Improved state-space models for inference about spatial and temporal variation in abundance from count data

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Abstract

Models of population dynamics play a central role in theoretical and applied ecology where they are used for purposes such as testing hypotheses about density dependence and predicting species' responses to future environmental change or conservation actions. Accounting for process variation and observation error in such efforts is necessary to achieve unbiasedness, and doing so is possible using recently developed state-space models. Conventional state-space models, however, have three important limitations: (1) the parameters are not identifiable in many common situations, (2) they do not admit spatial variation in population dynamics, and (3) there is no clear interpretation of the observation error. We demonstrate how each of these problems can be resolved using a class of hierarchical models for spatially-replicated time-series data recently proposed by Dail and Madsen (2011, Biometrics). We expand this class of models to accommodate classical growth models, zero-inflation, and random effects such as observer-specific detection probabilities. We also present methods for forecasting population size under future environmental conditions. Implementation of these ideas is possible using either frequentist or Bayesian methods, and code to fit these models using the **R** package `unmarked` or **JAGS** is also provided. A simulation study indicated that bias was negligible and coverage nominal and an analysis of North American Breeding Bird Survey is presented for illustration.

Key words: abundance, Dail and Madsen model, density-dependence, Gompertz model, immigration, open population point count models, random observer effects, range, Ricker model, zero-inflated

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Theoretical ecology requires models of population dynamics for testing hypotheses regarding spatial and temporal variation in abundance. For example, much theoretical work has focused on understanding the importance and existence of phenomenon such as density-dependent population regulation, population cycling, and spatial synchrony (May, 1975; Royama, 1977; Turchin, 1990; Dennis and Taper, 1994; Bjørnstad et al., 1999), and population models are required to evaluate associated hypotheses. In applied contexts, population models are used for estimating extinction probabilities (Schoener and Spiller, 1992; Nadeem and Lele, 2011) and for predicting the effects of future environmental conditions or conservation actions on population size (Jamieson and Brooks, 2004; Hatfield et al., 2012). In order to address these questions, two complicating factors must be confronted when fitting population models to data. First, deterministic models of population dynamics are virtually always inadequate due to process variation, the inherent stochasticity in demographic parameters and environmental conditions (Bjørnstad and Grenfell, 2001; Sæther and Engen, 2002). Second, abundance—the natural state variable in studies of population dynamics—can rarely be observed perfectly in field studies because of observation error, such as imperfect detection (Link and Nichols, 1994; Kery et al., 2009).

State-space models are a widely used approach for studying population dynamics while accounting for process variation and observation error (de Valpine and Hastings, 2002; Buckland et al., 2004; Dennis et al., 2006). Classical state-space models are time-series models in which the true state of the system (e.g. population size during each year) is observed imperfectly. One reason for the widespread adoption of state-space models in ecology is that failure to account for process variation and observation error can bias estimators of abundance and population growth parameters. For instance, the strength of density dependence will be over-estimated if observation error is ignored (Link and Nichols, 1994; Shenk et al., 1998).

A simple state-space models can be described as follows. Let N_t be the abundance of a species during year t, for $t = 1, \ldots, T$, and let X_t be the observed data, which differs from N_t due to observation error, a random effect denoted ζ_t. Temporal variation in N_t is modeled using a population growth model, $\mu(N_{t-1})$, coupled with a stochastic model allowing for random process variation. The deterministic model may be density-dependent, for example logistic, or it might be density-independent, as in the case of exponential growth, in which $\mu(N_{t-1}) = N_{t-1}e^r$ where r is the intrinsic rate of increase. The full model can now be written as:

$$N_1 = X_1 \tag{1a}$$

$$N_t = \mu(N_{t-1}) + \grave{\partial}_{t-1} \quad \text{for } t = 2, \ldots, T \tag{1b}$$

$$X_t = N_t + \zeta_t \qquad \text{for } t = 1, \ldots, T \tag{1c}$$

where $\grave{\partial}_t$ is the random effect allowing for process variation unaccounted for by the deterministic model. In classical state-space models, the two sets of random effects are assumed to be i.i.d Gaussian deviates: $\grave{\partial}_t \sim \mathrm{N}(0, \sigma)$ and $\zeta_t \sim \mathrm{N}(0, \tau)$. It is also standard practice to ignore process variation associated with N_1, as indicated by Eq 1a.

Even though state-space models such as that shown in Eq. 1 are the most widespread approach for modeling population dynamics using time-series data, several problems are evident. Namely, (1) time-series data and the underlying abundance parameters of interest are typically integer-valued, as in the case of count data, raising concerns about the use of Gaussian distribution for the random effects, (2) the model for observation error has little biological basis, (3) spatial variation in abundance is not allowed, and (4) some of the paramters of the model are not estimable. We briefly discuss each of these points before describing a general approach to resolving these shortcomings.

Use of the Gaussian distribution for modeling random process variation and observation error is motivated by convenience rather than biology. Specifically, the Gaussian assumptions allow for parameter estimation using the Kalman filter (Dennis et al., 2006), which is much more computationally efficient than estimation methods when random effects are not Gaussian distributed (de Valpine and Hastings, 2002). The problem with this is that it allows for negative values of the state-variable, which is inconsistent with the observed data. Nonetheless, efforts have been made to adhere to the Gaussian assumptions by tranforming abundance to density by replacing N_t with $Y_t = \log(N_t/A)$ where A is the area surveyed. However, this transformation is problematic since local abundance may be zero and thus $Y_t = \log(0) = -\infty$. Generally, zeros are replaced with some small number, although the effect of this is rarely discussed.

