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. Failure to account for observation error in such models can result in bias, and thus ecologists have increasingly relied on state-space models to directly model both the observation error and the ecological process of interest. 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 proposed by Dail and Madsen (2011, Biometrics) for spatially-replicated time-series data that attributes observation error to imperfect detection. We expand this class of models to accommodate classical growth models (e.g. exponential, Ricker, etc . . .), 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 for the proposed model extensions. An analysis of data from the North American Breeding Bird Survey highlighted how these methods can be readily applied to existing data, but it also suggested the that precision will be low when direct information about detection probability (such as is collected using distance sampling or replicated counts) is unavailable.

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, $\mu(N_{t-1})$ and random process variation denoted $\grave{o}_t$. The growth model may be density-dependent, as in the case of the Ricker model, or it might be density-independent, such as when growth is exponential. The full model can now be written as:

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

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

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

where $\grave{o}_t$ 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: $\grave{o}_t \sim \mathrm{N}(0, \sigma)$ 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. Alternatively, the population is assumed to be at equilibrium such that the N_1 can be regarded as an outcom of the equilibrium distribution.

Even though state-space models such as that shown in Eq. 1 are among the most widespread approaches 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 and non-integer values of the state-variable, which is inconsistent with the observed data, and may result in implausible predictions. Transforming the count data and the underlying abundance variables do little to resolve these issues (O'Hara and Kotze, 2010).

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 (i.e., $[Y|\Omega]$ is interpretted as the probability distribution of the random variable Y given the parameter Ω). The three probability distributions required for a state-space model are:

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

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

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

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. As mentioned previously, Eq. 2b and Eq. 2c are assumed to be Gaussian in classical state-space models, but what should be the distribution for Eq. 2a? And how could $\boldsymbol{\theta}$ be estimated given that there is only a single observation available? Often, these problems are simply assumed away. For example, sometimes researchers assume that there is no process variation in the first year, although this seems unjustified. Alternatively, the population may be assumed to be at equilibrium such that the expected value of N_t is constant through time. Although this makes the parameters $\boldsymbol{\theta}$ 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, only the work by Kery et al. (2009) addressed several of these limitations simultaneously. However, their model did not include serial dependence, which is a hallmark of population models. This limits the utility of their model for making inferences about explicit population processes.

In this paper, we focus on the model of Dail and Madsen (2011, henceforth the DM model;) 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 deficiencies 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 ecological time-series. Specifically, we describe methods for accomodating 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. In Section 4, 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 variation 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 primary sampling periods. A site is ideally a well-defined region of a study area, such as a wetland or a patch of early-successional habitat, although it could be an arbitrarily defined region such as a randomly located survey plots. The timeframe of the study is arbitrary, but in general it will be sufficiently long to allow for temporal variation in abundance. For instance, a primary sampling period could be a one month long breeding season, which could be surveyed once per year for T years. If the a site is surveyed on J occassions during a primary period, these are called secondary sampling occasions. In the case where no secondary sampling was conducted, i.e. $J = 1$, let $X_{it} : i = 1, \ldots, R; t = 1, \ldots, T$ denote the count data at site i and primary period t. If secondary sampling periods were used, an extra dimension is added so tha twe have $X_{ijt} : j = 1, \ldots, J$. Typically, we X_{it} will be lower than the actual quantitiy of interest, abundance, denoted X_{it}. In cases where detection probability is perfect, abundance is observed directly such that $X_{it} \equiv N_{it}$.

1.2 The Original Formulation of the Model

As with traditional state-space models, the DM model includes the three conditionally related processes shown in Eq. 2, which correspond to (1) initial abundance, i.e. the abundance at site i during the first primary period, denoted (2) abundance at time t (for $t > 1$) which depends upon abundance at $t-1$, and (3) the detection process (Dail and Madsen, 2011). The first two processes describe the state process—the variation in abundance in space and time. The third process simply describes the the relationship between abundance and the observed count data.

