

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 are frequently used for purposes such as testing hypotheses about density dependence and predicting species' responses to future environmental change or conservation actions. Fitting models of population dynamics to field data is challenging because most data sets are characterized by observation error, which can inflate estimates of process variation if ignored. Recently, state-space models have been developed to deal with this problem by directly modeling both the observation error and the ecological process of interest. Conventional state-space models, however, have several important limitations: (1) they assume that random effects are Gaussian distributed, which implies that abundance can be negative and that false positive observation errors are equally likely as false negative errors; (2) they do not admit spatial variation in population dynamics; and (3) some of the parameters of the model are not estimable. We demonstrate how each of these problems can be resolved using a class of hierarchical models proposed by Dail and Madsen (2011) that attributes observation error to imperfect detection. We expand this class of models to accommodate classical growth models (e.g., exponential and Ricker-logistic), zero-inflation, and random effects. We also present methods for forecasting population size under future environmental conditions. Implementation of these ideas is possible using either frequentist or Bayesian methods, as demonstrated by accompanying R and JAGS code. Results of a simulation study suggest that bias is negligible and coverage nominal in most cases for the proposed model extensions. An analysis of data from the North American Breeding Bird Survey highlights how these methods can be readily applied to existing data, but it also suggests that precision will be low when direct information about detection probability (such as is collected using distance sampling or replicated counts) is lacking.

Key words: abundance; Dail and Madsen model; density dependence; detectability; Gompertz model; immigration; North American Breeding Bird Survey; population dynamics; Ricker model; state-space model; zero-inflated distribution.

INTRODUCTION

Models of population dynamics are vital in both theoretical and applied ecological research. For instance, the importance and existence of phenomena such as density-dependent population regulation, population cycling, and spatial synchrony have been studied by comparing data from natural populations with theoretical models (May 1975, Turchin 1990, Bjørnstad et al. 1999). In applied contexts, population models are used for estimating extinction risk (Nadeem and Lele 2011, Hostetler et al. 2013) and for predicting the effects of future environmental conditions or conservation actions

on population size (Jamieson and Brooks 2004, Hatfield et al. 2012).

Two challenges are routinely encountered when trying to fit models of population dynamics to data from field studies. First, deterministic models of population dynamics are generally inadequate due to process variation, the 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, Kéry et al. 2009).

Recently developed state-space models have made it possible to study population dynamics while accounting for both 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 modeled as a latent process, and the observed data are modeled conditional

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on this process and the observation error. One reason for the widespread adoption of state-space models in ecology is that failure to account for observation error can bias estimators of abundance and population growth parameters. For instance, the strength of density dependence will be overestimated if observation error is ignored (Link and Nichols 1994, Shenk et al. 1998).

A simple state-space model 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. Temporal variation in N_t is modeled using a probability distribution whose expected value is determined by a population growth model, $\mu(N_{t-1}, \theta)$, such as a density-dependent Ricker-logistic model (henceforth Ricker model) or a density-independent exponential model, with parameter vector θ . Such a model can be written:

$$\begin{aligned} N_1 &\sim \text{Normal}(\mu_1, \sigma_0^2) \\ N_t &\sim \text{Normal}(\mu(N_{t-1}, \theta), \sigma^2) \quad \text{for } t = 2, \dots, T \\ X_t &\sim \text{Normal}(N_t, \tau^2) \quad \text{for } t = 1, \dots, T \end{aligned} \quad (1)$$

where σ_0^2 and σ^2 are variance parameters of the underlying abundance process, and τ^2 describes variation in observation error.

Even though state-space models overcome many of the limitations associated with the application of classical models of population dynamics, several problems exist. The Gaussian assumptions make it easier to estimate parameters because methods such as the Kalman filter can be applied (Dennis et al. 2006); however, these models allow for implausible predictions such as negative values of abundance. Transforming the count data and the underlying abundance variables do little to resolve these issues (O'Hara and Kotze 2010).

With respect to the observation error, the Gaussian assumption implies that false positive detections are as likely as false negatives, a pattern inconsistent with most findings (Miller et al. 2011). 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 being present but unavailable for detection, or to individuals being available but missed by the ecologist collecting the data in the field. Although a vast number of methods have been devised to account for this form of observation error, rarely have these methods been integrated into state-space models of population dynamics. Of the exceptions that exist, none provide software to facilitate model fitting (Buckland et al. 2004).

Other limitations of state-space models, as commonly applied in ecology, include the failure to admit spatial variation in abundance and the fact that some parameters are not identifiable (Polansky et al. 2009). Ignoring spatial variation reduces the scope of the inferences, reduces the information about the parameters of interest, and can lead to underestimation of variances

(Dennis et al. 2010). Even more problematic is the issue that without some form of replication in the first year, abundance cannot be estimated without making strong assumptions about the initial distribution. For example, practitioners either assume that there is no observation error in the first year, or they assume that the population is at equilibrium, which may defeat the purpose of many studies of population dynamics.