Another problem with standard state-space models is that the observation error has no clear interpretation. The use of a mean zero Gaussian distribution implies that X_t will be higher than N_t as often as it is lower than N_t. It is hard to identify a mechanism that would cause such symmetric errors. A more likely form of observation error, and one that has been recognized for well over a century, results from failing to detect individuals that are present. Imperfect detection may be attributable to characteristics of the species under study, such as its elusiveness, or to the failings of the ecologist collecting the data in the field. Although a vast number of methods have been devised for accounting for this form of observation error, rarely have these methods been integrated into state-space models (but see Buckland et al., 2004).

A more serious problem than the ones associated with the Gaussian assumptions is that the parameters of the simple state-space models such as Eq 1 are not identifiable in many circumstances (Polansky et al., 2009). Recall that the Eq. 1 did not specify distributions for N_1; however, N_1 is a random variable and hence there is uncertainty that should be accounted for. To be more specific, a fully-specified state-space model requires at least three probability distributions, which we represent using bracket notation:

$$[N_1|\boldsymbol{\theta}] \tag{2a}$$

$$[N_t|N_{t-1}, \boldsymbol{\Theta}] \quad \text{for } t = 2, \ldots, T \tag{2b}$$

$$[X_t|N_t, \boldsymbol{p}] \quad \text{for } t = 1, \ldots, T \tag{2c}$$

where $\boldsymbol{\theta}$ are the process variation parameters for the initial state, $\boldsymbol{\Theta}$ are the process variation parameters influencing how abundance changes over time, and $\boldsymbol{p}$ are the observation error parameters. The three lines of general model described by Eq. 2 correspond to the three equations shown for the specific example in Eq 1. However, in this case, we allow N_1 to be a random variable. But what should its distribution, $[N_1|\boldsymbol{\theta}]$ be? And how could $\boldsymbol{\theta}$ be estimated since there is only a single observation available? One approach to estimating the $\boldsymbol{\theta}$ is to assume that the population is in equilibrium, i.e. that the expected value of N_t is constant through time. Althought this makes the parameters identifiable, assuming equlibrium defeats the objective of many studies of population dynamics, namely determining why a population varies over time.

A fourth problem with these models is that they do not admit spatial variation. This reduces the scope of the inferences that can be drawn from the models and it ignores the importance of space in population regulation.

Several extensions of state-space models have been proposed to overcome the limitations described above. de Valpine and Hastings (2002) and Kery et al. (2009) described methods for fitting models with non-Gaussian distributions for the process and observation errors. Observation models with more intuitive interpretations, such

as those that explicitly model detection probability, have been proposed by Kery et al. (2009). Lele et al. (1998) and Kery et al. (2009) developed models allowing for inference about spatial and temporal variation in abundance, and their developments also resolved the problems of non-identifiability for the parameters of the initial state at time $t = 1$. Of these extensions, the work by Kery et al. (2009) is unique in that it addressed multiple limitations simultaneously. However, their model did not include serial depedence, which is a hallmark of population models. This limits the utility of their model for making inferences about explicit population processes. In contrast, recent work has sought to use state-space models for inference about population processes such as mortality and recruitment. To do so, methods have been developed to combine multiple sources of information, such as counts and mark-recapture data (Besbeas et al., 2002; Buckland et al., 2004; Schaub et al., 2007). Although these integrated population models may be viewed as the gold standard in state-space modeling, ecologists are not always so fortunate to have direct information about vital rates, especially at large spatial scales. Rather, count data are much more common, and are produced by many of the largest monitoring programs in the world, such as the North American Breeding Bird Survey (BBS; Robbins et al., 1986).

In this paper, we focus on the model of Dail and Madsen (2011) that simultaneous resolves each of the abovementioned problems with traditional state-space models, and is designed for simple count data. In the following section, we describe the DM model in its original form and explain how it resolves each of the deficieinces with standard state-space models. In Section 3, we extend the model to accomodate classical models of population growth and to handle several features common to eco-logical time-series. Specifically, we describe methods for accomodating excess zeros and nuisance variables such as random observer effects. Both frquentist and Bayesian methods of inference are discussed, and code for fitting models is presented in the appendices. In Section 5, we evaluate the performance of the model extensions using a simulation study and by analyzing data from the North American Breeding Bird Survey (BBS), one of the most spatially and temporally extensive sets of count data on vertebrate populations (Robbins et al., 1986). The overarching aim of the paper is to provide ecologists with flexible and accessible means of adressing important questions related to the variaion of abundance in space and time.

1   The Dail-Madsen Model

The DM model is an extension of the N-mixture model (Royle, 2004), which allows for inference about spatial variation in abundance when individuals cannot be detected with certainty. To estimate both abundance parameters and parameters of the detection process, the original N-mixture model uses replicate observations at each site, which are collected during sufficiently short time intervals such that the population can safely be assumed to be closed with respect to births, deaths, and movement. The DM model relaxes this closure assumption and includes explicit parameters describing population change over time.

1.1   The Data

The DM model requires count data collected at R sites, each of which is surveyed on T time periods. A site is ideally, but not necessarily, a well-defined region of a study area, such as a wetland or a patch of early-successional habitat. In some cases, a site may not have a clear biological significance, for instance in the case of randomly located survey plots. The timeframe of the study is arbitrary, but

the general situation is one in which the time period is sufficiently long such that abundance changes at each site. We will call these time periods primary sampling periods to distinguish them from secondary sampling periods, which are repeated surveys within a primary period. In the case where no secondary sampling was conducted, let $n_{it} : i = 1, \ldots, R; t = 1, \ldots, T$ denote the count data at site i and primary period t. If J secondary sampling periods were used, $n_{ijt} : j = 1, \ldots, J$ is the count at site i during secondary sampling occasion j within year t. These are the observed data, which typically will less than the actual quantitiy of interest, abundance, denoted N_{it}. In cases where detection probability is perfect, abundance is observed directly such that $\{N_{it}\}$ are the data.

