

Making better sense of monitoring data from low density species using a spatially explicit modelling approach

Max Post van der Burg^{1*†}, Bartholomew Bly², Tammy VerCauteren³ and Andrew J. Tyre¹

¹School of Natural Resources, 3310 Holdrege Street, University of Nebraska-Lincoln, Lincoln, NE 68583, USA;

²Nebraska Prairie Partners, PO Box 489, Scottsbluff, NE 69363, USA; and ³Rocky Mountain Bird Observatory, PO Box 1232, Brighton, CO 80601, USA

Summary

1. Wildlife managers are limited in the inferences they can draw about low density populations. These limits are imposed by biases in monitoring data not regularly accounted for.

2. We developed a Bayesian hierarchical model to correct biases arising from imperfect detection and spatial autocorrelation. Our analysis incorporated model selection uncertainty by treating model probabilities as parameters to be estimated in the context of model fitting. We fitted our model to count data from a monitoring programme for the mountain plover *Charadrius montanus*, a low density bird species in Nebraska, USA.

3. Our results demonstrated that previous accounts of the abundance and distribution of plovers in Nebraska were impacted by low detection probabilities (~5–20%). Uncorrected relative abundance estimates showed that the average number of birds per agricultural section increased over time, whereas corrected estimates showed that average abundance was stable.

4. Our method spatially interpolated relative abundance to produce distribution maps. These predictions suggested that birds were selecting some sites more frequently than others based on some habitat feature not explored in our study. Variation in mountain plover abundance appeared more heavily influenced by changes in the number of individuals occupying a few high quality sites, rather than from changes in abundance across many sites. Thus, conservation efforts may not be as efficient when focusing on low to moderate quality sites.

5. *Synthesis and applications.* Managers who must make decisions based on data-poor systems should adopt rigorous statistical approaches for drawing inferences. Spatial predictions provide information for deciding where to implement management, which is just as important as knowing what kind of management to apply. Our approach provides a step in the direction of making the biological signal in data-poor monitoring programmes more informative for conservation and management.

Key-words: Bayesian hierarchical models, detection error, modelling uncertainty, spatial statistics

Introduction

Wildlife managers are limited in the inferences they can draw from surveys of low density populations. These limits are partially caused by biases in monitoring data induced by detection errors and errors arising from spatial autocorrelation. Detection errors arise in surveys as a result of factors such as species-

specific behaviour or differing observer abilities (Royle 2004; Field, Tyre & Possingham 2005a; Johnson 2008). Accounting for variation in detectability has garnered much attention in the ecological literature because it erodes the power to estimate population parameters (Royle & Nichols 2003; Tyre *et al.* 2003; Field *et al.* 2005b).

Failure to account for detectability also affects our understanding of species' distributions. This is important for agencies tasked with targeting management. Often, distributional data is derived from the location of positive detections in the context of monitoring (e.g. McConnell *et al.* 2009). However, methods such as point counts or presence-absence

*Correspondence author. E-mail: mzp0022@auburn.edu

†Present address: School of Forestry and Wildlife Sciences, Auburn University, 3203 Forestry and Wildlife Sciences Building, Auburn, AL, 36849, USA.

surveys do not cover all occupied sites which could make observed distributions biased. Rigorous distributional predictions can be derived from capturing spatial autocorrelation between observations and using estimates of spatial dependence to map predicted abundance or occupancy (e.g. Latimer *et al.* 2006; Thogmartin, Knutson & Sauer 2006). Few studies have dealt with both detection and spatial coverage biases in the context of estimating abundance (but see Royle *et al.* 2007).

These combined errors could be of concern for low density populations for two reasons. First, low density populations are difficult to find and it would be helpful to know whether this low density is because of a biological process that warrants management action. Secondly, the non-random distribution of habitat is a likely source of spatial autocorrelation in count data (Legendre 1993). Non-random sampling of habitat patches will increase detections, but will also compromise the estimation of variability of abundance within a particular region. Therefore, accounting for the spatial non-independence of sampling sites and detection error is necessary to accurately predict a species' abundance and distribution.

We developed and applied a Bayesian hierarchical modelling approach that accounts for detection and spatial errors in count data. Our approach also deals with model selection uncertainty by treating model selection as a part of the fitting procedure. We fitted our model to data from a 3 year monitoring programme for the mountain plover *Charadrius montanus*, a low density bird species in Nebraska, USA. We had four main goals with this study. First, to compare detection-corrected and uncorrected relative abundance estimates for mountain plovers. Secondly, to compare mountain plover abundance between two types of agricultural habitats: grazed lands and arable fields. Thirdly, to compare abundance between sites that were actively managed to improve the reproductive success of plovers versus those that were not. Lastly, to generate predictions of mountain plover distributions to inform management.

Materials and methods

CASE STUDY: THE MOUNTAIN PLOVER

Mountain plovers are of conservation concern within North America (Knopf & Wunder 2006). The eastern edge of this species' range extends into a small portion of Nebraska, USA, where previous surveys indicated that plovers rarely occupied the state (Clausen 1990; Dinsmore 1997). Bly, Snyder & VerCauteren (2008) conducted patch surveys in the southwestern corner of the Nebraska panhandle and concluded that mountain plovers were more numerous than previously believed. Thus, it is likely that mountain plovers in Nebraska had been under-sampled. This is problematic for the conservation of this population for at least two reasons. First, the population in Nebraska is at the edge of the species' range and might be expected to experience wide fluctuations. Therefore, distinguishing between measurement and process error is crucial for conservation. Secondly, identifying locations that have high conservation value will be compromised by biased abundance estimates. This could lead to inefficient or misdirected allocation of conservation effort.

Numerous studies have recognized that mountain plovers are difficult to detect because they are cryptically coloured and often encountered in relatively low densities (Knopf & Wunder 2006). Past studies have accounted for detectability by using distance sampling (Wunder, Knopf & Pague 2003; Plumb, Knopf & Anderson 2005), mark-recapture methods (Dinsmore, White & Knopf 2003), repeated visits (Dreitz, Lukacs & Knopf 2006; Tipton, Dreitz & Doherty 2008) and removal methods (McConnell *et al.* 2009; Tipton, Doherty & Dreitz 2009).

