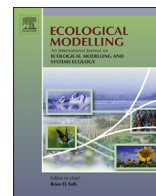




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Reprint of: Fitting population growth models in the presence of measurement and detection error[☆]

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ABSTRACT

Population time series data from field studies are complex and statistical analysis requires models that describe nonlinear population dynamics and observational errors. State-space formulations of stochastic population growth models have been used to account for measurement error caused by the data collection process. Parameter estimation, inference, and prediction are all sensitive to measurement error. The observational process may also result in detection errors and if unaccounted for will result in biased parameter estimates. We developed an N-mixture state-space modeling framework to estimate and correct for errors in detection while estimating population model parameters. We tested our methods using simulated data sets and compared the results to those obtained with state-space models when detection is perfect and when detection is ignored. Our N-mixture state-space model yielded parameter estimates of similar quality to a state-space model when detection is perfect. Our results show that ignoring detection errors can lead to biased parameter estimates including an overestimated growth rate, underestimated equilibrium population size and estimated population state that is misleading. We recommend that researchers consider the possibility of detection errors when collecting and analyzing population time series data.

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1. Introduction

Relating population growth models statistically to field data is essential for answering important questions in ecology and natural resource management (May, 1999). One statistical tool to do this is the population viability analysis (PVA), which use population abundance data and population growth models to estimate the probability that a population will persist for a specified time into the future (Beissinger and McCullough, 2002). Worthwhile PVAs require reliable estimates of population growth model parameters to answer population related questions (de Valpine and Hastings, 2002; Nadeem and Lele, 2012). At minimum, a typical analysis using population growth models begins with data collection, which often involves surveys to count individuals. In many surveys, the observation process can result in a substantial amount of

observational error. For example, an analysis of the North American Breeding Bird Survey (BBS), which consists of spatially and temporally replicated point counts over a large portion of North America since 1966, found that over 70% of the noise in the estimated growth rate for a population growth model was due to observation error (Dennis et al., 2006). Accounting for this observation error has been an important area of research for ecological statistics, and we hope to build upon previous work by incorporating two types of observation error that occur simultaneously, but have not been appropriately combined in a single modeling framework.

There are at least two distinct components of observation error, including measurement error and detection error. State-space models (SSMs) were developed over the last decade to model population dynamics and measurement error, with the goal of obtaining unbiased parameter estimates and improving ecological inference (de Valpine and Hastings, 2002; de Valpine, 2003; Williams et al., 2003; Clark and Bjørnstad, 2004; Dennis et al., 2006; Freckleton et al., 2006; Nadeem and Lele, 2012). To date, detection error has been ignored or it was assumed that accounting for measurement error was sufficient to result in unbiased parameter estimates and improved inference when population growth models were fit to time series data (de Valpine and Hastings, 2002; Williams et al., 2003; Clark and Bjørnstad, 2004; Dennis et al., 2006; Wang, 2007; Pedersen et al., 2011; Nadeem and Lele, 2012).

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Measurement error and detection error, however, are two distinct forms of observation error. For example, [Ponciano et al. \(2009\)](#) applied SSMs that considered several stochastic population growth models combined with a Poisson measurement error model. Using Gause's classic *Paramecium* data, which involved counting the number of cells on 0.5 cm³ samples of culture media daily, the authors estimated parameters of SSMs. In this example the Poisson measurement error model seems appropriate. We could imagine taking additional samples from each culture media in Gause's experiment. The number of cells counted on additional samples from a single culture on any given day may be different due to variability in the sampling process; the underlying population growth process, however, is the same for all samples. Non-detection occurs when fewer organisms are observed than are actually present. For Gause's data this would have occurred if some of the cells on the sample culture media were not counted. It is well known that non-detection can lead to biased parameter estimates in other types of models of populations, such as estimating trends in occupancy or abundance ([Tyre et al., 2003](#); [Royle, 2004](#); [Royle and Dorazio, 2008](#); [Kéry et al., 2009](#)). Methods correcting for non-detection in SSMs have only recently been applied and include distance sampling ([Moore and Barlow, 2011](#)) or incorporating prior knowledge derived from other studies ([Pagel and Schurr, 2012](#); but see [Wilberg et al., 2010](#) for review of catchability in fisheries stock assessment models). However, both distance sampling and prior knowledge of the detection process require more complex survey designs and additional data that may not be available for long-term time series data such as the BBS.