1.2 The Model

As originally formulated, the DM model includes submodels for three conditionally related processes: (1) initial abundance, i.e. the abundance at site i during the first primary period, denoted $[N_{i1}]$, (2) subsequent abundance, which is dependent upon abundance in previous years $[N_{it}|N_{it-1}]$, and (3) the detection process, $[n_{it}|N_{it}]$ (Dail and Madsen, 2011). The first two processes describe the state process—the variation in abundance in space and time. The third item in the list is the observation process, which describes the relationship between the true state, abundance, and the observed count data.

1.2.1 Initial abundance

In the original formulation, initial abundance was modeled using either the Poisson or negative binomial distributions:

$$N_{i1} \sim \text{Pois}(\Lambda_i)$$
$$\text{or}$$
$$N_{i1} \sim \text{NB}(\Lambda_i, \alpha) \tag{3}$$

where Λ_i is the expected abundance at site i during year 1. The Poisson distribution assumes that the mean of N_{i1} is equal to its variance, whereas the negative binomial distribution allows the variance to be greater than the mean with the amount of overdispersion determined by the parameter α.

Regardless of the specified distribution, the model for initial abundance has two distinguising features. First, it provides a mechanism for characterizing spatial variation in abundance. For instance, one might consider the influence of some environmental covariate (x_i) on abundance using a log-linear model such as $\log(\Lambda_i) = \beta_0^\Lambda + \beta_1^\Lambda x_i$. The second important point is that the spatial replicates resolve the problem of parameter non-identifiability that are common to standard state-space models because, as demonstrated by Royle (2004), process variation and observation error can be estimated from spatially-replicated count data. Hence, the first component of the model addresses issues (1) and (2) identified in the introduction.

1.2.2 Abundance in subsequent time periods

The DM model assumes that abundance in time t is a function of abundance in time $t-1$, i.e. abundance at each site evolves as a first order Markovian process, although higher order processes are also possible. Dail and Madsen (2011) considered several models to describe the temporal dynamics; however, in each case they modeled N_t as the sum of two random variables: S_t, the number of indivduals surviving from $t-1$

and not emigrating; and G_t the number of new individuals entering the population. Their most general model was

$$\left.\begin{array}{c} S_{it}|N_{it-1} \sim \text{Bin}(N_{it-1}, \omega) \\ G_{it}|N_{it-1} \sim \text{Pois}(\gamma(N_{it-1})) \\ N_{it} = S_{it} + G_{it} \end{array}\right\} \quad \text{for } t = 2, \dots, T \tag{4}$$

where ω is the apparent survival probability and γ is the recruitment rate (which can depend on N_{it-1}). In the absence of movement, ω is exactly the probability of surviving from year t to $t-1$, and γ is the per-capita birth rate. However, in the more common scenario when immigration and emigration occur, ω is the probability of surviving and not emigrating, and γ is product of the birth rate and the emigration rate, i.e. the recruitment rate. Dail and Madsen (2011) proposed three models for γ: the constant model, $G_t \sim \text{Pois}(\gamma)$ where recruitment does not depend on N_{it-1}, and which simulates a "propagule rain" of new individuals; the autoregressive model, $G_t \sim \text{Pois}(\gamma(N_{it-1}))$, which simulates geometric or density independent growth; and the "no-trend" model, $\gamma = (1 - \omega)\Lambda$, which keeps expected abundance constant over time. As before, covariates of ω and γ can be easily accomodated, for example using logit- and log-linear models respectively.

In cases where no movement occurs, the DM model can directly estimate demographich parameters, and this mechanistic description of population change is much more appealing than classical population growth models such as the logistic model. However, movement complicates the interpretation of the the parameters, reducing the connection to specific population processes. In such cases, the model of dynamics shown in Eq 4 can be replaced with standard population models as described in Sect 3. Irrespective of the model for population dynamics, it is worthwhile to note that the discrete distributions used in the DM model avoid the issues associated with the Gaussian distribution used to model process variation in standard state-space models.

1.2.3 Observation process

Eqs. 3 and 4 fully specify the state model—the model for spatial and temporal variation in abundance. The observation model assumes that individuals are missed due to imperfect detection. The simplest model for imperfect detection is

$$n_{it} \sim \text{Bin}(N_{it}, p) \tag{5}$$

Surprsingly detection probability, p, can be estimated without secondary sampling occasions. However, this is only possible because if the parameteric assumptions of the population dynamics are met exactly. In practice, it is preferable to obtain direct information about p using secondary sampling occassions or some other auxiliary data, as is demonstrated in section

2 Statistical Inference

2.1 Maximum likelihood

Maximum likelihood estimation of parameters in models with random effects requires removing the random effects by integration or summation.

2.2 Bayesian inference

Bayesian inference has several appealing features. First, it allows direct probability statements to be made about a hypothesis given data. Second, priors are cool. We can combine data from multiple sources or use existing estimates of parameters as prior distributions. MCMC has a bad rap for being slow, but actually, in the case of state-space models it may be one of the few options for estimation, and in fact may be faster than maximizing likelihoods.