1.2.1 Initial abundance

Recall that conventional state-space models assume that the distribution for the initial time period, $[N_1|\boldsymbol{\theta}]$, is either the equilibrium distribution, or has zero variance. In contrast, Dail and Madsen (2011) proposed modeling N_{i1} as either a Poisson or negative binomial random variable:

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

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. In the Poisson case, the eqivalent expression of $[N_1|\boldsymbol{\theta}]$ (Eq. 2a) is

$$[N_{i1}|\Lambda] = \frac{\Lambda^{N_{i1}} e^{-\Lambda}}{N_{i1}!}. \tag{4}$$

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 both the issues of spatial inference and parameter identifiability discussed previously.

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_{it}, the number of indivduals surviving from $t-1$ and not emigrating; and G_{it} the number of new individuals entering the population. Their most general model was

$$\left.\begin{array}{c} S_{it}|N_{it-1} \sim \mathrm{Bin}(N_{it-1}, \omega) \\ G_{it}|N_{it-1} \sim \mathrm{Pois}(\gamma(N_{it-1})) \\ N_{it} = S_{it} + G_{it} \end{array}\right\} \quad \text{for } t = 2, \ldots, T \tag{5}$$

where ω is the apparent survival probability and γ is the recruitment rate (which can depend on N_{it-1}). Dail and Madsen (2011) proposed three models for γ: the constant model, $G_{it} \sim \text{Pois}(\gamma)$ where recruitment does not depend on N_{it-1}, and which simulates a "propagule rain" of new individuals; the autoregressive model, $G_{it} \sim \text{Pois}(\gamma(N_{it-1}))$, 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.

To make the connection between conventional state-space models and the DM model, we need to replace $[N_t|N_{t-1}, \boldsymbol{\Theta}]$, Eq. 2b, with an expression derived from Eq. 5. This requires summing over all possible values of S and G, which is accomplished using the discrete convolution:

$$[N_{it}|N_{it-1}, \omega, \gamma] = \sum_{S_{it-1}=0}^{\min(N_{it}, N_{it-1})} \binom{N_{it-1}}{S_{it-1}} \omega^{S_{it-1}} (1-\omega)^{N_{it-1}-S_{it-1}} \times \frac{\gamma^{N_{it}-S_{it-1}} e^{-\gamma}}{(N_{it}-S_{it-1})!} \quad (6)$$

where here we assumed no dependenced of γ 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 (under the geometric growth model). This ability to directly estimate demographic parameters from simple count data is one of the DM model's most appearling features. However, in the more common scenario when immigration and emigration occur, ω and γ no longer can be intepretted as vital rates. Rather, ω is the probability of surviving and not emigrating, and γ is the sum of the birth rate and the immigration rate, i.e. the recruitment rate. In such cases, we propose replacing Eq. 5 with standard population models.

1.2.3   Observation process

Eqs. 3 and 5 fully specify the state model, i.e. the model for abundance dynamics. This state model has allowed us to replace the initial abundance distribution and transition models of conventional state-space models, with alternatives that (1) allow for modeling spatial variation in abundance, (2) respect the discrete nature of the counts, and (3) have parameters that are estimable. The one remaining task is to replace the observation model $[X_t|N_t, \boldsymbol{p}]$ (Eq. 2c) with one that can be more easily interpretted. The observation model assumes that individuals are missed due to imperfect detection. The simplest model for imperfect detection, and the one considered in the original formulation, is

$$X_{it} \sim \text{Bin}(N_{it}, p) \quad (7)$$

or equivalently,

$$[X_{it}|N_{it}, \boldsymbol{p}] = \binom{N_{it}}{X_{it}} \boldsymbol{p}^{X_{it}} (1-\boldsymbol{p})^{N_{it}-X_{it}}. \quad (8)$$

Under this model, $\boldsymbol{p}$ are interpretted as detection probability parameters...

