ESTIMATING DENSITY DEPENDENCE, PROCESS NOISE, AND OBSERVATION ERROR

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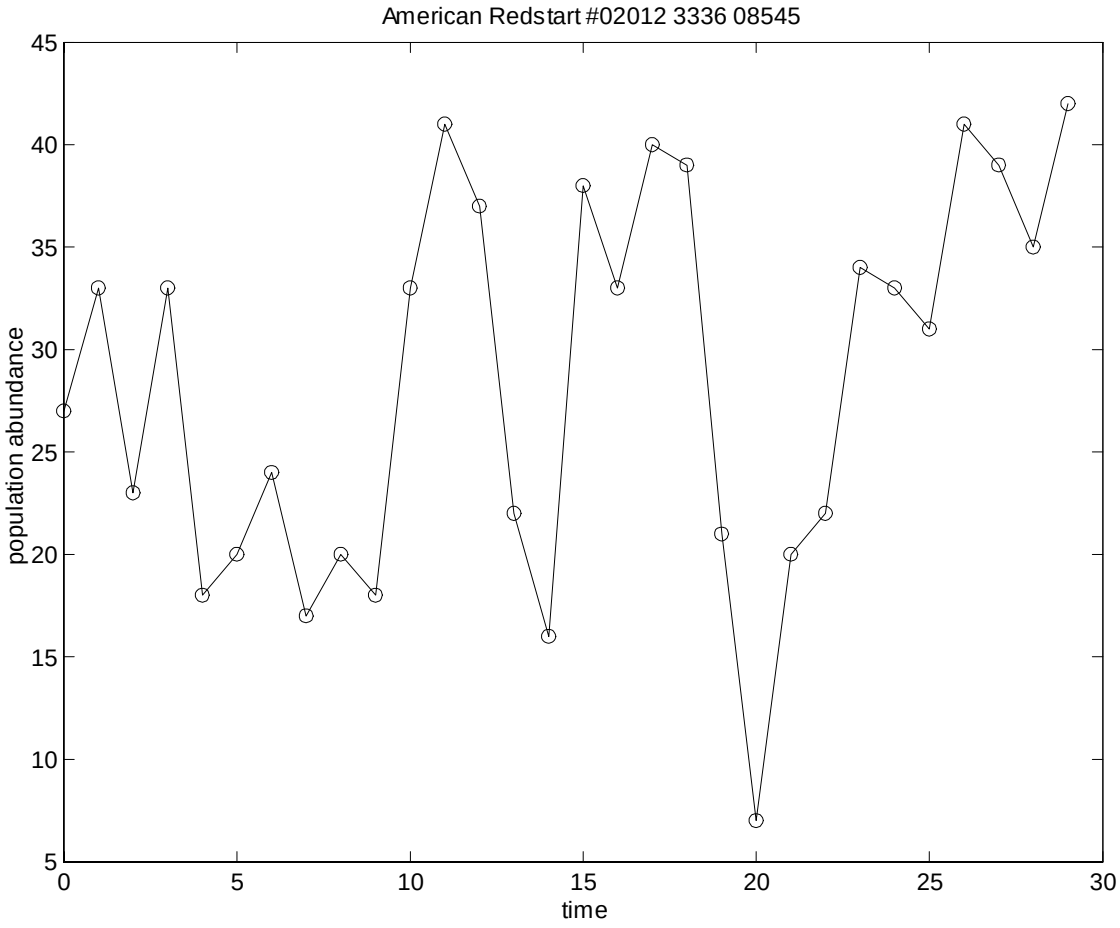
Model:

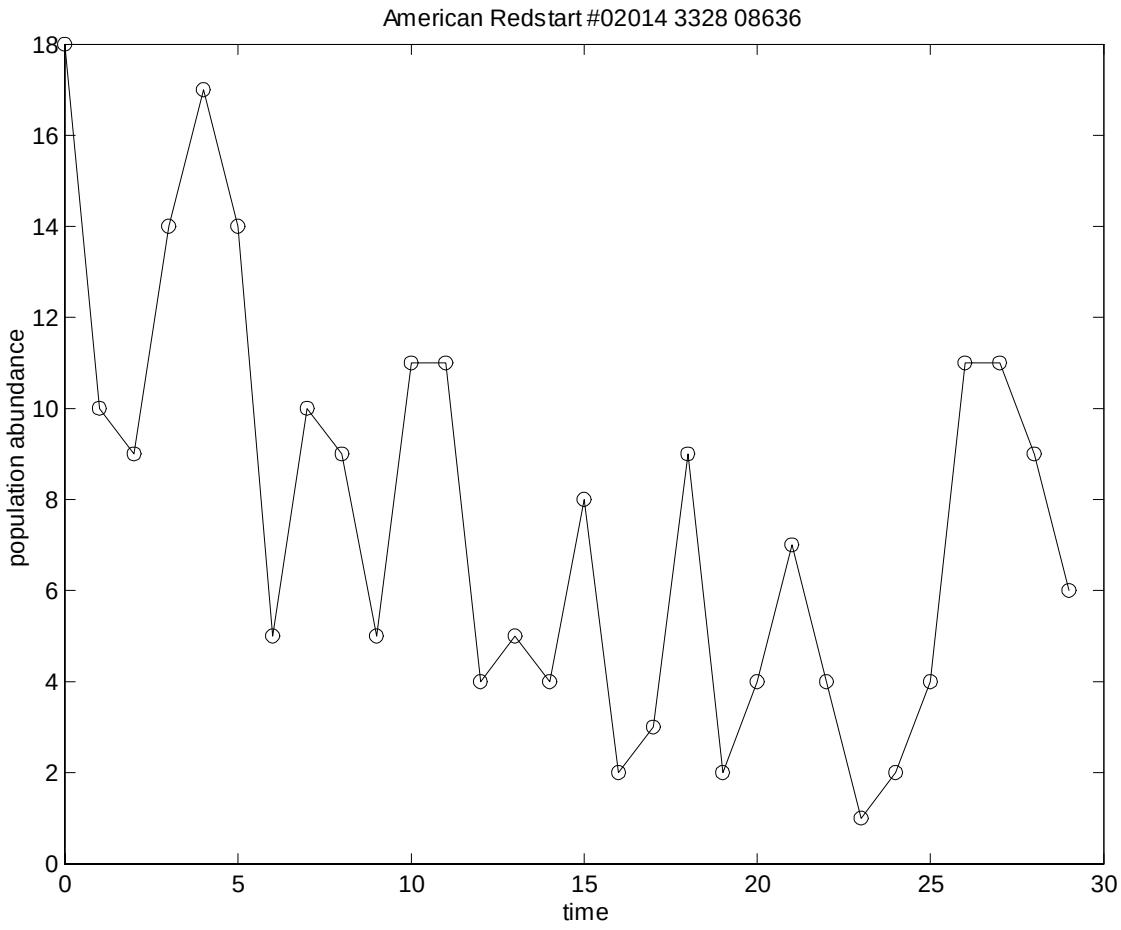
$$N_t = g(N_{t-1}, \theta)$$

where N_t is population abundance at time t
θ is a vector of parameters

Data:

American Redstart BBS # 02012 3336 08545
02014 3328 08636


American Redstart #02012 3336 08545
population abundance
time
45
40
35
30
25
20
15
10
5
0
5
10
15
20
25
30


American Redstart #02014 3328 08636
population abundance
time
0
2
4
6
8
10
12
14
16
18
0
5
10
15
20
25
30

1. OVERVIEW: CONNECTING ECOLOGICAL MODELS WITH TIME SERIES DATA

Approach: convert deterministic population models into stochastic time series models (explicitly model fluctuations)

A. Process noise

Types: demographic, environmental, catastrophic, etc.
ex. environmental

$$N_t = g(N_{t-1}, \theta) \qquad \text{(deterministic)}$$

$$\ln N_t = \ln g(N_{t-1}, \theta) + E_t \quad \text{(stochastic)}$$

where E_t is a random noise process; typical assumption is that $E_t \sim$ normal(0, σ^2) and E_1, E_2, E_3, ... are uncorrelated.