Here is some BUGS code:

```
model {
lambda ~ dunif(0, 5)
r ~ dunif(-5, 5)
p ~ dunif(0,1)
for(i in 1:nSites) {
  N[i,1] ~ dpois(lambda)
  y[i,1] ~ dbin(p, N[i,1])
  for(t in 2:nYears) {
    mu[i,t-1] = N[i,t-1]*exp(r)
    N[i,t] ~ dpois(mu[i,t-1])
    n[i,t] ~ dbin(p, N[i,1])
    }
  }
}
```

3 Model Extensions

3.1 Population growth models

Preliminary DM model runs for several species tended to lead to estimates of survival that were unrealistically high and recruitment that were unrealistically low, or the reverse (compared to independent demographic analyses). The DM models are able to partition changes in abundance to survival and recruitment in part by making strong distributional assumptions. When those assumptions are heavily violated the models may proportion population growth incorrectly into survival and recruitment, even if they estimates population growth accurately.

Although partitioning population growth into survival and recruitment is informative, it is not needed for all applications. Furthermore, a simpler model would have several merits: faster running time, fewer total model combinations, and possibly more realistic estimates. Therefore, we developed a version of the DM model that estimates and models population growth directly. In this model, Eq. 4 is simplified to:

$$N_{it} \sim \text{Pois}(\exp(r)N_{it-1}) \tag{6}$$

where r represents the instantaneous population growth rate. This, like the autoregressive version of the model, is a variant on a simple density-independent exponential model of population growth. Density-dependent versions of the model are also possible. For example:

$$N_{it} \sim \text{Pois}(N_{it-1}\exp(r(1 - N_{it-1}/K))) \tag{7}$$

where K is the stable equilibrium of the population and r is the instantaneous population growth rate at low population densities, and both parameters are constrained

to be positive. This model is based on the Ricker (1954) discrete time version of the logistic population growth model. We also implemented the Gompertz (1825) density-dependent model:

$$N_{it} \sim \text{Pois}(N_{it-1}\exp(r(1 - \log(N_{it-1})/\log(K)))) \tag{8}$$

where the log of N_{it-1} is only taken when $N_{it-1} > 0$ (when $N_{it-1} \equiv 0$, the full expression simplifies to 0 anyway). Here the interpretations of r and K are similar to in the Ricker model, but K is constrained to be greater than one.

Because a single Poisson distribution controls the distribution of N_{it} in each of these models, the discrete convolution used by Dail and Madsen (2011) is not required, speeding up processing time.

3.2 Immigration models

The autoregressive, population growth, Ricker, and Gompertz versions of the DM models all share a common feature (or bug): once the population at a site reaches 0, it must remain at 0. This is because all contributions to population growth are local in these models. We generalized each these models that include both internal and external (immigration) contributions to population growth. The population growth plus immigration model is:

$$N_{it} \sim \text{Poisson}(\exp(r)N_{it-1}) + \text{Poisson}(\iota) \tag{9}$$

or equivalently

$$N_{it} \sim \text{Poisson}(\exp(r)N_{it-1} + \iota) \tag{10}$$

where ι represents the immigration rate. This model is close to the constant DM model (equation 4), with $\exp(r)$ instead of ω and ι instead of γ, except that the first process is Poisson distributed instead of binomial. The Ricker and Gompertz models can be extended to allow for immigration in the same way.

We have implemented all preceding models in a maximum likelihood framework by extending the `unmarked` package (Fiske and Chandler, 2011) in **R** (R Development Core Team, 2012).

3.3 Excess zeros

Dail and Madsen (2011) suggested two distributions for modeling initial abundance: Poisson and negative binomial. We have extended their model to include another distribution, the zero-inflated Poisson. This could be useful when, for example, one is modeling the abundance of several bird species with the same set of BBS routespoint count surveys for all species, but this set includes routes sites outside the range of some of the bird species. The distribution of initial abundances can be represented as:

$$N_{i1} \sim \begin{cases} 0 \text{ with probability } \psi \\ \Lambda \text{ with probability } (1 - \psi) \end{cases} \tag{11}$$

where ψ represents the proportion of extra zeros.

These models allow three sources of zero counts by observers: a species was at a route but not detected; the route was within the species' range but there were no birds at that site in that year; and the route was outside the species' range. Furthermore, detection, abundance, and zero-inflation can be modeled separately as functions of different (or the same) covariates. For example, detection of species x at site y in year z might depend on wind speed, abundance on forest type and weather,

and zero-inflation upon elevation and climate. This approach combines elements of occupancy modeling (MacKenzie et al., 2006) and abundance modeling.

The zero inflation factor can also affect recruitment or population dynamics (see below). We also considered a zero-inflated negative binomial model of initial abundance, but this model did not perform well in preliminary tests.

The zero-inflated Poisson distribution can be applied to not only initial abundance but also to recruitment and population growth terms. For example, the recruitment term of the constant DM model (equation 4) can be modified as follows:

$$G_{it} \sim \begin{cases} 0 \text{ with probability } \psi \\ \text{Poisson}(\gamma) \text{ with probability } (1 - \psi) \end{cases} \tag{12}$$

When both initial abundance and dynamics are modeled as zero-inflated, ψ can be modeled as time-varying or not (in either case, ψ can also be modeled as varying over space). In the latter case, it makes sense for the model to "remember" which sites are inside the range of the species between the initial abundance stage and each time step of the dynamics stage (see code sample?). Adding zero-inflation to the dynamics of the autoregressive, trend, Ricker, or Gompertz models (without immigration) should have no effect when initial abundance is also zero-inflated unless ψ is time-varying (because these dynamic models cannot recover from zero abundance). We have implemented zero-inflated dynamics in the Bayesian framework using program JAGS (Plummer, 2003, version 3.2.0).

