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Fitting population growth models in the presence of measurement and detection error

Trevor J. Hefley[a,b,*], Andrew J. Tyre[b], Erin E. Blankenship[a]

[a] Department of Statistics, University of Nebraska-Lincoln, 3310 Holdrege Street, Lincoln, NE 68583, USA
[b] School of Natural Resources, University of Nebraska-Lincoln, 3310 Holdrege Street, Lincoln, NE 68583, USA

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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).

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

* Corresponding author at: Department of Statistics, University of Nebraska-Lincoln, 3310 Holdrege Street, Lincoln, NE 68583, USA. Tel.: +1 402 472 4054; fax: +1 402 472 2946.
E-mail addresses: thefley@huskers.unl.edu (T.J. Hefley), atyre2@unl.edu (A.J. Tyre), erin.blankenship@unl.edu (E.E. Blankenship).

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Gause's classic *Paramecium* data, which involved counting the number of cells on 0.5 cm^3 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; Knape 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 the 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

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