Notes:

- N_0, N_1, N_2, ... are *dependent*

- conditional distribution of $\ln N_t$ given $N_{t-1} = n_{t-1}$ is normal($\ln g(n_{t-1}, \theta)$, σ^2)

Observations: n_0, n_1, n_2, ..., n_q

Likelihood:

$$L\left(\theta, \sigma^2\right) \;=\; f\left(n_1 \middle| n_0\right) f\left(n_2 \middle| n_1\right) \cdots f\left(n_q \middle| n_{q-1}\right)$$

where

$$f\left(n_t \middle| n_{t-1}\right) \;=$$

$$\left(\sigma^2 2\pi\right)^{-1/2} \exp\left[-\frac{\left(\ln n_t - \ln g(n_{t-1}, \theta)\right)^2}{2\sigma^2} \right]$$

ML estimates of parameters in θ minimize:

$$\text{CSS} \;=\; \sum_{t=1}^{q} \left[\ln n_t \;-\; \ln g(n_{t-1}, \theta)\right]^2$$

conditional sum of squares

B. Observation (sampling) error

$$N_t = g(N_{t-1}, \theta)$$

$$Y_t = N_t + F_t$$

where $F_t \sim$ normal(0, τ^2) and F_0, F_1, F_2, ... are uncorrelated.

Notes:

- $N_t = h(t, \theta)$ is deterministic solution trajectory
- Initial pop. size $N_0 = n_0$ is an unknown model parameter
- Y_0, Y_1, ..., Y_q are *independent*

Observations: y_0, y_1, y_2, ..., y_q

Likelihood:

$$L\left(\theta, \tau^2, n_0\right) \;=\; f(y_0) f(y_1) \cdots f(y_q)$$

where

$$f(y_t) \;=$$

$$\left(\tau^2 2\pi\right)^{-1/2} \exp\left[-\frac{\left(y_t - h(t,\theta)\right)^2}{2\tau^2} \right]$$

ML estimates of parameters in θ minimize:

$$\text{TSS} \;=\; \sum_{t=0}^{q} \left[y_t \;-\; h(t,\theta) \right]^2$$

trajectory sum of squares

C. Combining process noise and observation error

$$\ln N_t \;=\; \ln g(N_{t-1}, \theta) \;+\; E_t$$

$$Y_t \;=\; N_t \;+\; F_t$$

"state space model"

Notes:

- Observations Y_0, Y_1, ..., Y_q are not just *dependent*, they are also *not* Markov
- Usually, likelihood function (a repeated integral) cannot be written in simple form
- Various approaches: likelihood via numerical simulation, Bayesian, etc (reviews by de Valpine 2002 *Bulletin of Marine Science*, and Clark and Bjørnstad 2004 *Ecology*)
- Parameter estimates (especially of σ^2 and τ^2) tend to be *biased* and *confounded*

2. THE MODEL

A. The process model

Population abundance is assumed to change according to a discrete-time, stochastic Gompertz model. The Gompertz growth process takes the density dependence term to be proportional to $\ln N_{t-1}$:

$$N_t = N_{t-1}\exp(a + b \ln N_{t-1} + E_t) .$$

Here a and b are constants, and E_t has a normal distribution with mean 0 and variance σ^2, written $E_t \sim \text{normal}(0, \sigma^2)$. Also, E_1, E_2, ... are assumed to be uncorrelated.

Let $X_t = \ln N_t$. On the logarithmic scale,

$$X_t = a + cX_{t-1} + E_t .$$

Here $c = (b + 1)$. Note: X_t is a first-order autoregressive process (AR(1) process).