3.4   Random effects of observers

Differences in observers' ability to see, hear, or identify birds has long been recognized as a potential source of error in avian point count surveys such as the BBS (Robbins et al., 1986; Diefenbach et al., 2003; Sauer et al., 1994; Alldredge et al., 2007; Campbell and Francis, 2011). Estimating a separate detection probability for each observer can be difficult and reduces one's ability to estimate the quantities of interest. This problem is compounded by the fact that observers differ greatly in the number of surveys they have run (so that many observers' separate detection probabilities could not be accurately estimated).

Current BBS trend estimators deal with this problem by treating observer identity as a random (as opposed to a fixed) effect (Link and Sauer, 2002; Sauer and Link, 2011). This allows observer-specific differences in detection probability, but assumes that observers are selected at random from a pool of potential observers. Models that contain both random and fixed effects are referred to as mixed models. Often in mixed models (as in this case), the random effect is modeled not because it of interest in itself, but to avoid bias in the estimates of the fixed effects.

To include random observer effects in DM models and these extensions, Eq. 5 can be modified to:

$$n_{ijt} \sim \text{Bin}(N_{it}, p_j)$$
$$\text{logit}(p_j) \sim \text{Normal}(\mu_p, \sigma_p) \tag{13}$$

where n_{ijt} is the number of bird recorded at site i by observer j in year t, p_j is observer-specific detection probability, μ_p is the mean detection probability (on the logit scale), and σ_p is the standard deviation of the random observer effects (also on the logit scale). We have implemented random observer effects in the Bayesian framework using program **JAGS** (Plummer, 2003, version 3.2.0) with the **R** (R Development Core Team 2011) package `rjags` (Plummer, 2011) interface.

4 Forecasting Future Population Size

5 Applications

5.1 Simulation Study

We simulated data for 100 sites over 40 years. All simulations assumed initial abundance was Poisson distributed and no covariates affected initial abundance, dynamics, or detection probability. Our first series of simulations assumed dynamics were exponential. We ran 1000 simulations for each combination of low, medium, and high $\Lambda \in \{1, 5, 10\}$, $r \in \{-0.005, 0, 0.005\}$, and $p \in \{0.05, 0.25, 0.5\}$.

Our second series of simulations changed dynamics to the Ricker model. We used an initial abundance of 10, a maximum growth rate of 0.005, and a detection probability of 0.25, and simulated low, medium, and high values of equilibrium abundance, each with 500 simulations (Table 1). Our third series of simulations was based on the Ricker + immigration dynamics model; here we fixed all parameters the same as the Ricker model (with K = 10) and simulated low, medium, and high values of immigration rate with 500 simulation each (Table 1).

We estimated the parameters for each simulation using the same initial abundance (Poisson) and dynamics models as were simulated, implemented in the unmarked library in **R**. When run in a maximum likelihood framework, these models require a maximum abundance to integrate over (Royle, 2004; Dail and Madsen, 2011); we used 200. We report bias of estimates, root mean squared error, and coverage (percentage of 95% confidence intervals for parameters that overlap the true values).

Ideas: I. Test importance of random effects modeling, and other differences between JAGS and unmarked II. Model with low p values, or a range of p values III. Ability to distinguish correct initial abundance and dynamics models IV. When can you detect DD if it exists (power)? V. Building on the last two: what if your model set doesn't include the correct DD model? When will the wrong DD model be favored over the wrong DID model?

5.2 Analysis of Breeding Bird Survey Data

We applied these models to North American Breeding Bird Survey (BBS) data from 1966-2010 for two species in the bordering US states Maryland and Virginia. For our focal species, we selected ovenbirds (*Seiurus aurocapilla*), an abundant and widespread forest breeding migrant with a stable or increasing trend in the region (CITE) and golden-winged warblers (*Vermivora chrysoptera*), which only breeds in the western parts of these states and has been declining in the region (CITE). MORE INFORMATION ABOUT THE SPECIES?

GENERAL ABOUT BBS DATA. We only used data marked as acceptable for use in the annual BBS analysis. We summed the total birds of each species seen on each route and year and used the routes (rather than the individual stops) as our sites. Strong winds can interfere with point count observers' ability to hear birds ((Simons et al., 2007)); we tested the effects of wind speed on detection probability. BBS volunteers record wind conditions at the beginning and end of each route on the Beaufort Scale (Robbins et al., 1986, start and end wind 0-9). When start or end wind was not recorded we imputed those values with the start or end mean. We took the mean of start and end wind for each route and put this average wind scale value into four categories: $0 \leq \text{wind} < 1$; $1 \geq \text{wind} < 2$; $2 \leq \text{wind} < 3$; and wind ≥ 3 (maximum of 3.5). Following Link and Sauer (2002), we also included the first time an observer ran a route as a predictor variable for detection probability.

HOW WE OBTAINED AND MANIPULATED PRISM DATA We ran a series of maximum-likelihood based models for each species, and then a series of Bayesian models. We started by testing three models of initial abundance (Poisson, negative binomial, and zero-inflated Poisson) with population growth dynamics (equation 7) and no covariates. We selected the minimum Akaike's Information Criterion (AIC) model from that set to test three additional models for p: wind, first, and wind + first. We selected the minimum AIC model from that set to test eight additional models of dynamics: constant, autoregressive, Ricker, Gompertz, autoregressive + immigration, population growth + immigration, Ricker + immigration, and Gompertz + immigration. We then tested the effect of average minimum temperature for June and July on all dynamics parameters from the minimum AIC dynamics model. When run in a maximum likelihood framework, these models require a maximum abundance to integrate over (Royle 2004, Dail and Madsen 2011); we used 600 for ovenbirds and 350 for GWWA.

We ran the top ranked models from the maximum likelihood analyses in a Bayesian framework. We added random observer effects and, where appropriate, zero-inflated dynamics. WILL ADD MORE HEREWe used non-informative priors. We tested for lack of convergence using X Markov chains for each model (Gelman and Rubin, 1992). For each chain we sampled the MCMC for Y iterations, after Z tuning samples. Latent inclusion factors for temperature effects?