The entire model can now be written:

$$\begin{aligned}
N_{i1} &\sim \text{Pois}(\Lambda) \\
S_{it}|N_{it-1} &\sim \text{Bin}(N_{it-1}, \omega) \\
G_{it}|N_{it-1} &\sim \text{Pois}(\gamma(N_{it-1})) \\
N_{it} &= S_{it} + G_{it} \\
X_{it} &\sim \text{Bin}(N_{it}, p)
\end{aligned} \quad (9)$$

2 Statistical Inference

2.1 Maximum likelihood

Maximum likelihood estimation of parameters in models with discrete random effects requires removing them by summation. For Markovian models, this can be done recursively, making the likelihood tractible. A general expression of the likelihood can be written:

$$
\mathcal{L}(\Lambda, \boldsymbol{\Theta}, p | \{X_{it}\}) =
$$

$$
\prod_{i=1}^{R} \left\{ \sum_{N_{i1}=0}^{\infty} [X_{i1}|N_{i1}, p][N_{i1}|\Lambda] \left\{ \sum_{N_{i2}=0}^{\infty} \cdots \sum_{N_{iT}=0}^{\infty} [X_{it}|N_{it}, p][N_{it}|N_{it-1}, \boldsymbol{\Theta}] \right\} \right\} \quad (10)
$$

where ∞ is replaced by a finite upper bound K, which should be high enough such that the MLEs are not affected by increasint it further. This likelihood can be maximized numerically using the **R** package `unmarked` (Fiske and Chandler, 2011). Examples are given in the Appendix.

2.2 Bayesian inference

Bayesian inference has several appealing features. First, it allows direct probability statements to be made about a hypothesis given data. [EXPLAIN POSTERIORS AND PRIORS] Second, Bayesian methods offer straight-forward appraoches for combine data from multiple sources or use existing estimates of parameters as prior distributions. In practice, simulation methods such as Markov chain Monte Carlo (MCMC) are used to simulate the posterior distributions. Although MCMC can be slow, our experience is that it may actually converge faster than the amount of time required to maximize the likelihood shown in Eq.10, especially when the upper bound of the summation must be high, e.g. $K > 200$. Furthermore, MCMC may be the only possible option for estimating parameters using some of the extensions described below, such as allowing for additional random effects.

Writing custom MCMC algorthims is often tedious and foreign to ecologists, but software packages such as **WinBUGS** and **JAGS** overcome the technical difficulties by allowing users to specify the model using a simple symbolic descriptions. For example, here is **BUGS** code for the "geometric" model described shown in Eq. 1.2.3:

```
model {
lambda ~ dunif(0, 5)
omega ~ dunif(0,1)
gamma ~ dunif(0, 10)
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) {
    S[i,t-1] ~ dbin(omega, N[i,t-1])
    G[i,t-1] ~ dpois(gamma*N[i,t-1])
    N[i,t] <- S[i,t-1] + G[i,t-1]
    n[i,t] ~ dbin(p, N[i,1])
    }
  }
}
```

3 Model Extensions

3.1 Population growth models

Although partitioning population growth into survival and recruitment is ideal in terms of providing a mechanistic description of population dynamics, it is not always possible using simple count data, especially when the sites are not closed with respect to immigration and emigration. If the mechanistic model must be sacrificed, we suggest replacing it with classical population growth models that have a long history in ecology. The simplest of which is the exponential growth model: $f(N_{it-1}) = N_{it-1}e^r$ where r is the intrinsic rate of increase. Although demographic and environmental stochasticity in r could be modeled as functions of covariates or random effects, a simpler way of allow for stocasticity is to regard N_{it} as a Poisson random variable, simplifying Eq. 5 to:

$$N_{it} \sim \text{Pois}(\exp(r)N_{it-1}). \tag{11}$$

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:

$$N_{it} \sim \text{Pois}(N_{it-1}\exp(r(1 - N_{it-1}/K)) \tag{12}$$

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 is a stochastic version of the Ricker-logistic population growth model (Ricker, 1954). We also implemented a modified Gompertz-logistic density-dependent model (Hart and Gotelli, 2011):

$$N_{it} \sim \text{Pois}(N_{it-1}\exp(r(1 - \log(N_{it-1} + 1)/\log(K + 1))) \tag{13}$$

Here the interpretations of r and K are similar to in the Ricker model.