Correcting for non-detection when applying SSMs based on statistical methods used to correct for detection error would be a useful addition to the literature on population time series and is the goal of this paper. Many methods have been developed to correct for non-detection in other types of models of population abundance, such as regression models describing the temporal trends and spatial variability in abundance due to habitat covariates ([Kéry et al., 2009](#)). One of the most ingenious and practical methods to correct for non-detections is the N-mixture model ([Royle, 2004](#)). The N-mixture model explicitly models population abundance and detection using only observed abundance data and can be applied to time series data. Often analyses using N-mixture models assume a binomial distribution for the detection model and a Poisson distribution for the abundance model ([Royle, 2004](#); [Royle and Dorazio, 2008](#)). The detection process (and thus detection error) is modeled with discrete and continuous covariate effects that vary with the probability of detection through the logit link. Similarly, the true population abundance (number of individuals present) is related to the underlying intensity of abundance with the Poisson measurement error model. The true abundance is modeled with discrete and continuous covariate effects that vary with the intensity of the Poisson distribution through the log link.

State-space models have been applied to time series data where detection errors may have occurred but replicated site visits were not available and a closed population could not be assumed ([Williams et al., 2003](#); [Dennis et al., 2006, 2010](#)). Until recently, N-mixture models had only been applied when replicated site visits were available and a closed population could be assumed ([Royle, 2004](#); [Kéry et al., 2009](#); [Sólymos et al., 2012](#)). Recently, [Sólymos et al. \(2012\)](#) developed the N-mixture model for data from single site visits that could be used in an open population. The authors showed numerically that all components of N-mixture models were estimable from data with no replication when detection and abundance depended on at least one unique continuous covariate. The authors suggested that the requirements of single site visit N-mixture models were satisfied by many situations and provided an illustrative analysis using a spatially replicated subset of the BBS data.

We show that the N-mixture model can be extended to correct for non-detection while simultaneously estimating the parameter of the SSM from population time series data. The simplest population growth models, however, do not depend on covariates and assume that model parameters are constant. The most common SSM applications have assumed that the model parameters are constant; therefore, it may appear that correcting for detection using an N-mixture model for single replicate time series data is not possible ([de Valpine and Hastings, 2002](#); [Dennis et al., 2006](#), [Nadeem and Lele, 2012](#)). However, population model parameters could depend on covariates ([Williams et al., 2003](#); [Knappe and de Valpine, 2012](#); [Pagel and Schurr, 2012](#)) or vary stochastically due to some hierarchical structure ([Newman and Lindley, 2006](#)). In addition, stochastic variation in population abundance may be equivalent to the requirement of a unique covariate effect on abundance for single site visit N-mixture models. That is, if the population state is varying over time, detection may be accounted for in SSMs without covariates that influence abundance, replicated site visits or other auxiliary estimates of detection.

In the population dynamics stock assessment models used in fisheries research and management variable catchability is a similar issue ([Wilberg et al., 2010](#)). Variable catchability has been incorporated into some state-space population dynamics models in fisheries, but we are unaware of methods for modeling discrete counting processes that are common to point count data such as the BBS. With regard to time-varying catchability, we quote the text of [Wilberg et al. \(2010\)](#), because it is equally true when detectability is dynamic: "Fisheries scientists, and most importantly, stock assessment practitioners must understand that (1) ecological theory and a large body of evidence suggests that time-varying catchability is a common phenomenon, (2) failing to incorporate time-varying catchability into stock assessments may produce biased results, (3) multiple methods to incorporate time-varying catchability exist, and (4) additional studies are needed to compare the performance of alternate methods and to develop new and improved methods to incorporate time-varying catchability." In this paper we combine SSMs and N-mixture models to develop a modeling framework to account for non-detection and measurement error simultaneously when fitting population growth models. We rigorously test our N-mixture state-space models using simulated data sets that emulate data that an ecologist is likely to collect and analyze.

2. Materials and methods

2.1. Model description

A state-space model describes the dynamics of an unobserved population state (N_t) at each time (t) and how the observed population abundance with perfect detection (A_t) relates to the population state. The utility of a SSM is in the ability to model random variation in the population state due to process error such as environmental stochasticity and random variation in the data due to measurement error. The general system and observation probability distribution functions (PDF) for SSMs are $N_t \sim f(t, N_{t-1}; \alpha)$ and $A_t \sim g(t, N_t; \lambda)$ respectively, where α is the vector of stochastic population model parameters and λ is the vector of measurement error model parameters. Both $f(t, N_{t-1}; \alpha)$ and $g(t, N_t; \lambda)$ may be discrete or continuous distributions. The $g(t, N_t; \lambda)$, however, must be discrete to correct for detection with the N-mixture model and because of this requirement alternative detection models would need to be developed for continuously distributed population abundances.