STUDY AREA

Data used in this study came from surveys described in Bly, Snyder & VerCauteren (2008). These surveys were conducted in the southwestern portion of the Nebraska panhandle (Kimball, Banner and Cheyenne counties) and covered approximately 4500 km². Roughly 90% of the land in this region was privately owned and used for agricultural production (Hiller *et al.* 2009). Approximately 59% of the landscape was used for grazing livestock and the remaining 41% was used for growing crops. Both intensively grazed lands with bare ground and wheat fields provide mountain plovers with breeding habitat in Nebraska: relatively flat areas with greater than 30% bare ground (Knopf & Miller 1994). Mountain plovers nest in agricultural fields, where their nests are exposed to tillage operations (Knopf & Rupert 1999; Shackford, Leslie & Harden 1999). In Nebraska, the Rocky Mountain Bird Observatory and Nebraska Game and Parks Commission had been applying a nest marking management programme in some of the same areas that the count data was recorded within. The nest marking programme focused on reducing nest loss due to agricultural tillage by marking nests so that soil tillage operations could avoid them.

SURVEY METHODOLOGY

Data were collected in the 2005, 2006 and 2007 breeding seasons. Counts were conducted within the primary land division unit, 2.56 km² sections. Our analysis was based on 102 randomly selected sections in 2005 (43 previously occupied sections, 59 randomly selected sections), 111 sections in 2006 (73 previously occupied sections, 38 randomly selected sections), and 150 sections in 2007 (88 previously occupied sections, 62 randomly selected sections). In each section, surveyors aimed to maximize the number of detections by selecting a 4 ha patch that contained suitable nesting habitat. Scaling from the level of the patch to the agricultural section has the potential to influence our ability to accurately predict mountain plover abundance. For instance, if the patch contained a portion of the plovers in a section, scaling could underpredict average abundance. However, we were only interested in predicting relative abundance at the scale of the section so scaling issues were not as important for our analysis as they might be for finer scale habitat selection analyses.

In all three years, roughly 25% of the patches were located in rangeland sections and about 75% of the patches were located in arable sections. Surveyors visited each patch three times in 2005, four times in 2006 and three times in 2007. Surveys were conducted from mid-April to the beginning of June each year. Different observers conducted the surveys in 2005 and 2006, but were the same in 2006 and 2007. Each visit consisted of two three-minute point counts: one prior to playing a territorial or alarm call and one post call playback. Call playback was standardized so that calls were played in the same direction and location during each visit. Surveys were conducted between sunrise and 10:00 or between 17:00 and sunset when it was not raining and winds were < 32 km h⁻¹.

STATISTICAL ANALYSIS

We performed all analyses using the statistical computing language R (R Development Core Team 2008). We used a hierarchical Bayesian approach because it accommodated multi-level processes and included prior information. Our approach was based on the work of Royle, Link & Sauer (2002) and Royle *et al.* (2007).

Our model of the count process followed Royle (2004):

$$p(y_{ij}|\lambda_i, p) = \prod_{i=1}^I \left(\left(\prod_{j=1}^J \text{Bin}(y_{ij}; N_i, p) \right) \text{Pois}(N_i; \lambda_i) \right) \quad \text{eqn 1}$$

where y_{ij} were observed counts arising from a binomial process at patch i and visit j , N_i was the unobserved patch-specific abundance and p was the rate at which individuals were detected. Notice that including N in the binomial model says that there was some true number of individuals, but that observers could only find some proportion of them. We assumed that N was distributed as a Poisson process where λ_i was the patch specific Poisson mean (i.e. detection-corrected average relative abundance). We assumed that N had a constant uniform prior distribution. We believe our method corrected our observations for detection error based on simulations (not presented). Others have found that similar methods may not always yield fully corrected estimates of ‘true’ abundance (Efford & Dawson 2009). Thus, to be conservative, we refer to our estimates as corrected relative abundance.

We modelled detection rate p as a function of temporal and observer-specific covariates using a logistic model. We assumed that p did not vary across sites. This assumption was reasonable because our sites did not contain factors, such as vegetation, that would make detection vary. We modelled the patch-specific mean abundance $u(s)$ using an overdispersed log linear model:

$$u(s) = \log_e(\lambda(s)) = \mu(s) + z(s) + \varepsilon(s) \quad \text{eqn 2}$$

where $\mu(s) = \sum \beta_0 + \beta_1 x_1 + \dots + \beta_m x_m$ was the sum of spatially indexed covariates, $z(s)$ was a random effect representing spatially autocorrelated error, and $\varepsilon(s)$ was a random effect representing uncorrelated residual error. We assumed a normal prior with a mean of zero and variance of 10 on the detection covariates and a constant prior (i.e. equal to 1) on the abundance covariates. Each of the sets of covariate parameters was drawn from a set of candidate models with a uniform prior (1/number of models). By updating the model parameters conditionally on the chosen model, we model averaged our posterior estimates and simultaneously estimated the probability of the model. We used the term ‘model averaging’ (*sensu* Burnham & Anderson 2002) to refer to the process of estimating model parameters conditional on model probabilities. The frequency with which each model was drawn can then be used to calculate Bayes’ factors, which we used to calculate posterior model probabilities (Link & Barker 2006).