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.

```
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])
    }
  }
}
```

3.2 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:

$$N_{it} \sim \text{Poisson}(\exp(r)N_{it-1} + \iota) \tag{14}$$

where ι represents the immigration rate, and is constrained to be positive (this is equivalent to separate Poisson processes for growth and immigration). This model is close to the constant DM model (Eq. 5), 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:

$$N_{i1} \sim \begin{cases} 0 \text{ with probability } \psi \\ \Lambda \text{ with probability } (1 - \psi) \end{cases} \tag{15}$$

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-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 (Eq. 5) can be modified as follows:

$$G_{it} \sim \begin{cases} 0 \text{ with probability } \psi \\ \text{Poisson}(\gamma) \text{ with probability } (1 - \psi) \end{cases} \tag{16}$$

We have implemented zero-inflated dynamics in the Bayesian framework using program JAGS (Plummer, 2003, version 3.2.0).

3.4   Environmental and demographic stochasticity

Even though the DM model is conceptually very simple, even in its most stripped down form it includes many random effects (the N's) making it challenging to compute the likelihood or implement MCMC algorithms. Nonetheless, in some cases additional random effects may be of interest. For example, in conventional state-space models, demographic stochasticity is often modeled as $r_t \sim \text{Norm}(\mu_r, \sigma_r)$.

3.5 Random effects of observers

Variation in detection probability among observers is another source of random variation that may need to be accounted for applying the DM model. For example, 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. 7 can be modified to:

$$X_{ijt} \sim \text{Bin}(N_{it}, p_j)$$
$$\text{logit}(p_j) \sim \text{Normal}(\mu_p, \sigma_p) \tag{17}$$

where X_{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** package `rjags` (Plummer, 2011; R Development Core Team, 2012) interface.

3.6 Alternative Observation Models

It would be cool to add something on this, but maybe it's asking too much

3.7 Forecasting Future Population Size

Ditto

4 Applications

4.1 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 and a detection probability of 0.25, and simulated low, medium, and high values of equilibrium abundance and maximum growth rate, each

with 1000 simulations (Table 1; 9 total combinations). 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 r = 0.05 and K = 10) and simulated low, medium, and high values of immigration rate with 1000 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).

4.2 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).

The BBS is an annual roadside survey implemented by trained observers in the United States and Canada. An observer conducts 50 3-minute point counts, with 400 m radiuses and 0.8 km apart from each other along a 39.4 km route. We only used data marked as acceptable for use in the annual BBS analysis (Sauer et al., 1994). 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: $0 \leq$ wind < 1; $1 \geq$ wind < 2; $2 \leq$ 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.

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 (Eq. 11) 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. As above, these models require a maximum abundance to integrate over when run in a maximum likelihood framework; 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. We used non-informative priors. We tested for lack of convergence using 5 Markov chains for each model (Gelman and Rubin, 1992). For each chain we sampled the MCMC for at least 40,000 iterations, after at least 3,000 tuning samples.

5 Results

5.1 Analysis of Breeding Bird Survey Data

The negative binomial distribution was strongly supported for ovenbird initial abundance over the Poisson and zero-inflated Poisson (Table 2A, 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 2A, 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 2A, 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.

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. 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 2B, models B.1 - B.3). The best supported model for p was an effect of first run (Table 2B, model B.4). The best supported dynamics model was population growth (Table 2B, 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). 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.