6 Results

The negative binomial distribution was strongly supported for ovenbird initial abundance over the Poisson and zero-inflated Poisson (Table 1A, models A.1 - A.3). Even compared to the Poisson, there was no evidence to support a zero-inflation factor for this species. The best supported model for p was additive effects of wind speed and first run (Table 1A, model A.4). First run and increasing wind speeds both decreased p. All dynamics models with immigration were better supported than models without immigration (Table 1A, models A.8 - A.16); the best supported of these was the Ricker + Immigration. The best supported model of those without immigration was the Gompertz, and the autoregressive and the constant model had the least support. There was little support for an effect of minimum June and July temperature on dynamics parameters of the Ricker + Immigration model (Table 1A, models A.17 - A.18).

Estimates for the top ranked model for OVEN (NB[$\Lambda(.)\alpha(.)$]Ricker+Imm.[$r(.)K(.)\iota(.)$]p(wind+1st)) were similar when run in the Bayesian framework, except that the estimate of r more than halved (from 0.026 ± 0.006 to 0.011 ± 0.005 [for Bayesian model estimates we present mean and SD]). When random observer effects were added, estimates for Λ and K increased dramatically (from 31.6 ± 4.9 to 42.5 ± 7.3 and from 56.2 ± 18.2 to 101.8 ± 21.1, respectively), and the estimate for r was intermediate (0.018 ± 0.006). The estimate of the intercept for p (on the logit scale) dropped from -1.5 ± 0.1 to -2.0 ± 0.1, and the estimate of σ_p was 0.35 ± 0.03. [Richard, I ran the temperature model in the Bayesian framework (w/ and w/o random effect) too. Should we include those results? As earlier, very little evidence for an effect of temperature on any of the parameters, although I couldn't get the latent inclusion parameter to work for r.] Gelman and Rubin diagnostics and visual examination of the ? plots provided some evidence for a lack of convergence in estimates of the intercept for p for all Bayesian models ran.

There was slightly more support for the ZIP distribution for initial abundance of GWWA than for the negative binomial; both were strongly supported over the

Poisson (Table 1B, models B.1 - B.3). The best supported model for p was an effect of first run (Table 1B, model B.4). The best supported dynamics model was population growth (Table 1B, model B.8); the estimate of r from this model was -0.058 ± 0.017 (SE). There was no support for immigration added to the population growth or autoregressive models (Table 1B, models B.10 and B.13). However, the Gompertz + immigration and Ricker + immigration models were supported over the corresponding models without immigration (Table 1B, models B.11, B.12, B.14, and B.15), despite low estimates of ι from these models (0.003 ± 0.003 and 0.003 ± 0.002, respectively). There was considerable support for an effect of average minimum June and July temperature on r in the population growth model (Table 1B, model B.17), with a negative slope.

Because of the closeness of rankings for the ZIP and negative binomial distributions for GWWA, we also ran the subsequent models with the negative binomial initial abundance. Rankings of subsequent models were similar, but with a p covariate (first) the negative binomial distribution outranked the ZIP.

STILL WORKING ON JAGS GWWA RESULTS Estimated detection probabilities were generally low. For OVEN, the estimated probability of detecting a bird with no wind and not the first time an observer had run a route varied between 0.046 ± 0.002 (model A.16) and 0.192 ± 0.015 (model A.11), among models that accounted for both. For GWWA, the estimated probability of detecting a bird by a non-first time observer varied between 0.025 ± 0.008 (model B.18) and 0.141 ± 0.027 (model B.16), among models that accounted for first but not wind.

For both species, constant dynamics models estimated very high survival probabilities ($\omega = 1 \pm 1.3\text{e-}05$ for OVEN and 0.935 ± 0.011 for GWWA). The autoregressive and autoregressive + immigration models estimated very low survival probabilities for OVEN ($\omega = 0.058 \pm 0.046$ and 0.026 ± 0.060, respectively), but not for GWWA ($\omega = 0.715 \pm 0.288$ for both models).

7 Discussion

Our work has highlighted the limitations of classical state-space models as applied to ecological time series data, and we have demonstrated how open population N-mixture models overcome these limitations. We extended this class of models in several important ways, while keeping in mind the practical issues ...

We made four important developments of the open population N-mixture model proposed by (Dail and Madsen, 2011) that make the model more applicable to long-term data such as is collected by the North American Breeding Bird Survey. First, we have reconciled the objectives of traditional state-space models with open population N-mixture models by illustrating how classical models of population dynamics can be embedded within the framework. Second, we have demonstrated methods of accounting for zero-inflation in the time-series. Third, we have illustrated how additional random effects such as observer-specific detection probabilities can be accommodated. Fourth, we presented a Bayesian analysis of the model, which, makes it possible to incorporate prior information when available, and in some cases, facilitates parameter estimation.