Our model structure allowed us to include the effects of spatial autocorrelation in terms of a departure from the systematic mean μ . The $z(s)$ term was modelled as a multivariate normal distribution: $z \sim MVN(0, \sigma_z^2 K)$, where σ_z^2 was the spatial variance and K was a correlation function that specified how correlated the error terms were. We used an exponential correlation model: $K = e^{-|d_i - d_j|/\theta}$, where θ represents the degree of spatial dependence in metres (i.e. range parameter in geostatistics). We assumed a uniform prior on θ ($U(0, 10\,000)$). We chose this correlation function because there is little theoretical justification for choosing complicated multiparameter correlation functions (Royle, Link & Sauer 2002). The uncorre-

lated error term represents the small scale variation in the data and was included to help account for overdispersion in our observations. We modelled uncorrelated error as $\varepsilon \sim Normal(\mathbf{0}, \sigma_\varepsilon^2)$, where σ_ε^2 was the residual variance. In our model, both σ_z^2 and σ_ε^2 were parameterized as $\tau_z = 1/\sigma_z^2$ and $\tau_\varepsilon = 1/\sigma_\varepsilon^2$, known as Bayesian precision parameters. We assumed inverse gamma priors with a mean of one and a variance of 10 on these parameters.

We used Markov chain Monte Carlo (MCMC) simulation to fit our models (Gilks, Richardson & Spiegelhalter 1995). Our algorithm was a Metropolized Gibbs sampler because it combined Gibbs sampling when the full conditional distribution was available and employed Metropolis–Hastings (M–H) when the full conditional was not available, as when updating based on the mixture likelihood (1) (Gilks, Richardson & Spiegelhalter 1995). We hierarchically centred our continuous covariates by subtracting the mean of each covariate from the data and dividing by the standard deviation in order to promote better mixing. We made additional improvements in mixing by reparameterizing the systematic mean and spatial random effect as: $z \sim MVN(\mu, \sigma_z^2 K)$ and $u \sim MVN(z, \sigma_z^2 K)$ (Gelfand, Sahu & Carlin 1995; Royle *et al.* 2007). For each iteration, we estimated the model parameters and then made spatial predictions by making draws from the full conditional distribution (Appendix S1–S4, Supporting information).

We analysed data for each year separately, with and without prior information on detectability. We assumed uninformative priors on all detection parameters for the 2005 data. We used the posteriors estimated from 2005 as priors on the 2006 analysis, and we used 2006 posteriors as priors on the 2007 analysis. Prior information did slightly influence our posterior detection parameter estimates and also reduced the posterior variance of those estimates, but did not influence our posterior abundance estimates. Our results were based on models including prior information.

We ran the models for 110 000 iterations, using three chains per model. We used more than one chain to ensure that we converged on the same answer each time we ran the algorithm. We discarded the first 10 000 iterations as a burn-in period. We made our inferences from the last 100 000 iterations, and to further reduce serial autocorrelation we thinned the chains using every 100th iteration. One chain took approximately 5–7 h to run on a computer with a 2.66 GHz processor. This long running time was largely due to the multivariate normal formulation of the spatial process, which is generally regarded as being more flexible than faster running conditional autoregressive models. Due to the long periods of time needed to run each model we adopted a parallel processing approach.

CANDIDATE MODELS

We considered four abundance models. Our first model assumed that average abundance was similar across patches (Null). Our second model contained an effect of the linear distance between the centre of the patch and the nearest road (Distance). We considered this because mountain plovers may select or avoid sites that experience more anthropogenic disturbance. Our third model included a binary variable (Grazed) for whether the site was in an arable field (0) or in grazed land (1). We considered these effects because mountain plover abundance could be higher in patches that were more similar to native grasslands (i.e. pastures and grazed lands) compared to arable fields. Our fourth model included a binary variable that described whether nest protection measures were applied in the section (1) or not (0). We considered this because mountain plovers might prefer sites with ongoing management. We did not consider models without the spatial random effects because we

wanted to make spatially explicit predictions of mountain plover abundance.

We considered three detection models. All three models contained an intercept and an effect of call playback (Call). We included this parameter in all the models because visual inspection of the data showed higher maximum counts after the call was played. Thus, our first model contained only an effect of call. Our second model added an observer effect (Observer). For these surveys there were only two observers in each year. We built our third model to include the effects of call, a quadratic effect of the time of day (Time + Time²) and a quadratic effect of the ordinal day in the breeding season (Day + Day²).

We presented all of our parameter estimates as posterior means and standard errors. These values were calculated by computing the mean and standard error of each parameter from values in the Markov chains. We then made predictions using our posterior parameter estimates. We presented these predictions as means with 95% Bayesian confidence intervals (BCI). Our spatial mountain plover predictions were made using the centre coordinates of 1720 sections within the survey area. For each iteration of the algorithm we drew 1720 predicted spatial random effects for each of the sections from the posterior predictive distribution (Royle, Link & Sauer 2002). We made spatial abundance predictions by combining these spatial random effects with the estimated model parameters for landuse. Within each section we specified whether the dominant form of landuse was arable land or grazed land using 2005 landcover data (obtained from Nebraska Department of Natural Resources) in ArcGIS 9.2 (ESRI 2008).

Results

We detected a total of 18 birds in 2005, 26 birds in 2006 and 86 birds in 2007. Thus, our surveys yielded low observed abundances of mountain plovers across years, but there was an increase in mean naïve abundances over time (Fig. 1a). Our results suggested that this increase was probably a result of increasing detectability across years (Fig. 1a). In our model selection exercise, we found that the detection error model with the highest posterior probability in 2005 included an effect of observer and call, whereas the model with the highest posterior in 2006 and 2007 contained call and time effects (Table 1). Our posterior parameter estimates suggested that playing a call had the strongest effect on detection error (Table 2). In general, playing a call increased detectability within each year and appeared to have caused the most dramatic increase in 2007 (Fig. 2). We found only weak effects of observer and time on detection error (Table 2).

Model selection results showed a high degree of uncertainty for models of abundance (Table 1). We found that average relative abundance seemed to have remained fairly constant through time (Fig. 1a). In terms of parameter effects, we found no effect of distance from road on mountain plover relative abundance (Table 2). We did, however, find a slight increase in relative abundance for patches located in grazed land compared to arable fields, and this effect was most pronounced in 2006 (Fig. 1b). We found virtually no correlation between nest management and observed abundance (Table 2).