Several extensions of state-space models have been proposed to overcome these limitations (Newman et al. 2014). Methods for fitting models with non-Gaussian distributions for the process and observation errors have been described by de Valpine and Hastings (2002) and Brooks et al. (2004). An observation model explicitly modeling detection probability has been proposed by Kéry et al. (2009). Lele et al. (1998) and Kéry et al. (2009) have developed models allowing for inference about spatial and temporal variation in abundance, and their developments also have resolved the problems of non-identifiability for the parameters of the initial state at time $t = 1$. Of these extensions, only the work by Kéry et al. (2009) addressed several of these limitations simultaneously; however, their model did not include serial dependence, which is a hallmark of classical population growth models as well as state-space models.

In this paper, we focus on the model of Dail and Madsen (2011; henceforth the DM model) that resolves each of the problems just outlined. Our aim is to extend the model to accommodate classical models of population growth and to handle several features common to ecological time series, such as excess zeros and unexplained random variation. Both frequentist and Bayesian methods of inference are discussed, and we evaluate the performance of the model 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 DAIL-MADSEN MODEL

The DM model is an extension of the Royle (2004) N -mixture model, which allows for inference about spatial variation in abundance when individuals cannot be detected with certainty. To estimate both abundance and detection parameters, the N -mixture model uses replicate observations at each site. The observations are made during sufficiently short time intervals such that the population can 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.

The DM model requires count data collected at R sites, each of which is surveyed on T primary sampling periods. Let $X_{i,t}$ (where $i = 1, \dots, R$; $t = 1, \dots, T$) denote the count data at site i and primary period t . In general, $X_{i,t}$ will be lower than abundance, $N_{i,t}$, but in cases

where detection is perfect, abundance is observed directly such that $X_{i,t} \equiv N_{i,t}$.

Like traditional state-space models, the DM model includes three conditionally related processes corresponding to: (1) initial abundance, i.e., the abundance at site i during the first primary period, denoted $N_{i,1}$; (2) abundance at time t (for $t > 1$), which depends upon abundance at $t - 1$; and (3) the detection process. The first two processes describe the variation in abundance in space and time. The third process describes the relationship between abundance and the observed count data.

Initial abundance

Conventional state-space models assume that the distribution for the initial time period is either the equilibrium distribution or has zero variance. In contrast, Dail and Madsen (2011) proposed modeling $N_{i,1}$ as either a Poisson ($N_{i,1} \sim \text{Pois}(\Lambda_i)$) or negative binomial random variable ($N_{i,1} \sim \text{NB}(\Lambda_i, \alpha)$), where Λ_i is the expected abundance at site i during year 1. The Poisson distribution assumes that the mean of $N_{i,1}$ is equal to its variance, and the negative binomial distribution allows the variance to be greater than the mean, with the amount of overdispersion determined by the parameter α .

Regardless of the specified distribution, the model for initial abundance has two distinguishing features. First, it provides a mechanism for characterizing spatial variation in abundance. For instance, one could model the effect of an environmental covariate (x_i) on abundance using a log-linear model such as $\log(\Lambda_i) = \beta_0^\Lambda + \beta_1^\Lambda x_i$. Second, the spatial replicates resolve the problem of parameter non-identifiability that are common to standard state-space models because process variation and observation error can be estimated from spatially replicated count data (Royle 2004).

Abundance in subsequent time periods

The DM model assumes that abundance at time $t > 1$ is a function of abundance at time $t - 1$, i.e., abundance at each site evolves as a first-order Markov process. 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: $S_{i,t}$, the number of individuals surviving from $t - 1$ and not emigrating; and $G_{i,t}$, the number of new individuals entering the population. Their most general model was

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

where ω is the apparent survival probability and γ is the recruitment rate, which can depend on $N_{i,t-1}$. Dail and Madsen (2011) proposed three models for G_t : the constant model, $G_{i,t} \sim \text{Pois}(\gamma)$ where recruitment does not depend on $N_{i,t-1}$; the “autoregressive” model, $G_{i,t} \sim \text{Pois}(\gamma N_{i,t-1})$ of geometric or density-independent growth; and the no-trend model, $\gamma = (1 - \omega)\Lambda$, which

assumes that the population is at equilibrium. Covariates of ω and γ can be accommodated, e.g., using logit- and log-linear models, respectively.

Observation process

The observation model adopted by Dail and Madsen (2011) is the same binomial model proposed by Royle (2004):

$$X_{i,t} \sim \text{Bin}(N_{i,t}, p) \quad (3)$$

where p is the probability of detecting each individual. Variation in detection probability can be modeled as a function of site-specific or occasion-specific covariates using, for example, a logit-linear model.

MODEL EXTENSIONS

Population growth models

Partitioning population growth into survival and recruitment is useful in terms of providing a mechanistic description of population dynamics, but this is not always possible using simple count data, especially when the sites are not closed with respect to movement. When the mechanistic model is unrealistic, we suggest replacing it with classical population growth models that have a long history in ecology. The exponential growth model, which describes population growth in an unlimited environment, is the simplest: $N_{i,t} = N_{i,t-1}e^r$, where r is the intrinsic or maximum per capita rate of increase. To allow for demographic stochasticity, we can regard $N_{i,t}$ as a Poisson random variable, simplifying Eq. 2 to

$$N_{i,t} \sim \text{Pois}(\exp(r)N_{i,t-1}). \quad (4)$$

Density-dependent versions of the model are also possible. For example:

$$N_{i,t} \sim \text{Pois}(N_{i,t-1}\exp(r(1 - N_{i,t-1}/K))) \quad (5)$$

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 (1954) model. In the Ricker model, density dependence becomes stronger as abundance increases well above K , leading to overcompensation (abundance goes from above K to below it; Sabo et al. 2004). Another option is a modified Gompertz-logistic density-dependent model (henceforth Gompertz model; Gompertz 1825, Hart and Gotelli 2011):

$$N_{i,t} \sim \text{Pois}(N_{i,t-1}\exp(r(1 - \log(N_{i,t-1} + 1)/\log(K + 1)))). \quad (6)$$

