

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

Richard B. Chandler

USGS Patuxent Wildlife Research Center  
Laurel, MD 20708

Jeffrey A. Hostetler \*

Smithsonian Conservation Biology Institute  
National Zoological Park, MRC 5503  
Washington, DC 20013-7012

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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 management actions. State-space models are widely used for these purposes because they allow for estimating parameters of classical growth models, such as exponential, logistic, and Gompertz, while accounting for demographic stochasticity and observation error. 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. Furthermore, we describe classical and Bayesian methods of parameter estimation. These new developments will allow researchers to apply these methods to address important questions regarding the factors affecting spatial and temporal variation in abundance. We demonstrate these developments by analyzing data from the North American Breeding Bird Survey. Code to fit these models using the **R** package **unmarked** and **JAGS** is also provided.

**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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\*Contact: HostetlerJ@si.edu, +001-202-633-4205

Theoretical ecology requires models of population dynamics for testing hypotheses regarding spatial and temporal variation in abundance—hypotheses relating to 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). 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). 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). Conventional state-space models are simply 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 (Kery et al., 2009). For instance, the strength of density dependence will be overestimated if observation error is ignored (Link and Nichols, 1994; Shenk et al., 1998).

One of the simplest state-space models can be described as follows. Let  $N_t$  be the abundance of a species during year  $t$ , for  $t = 1, \dots, T$ , and let  $X_t$  be the observed data, which differs from  $N_t$  due to observation error, a random effect denoted  $\zeta_t$ . Temporal variation in  $N_t$  is modeled using a deterministic population growth model (e.g. exponential, logistic, etc ...) and a stochastic model allowing for random process variation, which we denote  $\delta_t$ . As an example, under exponential population growth, the model could be written as:

$$\mu_t = N_{t-1} \exp(r) \tag{1a}$$

$$N_t \sim N(\mu_t, \delta_t) \tag{1b}$$

$$X_t \sim N(N_t, \zeta_t) \tag{1c}$$

where  $r$  is the intrinsic rate of increase. Although the exponential growth model shown here is often replaced with density dependent models, most state-space models share the common feature that the error terms are assumed to be i.i.d random effects distributed as  $\delta_t \sim N(0, \sigma)$  and  $\zeta_t \sim N(0, \tau)$ . The Gaussian assumption allows 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).

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, raising concerns about the use of Gaussian distribution shown in Eq 1b, (2) the model for observatoin error (Eq. 1c) 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.

The fact that both abundance ( $N_t$ ) and the observed data ( $X_t$ ) are typically non-negative integers suggests that the Gaussian assumption in Eq. 1b is not justified. Even so, efforts are often made to adhere to the Gaussian assumption by transforming 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 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 the observed data  $X_t$  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 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). Specifically, the Markovian nature of the model implies the following likelihood

$$\mathcal{L}(\Theta|\{X_t\}) = [N_1|\Theta] \prod_{t=2}^T [N_t|N_{t-1}, \Theta] \quad (2)$$

The first term is the probability density for the first observation in the time series,  $X_1$ , yet it is intuitively not possible to estimate the parameter(s) of this distribution using only a single observation. Two options have been proposed handling the identifiability problem. First, one can assume that the first observation in the time series is made without error. Second, one can assume that the population is at equilibrium so that that the  $x$  can be replaced with the equilibrium distribution. However, assuming equilibrium defeats the objective of many studies of population dynamics, namely determining if and why a population is at equilibrium.

A fourth problem with these models is that they do not admit spatial variation, which restrict the utility of their since it is typically impossible assess the impacts of factors such as habitat fragmentation or climate change on population dynamics without considering spatial variation in abundance. Indeed many populations are regulated by spatial processes such as source-sink dynamics.

Several extensions of state-space models have been proposed to overcome the limitations described above. de Valpine and Hastings (2002) described methods for fitting models with non-Gaussian distributions for the process and observation errors. Observation models with more intuitive interpretations have been proposed by Kery et al. (2009). Lele et al. (1998) 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  $t = 1$ . In spite of these improvements, until recently, few methods existed to address each issue simultaneously, and even fewer of these methods have been made readily available to applied ecologists.

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. Specifically, the model (1) recognizes the discrete nature of count data and the underlying true abundance state, (2) includes a realistic observation model with explicit

detection probability parameters (3) has estimable parameters, including those describing the initial state at time  $t = 1$ , and (4) allows for inference about both temporal and spatial variation in abundance. In some respects, the DM model can be viewed as a specific manifestation of the general state-space model formulated by (Buckland et al., 2004). However, their model was designed to allow for inference about demographic parameters, which will typically require mark-recapture data. Although this may be viewed as the gold standard in many studies of wildlife populations, in this paper, we focus on the analysis of count data, which is the typical source of information used in state-state modeling applications, and one of the most widely available forms of ecological data—it is also the data required by the DM model.