Our estimates of spatial autocorrelation in abundance among patches varied between years with the range parameter

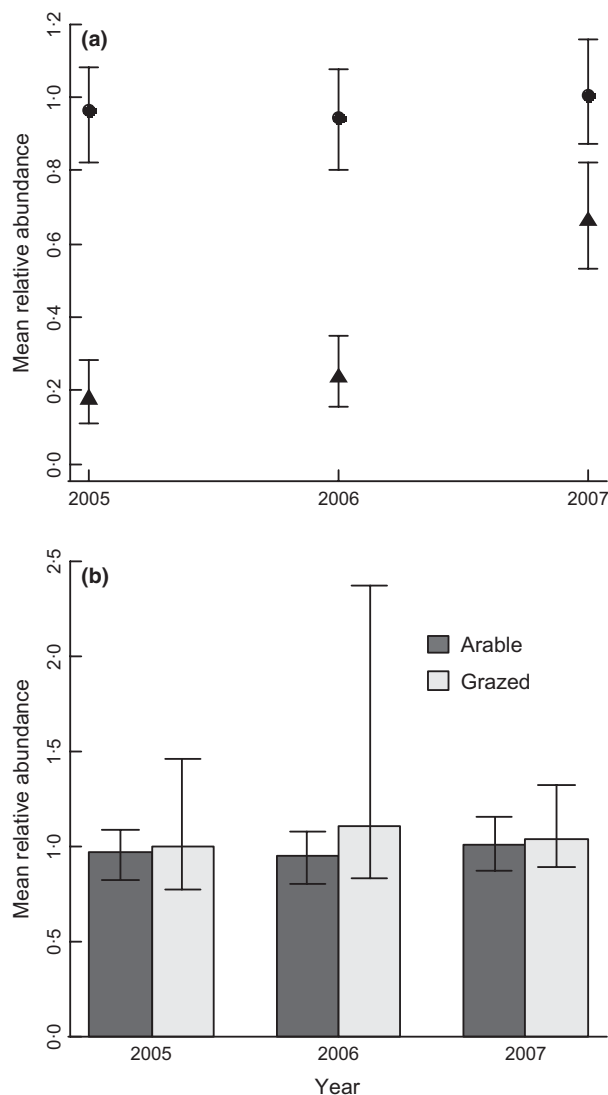


Fig. 1. (a) Mountain plover relative abundance estimates from western Nebraska during the breeding seasons of 2005–2007. Closed triangles represent mean naïve abundance estimates (with 95% BCI) based on the maximum number of observed individuals. Closed circles represent posterior detection corrected model estimates of mean relative abundance (with 95% BCI). (b) Bars represent posterior mean model abundance estimates (with 95% BCI) for arable and grazed patches over the course of 3 years.

(θ) being similar in 2005 and 2007, but lower in 2006 (Table 2). This parameter was difficult to interpret, but generally it is thought of as representing the distance at which the correlation between points weakens by a factor of 0.37 (i.e. $e^{-1} = 0.37$; Isaaks & Srivastava 1989). Across all 3 years, we found variation in mountain plover abundance could be attributed to variability between locations (τ_s) compared to variation within each location (τ_η). Recall, that these were precision parameters and must be inverse transformed. Our spatially explicit predictions of abundance showed a patchy distribution of mountain plovers across our study area (Fig. 3). This distributional pattern also changed between years with 2006 showing a weaker pattern compared with 2005 and 2007. Between years the spatial distribution shifted from a western to a southern

Table 1. Model selection table for linear models explaining variation in abundance and detection probability of mountain plovers in Western Nebraska for the 2005–2007 breeding seasons

	2005	2006	2007
Abundance models			
λ_{Null}	0.26	0.25	0.24
$\lambda_{\text{Distance}}$	0.26	0.27	0.27
λ_{Nests}	0.24	0.25	0.27
λ_{Grazed}	0.25	0.23	0.22
Detection models			
p_{Call}	0.07	0.02	0.00
$p_{\text{Call} + \text{Observer}}$	0.63	0.02	0.00
$p_{\text{Call} + \text{Time}^2 + \text{Day}^2}$	0.30	0.96	1.00

The abundance models included a null effect (Null), an effect of distance from road (Distance), the presence (Nests = 1) or absence (Nests = 0) of marked nests, and whether abundance varied between arable crop fields (Grazed = 0) and grazed land (Grazed = 1). The detection model set included a model with the effect of call (Call), an effect of call and observer (Observer) and quadratic effects of time of day (Time²) and ordinal day of the breeding season (Day²). Model probabilities were calculated using Bayes' factors.

Table 2. Posterior parameter estimates (standard errors) of abundance (λ) and detection probability (p) on the linear scale

	2005	2006	2007
$\log(\lambda)$	-0.03 (0.07)	-0.06 (0.08)	0.00 (0.07)
Distance	0.00 (0.03)	0.00 (0.03)	0.00 (0.03)
Grazing	0.03 (0.13)	0.15 (0.30)	0.04 (0.10)
Nests	0.01 (0.07)	-0.01 (0.07)	-0.06 (0.13)
$\text{logit}(p)$	-4.65 (0.56)	-4.25 (0.31)	-3.14 (0.34)
Call	1.35 (0.41)	1.37 (0.27)	1.38 (0.15)
Observer	0.64 (0.58)	0.00 (0.03)	0.00 (0.01)
Time	-0.30 (0.59)	0.01 (0.36)	-0.42 (0.35)
Time ²	0.99 (1.77)	1.61 (1.11)	2.09 (1.63)
Day	-0.08 (0.15)	-0.29 (0.12)	-0.32 (0.23)
Day ²	0.01 (0.10)	0.06 (0.08)	0.09 (0.08)
θ	5360.86 (2790.35)	2893.75 (2586.74)	4196.95 (2277.51)
τ_s	4.03 (3.03)	3.78 (2.40)	1.86 (0.91)
τ_η	7.35 (4.52)	6.31 (4.20)	7.01 (4.61)

The covariates for abundance were the effect of distance from road (Distance), landuse: arable field (Grazed = 0), grazed land (Grazed = 1) and whether managed nests were absent (Nests = 0) or present (Nests = 1). The detection covariates were the effect of call (Call), effect of observer (Observer), as well as a main and quadratic effect of both time and day. Additional model parameters included the range of spatial autocorrelation (θ), spatial precision (τ_s) and residual precision (τ_η).

distribution. Assuming we made predictions within the region of Nebraska where mountain plovers are likely to be found, we estimated the total abundance of plovers as 1650 (95% BCI: 400–6681); 1617 (95% BCI: 367–6966); and 1568 (95% BCI: 277–8681) for the 3 years, respectively.