Here the interpretations of r and K are similar to those in the Ricker model, but dynamics can only be overcompensatory at high values of r (approximately $r > \log(K)$). Because a single Poisson distribution controls the distribution of $N_{i,t}$ in each of these models, the discrete convolution used by Dail and Madsen

(2011) to construct the likelihood is not required, speeding up processing time.

Immigration models

One limitation of the geometric-recruitment, exponential, Ricker, and Gompertz versions of the DM models is that they include no mechanism for a local population to recover after extinction. However, these models can be generalized to allow immigration to contribute to population growth. For example, an exponential plus immigration model is:

$$N_{i,t} \sim \text{Pois}(\exp(r)N_{i,t-1} + \iota) \quad (7)$$

where ι represents the average number of immigrants per year, and is constrained to be positive (this is equivalent to separate Poisson processes for growth and immigration). The geometric-recruitment, Ricker, and Gompertz models can be extended to allow for immigration in the same way. Because the population contribution from immigration does not depend on current abundance, ι and other growth parameters are separately estimable. Deterministic versions of the Ricker plus immigration and the Gompertz plus immigration do reach stable equilibria, but the equilibria are not at K and cannot be solved for analytically (Otto and Day 2007). Therefore, we refer to K in these models as the semi-equilibrium abundance.

Excess zeros

The negative binomial distribution used in N -mixture models can have a very long right tail, and its mean to variance ratio may not be ideal in all cases. An alternative is to consider zero-inflated distributions, such as the zero-inflated Poisson:

$$N_{i,1} \sim \begin{cases} \text{Pois}(0) & \text{with probability } \psi \\ \text{Pois}(\Lambda) & \text{with probability } (1 - \psi) \end{cases} \quad (8)$$

where ψ represents the proportion of extra zeros. Under this formulation, detection, abundance, and zero-inflation can be modeled separately as functions of covariates. For example, detection of a species might depend on wind speed, abundance on forest type and weather, and zero-inflation upon elevation and climate.

The zero-inflated Poisson distribution can be applied to recruitment and population growth terms as well as initial abundance. For example, the recruitment term of the constant-recruitment DM model (Eq. 2) can be modified as follows:

$$G_{i,t} \sim \begin{cases} \text{Pois}(0) & \text{with probability } \psi \\ \text{Pois}(\gamma) & \text{with probability } (1 - \psi) \end{cases} \quad (9)$$

Environmental and demographic stochasticity

The original DM models allows for demographic stochasticity (variation in population growth rate due to the randomness of birth and death processes) via the binomial and Poisson distributions for apparent survival and recruitment. Our population growth extensions use

a single Poisson distribution for abundance. Conceptually, this is an appropriate method of modeling demographic stochasticity for semelparous populations with one generation per sampling interval (year) (Bonsall and Hastings 2004), and the DM models appropriate for modeling the demographic stochasticity of iteroparous populations, if they are underdispersed compared to the Poisson (but see *Discussion*). Dynamics of semelparous populations with more than one generation per year (many insects) may be overdispersed compared to the Poisson. If the number of generations per year is known, then this can be accounted for in our models by adding extra N 's between each count (see Supplement).

One way to model environmental stochasticity, the variation in population growth rate due to stochastic environmental conditions, is by explicitly modeling dynamic parameters as functions of environmental covariates. For example, in the Gompertz model (Eq. 6), r could be a function of temperature and K a function of rainfall.

Another way to model environmental stochasticity is as lognormal variation in the population growth rate (Bjørnstad 2001, Bonsall and Hastings 2004). This could be applied to both density-independent and density-dependent models. For example, for the Ricker plus immigration model:

$$N_{i,t} \sim \text{Pois}(N_{i,t-1}\exp(v_{i,t} + r(1 - N_{i,t-1}/K)) + \iota) \quad (10)$$

where v is a normally distributed random variable with mean 0 and variance σ_v^2 . We suggest three variations for spatial variation in environmental stochasticity. The first has independent environmental stochasticity between sites, and might be appropriate where sites are widely dispersed. In the second, all sites have the same environmental conditions in a given year (regional stochasticity, $v_{i,t} = v_t$), which might be appropriate where the geographic or environmental range is small (Hanski 1998). Third, where sites can be close together but the range of sites is broad, a multivariate normal distribution for $v_{i,t}$ with a distance-dependent covariance matrix might be appropriate.

Random observer effects

Variation in detection probability among observers is another source of random variation that may need to be considered when 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, Sauer et al. 1994, Campbell and Francis 2011).