A unique aspect of the Dail and Madsen model as originally devised was that it allowed for the estimation of demographic parameters under strict distributional assumptions and with the assumption of geographic closure. Clearly, estimating demographic parameters from count data is a loftyn ambitious goal, and the required assumption will not be valid in many cases. Nonetheless, their approach is important because it allows for the combination of count data with other data types
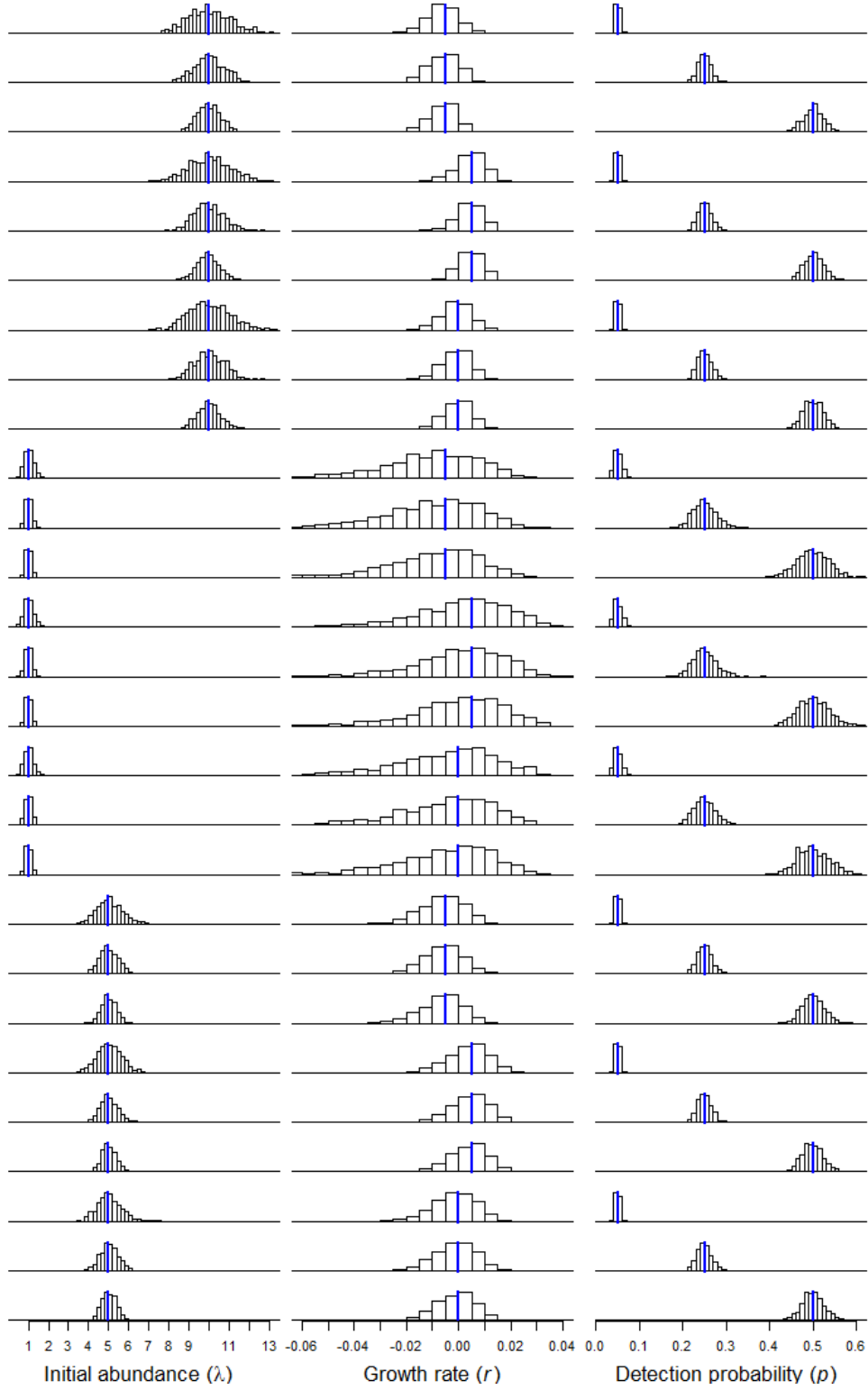
Figure 1: Histograms of 1000 parameter estimates for each of 27 simulation cases. The verticle lines are the data-generating values.

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such as capture-recapture data , which offers a means of making inferences about demographic processes at broad spatial scales. Models combining count data and demographic data are often referred to as integrated population models, and This topic has received much attention lately under t

In the absence of direct information about demographic parameters, and when the original assumptions of the model do not hold, we have offered extensions of the model to estimate derived parameters such as population growth rate. This has been the traditional emphasis of state-space models, and our approach resolves many of the factors limiting ...

[paragraph on zero-inflation]The zero-inflated models for initial abundance and dynamics allow one to estimate and model the proportion of sites outside of the range of a species. This could be especially useful when different factors control the range than the abundance or dynamics within the range. [some examples where that is the case?]

[paragraph on random effects]

[paragraph on Bayesian] The ability to fit this class of models using freely available MCMC software offers non-statisticians a powerful means .

In spite of the new extensions we have proposed, several aspects of the model could be improved. First, the precision with which the parameters of the state process can be estimated ultimately depends upon how well detection probability is estimated. When there is only a single survey per primary period, the information about detection probability comes from deviations from the parametric assumptions about population dynamics. Thus, without direct information about detection probability, the estimates will be determined by model based assumptions. Furthermore, there are multiple components of detection probability that should be accounted for to minimize bias and yield valid estimates of population size (Nichols et al., 2009).

Fortunately, it is easy to incorporate direct information about detection probability and we recommend that this be done whenever possible. The original method for proposed in the original paper was to collected replicated counts within the primary periods during a period in which the populations could be assumed to be closed. a robust design could be used to combine multiple surveys per primary period to increase the precision of the estimates. We envision that multiple other options are available as well. For instance, there should be no difficulty extending the model to accommodate traditional capture-recapture data collected during each primary period. Removal or time of detection etc.. Distance-related heterogeneity in detection probability is another source of variation that can bias estimators of abundance. Show some equations for the alternative observation models.