Discussion

The primary uses of monitoring data in species conservation should be to answer scientific questions or to assess the efficacy

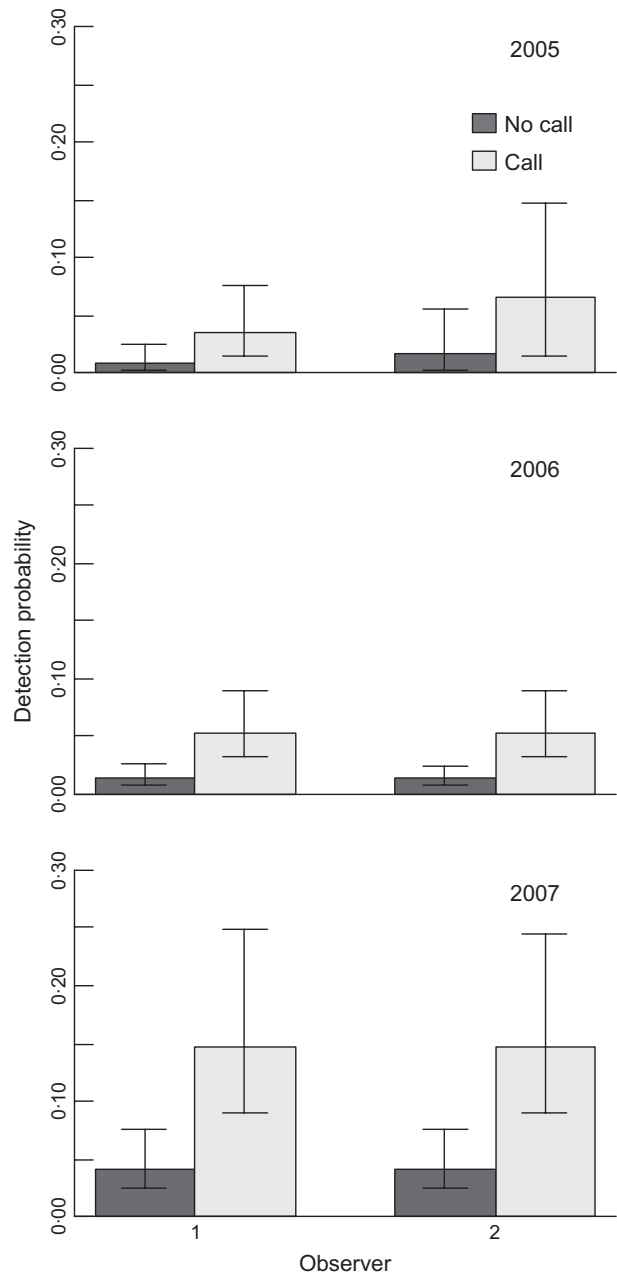


Fig. 2. Detection probability estimates for mountain plover surveys during the 2005–2007 breeding seasons. Bars represent the posterior mean estimates of detection probability between two observers and before and after alarm calls were played. Error bars represent 95% BCI.

of certain management practices (Nichols & Williams 2006). Inferences based on naïve estimates of abundance are likely to impact which steps are taken in terms of interpreting results and applying management action. For example, had we implemented a management practice to improve breeding habitat within agricultural sections in 2005, we would have drawn the wrong conclusion about the impact of management on the average number of birds expected in each section. Likewise, had we not accounted for spatial error we might not have detected changes in sections under management or identified portions of the landscape that warranted further attention.