Current BBS trend estimators deal with this problem by treating observer identity as a random effect (Link and Sauer 2002, Sauer and Link 2011). To include random observer effects in DM models, Eq. 3 can be modified to:

$$\begin{aligned} X_{i,j,t} &\sim \text{Bin}(N_{i,t}, p_j) \\ \text{logit}(p_j) &\sim \text{Normal}(\mu_p, \sigma_p^2) \end{aligned} \quad (11)$$

where $X_{i,j,t}$ is the number of individuals counted 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^2 is the logit-scale variance of the random observer effect.

Statistical inference

Dail and Madsen (2011) used likelihood-based methods for estimating the parameters of their model. The same likelihood functions can be used to accommodate the alternative population growth, immigration, and zero-inflation (initial abundance only) models that we have proposed. Methods for implementing these models using maximum likelihood estimation are included in the R package *unmarked* (Fiske and Chandler 2011). Examples are given in the Supplement.

Bayesian inference is an alternative to classical inference with several appealing features. First, it allows direct probability statements to be made about a hypothesis, given data (Link and Barker 2010). Second, Bayesian methods offer straightforward approaches for combining data from multiple sources or using existing estimates of parameters as prior distributions. Third, a common usage of state-space models is to predict future population size, and this is easily accomplished using Bayesian methods.

Simulation methods such as Markov chain Monte Carlo (MCMC) are used to estimate the posterior distributions. Although time consuming, MCMC may be the only viable approach for estimating parameters, especially for hierarchical models with many random effects. Software packages such as JAGS (Plummer 2003) make these methods readily available to ecologists, and we have provided examples in the Supplement.

APPLICATIONS

Simulation study to assess estimator accuracy

We simulated data for 100 sites over 40 years, with 1000 simulations of each combination of parameter values. All simulations assumed that initial abundance was Poisson distributed and no covariates affected initial abundance, dynamics, or detection probability. Our first series of simulations assumed that dynamics were exponential (Eq. 4). We ran each combination of low, medium, and high initial abundance, growth rate, and detection probability ($\Lambda \in \{1, 5, 10\}$, $r \in \{-0.005, 0, 0.005\}$, and $p \in \{0.05, 0.25, 0.5\}$). Our second series of simulations changed dynamics to the Ricker model (Eq. 5). We used $\Lambda = 10$ and $p = 0.25$, and simulated low, medium, and high values of equilibrium abundance (K) and r (Table A1; nine total combinations). Our third series of simulations was based on the Ricker plus 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 ι (Appendix A: Table A1).

We used the R package *unmarked* to estimate the parameters for each simulation with the same initial abundance (Poisson) and dynamics models as were simulated. We report bias of estimates, root mean squared error, and coverage (percentage of 95% confidence intervals for parameters that overlap the true values).

Robustness simulation study

Most of our DM model extensions assume Poisson process error for annual dynamics. Although we provide a variation for data overdispersed compared to the Poisson (see *Environmental and demographic stochasticity*), and the original DM models assume underdispersed data, we tested our models against violations of the Poisson assumption. We ran three alternative scenarios: (1) a geometric-recruitment model with $\omega = \gamma = 0.5$; (2) a Leslie matrix model with six age classes; and (3) a Gompertz model with two nonoverlapping generations per year (sampling occasion). The first two scenarios are underdispersed compared to the Poisson and the third is overdispersed. In the first two cases, we estimated parameters with both the exponential and geometric-recruitment models using the R package *unmarked*. We compared the bias, root mean squared error, and coverage of the model estimates as well as their Akaike's information criterion (AIC) values. For the third scenario, we estimated parameters with the Gompertz model with one generation per year, using both maximum likelihood and MCMC approaches, as well as allowing for two generations per year with MCMC. We compared the bias, root mean squared error, and coverage of all three model estimates. Details of the robustness simulation study can be found in Appendix A.

Analysis of Breeding Bird Survey data

We applied our model extensions to North American Breeding Bird Survey (BBS) data collected from 1966 to 2010 in Maryland and Virginia. For our focal species, we selected the Ovenbird (*Seiurus aurocapilla*), an abundant, forest-breeding migratory songbird with a stable or increasing trend in the region (Porneluzi et al. 2011).

The BBS is an annual roadside survey implemented by trained observers in the United States and Canada. An observer conducts 50 3-min point counts with 400 m radii, 0.8 km apart 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 number of Ovenbirds 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

TABLE 1. Simulation results from 27 cases of exponential dynamics (1000 Monte Carlo replicates for each): data generating values, mean estimate, root mean squared error (RMSE), and coverage for the initial abundance (Λ), growth rate (r), and detection probability (p) parameters.