The N-mixture model describes how the observed count data (Y_t) and probability of detection (p_t) relate to abundance if detection was perfect (A_t). Note that A_t must be estimated in an N-mixture model, whereas if detection was perfect it would be the observed

count. The general observation PDF of an N-mixture model is $Y_t \sim h(t, A_t; p_t | D_t)$. Here h is a discrete PDF, typically binomial. Unless replicated site visits are available, the probability of detection must depend on at least one continuous covariate (D_t), typically through the logit link (Sólymos et al., 2012). Combining the above PDFs yields a three-stage hierarchical N-mixture state-space model (NMSSM),

$$N_t \sim f(t, N_{t-1}; \alpha) \quad (1)$$

$$A_t \sim g(t, N_t; \lambda) \quad (2)$$

$$Y_t \sim h(t, A_t; p_t | D_t) \quad (3)$$

where (1) is the PDF of the stochastic population growth model, (2) is the discrete measurement error PDF and (3) is the discrete detection error PDF. We provide a data generating example based on our general model description in Section 2.4 (Eqs. (4)–(6)), which may provide a more concrete model description for some readers.

Although our NMSSM may appear specific to field studies of population dynamics, such temporal hierarchical models that account for the observational process have a wide application in ecology (Ives et al., 2003; Cressie and Wikle, 2011). For example, a wide array of dynamical systems models describing the temporal dynamics of an ecological process could be used in place of the population growth model. The idea of separating observation error into separate components, as we did with measurement error and detection error, may be crucial to successfully modeling the underlying ecological process.

2.2. Estimability

We agree with Lele (2010) that scientifically valid inference must be based on estimable parameters in a model, regardless of the statistical paradigm. Exact estimability conditions for the NMSSM are unknown. For SSMs, estimability is difficult to show for even the simplest case ($N_t \sim \text{normal}$, $A_t \sim \text{normal}$, and the population growth model is linear; Dennis et al., 2006; Knappe, 2008; Lele et al., 2010). Similarly, for N-mixture models, exact estimability criteria have not been obtained analytically. Sólymos et al. (2012) showed numerically that the parameters of the N-mixture model are estimable when detection and abundance depend on at least one unique continuous covariate. For the NMSSM we limit our methods to the situation when detection depends on at least one continuous covariate. We argue the requirement that abundance depends on at least one unique covariate is analogous to a requirement that N must be a random variable from a non-degenerate distribution (i.e., N must be non-constant). A degenerate distribution of N could occur if the population state was deterministic or if N was a constant. We expect that a constant N will never occur in any real population. We support our claims by using the data cloning algorithm to show numerically that the parameters of an NMSSM are estimable when at least one unique covariate of detection is available and N is a random variable from a non-degenerate distribution (Appendix A, Figure A1; Lele et al., 2010; Sólymos, 2010). Following Sólymos et al. (2012), we recommend checking estimability numerically with the data cloning algorithm for individual data sets and population growth model combinations (Lele et al., 2010; Sólymos, 2010). For our simulation study, it is not computationally feasible to check each simulated data set for parameter estimability using the data cloning algorithm, however, we do demonstrate estimability for one simulated data set (Figure A2).

Supplementary material related to this article found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2013.10.021>.

2.3. Estimation

Maximum likelihood estimation (MLE) of parameters for SSMs involves solving high-dimensional integrals (de Valpine and Hastings, 2002). For normal and non-normal measurement error SSMs, a data cloning algorithm based on the Markov chain Monte Carlo (MCMC) algorithm has been developed (Ponciano et al., 2009; Lele et al., 2010; Nadeem and Lele, 2012). Similarly, MLE for N-mixture model parameters requires computation of high dimensional infinite sums (Royle, 2004; Sólymos et al., 2012). The NMSSM requires both integration and summation. The MCMC algorithm offers a relatively easy and efficient method for parameter estimation when high dimensional integration or summation is required and can be used to estimate parameters based on a Bayesian paradigm or maximum likelihood. For our simulation study, MLE with the data cloning algorithm is impractical due to reduced computational efficiency, but would be a viable estimation method for single data sets. We therefore embrace a fully Bayesian paradigm for our study. We used the MCMC algorithm to simulate from the posterior distribution of the NMSSM and SSM. We used four independent Markov chains initialized from random draws from the prior distribution for each parameter. This procedure resulted in overdispersed starting values, judged by viewing a small portion of the trace plots from the simulated data sets. We determined the adaptation interval, burn-in interval, and thinning interval by examining trace plots, auto-correlation plots and Gelman–Rubin's multivariate potential scale reduction factor (Brooks and Gelman, 1998). Our goal was to produce posterior samples that had multivariate potential scale reduction factors of < 1.1 and similar autocorrelation. Details of the MCMC simulation are in Appendix B. We used program R (ver. 2.15.1) for all statistical computing (R project for Statistical Computing, Vienna, Austria). We use JAGS (ver. 3.2.0) for all MCMC sampling (Plummer, 2012) called from the dclone package (ver. 1.8-1) in R (Sólymos, 2010). Annotated R code to implement the NMSSM is in Appendix C.