[paragraph on spatially-explicit dispersal] [Other possible extensions we could mention: Spatially hierarchical model (so can use individual stops) Other models of variability in growth or recruitment (such as negative binomial) Add density dependence to survival and recruitment models] [Discuss causes of low p values (and other BBS results) here or in BBS results?] Our emphasis was on increasing the practical utility of this class of models, and so we avoided several conceptually-interesting extensions that we belive would be computationally prohibitive in many cases. Nonetheless, we will discuss one—spatially-explict models of immigration.

The modeling framework we described can be used to address many of the most pressing issue in ecology and conservation biology. For example, it is possible to test hypotheses about temporal and spatial population regulation. Furthermore, the Bayesian approach is very useful in that it can be used to combine multiple sources of data to develop mechanistic models of population dynamics. Thus one can test hypotheses about the effects of climate change on either explicit demographic parameters or in derived parameters such as population growth rate. Furthermore, under

the Bayesian approach , population viability analysis is trivial because projecting populations into the future can be done as a component of the MCMC analysis. This allows for the computation of posterior distributions of parameters such as quasi-extinction probability.

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Table 1: Changed parameter values, by series of simulations. We simulated 1000 sets of data each combination of parameter values for 100 sites over 40 years. We assumed that initial abundance (Λ) was Poisson distributed. For the exponential growth simulations we included all combinations of low, medium, and high Λ, growth rate (r), and detection probability (p). For the Ricker model simulations we used $\Lambda = 10$ and $p = 0.25$, and simulated low, medium, and high values of r and equilibrium density (K). For the Ricker + immigration dynamics model we fixed all parameters the same as the Ricker model (with $r = 0.05$ and $K = 10$) and simulated low, medium, and high values of immigration rate (ι).

	Exponential Growth			Ricker	Ricker + Immigration	
	Λ	r	p	r	K	ι
Low	1	-0.01	0.05	0.005	5	0.005
Med	5	0	0.25	0.05	10	0.05
High	10	0.005	0.5	0.1	20	0.5

Table 2: Model selection table for ovenbirds and golden-winged warblers in Maryland and Virginia, 1966-2010. We present model name and number, number of parameters (Par.), and difference in Akaike's information criterion between each model and the top model of that set (ΔAIC). For each species, the first section compares models for initial abundance, the second for detection probability, and the third for dynamics.

A. Ovenbirds			B. Golden-Winged Warblers		
Model	Par.	ΔAIC	Model	Par.	ΔAIC
A.1. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]$p(.)$	4	0	B.1. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]$p(.)$	4	0
A.2. P[$\Lambda(.)$]Growth[$r(.)$]$p(.)$	3	1262.7	B.2. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]$p(.)$	4	0.4
A.3. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]$p(.)$	4	1264.7	B.3. P[$\Lambda(.)$]Growth[$r(.)$]$p(.)$	3	37.8
A.4. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]p(wind+1st)	8	0	B.4. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]p(1st)	5	0
A.5. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]p(wind)	7	0.9	B.5. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]$p(.)$	4	3.5
A.6. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]p(1st)	5	5.0	B.6. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]p(wind+1st)	8	5.9
A.7. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]$p(.)$	4	6.4	B.7. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]p(wind)	7	9.3
A.8. NB[$\Lambda(.)\alpha(.)$]Ricker+Imm.[$r(.)K(.)\iota(.)$]p(wind+1st)	10	0	B.8. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]p(1st)	5	0
A.9. NB[$\Lambda(.)\alpha(.)$]Gompertz+Imm.[$r(.)K(.)\iota(.)$]p(wind+1st)	10	8.4	B.9. ZIP[$\Lambda(.)\psi(.)$]AR[$\gamma(.)\omega(.)$]p(1st)	6	1.7
A.10. NB[$\Lambda(.)\alpha(.)$]Growth+Imm.[$r(.)\iota(.)$]p(wind+1st)	9	36.5	B.10. ZIP[$\Lambda(.)\psi(.)$]Growth+Imm.[$r(.)\iota(.)$]p(1st)	6	2.0
A.11. NB[$\Lambda(.)\alpha(.)$]AR+Imm.[$\gamma(.)\omega(.)\iota(.)$]$p$(wind+1st)	10	38.6	B.11. ZIP[$\Lambda(.)\psi(.)$]Gompertz+Imm.[$r(.)K(.)\iota(.)$]p(1st)	7	2.6
A.12. NB[$\Lambda(.)\alpha(.)$]Gompertz[$r(.)K(.)$]p(wind+1st)	9	190.9	B.12. ZIP[$\Lambda(.)\psi(.)$]Gompertz[$r(.)K(.)$]p(1st)	6	3.0
A.13. NB[$\Lambda(.)\alpha(.)$]Ricker[$r(.)K(.)$]p(wind+1st)	9	195.1	B.13. ZIP[$\Lambda(.)\psi(.)$]AR+Imm.[$\gamma(.)\omega(.)\iota(.)$]$p$(1st)	7	3.7
A.14. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]p(wind+1st)	8	271.3	B.14. ZIP[$\Lambda(.)\psi(.)$]Ricker+Imm.[$r(.)K(.)\iota(.)$]p(1st)	7	4.2
A.15. NB[$\Lambda(.)\alpha(.)$]AR[$\gamma(.)\omega(.)$]p(wind+1st)	9	273.7	B.15. ZIP[$\Lambda(.)\psi(.)$]Ricker[$r(.)K(.)$]p(1st)	7	5.2
A.16. NB[$\Lambda(.)\alpha(.)$]Constant[$\gamma(.)\omega(.)$]p(wind+1st)	9	1856.7	B.16. ZIP[$\Lambda(.)\psi(.)$]Constant[$\gamma(.)\omega(.)$]p(1st)	6	12.5