Data generating values			Mean estimate			RMSE			Coverage		
Λ	r	p	Λ	r	p	Λ	r	p	Λ	r	p
10	-0.005	0.05	10.039	-0.0060	0.050	1.050	0.0061	0.004	0.959	0.945	0.96
10	-0.005	0.25	10.033	-0.0057	0.250	0.769	0.0060	0.015	0.951	0.942	0.945
10	-0.005	0.5	10.009	-0.0060	0.500	0.611	0.0053	0.024	0.949	0.957	0.945
10	0.005	0.05	10.068	0.0042	0.050	1.046	0.0058	0.004	0.955	0.939	0.949
10	0.005	0.25	10.036	0.0040	0.251	0.801	0.0053	0.017	0.934	0.954	0.921
10	0.005	0.5	9.967	0.0043	0.502	0.618	0.0049	0.025	0.934	0.957	0.92
10	0	0.05	10.065	-9×10^{-4}	0.050	1.061	0.0055	0.005	0.961	0.96	0.944
10	0	0.25	10.035	-0.0009	0.250	0.763	0.0056	0.016	0.953	0.943	0.936
10	0	0.5	10.003	-0.0007	0.501	0.581	0.0054	0.023	0.949	0.945	0.948
1	-0.005	0.05	1.047	-0.0125	0.050	0.241	0.0241	0.009	0.949	0.953	0.97
1	-0.005	0.25	1.016	-0.0117	0.250	0.154	0.0227	0.027	0.952	0.949	0.945
1	-0.005	0.5	1.011	-0.0114	0.500	0.135	0.0229	0.038	0.957	0.936	0.95
1	0.005	0.05	1.028	-5×10^{-5}	0.050	0.236	0.0206	0.010	0.939	0.948	0.947
1	0.005	0.25	1.014	-0.0014	0.250	0.161	0.0225	0.027	0.957	0.937	0.946
1	0.005	0.5	1.006	-0.0011	0.502	0.137	0.0206	0.037	0.947	0.945	0.95
1	0	0.05	1.036	-0.0068	0.050	0.237	0.0246	0.009	0.958	0.934	0.961
1	0	0.25	1.016	-0.0059	0.250	0.164	0.0213	0.026	0.944	0.945	0.953
1	0	0.5	1.005	-0.0053	0.500	0.134	0.0198	0.038	0.951	0.947	0.952
5	-0.005	0.05	5.075	-0.0064	0.050	0.656	0.0088	0.005	0.945	0.959	0.965
5	-0.005	0.25	5.026	-0.0062	0.250	0.473	0.0078	0.017	0.943	0.966	0.937
5	-0.005	0.5	5.013	-0.0066	0.501	0.362	0.0081	0.025	0.96	0.949	0.961
5	0.005	0.05	5.056	0.0040	0.050	0.624	0.0079	0.005	0.944	0.957	0.952
5	0.005	0.25	5.016	0.0041	0.250	0.446	0.0075	0.017	0.948	0.947	0.942
5	0.005	0.5	5.027	0.0037	0.499	0.367	0.0073	0.025	0.947	0.95	0.943
5	0	0.05	5.063	-0.0016	0.050	0.611	0.0084	0.005	0.96	0.96	0.956
5	0	0.25	5.044	-0.0014	0.249	0.465	0.0081	0.017	0.942	0.938	0.945
5	0	0.5	5.024	-0.0012	0.499	0.373	0.0075	0.025	0.952	0.964	0.946

effects of wind speed on detection probability, using the truncated mean of wind conditions at the start and end of each route on the Beaufort scale as a categorical predictor. Following Link and Sauer (2002), we also included the first time an observer ran a route as a predictor variable for detection probability.

We fit a series of models using maximum likelihood, and then a series of models using MCMC. We started by testing three models of initial abundance (Poisson, negative binomial, and zero-inflated Poisson) with exponential dynamics (Eq. 4) and no covariates. We selected the minimum AIC model from that set to test three additional models for p : wind, first, and wind plus first. We selected the minimum AIC model from that set to test eight additional models of dynamics: constant-recruitment, geometric-recruitment, Ricker, Gompertz, the previous three with immigration, and exponential plus immigration. These models require a finite upper bound to integrate over when run in a maximum likelihood framework; we used 600.

We ran the top-ranked models from the maximum likelihood analyses in a Bayesian framework with vague priors (Λ , α , and $K \sim \text{Uniform}(0, 200)$, $r \sim \text{Uniform}(0, 5)$, $\iota \sim \text{Uniform}(0, 15)$, and logit-linear p coefficients $\sim \text{Normal}(0, 100)$). We added random observer effects and environmental stochasticity, modeled as lognormal variation in regional population growth rate (Eq. 10). We also used the random observer effects model to obtain route- and year-specific abundance estimates. We

tested for lack of convergence using four or five Markov chains for each model (Gelman and Rubin 1992). For each chain, we drew at least 40 000 samples, after at least 3000 adaptation iterations.

RESULTS

Simulation study to assess estimator accuracy

Estimator bias and error were generally low with the exponential model, and coverage was nominal (93.4–97.0%; Table 1; Fig. A1 in Appendix A). However, estimates of r were imprecise (RMSE between 0.020 and 0.025; relative RMSE between 413% and 482% for nonzero true r) and biased low (between -0.008 and -0.005; relative bias between -151% and -101% for nonzero true r) when the true value of Λ was low. Simulations of the Ricker model generally performed well (Table 2; Fig. A2 in Appendix A), except when the true value of r was low (0.005). In this case, the estimates of r and K were inaccurate (relative RMSE between 87.4% and 2091.8%), biased high (between 65.4% and 198.9%), and had low coverage (between 77.6% and 94.3%). In other cases for the Ricker model, relative RMSE was between 6.7% and 55%, bias was between -6.4% and 5.8%, and coverage was between 91.9% and 96.4%. All three cases simulated for the Ricker plus immigration model performed fairly well (Table 3; Fig. A3 in Appendix A; relative RMSE between 7.2% and 62.9%, bias between -3.5% and 3.3%, and coverage between 93.2% and 96.4%).