Supplementary material related to this article found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2013.10.021>.

2.4. Simulation

The theta logistic population growth model, Poisson measurement error model and binomial detection error model were used for assessing the estimation performance of the NMSSM:

$$N_t \sim \text{log-normal}(N_{t-1} e^{r_0(1-(N_{t-1}/k)^\theta)}, \sigma^2) \quad (4)$$

$$A_t \sim \text{Poisson}(N_t) \quad (5)$$

$$Y_t \sim \text{binomial}(A_t, p_t | D_t) \quad (6)$$

where $\text{logit}(p_t) = \beta_0 + \beta_1 D_t$. Our methods did not attempt to estimate θ and considered it fixed. Estimating θ and determining the functional form of density dependence can be difficult, even when the data are simulated (Polansky et al., 2009).

Following Wang (2007) and Pedersen et al. (2011), two tests of the methods were carried out:

1. Estimation performance of state (N) and all five population model parameters ($r_0, K, \sigma^2, \beta_0, \beta_1$) from the NMSSM with known model functional form and parameter values from simulated data Y .
2. Compare test one to estimation performance of state and all model parameters to the SSM (r_0, K, σ^2) when detection is perfect with simulated data A and when detection is imperfect, but ignored or assumed to be perfect with simulated data Y .

The goal of test one was to evaluate the estimation and inferential properties of the NMSSM; test two gave a baseline to compare with the results of test one and illustrated that when detection is ignored the results obtained from a SSM are inadequate.

For both tests, $T=1000$ data replicates were simulated with $\theta = 1$, $K = 1000$, $\sigma^2 = 0.01$, $\beta_0 = -2$, $\beta_1 = 2$, and $r_0 = 0.1$ as in Wang (2007) and Pedersen et al. (2011). A single covariate of detection (D_t) was generated from a standard normal distribution. We simulated time series of two different lengths: $n = 200$ and $n = 40$. The longer time series simulation was designed to make the results of our tests obvious; the shorter time series simulations were designed to determine how our results might perform in more realistic situations encountered by ecologists. Although $n = 40$ may appear unrealistically long for any single time series, we suggest combining multiple time series from a population (e.g., four time series of $n = 10$) under a multivariate framework; doing so may produce results that are nearly equivalent to longer time series. For the $n = 40$ simulation we evaluate two sets of priors, which we considered to be weakly informative ($K \sim \text{uniform}(0,5000)$, $r_0 \sim \text{uniform}(0,4)$, $\log(\sigma^2) \sim \text{uniform}(-10,10)$, $\beta_0 \sim \text{uniform}(-4,4)$ and $\beta_1 \sim \text{uniform}(-4,4)$; \log is the natural logarithm) and highly informative ($K \sim N(1000,1000)$, $r_0 \sim N(0.1,0.25)$, $\log(\sigma^2) \sim N(\log(0.01),0.01)$, $\beta_0 \sim N(-2,0.25)$ and $\beta_1 \sim N(2,0.25)$ where $N(\mu, \sigma^2)$ is the normal distribution with mean μ and variance σ^2). For the $n = 200$ simulation we evaluated only weakly informative priors. Following Wang (2007) and Pedersen et al. (2011), the longer time series was started from the initial state $N_1 = 3$ and was assumed known for our SSM and NMSSM analysis. The shorter time series was started from K and allowed 100 burn-in iterations before we collected the time series used in our simulation analysis. For the shorter time series we assigned the initial state priors $\log(N_1) \sim N(\log(2Y_1), 1)$ for the NMSSM, $\log(N_1) \sim N(\log(A_1), 1)$ for the SSM when detection is perfect and $\log(N_1) \sim N(\log(Y_1), 1)$ when detection is ignored. The same priors on the initial state were used in both the weakly and highly informative short time series simulation.

The performance of state estimations of our methods was evaluated with the posterior mean of the root mean square error of the log population state

$$\text{RMSE} = \frac{1}{s} \sum_{i=1}^s \left(\frac{1}{n} \sum_{t=1}^n (\log(N_{t,i}) - \log(N_{t,i}))^2 \right)^{1/2} \quad (7)$$

where N is single draw from the posterior of the population state, N is the true population state, n is the total length of the time series and s is the number of posterior simulations. We choose evaluate the RMSE of the natural logarithm of the population state so that our results are comparable to previous SSM simulation studies (Wang, 2007; Pedersen et al., 2011). Model parameters were estimated using the posterior mean. The performance of the posterior mean as parameter estimates was evaluated with the mean of the root mean square error from 1000 data replicates (see Appendix B).

