increased by restricting samples to include only non-neighbouring plots (owing to a reduction in spatial correlation), the additional costs associated with increased transit times will often outweigh the benefits to collecting independent data (see e.g. Giudice *et al.* 2010). In our particular application, we sampled river systems using a single flight path. Although this resulted in a high degree of spatial correlation among survey units, the alternatives would be to fly in a less efficient manner or to 'throw away data' (i.e. not use neighbouring plots). Thus, the ability to account for spatial correlation is an important feature of our modelling approach.

We accounted for spatial correlation in our models using two different approaches. First, we used an intrinsic CAR prior on the logit occupancy scale to allow site-level occupancies to be correlated. Rather than induce spatial correlation via latent random effects (i.e. using the CAR prior), an alternative approach would be to directly model correlation among the site-level occupancy indicators (z_i) using an autologistic model (Besag 1974; Sargeant *et al.* 2005). The primary advantage of the CAR modelling approach is that it leads to simple MCMC routines that are easily implemented in WinBugs (Magoun *et al.* 2007). Second, we used a Markovian model to allow for spatial correlation in the availability of tracks for detection; a similar approach was used by Hines *et al.* (2010) to model the presence of tiger *Panthera tigris* sign. Notably, our track-laying parameters share similarities with parameters used to describe temporary emigration in mark–recapture models (i.e. both sets of parameters determine whether animals are available for detection at the time of a survey). Although our application focused on spatial correlation, we suspect Markovian models (e.g. for emigration parameters) may also prove useful for inducing temporal correlation in a wide range of modelling applications (Hines *et al.* 2010).

Many natural resource agencies monitor trends in abundance using indices based on surveys of animal sign (e.g. scat, scent marks, animal tracks), and our 3-level occupancy model has broad relevance to these types of studies. For example,