TABLE 2. Simulation results from nine cases of Ricker dynamics (1000 Monte Carlo replicates for each): data generating values, mean estimate, root mean squared error (RMSE), and coverage for initial abundance (Λ), maximum growth rate (r), equilibrium abundance (K), and detection probability (p) parameters.

Data generating values ($\Lambda = 10$, $p = 0.25$)		Mean estimate			RMSE				Coverage				
r	K	Λ	r	K	p	Λ	r	K	p	Λ	r	K	p
0.005	5	9.914	0.0098	6.368	0.252	0.785	0.0115	5.561	0.016	0.955	0.807	0.776	0.963
0.005	10	9.954	0.0087	10.989	0.252	0.775	0.0093	8.739	0.016	0.960	0.831	0.828	0.943
0.005	20	9.935	0.0083	59.778	0.251	0.761	0.0083	418.378	0.016	0.955	0.841	0.943	0.955
0.05	5	10.038	0.0529	4.682	0.252	0.896	0.0275	1.583	0.019	0.945	0.922	0.919	0.951
0.05	10	10.009	0.0527	9.718	0.252	0.834	0.0188	1.746	0.017	0.961	0.930	0.960	0.948
0.05	20	10.000	0.0514	19.790	0.251	0.839	0.0132	2.513	0.017	0.951	0.943	0.962	0.940
0.1	5	10.046	0.1013	4.833	0.250	0.913	0.0353	0.876	0.020	0.948	0.954	0.944	0.954
0.1	10	9.990	0.1025	9.893	0.251	0.884	0.0227	0.896	0.018	0.949	0.954	0.964	0.950
0.1	20	9.988	0.1018	19.916	0.251	0.858	0.0154	1.621	0.017	0.947	0.941	0.951	0.953

Robustness simulation study

In simulations of the geometric-recruitment model estimated with the exponential model, estimates of Λ were biased high and p biased low (Appendix A: Table A2). However, estimates of r had low bias and RMSE, with nominal coverage. The estimates from the geometric-recruitment model for Λ and p had low bias, but the estimates for γ and ω were somewhat biased and imprecise (Appendix A: Table A2 and Fig. A4). The geometric-recruitment model had lower AIC 71.3% of the time; when the geometric-recruitment model was favored, the mean ΔAIC was 6.0 and when the exponential model was favored the mean was 1.4. For the Leslie matrix simulations, bias in estimates of Λ and p from both the exponential and geometric-recruitment models were high, but the exponential biases were higher (Appendix A: Table A3 and Fig. A4). The geometric-recruitment model was favored in 100% of the simulations, with a mean ΔAIC of 89.0.

The Gompertz model with a single generation per year, fitted with both maximum likelihood and MCMC using data simulated from a Gompertz model with two

generations per year, underestimated Λ and K and overestimated p (Appendix A: Table A4 and Fig. A5). As a result, RMSEs for these parameters were all high and coverages all low, except that the coverage of K by the maximum likelihood model was 100%. However, the model with two generations per year estimated parameters well, with minimal bias and RMSE and nominal coverage.

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 B1A in Appendix B). The best-supported model for p included effects of wind speed and an observer's first run of a route (Appendix B: Table B1B, model B.1). First run and increasing wind speeds both decreased p . All dynamics models with immigration were better supported than models without immigration (Table B1C); the best-supported was Ricker plus immigration (see Appendix B: Fig. B1 for estimates). Constant-recruitment dynamics models estimated unrealistically high survival probabilities ($\omega = 1 \pm 1.3 \times 10^{-5}$, mean \pm SE), whereas

TABLE 3. Simulation results from three cases of Ricker and immigration dynamics (1000 Monte Carlo replicates for each): data generating values, mean estimate, root mean squared error (RMSE), and coverage for initial abundance (Λ), maximum growth rate (r), semi-equilibrium abundance (K), immigration (ι), and detection probability (p) parameters.

Statistic, with different data-generating ι values	For data-generating values, $\Lambda = 10$, $r = 0.05$, $K = 10$, $p = 0.25$; only ι is variable				
	Λ	r	K	ι	p
Mean estimate					
$\iota = 0.005$	9.997	0.0515	9.687	0.0051	0.251
$\iota = 0.050$	10.015	0.0517	9.758	0.0504	0.251
$\iota = 0.500$	10.000	0.0506	9.648	0.5081	0.251
RMSE					
$\iota = 0.005$	0.877	0.0181	1.777	0.0031	0.018
$\iota = 0.050$	0.875	0.0173	1.724	0.0105	0.018
$\iota = 0.500$	0.965	0.0194	2.683	0.0776	0.021
Coverage					
$\iota = 0.005$	0.951	0.944	0.964	0.947	0.942
$\iota = 0.050$	0.943	0.932	0.958	0.940	0.943
$\iota = 0.500$	0.947	0.940	0.952	0.951	0.941