Estimates for the top ranked model for GWWA (ZIP[$(.)(.)$]Trend[$r(.)$]p(1st)) were similar when run in the Bayesian framework. When random observer effects were added, the estimate for increased dramatically (from 22.4 7.6 to 55.5 30.9). The estimate of the intercept for p (on the logit scale) dropped from -3.5 0.2 to -5.6 1.1, and the estimate of p was 1.7 0.7. Adding zero-inflation to the dynamics (as well as the initial abundance) has no effect for trend models, because populations that started at 0 would stay at 0 in any case. Therefore, we tested zero-inflated dynamics on the Trend + Imm. model. Adding zero-inflation to the dynamics increased the estimate of from 0 to 0.091 0.049, but had only minor effects on the other parameters. Gelman and Rubin diagnostics and visual examination of the ? plots provided evidence for a lack of convergence in estimates of for all Bayesian models ran, and for most parameters when random effects were included.

Estimated detection probabilities were generally low. The estimated probability of detecting an OVEN in the top model (A.8) varied between 0.157 0.014 and 0.184 0.015, depending on wind speed and whether the observer had run that route before.

The estimated probability of detecting a GWWA went from 0.013 0.006 for first time observers to 0.028 0.008 for repeat observers for the top model (B.8). Accounting for random observer effects decreased average detection probability for both species.

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).

6 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 that should make them more suitable to typical ecological datasets that are characterized by sparse counts, zero-inflation, and observation error due to imperfect detection.

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 an ambitious goal, and the required assumption will not be valid in many cases. One advantage of the original DM models over our extensions here is that they model population dynamics more mechanistically, by focusing on survival and recruitment. As we report here, these models often provide unrealistic estimates of these vital rates and are generally less supported in model selection. Adding density dependence directly to one or both vital rates may solve both of these problems, although this might require very good data. Another strategy would be to use estimates of vital rates from demographic studies as priors in a Bayesian analysis using DM models. Finally, count data could be combined 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 (IPM; CITE), and we believe that a DM model would provide an effective part of an IPM.

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 (?Buckland et al., 2004; ?). 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 the context of IPMs, 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 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 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, such as removal, time of detection, and distance modeling ([cites]).

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.

In our models immigration is currently modeled as independent of population sizes in other sites. Several alternatives suggest themselves if we think about movement in a metapopulation context ([cite]): immigration depending on total or mean abundance across sites the previous time step; immigration depending on abundance in nearby sites only; and immigration depending on abundance at sites as a function of their distance from the receiving site (LOTS OF CITATIONS). These models would be based on the assumptions that either the study sites spatially cover the whole range of the metapopulation or the annual changes in the populations sampled are representative of a larger metapopulation. Initial tests suggest that it would be possible to fit some or all of these models, at least in the Bayesian framework.

[simulation results discussion]

We have presented a test case for these models using data from the BBS for two species. We demonstrate that these models can be used to model and estimate initial

abundance, detection probability, and density-independent and dependent functions for population dynamics. We tested these models in both the classical and Bayesian frameworks and found strengths and weaknesses of each approach. The Bayesian analyses permit more flexibility and allow the incorporation of random observer effects and zero-inflated dynamics. Our results suggest ignoring variation between observers can lead to underestimation of initial abundance and equilibrium population sizes. On the other hand, our Bayesian analyses did have convergence problems, particularly for the species (GWWA) with sparser data. It's likely that poor model fits are related to the low estimates of detection probability, which in turn are probably caused by the large 400 m radius used for BBS point counts. Again, we believe that direct information on detectability (such as repeated visits within a season) would greatly improve the fit of these models in both frameworks. [Alternatively, could put discussions of our results where they fit in by subject area, rather than separately. For instance, could discuss BBS population dynamics model selection in population models paragraph, BBS Bayesian vs. frequentist strengths and weakness in the Bayesian paragraph (currently not written), and GWWA ZIP results in ZIP paragraph.]

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.

7   Acknowledgements

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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 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). The first section compares models for initial abundance, the second for detection probability, and the third for dynamics.

