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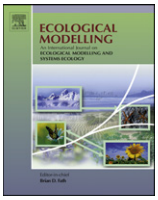

Population viability analysis for several populations using multivariate state-space models

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ABSTRACT

The International Union for the Conservation of Nature and Natural Resources (IUCN), the world's largest and most important global conservation network, has listed approximately 16,000 species worldwide as threatened. The most important tool for recognizing and listing species as threatened is population viability analysis (PVA), which estimates the probability of extinction of a population or species over a specified time horizon. The most common PVA approach is to apply it to single time series of population abundance. This approach to population viability analysis ignores covariability of local populations. Covariability can be important because high synchrony of local populations reduces the effective number of local populations and leads to greater extinction risk. Needed is a way of extending PVA to model correlation structure among multiple local populations. Multivariate state-space modeling is applied to this problem and alternative estimation methods are compared. The multivariate state-space technique is applied to endangered populations of pacific salmon, USA. Simulations demonstrated that the correlation structure can strongly influence population viability and is best estimated using restricted maximum likelihood instead of maximum likelihood.

1. Introduction

The International Union for the Conservation of Nature and Natural Resources (IUCN), the world's largest and most important global conservation network, has listed approximately 16,000 species worldwide as threatened (IUCN, 2007). Placing a species on this list, known as the Red List, brings threatened species special attention which can lead to the development of specific management plans to reduce the likelihood of extinction. The most important tool for recognizing and listing species as threatened is population viability analysis (PVA), which estimates the probability of extinction of a population or species over a specified time horizon.

The most common PVA approach is to apply it to a single time series of population abundance (e.g., Dennis et al., 1991). This approach ignores correlation structure which arises when a population actually consists of several local, possibly interbreeding, populations. Correlation structure of local populations actually has important implications for the viability of a species and should not be ignored. High population synchrony reduces the effective number of local populations, leading to greater extinction risk (Harrison and Quinn, 1989; Hill et al., 2002; Hilderbrand, 2003). Most PVA approaches, however, do not model correlation structure explicitly, and either lump the populations together, or run PVAs separately on each related population. In this paper, I analyze alternative methods to estimate correlation structure, while allowing the possibility of measurement error in population counts.

Another important consideration for PVA is measurement error in population counts. Measurement error, which arises because of population counting or sampling error, if ignored, can create bias in population viability analysis results (Holmes, 2001; McNamara and Harding, 2004). Several methods for treating measurement error include using a robust estimator that does not rely on information about the measurement error distribution (Holmes, 2001), or, applying a maximum likelihood (Lindley, 2003) or restricted maximum likelihood (Staples et al., 2004) to a state-space model. I extend the approach of Staples et al. (2004), originally developed to handle single populations, into multivariate framework, which models correlation structure of several local populations.

The main objective of this work is to develop a multivariate model to handle multiple local populations at once and make inferences on PVA model structures (e.g., population growth rate and covariance structure). I begin by demonstrating the importance of considering correlation structure in population viability using simulations. The state-space method is then applied in another simulation study that demonstrates the accuracy of estimating correlation structures and population growth rate differences between local populations. Three alternative estimation techniques for the

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multivariate PVA model are developed and compared: a multivariate Dennis approach (MVD), which ignores measurement error; a maximum likelihood (ML), and restricted maximum likelihood (REML). These estimation techniques are applied to two groups of local populations of chinook salmon (*Oncorhynchus tshawytscha)*: one group in the Snake River basin, USA, and the other in the Lake Washington basin, USA.

2. Methodology

2.1. State-space models

When detailed models of population structure are not possible because only population counts are available, the most common approach is to use a diffusion approximation approach (Holmes et al., 2007). The typical diffusion approximation approach, often called the Dennis Model, for the growth of a single population is a stochastic, discrete-time model of exponential growth that is described by

$$N_t = N_{t-1}\ \exp(\mu + e_t), \tag{1}$$

where $t = 1, 2,\ldots,T$; N_t represents population abundance at time t; and $\exp(\mu)$ is the deterministic per-unit-abundance growth rate in population density (Dennis et al., 1991). The error term, e_t, represents the stochastic deviations from long-term trend due to environmental effects. These errors are assumed to have a normal distribution with mean zero and constant variance. Defining $x_t = \log(N_t)$, the growth process can be expressed as

$$x_t = x_{t-1} + \mu + e_t, \tag{2}$$

which represents a discrete-time random walk with drift process.

This approach, although useful for single populations, must be extended to model several local populations simultaneously. Suppose that instead of a single population, there are n related local populations to model, which may have correlated growth rates. Further suppose that x_t is observed with error. The Dennis et al. (1991) model can be extended to this situation through a multivariate state-space approach (Dennis et al., 1998). The true (but unknown) log population abundances, denoted by the state variable vector $\boldsymbol{\alpha}_t$, are governed by the dynamic equation

$$\boldsymbol{\alpha}_t = \boldsymbol{\alpha}_{t-1} + \mathbf{c} + \boldsymbol{\eta}_t, \tag{3}$$

where $\mathbf{c}$ is a $n \times 1$ vector that represents the stochastic growth rates, and $\boldsymbol{\eta}_t$ is a $n \times 1$ vector of serially uncorrelated disturbances with mean zero and $n \times n$ covariance matrix $\mathbf{Q}$.

The observed values of log abundances, $\mathbf{y}_t$ are related to the true log abundances, $\boldsymbol{\alpha}_t$, through the measurement equation

$$\mathbf{y}_t = \boldsymbol{\alpha}_t + \boldsymbol{\varepsilon}_t, \tag{4}$$

for $t = 1, 2,\ldots,T$, where $\boldsymbol{\varepsilon}_t$ is a $n \times 1$ vector of serially uncorrelated disturbances with mean zero and $n \times n$ covariance matrix $\mathbf{H}$.