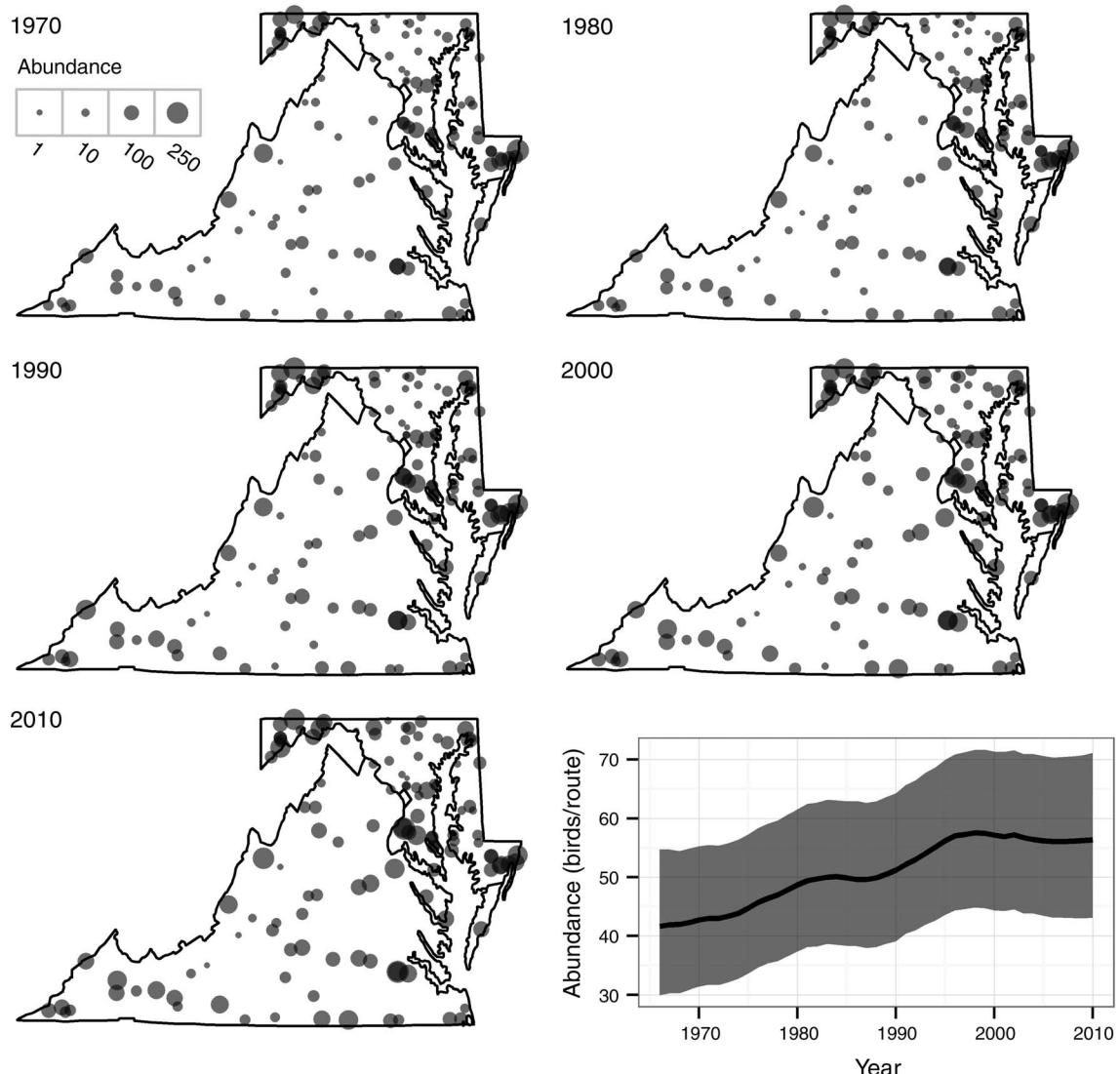


FIG. 1. Maps of Breeding Bird Survey (BBS) route and year-specific estimated Ovenbird (*Seiurus aurocapilla*) abundance (mean number of birds per route) for the years 1970, 1980, 1990, 2000, and 2010. Note that the abundance scaling in the key is continuous, not categorical; dot size is scaled by estimated abundance for that route and year and therefore provides examples of representative abundances, not categories. The lower right panel depicts estimated mean (with 95% credible interval) route abundance by year.

the geometric-recruitment and geometric-recruitment plus immigration models estimated nonviable low survival probabilities ($\omega = 0.058 \pm 0.046$ and 0.026 ± 0.060 , respectively).

Estimates for the top-ranked model were similar when run in the Bayesian framework, except that the estimate of r more than halved (Appendix B: Fig. B1). When random observer effects were added, estimates for Λ and K increased dramatically and the estimate for r was intermediate. The estimate of the intercept for p dropped. When environmental stochasticity was added, the estimate for K increased. The highest estimates of Λ and K came from the model that included environmental stochasticity and random observer effects.

We estimated Ovenbird abundance by route and year (and averaged over routes) using the Bayesian model with random observer effects (Fig. 1). Estimated average abundance over time alternated between growing and stable periods. Estimated Ovenbird abundance was highest in western and eastern Maryland in 1970 and 1980, but became more evenly distributed by 2010. Gelman and Rubin (1992) diagnostics and visual examination of the chain trajectory and density plots provided little evidence of lack of convergence for any of the Bayesian models ran.