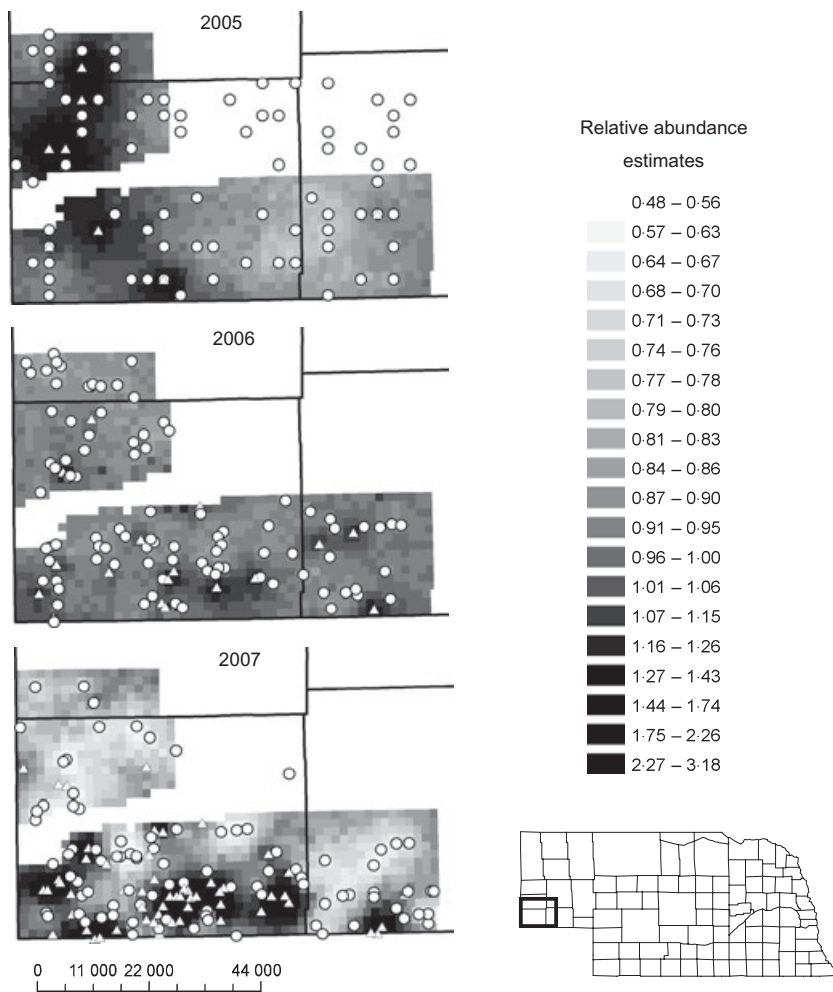


Fig. 3. Spatially explicit posterior mean predictions of mountain plover relative abundance in the panhandle of Nebraska for the 2005–2007 breeding seasons. Open circles represent count locations where no birds were detected. Triangles represent locations where one or more birds were detected. Grid cells represent 2.56 km² agricultural sections. Map scale is in metres.

Rather, our habitat effects would have told us that abundance was largely similar across patches and that the expected number of birds within a section was fairly uniform across the landscape. Therefore, in order to make progress in terms of creating new management plans for this species (or for any low density species), a rigorous modelling approach is necessary to make better sense of the data.

MOUNTAIN PLOVER ABUNDANCE

Our estimates of detection rate were, in general, lower than those found elsewhere: 0.94–0.65 in Oklahoma, USA (McConnell *et al.* 2009), 0.38 in Colorado, USA (Wunder, Knopf & Pague 2003). The overall pattern in our results mirrored those of other surveys designed to increase the number of detections within sampling locations (e.g. McConnell *et al.* 2009). Other studies of this species have shown that increasing the number of visits to the same site does reduce detection error (Dreitz, Lukacs & Knopf 2006). While such strategies can reduce variation in detection error, this reduction usually comes at the cost of increasing variation in abundance estimates (based on simulations, not shown). The amount of effort invested in revisits could also explain why we found a very weak effect of time on detection error. Dreitz, Lukacs & Knopf (2006) sampled some

sites as many as 12 times. In our study, effort remained fixed at three to four visits because of personnel and financial constraints. Tipton, Dreitz & Doherty (2008) found similar results for this species using fixed and comparatively low amounts of sampling effort. Thus, studies designed to monitor low density species should weigh the statistical trade-off between the number of sites and visits, as well as the financial trade-offs between costs associated with increased effort and costs of making decisions based on incorrect inferences (Field *et al.* 2004; Field, Tyre & Possingham 2005a). Within the limits of our data, our model-based estimates suggested that mountain plover relative abundance was higher in Nebraska than previously suggested in Bly, Snyder & VerCauteren (2008). Furthermore, past claims about the size of this population in Nebraska were probably confounded by chronic undersampling.

It would appear that mountain plover abundance did not respond to the types of agricultural landuse we considered. Our estimated effect of agricultural landuse was similar to that found elsewhere (Dreitz, Lukacs & Knopf 2006; Tipton, Dreitz & Doherty 2008; Tipton, Doherty & Dreitz 2009). There was also a great deal of variability in terms of mean relative abundance across the mountain plover's range. Our estimates of relative abundance on a per hectare basis were ~0.20–0.30 birds ha⁻¹. Others have found abundances as high as 1.56 birds ha⁻¹ (assuming 1.6 ha patches) in Colorado (Dreitz,

Lukacs & Knopf 2006) and as low as 0.003 birds ha⁻¹ in Oklahoma (McConnell *et al.* 2009). One possible explanation for this heterogeneity could be related to the methods of sampling and detection correction applied across the various surveys. Our study and that of Dreitz, Lukacs & Knopf (2006) both used a multiple revisit method of sampling and similar statistical methods. Plumb, Knopf & Anderson (2005) and Wunder, Knopf & Pague (2003) used distance sampling which requires a different sampling strategy and different statistical approach. Finally, McConnell *et al.* (2009) used a point count sampling approach and *post hoc* detection correction method, and Tipton, Doherty & Dreitz (2009) used a probability based sampling approach and a design based method of deriving abundance. Therefore, comparing multiple studies suggests that we may not clearly know whether abundance differences are attributable to a biological signal or whether these differences are attributable to variation in field and statistical methods.

SPATIAL PREDICTIONS

Without spatially explicit predictions we would have to estimate total mountain plover abundance in Nebraska by assuming that our model could be used to predict abundance at unobserved locations (i.e. extrapolation), which could lead to unreliable estimates. Instead, we estimated the spatial structure of abundance using the data and constructed predictions at unobserved locations between observed locations (i.e. interpolation). In many of the studies previously mentioned, total population estimates were arrived at using extrapolated estimates of density. However, our total population estimates for Nebraska, based on interpolated values, are less than those for Colorado (Wunder, Knopf & Pague 2003; Tipton, Doherty & Dreitz 2009) and Montana (Dinsmore, White & Knopf 2003), and are generally more uncertain. This was to be expected because ignoring spatial autocorrelation can result in biased parameter estimates and misleading inferences (Legendre 1993; Dormann 2007; Beale *et al.* 2010).

Our study was unable to tease apart the broader reasons for the spatial structuring in our data. Spatial structuring could be driven by either extrinsic (e.g. environmental or geomorphic) factors or intrinsic (e.g. behavioural or phenotypic) factors. Because habitat variables did not adequately account for the variability in our data it is likely that much of the intrinsic and extrinsic structuring was swept into the spatial autocorrelation term. Therefore, it could be that the temporal variation in our spatial predictions was caused by interacting static and dynamic spatial processes. Additionally, including a spatial error term, as we did, does not necessarily mean that we accounted for all of the spatial variation in our data. For instance, Wintle & Bardos (2006) show that including a spatial autocorrelation term in a model reduces residual spatial error in data with intrinsic structuring, but not completely. Thus, it is possible that there may be lingering spatial variation in our data that we did not account for. The way to solve this would be to include additional linear and non-linear spatially indexed covariates in our abundance models and utilize the Bayesian

model averaging approach to compare the performance of those additional predictors.