Model	Par.	ΔAIC
A. Initial Abundance		
A.1. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]$p(.)$	4	0
A.2. P[$\Lambda(.)$]Growth[$r(.)$]$p(.)$	3	1262.7
A.3. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]$p(.)$	4	1264.7
B. Detection Probability		
B.1. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]p(wind+1st)	8	0
B.2. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]p(wind)	7	0.9
B.3. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]p(1st)	5	5.0
B.4. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]$p(.)$	4	6.4
C. Dynamics		
C.1. NB[$\Lambda(.)\alpha(.)$]Ricker+Imm.[$r(.)K(.)\iota(.)$]p(wind+1st)	10	0
C.2. NB[$\Lambda(.)\alpha(.)$]Gompertz+Imm.[$r(.)K(.)\iota(.)$]p(wind+1st)	10	8.4
C.3. NB[$\Lambda(.)\alpha(.)$]Growth+Imm.[$r(.)\iota(.)$]p(wind+1st)	9	36.5
C.4. NB[$\Lambda(.)\alpha(.)$]AR+Imm.[$\gamma(.)\omega(.)\iota(.)$]$p$(wind+1st)	10	38.6
C.5. NB[$\Lambda(.)\alpha(.)$]Gompertz[$r(.)K(.)$]p(wind+1st)	9	192.8
C.6. NB[$\Lambda(.)\alpha(.)$]Ricker[$r(.)K(.)$]p(wind+1st)	9	195.1
C.7. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]p(wind+1st)	8	271.3
C.8. NB[$\Lambda(.)\alpha(.)$]AR[$\gamma(.)\omega(.)$]p(wind+1st)	9	273.7
C.9. NB[$\Lambda(.)\alpha(.)$]Constant[$\gamma(.)\omega(.)$]p(wind+1st)	9	1856.7

Table 3: Model selection table for 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). The first section compares models for initial abundance, the second for detection probability, and the third for dynamics.