In the following section, we describe the DM model in its original form, and we explain how it resolves each of the deficiencies with standard state-space models. In Section 2, we extend the model to accommodate classical models of population growth and to handle several features common to ecological time-series. Specifically, we describe methods for accommodating excess zeros and nuisance variables such as random observer effects. Both frequentist and Bayesian methods of inference are discussed, and code for fitting models is presented in the appendices. The Bayesian method is attractive in that it can accommodate prior information about detection parameters, which is available for many species, yet not collected as part of many existing monitoring programs. In Section 3, 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 a flexible and accessible means of addressing important questions related to the variation of abundance in space and time. We believe these extensions will increase the utility of the model for application to existing datasets such as the Breeding Bird Survey.

# 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 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  $n_{it} : i = 1, \dots, R; t = 1, \dots, T$  denote the count data at site  $i$  and primary period  $t$ . If  $J$  secondary sampling periods were used,  $n_{ijt} : j = 1, \dots, J$  is the count at site  $i$  during secondary sampling occasion  $j$  within year  $t$ . These are the observed data, which typically will be less than the actual quantity 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:

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

where  $\Lambda_i$  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  $\alpha$ .

Regardless of the specified distribution, the model for initial abundance has two distinguishing 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 individuals surviving from  $t - 1$  and not emigrating; and  $G_t$  the number of new individuals entering the population. Their most general model was

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

where  $\omega$  is the apparent survival probability and  $\gamma$  is the recruitment rate (which can depend on  $N_{it-1}$ ). In the absence of movement,  $\omega$  is exactly the probability of surviving from year  $t$  to  $t - 1$ , and  $\gamma$  is the per-capita birth rate. However, in the more common scenario when immigration and emigration occur,  $\omega$  is the probability of surviving and not emigrating, and  $\gamma$  is product of the birth rate and the emigration rate, i.e. the recruitment rate. Dail and Madsen (2011) proposed three models for  $\gamma$ : 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.

In cases where no movement occurs, the DM model can directly estimate demographic 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 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 2.

### 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

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

Initial abundance, apparent survival, recruitment, and detection can all be modeled as functions of covariates, allowing fairly sophisticated inference about population processes and dynamics from point count data.

## 2 Model Extensions

### 2.1 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:

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

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:

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

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:

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

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.

## 2.2 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:

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

or equivalently

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

where  $\iota$  represents the immigration rate. This model is close to the constant DM model (equation 4), with  $\exp(r)$  instead of  $\omega$  and  $\iota$  instead of  $\gamma$ , 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).

## 2.3 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 route point 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:

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

where  $\psi$  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:

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

When both initial abundance and dynamics are modeled as zero-inflated,  $\psi$  can be modeled as time-varying or not (in either case,  $\psi$  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  $\psi$  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).

## 2.4 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:

$$\begin{aligned} n_{ijt} &\sim \text{Bin}(N_{it}, p_j) \\ \text{logit}(p_j) &\sim \text{Normal}(\mu_p, \sigma_p) \end{aligned} \quad (13)$$



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,  $\mu_p$  is the mean detection probability (on the logit scale), and  $\sigma_p$  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.

## 2.5 Bayesian inference

priors are good

# 3 Applications

## 3.1 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?

## 3.2 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:  $0 \leq \text{wind} < 1$ ;  $1 \leq \text{wind} < 2$ ;  $2 \leq \text{wind} < 3$ ; and  $\text{wind} \geq 3$  (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 HERE**We 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?

## 4 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 ( $\text{NB}[\Lambda(.)\alpha(.)]\text{Ricker+Imm.}[r(.)K(.)\iota(.)]p(\text{wind}+1st)$ ) were similar when run in the Bayesian framework, except that the estimate of r more than halved (from  $0.026 \pm 0.006$  to  $0.011 \pm 0.005$  [for Bayesian model estimates we present mean and SD]). When random observer effects were added, estimates for  $\Lambda$  and  $K$  increased dramatically (from  $31.6 \pm 4.9$  to  $42.5 \pm 7.3$  and from  $56.2 \pm 18.2$  to  $101.8 \pm 21.1$ , respectively), and the estimate for r was intermediate ( $0.018 \pm 0.006$ ).