Despite this, we can view our relative spatial predictions as measures of habitat quality if we assume that the number of birds in a section is proportional to the number and quality of habitat patches in a section (Fretwell & Lucas 1970). Treating our corrected mean estimate of relative abundance as a Poisson random variable representing birds per section (our unit of prediction), we could expect to find one to two mountain plovers in each section, but could occasionally find a maximum of five. When we consider the spatial heterogeneity in mountain plover habitat use, as measured by our map, we might expect to see as many as ten birds in some sections and almost none in others. This is interesting biologically, because our mean abundance estimate suggests that, in the absence of a spatial process, mountain plovers should be spacing themselves so that their densities are fairly low (around 1–2 birds per section). This would only work if there were one or two high quality patches in each section. If we drew inferences from only this value we might have expected that an increase in the abundance of mountain plovers would lead to more sections being occupied by individuals. In terms of management, this would be an important aspect of mountain plover biology to understand because it should inform the scale at which management is applied. In the case of mountain plovers, this would suggest that a larger area was necessary to increase the population.

However, this is not what our results indicate. Our spatial predictions show that the number of mountain plovers in some sections increased. We might expect this result if something were improving the number of high quality patches within each section. One potential explanation for this within-section increase could be that mountain plovers were selecting nesting sites in response to nest success (Greenwood 1980). Our modelling results indicated that nest management had little effect on our estimates of relative abundance. This is likely to be due to the fact that few of the sites where nests were marked corresponded to survey locations. However, the survey locations with the highest predicted numbers of mountain plovers in our 2007 map overlap the regions where the highest densities of nests were found between 2004 and 2007 (B. Bly, unpublished data). If we compare the average predicted abundances between sections that contained marked nests (1.51) and those that did not (0.89) we see that plover abundance is slightly higher in the managed sections. Bly, Snyder & VerCauteren (2008) also found that the observed number of mountain plover nests in these sections had increased from 49 nests in 2005 to 112 nests by 2007. Average nest success rates in this region are high (~75%) and similar between years (B. Bly, M. Post van der Burg, A. Tyre, L. Snyder, J. Jorgensen & T. Vercauteren, unpublished data). However, we are still unsure whether these sections contain some as yet unobserved habitat characteristic that could be attracting breeding plovers, thus giving the impression that the increase in abundance is due to management efforts.

Knowing this information would be particularly useful in a largely homogeneous landscape like our study area. Our

analysis suggested that small-scale conservation programmes, which tend to be more expensive in terms of money and labour, might be more beneficial for some subsets of the continental population of mountain plovers. This might be particularly true when preferred habitats, such as prairie dog *Cynomys ludovicianus* colonies, are nearly absent from the landscape. The population level benefit of management could also vary with regional shifts in preferred tillage techniques.

Variation in the value of management strategies across a species' range raises questions of where to put conservation effort, rather than how to implement it across the landscape. Conservation practices certainly accrue greater benefit when they are coordinated at larger scales (Kark *et al.* 2009). The types of conservation practices for migratory species like mountain plovers appear fragmented from one region to another. Federal and regional agencies can make recommendations, but have no regulatory authority to compel state agencies or funding bodies to direct funds to species where the greatest local benefit would accrue. Our study does not provide 'rules-of-thumb' for low density population management, but it does provide a modelling framework to study spatial variation that can be used to target management across the landscape. Considering the variability in approaches and methods for surveys and analysis of population trends, we suggest that a more synthetic study of these methodologies is warranted.

Acknowledgements

We would like to thank the Nebraska Game and Parks Commission (NGPC) for financial support. Our research was funded with State Wildlife Grant (T-47), Nebraska Environmental Trust Grant (05-182), and NGPC Nongame and Endangered Species Conservation Funds. The UNL Research Computing Facility provided the computational resources for fitting the models. We especially would like to thank Joel Jorgenson, Matthew Giovanni, Wayne Thogmartin, Carsten Dormann, the editor and one anonymous reviewer for helpful comments on this manuscript. This research would not have been possible without the help of Larry Snyder and his knowledge of local landowners. Likewise, without those landowners granting us access to their property, our observations would have been more limited. We would also like to acknowledge the previous work that Cris Carnine and Courtney Kerns did to establish mountain plover surveys in Nebraska. Finally, we thank the technicians for their work in the field: Travis Wooten, Cameron Shelton and Brian Monser.

References

Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J. & Elston, D.A. (2010) Regression analysis of spatial data. *Ecology Letters*, **13**, 246–264.

Bly, B.L., Snyder, L. & VerCauteren, T. (2008) Migration chronology, nesting ecology, and breeding distribution of Mountain Plover (*Charadrius montanus*) in Nebraska. *Nebraska Bird Review*, **76**, 120–128.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York, USA.

Clausen, M.K. (1990) Mountain Plover sighted in Kimball County. *Nebraska Bird Review*, **58**, 98–99.

Dinsmore, S.J. (1997) Mountain Plover nest in Kimball County. *Nebraska Bird Review*, **65**, 131.

Dinsmore, S.J., White, G.C. & Knopf, F.L. (2003) Annual survival and population estimates of mountain plovers in southern Philips County, Montana. *Ecological Applications*, **13**, 1013–1026.

Dormann, C.F. (2007) Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Global Ecology and Biogeography*, **16**, 129–138.

Dreitz, V.J., Lukacs, P.M. & Knopf, F.L. (2006) Monitoring low density avian populations: an example using Mountain Plovers. *Condor*, **108**, 700–706.

Efford, M.G. & Dawson, D.K. (2009) Effect of distance-related heterogeneity on population size estimates from point counts. *Auk*, **126**, 100–111.