2.2. Alternative model structures

Covariance and growth rate structures are inferred by fitting alternative forms of the state-space model to population data, then determining which is best supported by the data. This represents a distinct advantage over univariate approaches which do not allow for relationships among the viability parameters of local populations. Several alternative forms of the stochastic growth rate and variance structures are possible. In this paper, the stochastic growth rate structures I explore are: population-specific stochastic growth rates, and a stochastic growth rate common to all local populations. The four alternative forms for the process error, $\mathbf{Q}$, I explore are: an unrestricted covariance matrix; a diagonal covariance matrix with unequal diagonal entries; a diagonal covariance matrix with equal variances; and a matrix with equal variances and equal covariances. The unrestricted covariance matrix contains no restrictions on its elements, such as common variances, covariances, or zeroes, while the other forms do contain such restrictions. These four alternative covariance matrix forms were also used for the measurement error covariance matrix $\mathbf{H}$ To determine which state-space model was best supported by the data, AIC was used (Akaike, 1973).

2.3. Estimation of state-space models

To determine which approach is best for estimating alternative stochastic growth rate and covariance structures, I evaluated three alternative estimation procedures: ML, MVD, and restricted maximum likelihood (REML). All of the methods work by forming likelihood functions based on differences of the observed log abundances, which have multivariate normal distributions. The first differences series of log-transformed counts can be written

$$\mathbf{w}_t = \mathbf{y}_{t+1} - \mathbf{y}_t = \mathbf{c} + \boldsymbol{\eta}_{t+1} + \boldsymbol{\varepsilon}_{t+1} - \boldsymbol{\varepsilon}_t. \tag{5}$$

Now form the $n(T-1) \times 1$ vector $\mathbf{W}$ by stacking all of the $\mathbf{w}_t$ vectors into a single column. The distribution of $\mathbf{W}$ is multivariate normal with mean $\mathbf{Ec}$ and variance–covariance matrix $\boldsymbol{\Sigma}$, where $\mathbf{E}$ is a $n(T-1) \times n$ matrix formed by stacking $(T-1)$ copies of the $n \times n$ identity. Using the fact that $\mathrm{E}[\mathbf{w}_t - \mathbf{c})(\mathbf{w}_t - \mathbf{c})'] = 2\mathbf{H} + \mathbf{Q}$ and $\mathrm{E}[\mathbf{w}_{t+1} - \mathbf{c})(\mathbf{w}_t - \mathbf{c})'] = -\mathbf{H}$, we can express the variance–covariance matrix for $\mathbf{W}$ as

$$\sum = \begin{bmatrix} 2\mathbf{H}+\mathbf{Q} & -\mathbf{H} & \mathbf{0} & \mathbf{0} & \cdot & \cdot & \cdot & & 0 \\ -\mathbf{H} & 2\mathbf{H}+\mathbf{Q} & -\mathbf{H} & \mathbf{0} & \cdot & \cdot & \cdot & & \cdot \\ \mathbf{0} & -\mathbf{H} & 2\mathbf{H}+\mathbf{Q} & -\mathbf{H} & \mathbf{0} & & & & \cdot \\ \mathbf{0} & \mathbf{0} & -\mathbf{H} & \cdot & \cdot & \cdot & \cdot & & \cdot \\ \cdot & & \mathbf{0} & \cdot & \cdot & \cdot & \cdot & & \cdot \\ \cdot & & & \cdot & \cdot & \cdot & \cdot & & \mathbf{0} \\ \cdot & & & & \cdot & \cdot & \cdot & & -\mathbf{H} \\ \mathbf{0} & \cdot & \cdot & \cdot & \cdot & \mathbf{0} & -\mathbf{H} & & 2\mathbf{H}+\mathbf{Q} \end{bmatrix}. \tag{6}$$

Notice that the entries in the variance–covariance matrix consist entirely of the parameters contained in the process error and measurement error matrices.

The maximum likelihood approach, ML, proceeds by maximizing the likelihood formed by the distribution of $\mathbf{W}$ with respect to the elements of $\mathbf{c}$, $\mathbf{Q}$, and $\mathbf{H}$. This log likelihood function is given by

$$L_{\mathbf{W}} = -\frac{1}{2}\ \log|2\pi\boldsymbol{\Sigma}| - \frac{1}{2}\mathbf{W}'\,\boldsymbol{\Sigma}^{-1}\mathbf{W}. \tag{7}$$

The multivariate Dennis approach (MVD) proceeds by maximizing this likelihood after fixing $\mathbf{H} = 0$. I call this the MVD because when applied to a single population, it yields precisely the Dennis model estimates.

Staples et al. (2004) observed that, in the univariate case, maximum likelihood (ML) estimators obtained by maximizing $L_{\mathbf{W}}$ directly were strongly biased. They suggested using the restricted maximum likelihood is used to overcome this bias (Searle et al., 1992). In order to use REML for the estimation problem in this paper, I generalized the univariate approach of Staples et al. (2004) to a multivariate framework. The REML proceeds by using another difference of the log count data:

$$\mathbf{j}_t = \mathbf{w}_{t+1} - \mathbf{w}_t, \tag{8}$$

where $\mathbf{j}_t$ is a $n \times 1$ vector and $t = 1, 2,\ldots,T–2$. Next construct the $n(T-2) \times 1$ vector $\mathbf{J}$ by stacking all of the vectors $\mathbf{j}_t$ into a single