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We assessed the frequentist coverage probability of the 95% credible intervals (CI) and report the percent length reduction (PLR)

$$\text{PLR} = \frac{U_{\theta|y} - L_{\theta|y}}{U_{\theta} - L_{\theta}} \quad (8)$$

where $P(\theta > U_{\theta|y}|y) = P(\theta < L_{\theta|y}|y) = P(\theta > U_{\theta}) = P(\theta < L_{\theta}) = 0.025$, θ is the parameter of interest, U is the upper CI limit and L is the lower. The subscripts θ indicate that the CI is from the prior, whereas $\theta|y$ is from the posterior. The PLR is a metric of the information in the data and the efficiency of our estimation procedure. Therefore a

PLR close to zero would indicate that the data are highly informative compared to the prior and that our estimation procedure is extracting the information efficiently. We plotted CI coverage probability against PLR to allow for simultaneous evaluation of coverage probability and PLR. We also report the raw average CIs coverage probability and length (see Appendix B). Ninety-five percent CIs were constructed from the 2.5 and 97.5 percentiles of the posterior distribution for each model parameter. Assessing the frequentist properties of Bayesian methods is used to determine if the method is well calibrated (Little, 2006). For example, a 95% CI (or confidence interval) that has a coverage probability of 0.95 is said to be perfectly calibrated. Estimation methods that result in well calibrated statistics are highly desirable under any inferential paradigm.

3. Results

3.1. Simulation results

In a single simulation, the observed data (Y_t) hardly resemble abundance (A_t); however, as a result of our Poisson measurement error model, A_t tracks the population state (N_t) well (Fig. 1). The true probability of detection varied effectively between zero and one due to the effect of the covariate of detection and resulted in a low average probability of detection ($\bar{p} = 0.23$) that was highly variable ($\text{SD} = 0.24$) between time steps. For the NMSSM estimated population model parameters were similar to the SSM when detection was perfect (Fig. 2). Both statistical models resulted in well-estimated population model parameters for all sample sizes and priors combinations. The parameter K was biased high when $n = 40$ with weakly informative priors (Fig. 2). When detection was imperfect and ignored, all model parameters were poorly estimated and highly biased. The mean RMSE between the estimated population state and true population state was small for the SSM with perfect detection (0.13, $\text{SD} = 0.01$, $n = 200$; Fig. 2). The NMSSM produced a similar mean RMSE of 0.16 ($\text{SD} = 0.02$). When the data were generated with detection errors ignored, the mean RMSE (2.81, $\text{SD} = 0.13$) was approximately 18 times greater than when detection was accounted for. The mean RMSE did not increase substantially when sample size was decreased ($n = 40$) or improve substantially with informative priors (Fig. 2). Root mean square error for posterior means of population model parameters was similar for the NMSSM and SSM with perfect detection; however, when detection was perfect the SSM outperformed the NMSSM (Table B1). As expected, highly informative priors reduced root mean square error of parameter estimates.

With weakly informative priors, coverage probabilities for the NMSSM and SSM with perfect detection were near the nominal coverage (0.95) for all model parameters at both sample sizes. With highly informative priors, coverage probability was one or near one (Fig. 3). The coverage probability of the SSM when detection was ignored was zero for most of the model parameters (Table B2). The PLR was less than one for all model parameters in all tests indicating that CIs of the posterior were shorter than the CIs of the priors for all cases (Fig. 3). The greatest reduction in PLR occurred with the weakly informative priors. As expected, the NMSSM model had larger values of PLR compared to SSM with perfect detection. This indicates that simultaneously estimating the detection and population model parameters results in reduced efficiency; however, loss of efficiency is minimal.