The estimate of the intercept for  $p$  (on the logit scale) dropped from  $-1.5 \pm 0.1$  to  $-2.0 \pm 0.1$ , and the estimate of  $\sigma_p$  was  $0.35 \pm 0.03$ . [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  $-0.058 \pm 0.017$  (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  $\iota$  from these models ( $0.003 \pm 0.003$  and  $0.003 \pm 0.002$ , 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  $0.046 \pm 0.002$  (model A.16) and  $0.192 \pm 0.015$  (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  $0.025 \pm 0.008$  (model B.18) and  $0.141 \pm 0.027$  (model B.16), among models that accounted for first but not wind.

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

## 5 Discussion

We made four important developments of the open population N-mixture model proposed by Dail and Madsen 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 much easier to estimate parameters and to fine tune the model for specific purposes.

A unique aspect of the Dail and Madsen model as originally devised was that

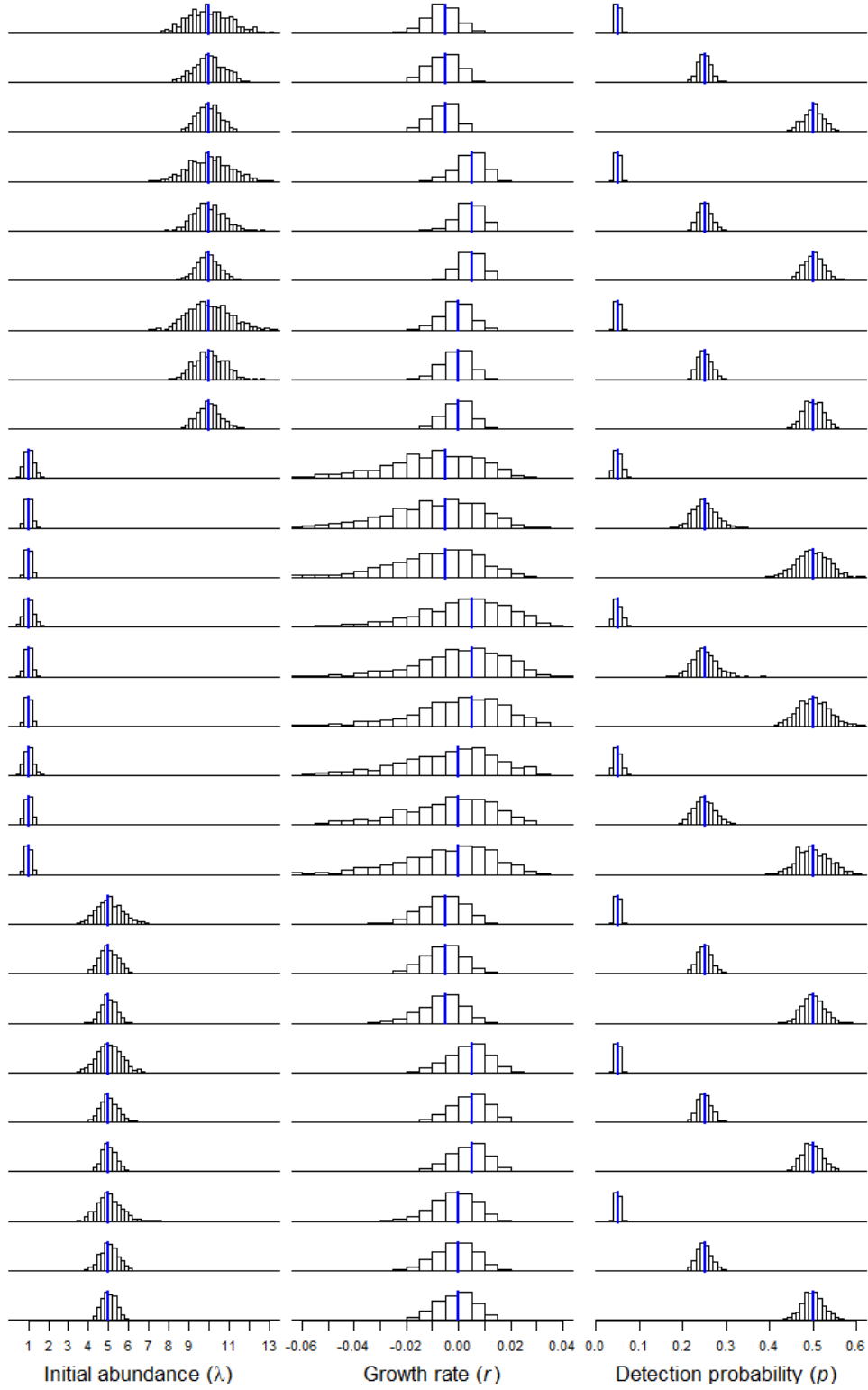


Figure 1: Histograms of 1000 parameter estimates for each of 27 simulation cases. The vertical lines are the data-generating values.

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 lofty 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 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] 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 EURING paper] .

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?]

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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