| Model	Par.	ΔAIC
A. Initial Abundance		
A.1. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]$p(.)$	4	0
A.2. NB[$\Lambda(.)\alpha(.)$]Growth[$r(.)$]$p(.)$	4	0.4
A.3. P[$\Lambda(.)$]Growth[$r(.)$]$p(.)$	3	37.8
B. Detection Probability		
B.1. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]$p(1st)$	5	0
B.2. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]$p(.)$	4	3.5
B.3. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]$p(wind+1st)$	8	5.9
B.4. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]$p(wind)$	7	9.3
C. Dynamics		
C.1. ZIP[$\Lambda(.)\psi(.)$]Growth[$r(.)$]$p(1st)$	5	0
C.2. ZIP[$\Lambda(.)\psi(.)$]AR[$\gamma(.)\omega(.)$]$p(1st)$	6	1.7
C.3. ZIP[$\Lambda(.)\psi(.)$]Growth+Imm.[$r(.)\iota(.)$]$p(1st)$	6	2.0
C.4. ZIP[$\Lambda(.)\psi(.)$]Gompertz+Imm.[$r(.)K(.)\iota(.)$]$p(1st)$	7	2.5
C.5. ZIP[$\Lambda(.)\psi(.)$]Gompertz[$r(.)K(.)$]$p(1st)$	6	3.0
C.6. ZIP[$\Lambda(.)\psi(.)$]AR+Imm.[$\gamma(.)\omega(.)\iota(.)$]$p(1st)$	7	3.7
C.7. ZIP[$\Lambda(.)\psi(.)$]Ricker+Imm.[$r(.)K(.)\iota(.)$]$p(1st)$	7	4.2
C.8. ZIP[$\Lambda(.)\psi(.)$]Ricker[$r(.)K(.)$]$p(1st)$	7	5.2
C.9. ZIP[$\Lambda(.)\psi(.)$]Constant[$\gamma(.)\omega(.)$]$p(1st)$	6	12.5
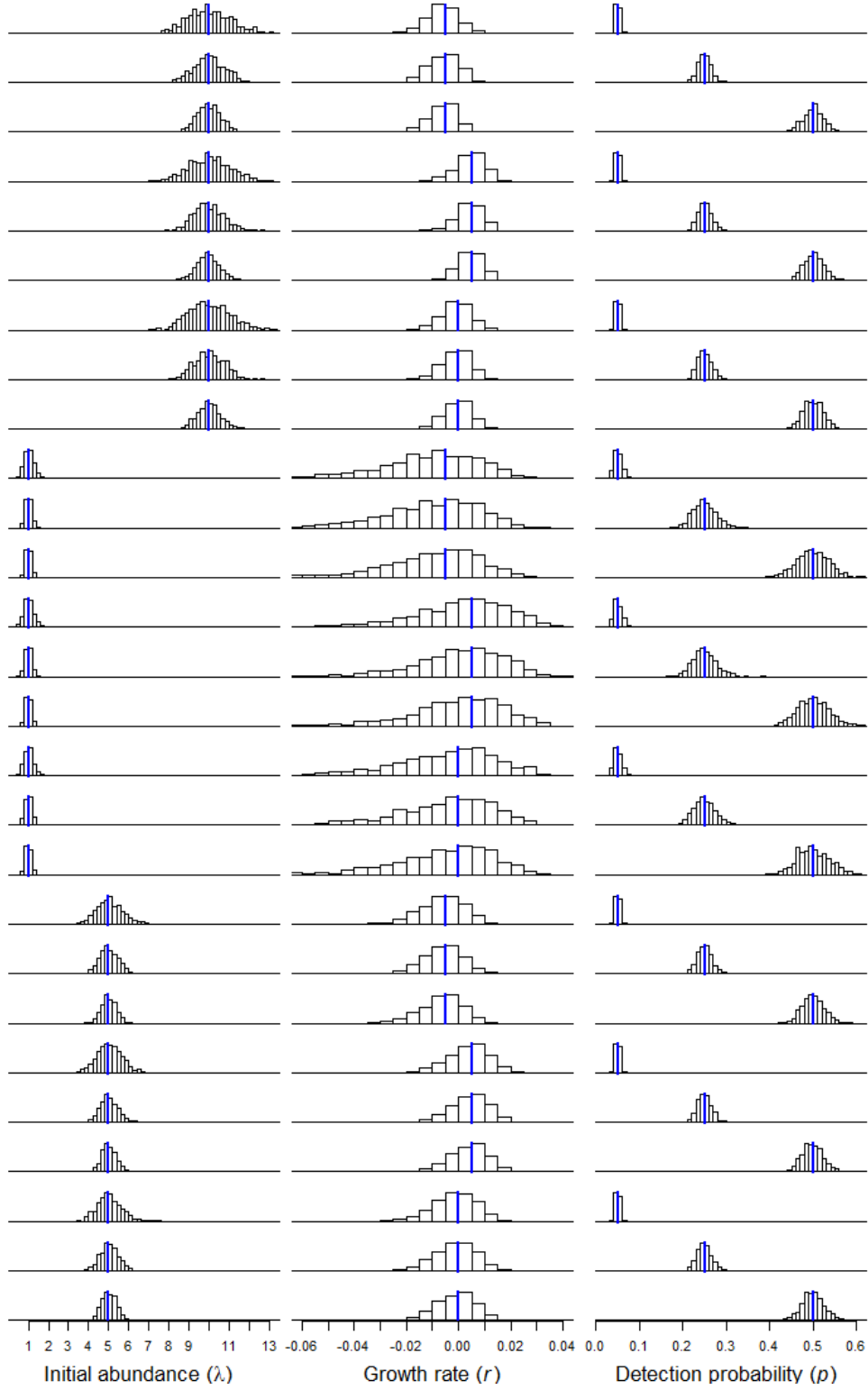
Figure 1: Histograms of 1000 parameter estimates for each of 27 simulation cases. The verticle lines are the data-generating values.