4. Discussion

Ignoring detection errors can result in highly biased population model parameters and population state estimates. Given the prevalence of detection errors in population survey data we

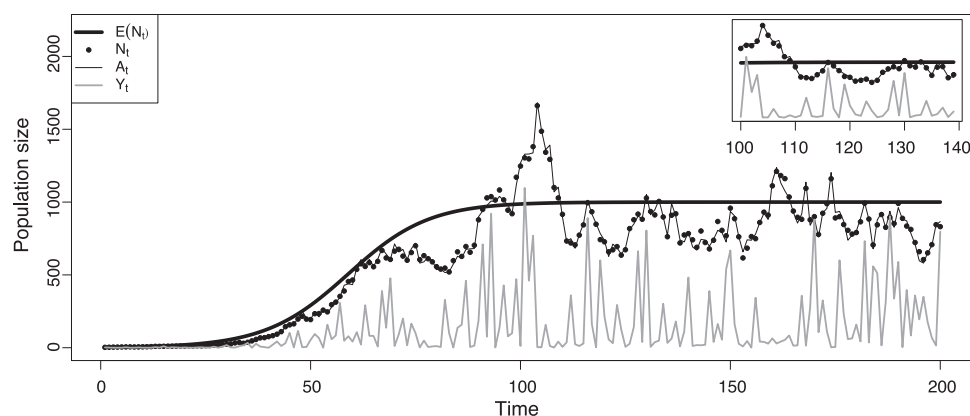


Fig. 1. Example simulated population time series data. The $E(N_t)$ is the deterministic population model trajectory, N_t is the unobserved population state, A_t is the observed abundance when detection is perfect and Y_t is the observed abundance when detection error are present. The full time series ($t = 0-200$) was used to evaluate the large sample properties, whereas, the time series in the inset plot ($t = 100-140$) was used to evaluate the small sample properties of our model.

suggest that researchers consider the possibility of imperfect detection when fitting population growth models to field data. The NMSSM modeling framework we developed appears to perform well under a range of scenarios and priors. In our simulation the NMSSM was efficient, in that mean RMSE and the root mean square errors of NMSSM parameters were not much larger than those for the SSM when detection was perfect and are comparable to

results from SSMs in other studies (Wang, 2007; Pedersen et al., 2011). We were surprised that the coverage probability of the NMSSM and the SSM with perfect detection were near nominal with weakly informative priors. Near nominal coverage probability is surprising because the NMSSM is a complex hierarchical model evaluated with relatively small (i.e., non-asymptotic) sample sizes.