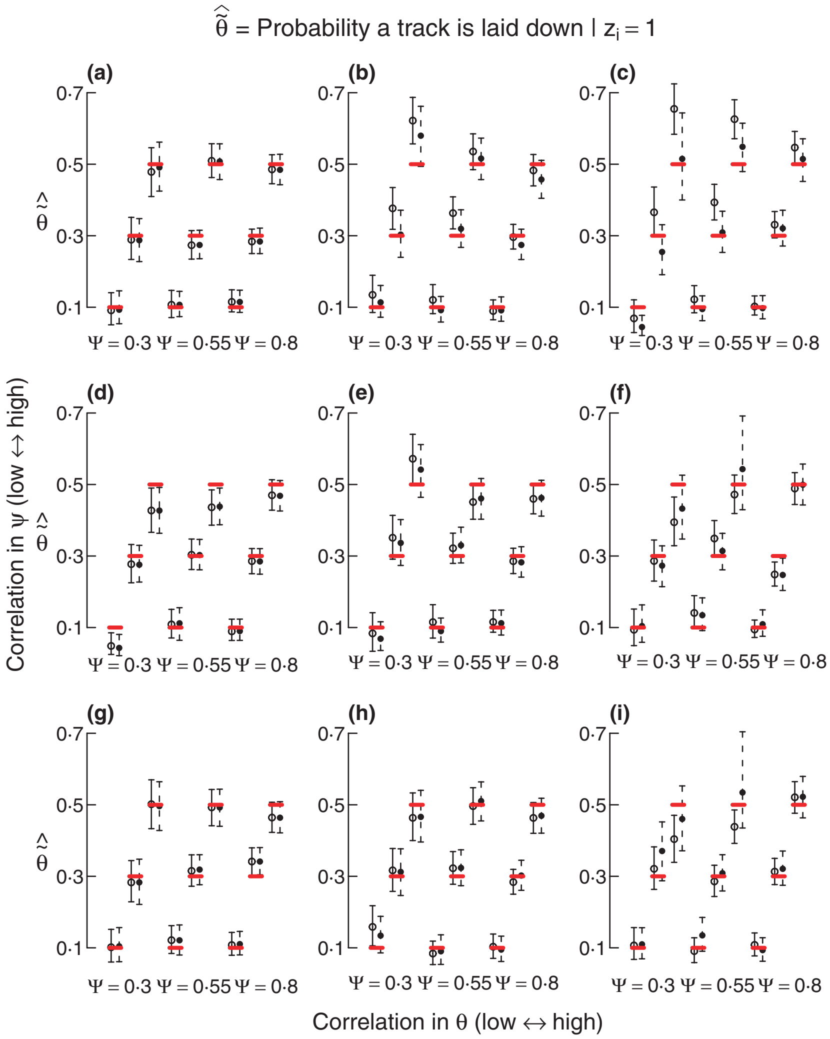

Fig. 3. Posterior means and 95% credibility intervals for $\tilde{\theta}$ = probability of laying down a track one day after a snowfall $|z_i = 1$, from fitting the baseline model (open circle, solid lines) and the spatial model (solid circles, dashed lines) to simulated data. True parameter values are given by horizontal red lines. Data were simulated based on a complete, four-way, three-level factorial design with variables: (i) occupancy correlation [levels: 0 (g–i), medium (d–f) and high (a–c), represented by separate rows in the figure], (ii) track-laying correlation [levels: 0 (a, d, g), medium (b, e, h) and high (c, f, i), represented by separate columns in the figure], (iii) occupancy probability ($E[\psi_i]$ = 0·3, 0·55, and 0·8) and (iv) track-laying parameter $\tilde{\theta}$ (equation 2) = (0·1, 0·3 and 0·5). The latter two factors are varied within each panel.

Table 1. Coverage rates for model parameters*

Model	Ψ	$\tilde{\theta}$	β	p_1	p_2	p_3	e_1	e_2	e_3
Spatial	95 (77)	93 (75)	95 (77)	95 (77)	95 (77)	91 (74)	94 (76)	98 (79)	93 (75)
Baseline	91 (74)	78 (63)	NA	93 (75)	96 (78)	91 (74)	95 (77)	91 (74)	94 (76)

*Percent (number out of 81) of simulations in which Bayesian 95% credibility interval contained the true value.

large carnivores are often monitored using scent station surveys, with scent stations distributed uniformly along transects or in a 2-dimensional grid (e.g. Sargeant, Johnson & Berg 1998). Similar 3-level occupancy models could be constructed for these types of survey designs, with track-laying parameters replaced with ‘deposition’ parameters, and each scent station serving as a unique site. A benefit of the 3-level model, particularly for snow-track surveys, is that it offers the potential to account for a significant source of heterogeneity in the detection process (i.e. that owing to temporal variability in the presence of tracks).

The benefit of the 3-level modelling approach can be seen by considering a recent study by Gardner *et al.* (2010), in which they performed wolverine snow-track surveys over the course of a month. Surveys were conducted provided that at least 24 h had passed since the previous snowfall (with no upper

Table 2. Model estimates (Bayesian 95% credibilty intervals) for the baseline (independence) and spatial occupancy models fit to Mississippi River data

	Estimate (95% credibility interval)	
Parameter	Baseline model	Spatial model
e_1	0·02 (0·00, 0·04)	0·01 (0·00, 0·02)
e_2	0·05 (0·03, 0·07)	0·04 (0·02, 0·06)
e_3	0·03 (0·01, 0·05)	0·03 (0·01, 0·05)
p_1	0·67 (0·61, 0·75)	0·65 (0·60, 0·72)
p_2	0·69 (0·61, 0·79)	0·66 (0·62, 0·70)
p_3	0·62 (0·60, 0·67)	0·61 (0·60, 0·65)
ψ	0·59 (0·43, 0·76)	0·82 (0·67, 0·97)
θ	0·15 (0·11, 0·20)	0·12 (0·09, 0·16)
β		0·53 (0·39, 0·66)

time limit). They detected an increasing trend in detection rates with Julian date. If this trend was owing to an increased opportunity for tracks to be laid down over time, then our model might offer several advantages. First, a mechanistic approach to modelling this detection component might do a better job of adjusting for temporally varying detection probabilities. Secondly, it could provide an explanation for this temporal trend, which would be useful when exploring alternative survey designs. When conducting simulations to look at the power to detect changes in abundance over time, Gardner *et al.* (2010) had to standardize predictions to a common date. By contrast, our 3-level model would provide a means to explore the power to detect changes across a range of historical snowfall patterns.

For complex models and small numbers of sites, simulations provide the best way to explore sample design questions (Guillera-Arroita, Ridout & Morgan 2010). Our pilot data and 3-level models suggest that the detection process is largely driven by otter movement following snow events and much less so by difficulties associated with observing tracks from the air once present. Importantly, the spatial model predicted lower track-laying rates than the baseline model but with a high degree of spatial correlation. Because we believed the spatial model better represented the true detection process, we used it to evaluate future survey design choices. We considered a fixed set of parameters (based on our fits to real data) and recommended a minimum sampling effort of 15–20 flights, distributed over at least three unique snow events, with at least three successive daily surveys following each event.