ESRI (2008) *ArcGIS: Release 9.3*. Environmental Systems Research Institute, Redlands, CA.

Field, S.A., Tyre, A.J. & Possingham, H.P. (2005a) Optimizing allocation of monitoring effort under economic and observational constraints. *Journal of Wildlife Management*, **69**, 473–482.

Field, S.A., Tyre, A.J., Jonzen, N., Rhodes, J.R. & Possingham, H.P. (2004) Minimizing the cost of environmental management decisions by optimizing statistical thresholds. *Ecology Letters*, **7**, 669–675.

Field, S.A., Tyre, A.J., Thorn, K.H., O'Connor, P.J. & Possingham, H.P. (2005b) Improving the efficiency of wildlife monitoring by estimating detectability: a case study of foxes (*Vulpes vulpes*) on the Eyre Peninsula, South Australia. *Wildlife Research*, **32**, 253–258.

Fretwell, S.D. & Lucas, H.L. (1970) On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, **19**, 16–36.

Gelfand, A.E., Sahu, S.K. & Carlin, B.P. (1995) Efficient parametrizations for normal linear mixed models. *Biometrika*, **82**, 479–488.

Gilks, W., Richardson, S. & Spiegelhalter, D. (1995) *Markov Chain Monte Carlo in Practice*. Chapman and Hall, London.

Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behavior*, **28**, 1140–1162.

Hiller, T.L., Powell, L.A., McCoy, T.D. & Lusk, J.J. (2009) Long-term agricultural land-use trends in Nebraska, 1866–2007. *Great Plains Research*, **19**, 225–237.

Isaaks, E.H. & Srivastava, R.M. (1989) *An Introduction to Applied Geostatistics*. Oxford University Press, New York, USA.

Johnson, D.H. (2008) In defense of indices: the case of bird surveys. *Journal of Wildlife Management*, **72**, 857–868.

Kark, S., Levin, N., Grantham, H.S. & Possingham, H.P. (2009) Between-country collaboration and consideration of costs increase conservation planning efficiency in the Mediterranean Basin. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 15360–15365.

Knopf, F.L. & Miller, B.J. (1994) *Charadrius montanus*: montane, grassland, or bare-ground plover? *Auk*, **111**, 504–506.

Knopf, F.L. & Rupert, J.R. (1999) Use of cultivated fields by breeding mountain plovers in Colorado. *Studies in Avian Biology*, **19**, 81–86.

Knopf, F.L. & Wunder, M.B. (2006) Mountain Plover (*Charadrius montanus*). *The Birds of North America Online* (ed. A. Poole). Cornell Lab of Ornithology, Ithaca; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/211>

Latimer, A.M., Wu, S.S., Gelfand, A.E. & Silander, J.A. (2006) Building statistical models to analyze species distributions. *Ecological Applications*, **16**, 33–50.

Legendre, P. (1993) Spatial autocorrelation – trouble or new paradigm. *Ecology*, **74**, 1659–1673.

Link, W.A. & Barker, R.J. (2006) Model weights and the foundations of multi-model inference. *Ecology*, **87**, 2626–2635.

McConnell, S., O'Connell, T.J., Leslie, D.M. & Shackford, J.S. (2009) Mountain Plovers in Oklahoma: distribution, abundance, and habitat use. *Journal of Field Ornithology*, **80**, 27–34.

Nichols, J.D. & Williams, B.K. (2006) Monitoring for conservation. *Trends in Ecology and Evolution*, **21**, 668–673.

Plumb, R.E., Knopf, F.L. & Anderson, S.H. (2005) Minimum population size of mountain plovers breeding in Wyoming. *Wilson Bulletin*, **117**, 15–22.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Royle, J.A. (2004) N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, **60**, 108–115.

Royle, J.A., Link, W.A. & Sauer, J.R. (2002) *Statistical Mapping of Count Survey Data. Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Washington, D.C.

Royle, J.A. & Nichols, J.D. (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology*, **84**, 777–790.

Royle, J.A., Kery, M., Gautier, R. & Schmid, H. (2007) Hierarchical spatial models of abundance and occurrence from imperfect survey data. *Ecological Monographs*, **77**, 465–481.

Shackford, J.S., Leslie, D.M. & Harden, W.D. (1999) Range-wide use of cultivated fields by Mountain Plovers during the breeding season. *Journal of Field Ornithology*, **70**, 114–120.

- Thogmartin, W.E., Knutson, M.G. & Sauer, J.R. (2006) Predicting regional abundance of rare grassland birds with a hierarchical spatial count model. *Condor*, **108**, 25–46.
- Tipton, H.C., Doherty, P.F. & Dreitz, V.J. (2009) Abundance and density of mountain plover (*Charadrius montanus*) and burrowing owl (*Athene cunicularia*) in eastern Colorado. *Auk*, **126**, 493–499.
- Tipton, H.C., Dreitz, V.J. & Doherty, P.F. (2008) Occupancy of mountain plover and burrowing owl in Colorado. *Journal of Wildlife Management*, **72**, 1001–1006.
- Tyre, A.J., Tenhumberg, B., Field, S.A., Niejalke, D., Parris, K. & Possingham, H.P. (2003) Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications*, **13**, 1790–1801.
- Wintle, B.A. & Bardos, D.C. (2006) Modeling species–habitat relationships with spatially autocorrelated observation data. *Ecological Applications*, **16**, 1945–1958.
- Wunder, M.B., Knopf, F.L. & Pague, C.A. (2003) The high-elevation population of Mountain Plovers in Colorado. *Condor*, **105**, 654–662.

Received 1 February 2010; accepted 20 October 2010
 Handling Editor: Brendan Wintle

Supporting Information

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

Appendix S1. R code for MCMC algorithm for analysis of spatial data.

Appendix S2. R script file for proposal and likelihood functions used in Appendix S1.

Appendix S3. Comma delimited Microsoft Excel file containing data for analysis.

Appendix S4. Comma delimited Microsoft Excel file with data used in spatial interpolation.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.