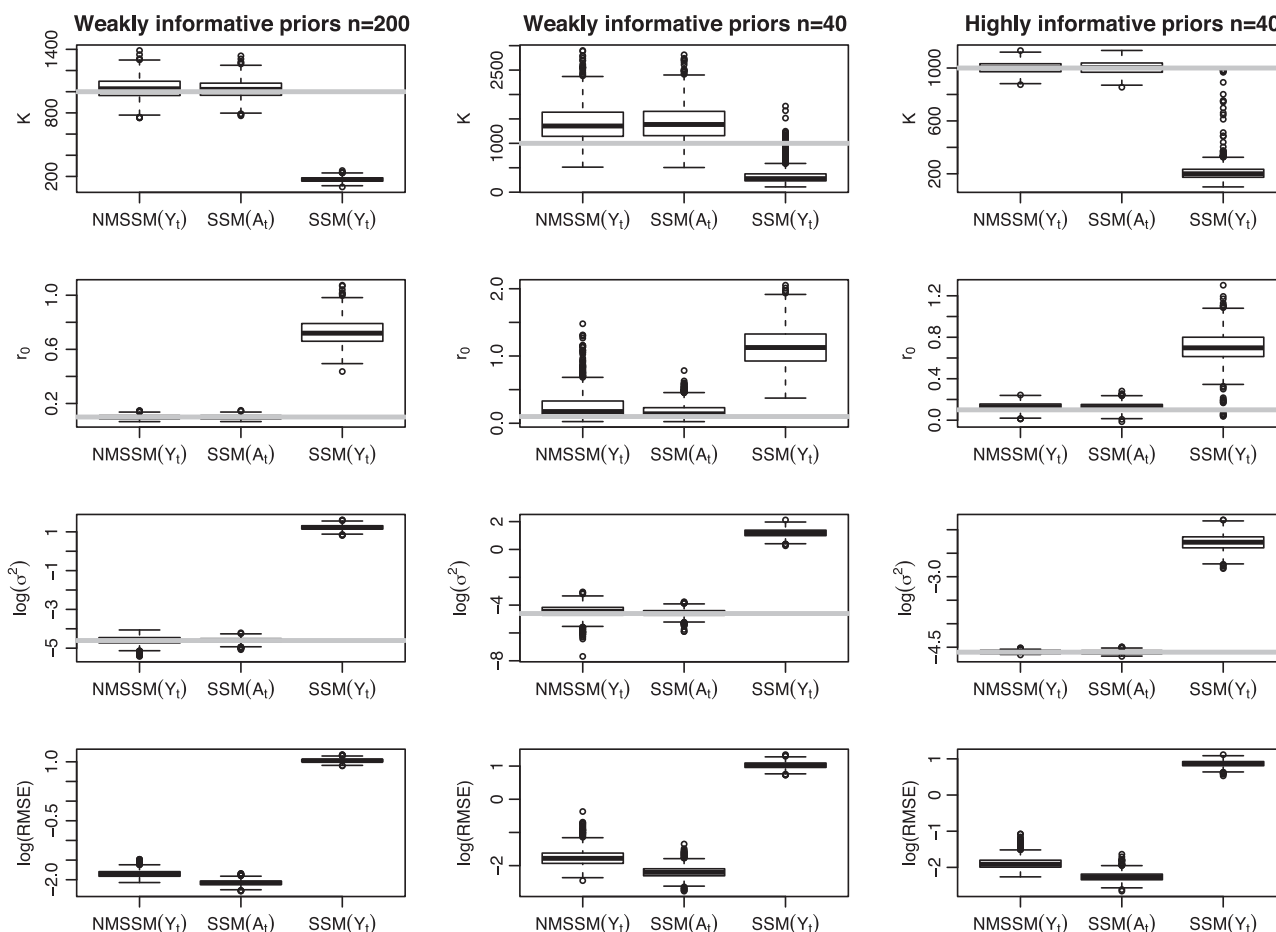


Fig. 2. Simulation results for population model parameters (K , r_0 , and σ^2) and root mean square error (RMSE) of the natural log of population state estimates for three scenarios with two different sets of priors and two lengths of time series (weakly informative with $n = 200$ and $n = 40$ and highly informative with $n = 40$). The scenarios include an N-mixture state-space model (NMSSM(Y_t)) when detection is imperfect and estimated, a state-space model (SSM) analysis when detection is perfect (SSM(A_t)) and an SSM analysis when detection is imperfect, but assumed perfect (SSM(Y_t)). Each box and whisker plot corresponds to the posterior mean of 1000 simulated data replicates. Gray lines show the true parameter value.