DISCUSSION

Our work demonstrates how a class of open-population N -mixture models proposed by Dail and

Madsen (2011) overcomes many of the limitations of classical state-space models as applied to ecological time series data. We extended their model in several important ways to accommodate common features of ecological data sets, including sparse counts, zero-inflation, environmental stochasticity, and random variation in observation error. We also demonstrated how many of the objectives of conventional state-space modeling can be accomplished within this expanded framework. For example, one of the primary aims of our paper was to demonstrate how classical population growth models can be embedded in the DM model.

Although we view this as an important connection to make between the two different classes of state-space models, we believe that such population growth models are more phenomenological than mechanistic, and this runs counter to the motivation for the DM model. However, estimating demographic parameters from count data is an ambitious goal, and the required assumptions will not be valid in many cases, especially when immigration and emigration occur. This was supported by the unrealistic estimates of vital rates reported here and by the lack of support for the mechanistic models relative to the population growth models. A separate analysis of BBS data for 11 other forest passersines found similar poor support and unrealistic estimates for the mechanistic models (J. Hostetler, *unpublished analyses*), suggesting that some process, possibly individual heterogeneity (Vindenes et al. 2008), is increasing variances above the levels expected from demographic stochasticity alone. It is also possible that similar values for recruitment and survival rates in songbirds and low detection probabilities for the BBS have contributed to the DM model issues.

DM models and our extensions are conceptually simple, but even in their most basic form they include many random effects (the N 's, which incorporate demographic stochasticity), making it challenging to compute the likelihood or implement MCMC algorithms. Nonetheless, in some cases additional random effects may be of interest. We have shown a few approaches for incorporating some of these (environmental stochasticity and random observer effects). Although incorporating these random effects can increase the difficulty of achieving model convergence and decrease estimate precision, they can be important. For example, the estimate of semi-equilibrium abundance for the Ovenbird increased by more than 150% when environmental stochasticity and random observer effects were included.

Another important benefit of this class of models is that it can be readily implemented using frequentist or Bayesian methods by ecologists lacking skills in computer programming and advanced statistics. The Supplement includes code to simulate and fit many of the extensions discussed in this paper. In spite of the new extensions that 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. With 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 the model's parametric assumptions. Furthermore, properly modeling detection probability can involve accounting for nuances such as difference among individuals and probabilities of being available for detection (Nichols et al. 2009).

Fortunately, incorporating direct information about detection probability is straightforward and we recommend that this be done whenever possible. Dail and Madsen (2011) proposed that replicated counts be conducted within an interval in which the populations can be assumed to be closed. A robust design (Pollock 1982) 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, multiple observer, and distance sampling (Williams et al. 2002). These could be accomplished by extending the open-population N -mixture model in exactly the same way as the closed-population version has been extended (e.g., Royle et al. 2004).

Our emphasis was on increasing the practical utility of this class of models, and so we avoided several conceptually interesting extensions that we believe would be computationally prohibitive in many cases. Nonetheless, we will discuss one: spatially explicit models of immigration. In our models, immigration is currently modeled as independent of population sizes in other sites, and emigration is included only as an implicit piece of apparent survival or population growth. We suggest alternatives that put movement in a metapopulation context: immigration conditional on total or mean abundance across sites in the previous time step; immigration conditional on abundance in nearby sites only; and immigration conditional on abundance at sites as a function of their distance from the receiving site (Hastings 1991, Hanski 1998). These models would require that all sites in the metapopulation are sampled, or that abundance at unsampled locations can be estimated (Lele et al. 1998). Initial tests suggest that it would be possible to fit some or all of these models, at least in the Bayesian framework. It may also be possible to model an explicit emigration process or rate and tie immigration at nearby sites to this rate.

Our models generally estimated parameters well in analysis of data simulated with the same model. Two exceptions were the estimates of instantaneous growth rate in the exponential model when the true value of initial abundance was low, and the estimates of equilibrium abundance and maximum growth rate in the Ricker model when the true value of maximum

growth rate was low. The failure of the first case was probably due to a large number of sites starting at abundance 0 or reaching it early in the simulation. Because a site that hit abundance 0 in this simulation stayed at 0, this provided little information with which to estimate growth rate. The failure of the second case is also reasonable: with very slow movement toward the equilibrium abundance comes little information for estimating that abundance or the rate of growth. In other cases, bias was low and coverage nominal. However, we simulated 40 years of data; with fewer years of data these models might experience more problems.

Our models generally did not estimate parameters well in simulations when data were underdispersed or overdispersed compared to the model assumptions. However, we present models for both Poisson-distributed and overdispersed data, and the original DM model and the stage-structured model of Zipkin et al. (2014) are available for underdispersed data. The AIC model selection did a good job of picking the most appropriate distribution. Appropriate density-dependent models for underdispersed data remain to be developed.

The modeling framework that we have described can be used and extended to address many pressing issues in ecology and conservation biology. For example, it allows for inference about the effects of climate change on either explicit demographic parameters or in derived parameters such as population growth rate. Furthermore, in addition to assessing past climate change on population parameters, projecting populations under future climate scenarios is also possible. Thus, we expect that this modeling methodology can be used to make quantitative assessments of species vulnerability to climate change and other important human-induced drivers of population dynamics.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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