An interesting alternative approach and avenue for future research would be to investigate optimal survey design questions using Bayesian experimental design principles, allowing for parameter uncertainty (Chaloner & Verdinelli 1995). For example, one could compare designs across a range of simulation scenarios, with parameters in each scenario chosen randomly from fitted posterior distributions. A Bayesian approach to experimental design would also allow one to incorporate uncertainty in the number of annual snow events and the likelihood of missed flights (e.g. as a result of poor weather conditions or difficulties associated with helicopter availability). Because these variables are not under user control, a Bayesian approach to experimental design would arguably provide a much more realistic test of whether survey goals (e.g. standard error of $\hat{\Psi} < 0{\cdot}05$) are likely to be met. Cost-benefit trade-offs related to collecting repeat survey data (multiple observers, multiple surveys after each snow event) could also be evaluated by quantifying the power to detect trends in occupancy rates over time (for specific alternative sampling and analysis strategies). We hope to explore these issues in future work.

In developing our approach, we assumed that detection probabilities were constant once tracks were laid down (i.e. detection rates do not increase if tracks are laid down on multiple days). This assumption may be reasonable if detection rates are high and track-laying rates are low (as in our applied example). In that case, few sites will contain more than one set of tracks, and those that do will have only slightly higher detection probabilities. Yet, our models can easily be modified to handle violations of this assumption. For simplicity, consider only a single observer and recognize that the parameter p in our models is really a classification (rather than a detection) parameter (i.e. it gives the probability of correctly recording a track when one is present). As discussed by Royle & Link (2006), correct classifications can occur by mistake (e.g. otter tracks may be missed, but tracks of another species may be misidentified as otter tracks). Royle & Link (2006) describe an alternative, equivalent parametrization of the model specified in terms of two detection parameters, say δ_a and δ_b: $\delta_a =$ the probability of correctly detecting a track at a site that contains a track.

$\delta_b =$ the probability of incorrectly detecting a track at a site (the site may or may not contain a track).

Our $p = \delta_a + \delta_b - \delta_a\delta_b$, and $e = \delta_b$ (Royle & Link 2006). We will need to use this latter formulation of the model and rather than keep track of the latent variables $w_{i,j,k}$ (=1 if tracks are present in site i on the kth day of the jth snowfall event, 0 otherwise), we will need to keep track of the number of days in which a track is laid down (call this $w_{i,j,k}'$, which can take on values of 0, 1, 2, or 3). If we assume tracks within a site are detected independently, then the probability of correctly recording a track when present (p in our original formulation of the model) is given by: $1-(1-\delta_a)^{w_{i,j,k}'} + \delta_b - \delta_b(1-(1-\delta_a)^{w_{i,j,k}'})$.

We modified our models as described above and fit them to the otter survey data. Estimates of Ψ, θ, $\tilde{\theta}$, and β were virtually unchanged. This result was not unexpected, given the high estimates of p and low estimates of e and θ.

Unfortunately, sites in our motivating problem were not defined *a priori*. Rather than collect way points in a semi-continuous manner and then create sites post hoc, it would be desirable in the future to define a grid *a priori* and use Global Positioning System information to more accurately record presence/absence data to spatial units, thereby reducing misclassification rates. False positives, in general, deserve more attention in occupancy models because they can have large impacts on estimates of occupancy rates (Royle & Link 2006; McClintock *et al.* 2010). Adaptations that allow for false positives significantly increase model complexity, solutions are relatively new, and models may perform in unexpected ways because of the challenges associated with parameter identifiability. In particular, McClintock *et al.* (2010) recently found that false positives, combined with heterogeneous detection probabilities, resulted in poorly identified parameters that were often estimated with significant biases. We expect the theory underlying these models to continually develop as modellers attempt to address increasingly complex problems. In the meantime, we strongly recommend testing models with simulated data as a means of better understanding their statistical properties.

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Supporting Information

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

Appendix S1. R code to simulate data for 3-level occupancy model, assuming site-level independence for occupancy and track laying processes.

Appendix S2. R code to simulate data for 3-level occupancy model, assuming site-level occupancy and track laying processes are spatially correlated.

Appendix S3. R code for fitting 3-level occupancy model, assuming site-level independence for occupancy and track laying processes.

Appendix S4. R code for fitting 3-level occupancy model, assuming site-level occupancy and track laying processes are spatially correlated.

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