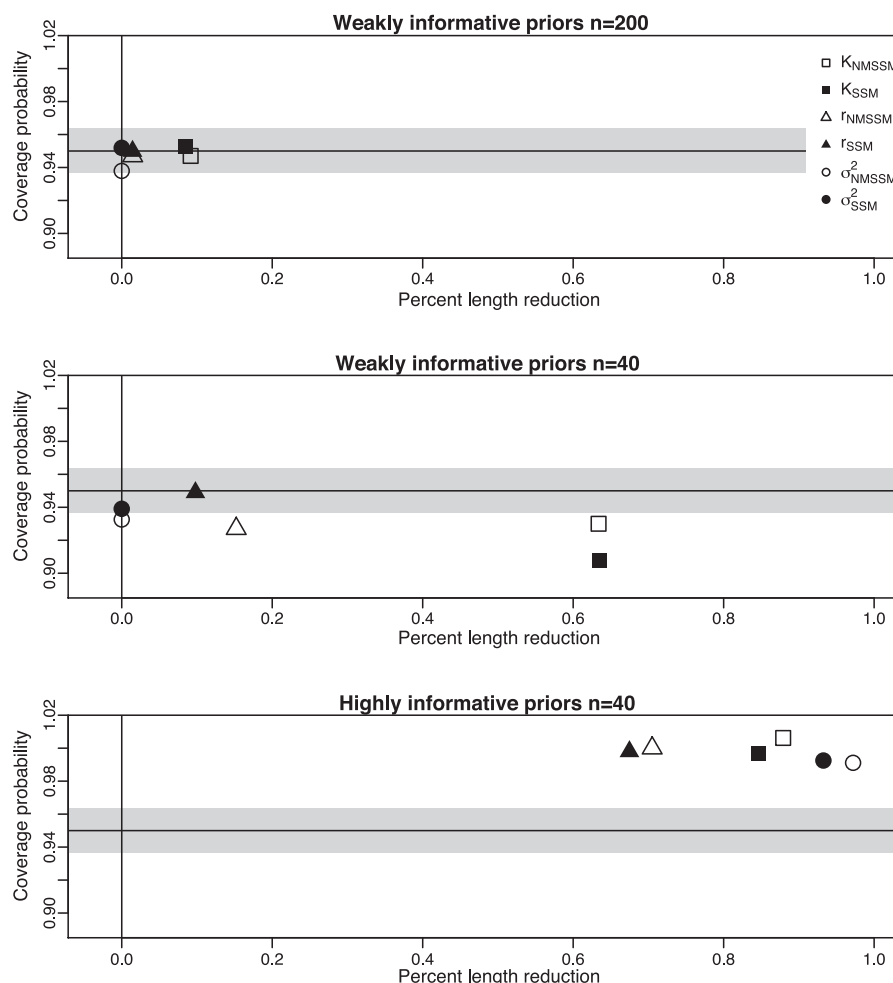


Fig. 3. Coverage probability plotted against ratio of the posterior credible interval length to prior credible interval length (percent length reduction) for population model parameters (K , r_0 , and σ^2) with two lengths of time series and with two different sets of priors (weakly informative with $n=200$ and $n=40$ and highly informative with $n=40$). The two scenarios include a state-space model (SSM) analysis when detection is perfect and an N-mixture state-space model (NMSSM) when detection is imperfect and estimated. Each symbol is the mean of 1000 simulations. The vertical line at zero is the limit of the percent length reduction and the horizontal line is at the nominal 95% credible interval coverage probability with 95% confidence interval coverage based on a normal approximation (gray shading). Symbols that overlapped were jittered a small amount.

We recommend that the NMSSM can be applied under a Bayesian estimation paradigm with weakly or strongly informative priors. Although initially our weakly informative priors may seem to contain more information than what is available for many applications, we argue that this may not be the case. For example, the uniform prior on the population growth rate r_0 covers a wide range of population dynamics including a stable equilibrium, limit cycle, and chaos. Surely a biologist can exclude values of $r_0 > 3$ that result in chaos based on prior knowledge of the species. Another example where prior knowledge may be used is to inform the coefficient in the detection model (β_1). For example, in point counts of bird species it may be known that detection decreases as wind velocity increases. For our scenario with weakly informative priors we assumed $\beta_1 \sim \text{uniform}(-4,4)$. If reliable prior knowledge of the sign of the relationship between detection and the covariate is available this can be incorporated by limiting the support of the prior (e.g., $\beta_1 \sim \text{uniform}(-4,0)$ for wind velocity). Alternatively, if specification of priors is not feasible, we recommend maximum likelihood estimation of the parameters using the data cloning algorithm and we have provided code to do so (Appendix C). Although it was not computationally feasible to evaluate the properties of the maximum likelihood estimates using numerical simulation, it would be feasible to estimate NMSSM parameters for most data sets. Ideally both Bayesian and maximum likelihood estimates could be obtained and

compared; this would be especially beneficial when informative priors are used and would allow one to evaluate the influence of the priors.

When SSM were first introduced to ecologists, they were advertised as an approach to improve population model parameter estimation, statistical inference, and prediction when the data collection process resulted in measurement error (de Valpine and Hastings, 2002; de Valpine, 2003; Freckleton et al., 2006). Prior to this advancement, an ecologist who fit population models to field data had to assume that measurement error was negligible or that all stochastic variability in the time series was measurement error (de Valpine and Hastings, 2002). Similarly, N-mixture models introduced a novel method to estimate detection probabilities and corrected abundance when replicated site visits were conducted (Royle, 2004). The combination of SSM and N-mixture models would correct for the inadequacy of ignoring errors in detection when fitting SSM. However, most applications of SSM involved data with only one site visit between time intervals when it was known that the population abundance changed, rendering the combination SSMs and the N-mixture useless for most applications. With the extension of N-mixture models to single site visit survey data by Sóllymos et al. (2012), it is now possible to usefully combine these two models.

Prior to the advancement we propose here, ecologists who fit population models to field data under the SSM framework had to assume that the only type of observational error was measurement error (Williams et al., 2003; Dennis et al., 2006). This assumption is equivalent to assuming that detection is perfect and may result in biased parameter estimates. Perfect detection is unlikely under most field conditions, as evidenced by the extensive literature on remedial methods for data with errors in detection. The NMSSM modeling framework we present here is applicable to situations for discrete data such as point counts and our results show that the detection process can be accounted for when the probability of detection depends on at least one continuous covariate. We argue that continuous covariates can be obtained from the most basic characteristics of the survey such as time of day and environmental conditions (e.g. wind velocity; Sólymos et al., 2012). Furthermore, it can be determined if detection is imperfect from the data using model selection tools that are commonly applied to SSMs (Knappe et al., 2011; Nadeem and Lele, 2012). Given the potential for large bias in population model parameter estimates, erroneous inference, and dangerously incorrect predictions when detection errors are ignored, ecologists should collect relevant covariates of detection with each survey and consider the NMSSM when estimating population model parameters.

The methods we developed are useful when the measurement error is discrete and when detection error results in discrete observed abundance. We envision that our methods will be used for point count data. However, population abundance data may be continuous, for example biomass. In addition to application of the NMSSM, future research should focus on accounting for detectability or catchability and provide a framework that allows for both continuous and discrete measurement and detection error model (Wilberg et al., 2010).

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