B. Properties of the process model

• If $c < 1$, then the probability distribution for X_t approaches a *stationary distribution* as t becomes large:

$$X_\infty \sim \text{normal}\left(\frac{a}{1-c}, \frac{\sigma^2}{1-c^2}\right).$$

The stationary distribution for $N_\infty = \exp(X_\infty)$ is a *lognormal distribution*.

• If $c = 1$, then the model for X_t is a discrete-time version of *Brownian motion with drift*. The corresponding model for N_t is a discrete-time, stochastic model of exponential population growth (or decline). This is the density-independent population growth model studied by Dennis et al. (1991 *Ecological Monographs*).

C. Model with process noise and sampling error

Let Y_t denote the *estimated logarithmic* population abundance (estimated value of X_t). The error is assumed to be normally distributed. Thus the full model is:

$$X_t = a + cX_{t-1} + E_t\,,$$

$$Y_t = X_t + F_t\,.$$

Here $E_t \sim$ normal$(0, \sigma^2)$, $F_t \sim$ normal$(0, \tau^2)$, and the random errors/noises are assumed free of auto- or cross-correlations. The model implies that the sampling error inherent in estimating N_t is *lognormal*. The model is a *state-space model* with an underlying, unobserved process X_t and an observed process Y_t. The parameter τ^2 is the variance of the log-scale estimation error.

D. Properties of the model with process noise plus sampling error

• If $c < 1$, then the probability distribution for Y_t approaches a *stationary distribution* as t becomes large:

$$Y_\infty \sim \text{normal}\left(\frac{a}{1-c}, \frac{\sigma^2}{1-c^2} + \tau^2\right).$$

• If $c = 1$, then the model for Y_t is a discrete-time version of error-corrupted Brownian motion with drift. The model represents a discrete-time, stochastic model of exponential population growth (or decline) with lognormal sampling error. This is the model studied by Holmes (2001 *Proceedings of the National Academy of Sciences USA*) and Holmes and Fagan (2002 *Ecology*). They proposed a variance regression method for estimating parameters.

3. THE LIKELIHOOD FUNCTION: PROCESS NOISE PLUS SAMPLING ERROR

A. Multivariate normal likelihood

It can be shown that the observations Y_0, Y_1, Y_2, ..., Y_q have a joint multivariate normal distribution, provided Y_0 arises from the stationary distribution, with:

$$\mathrm{E}(Y_t) \;=\; \frac{a}{1-c}\,,$$

$$\mathrm{V}(Y_t) \;=\; \frac{\sigma^2}{1-c^2} \;+\; \tau^2\,,$$

$$\mathrm{Cov}(Y_t, Y_{t+s}) \;=\; \frac{\sigma^2}{1-c^2}c^{|s|}\,.$$

The likelihood function is the multivariate normal pdf, evaluated at the data $\mathbf{y} = [y_0, y_1, ..., y_q]'$:

$$L(a, c, \sigma^2, \tau^2) \;=$$

$$\left(\frac{1}{(2\pi)^{(q+1)/2}|\mathbf{V}|^{1/2}}\right)\exp\left[-\frac{1}{2}(\mathbf{y}-\boldsymbol{\mu})'\mathbf{V}^{-1}(\mathbf{y}-\boldsymbol{\mu})\right].$$

Interestingly, the likelihood function is identical to that of an AOV mixed effects model with repeated measures. SAS PROC MIXED can be “tricked” into calculating parameter estimates!

The AOV model: one subject (fixed intercept), with repeated measures on the subject (having AR(1) covariance structure), and random time effect. SAS program is appended with these notes.

B. The Kalman filter

Like the process-noise-only case, the likelihood $L(a, c, \sigma^2, \tau^2)$ for the model with process noise and sampling error can be decomposed into a product of univariate normal pdfs. However, the process Y_t is *not* a Markov process: that is, given $Y_{t-1} = y_{t-1}$, the distribution of Y_t (or any future value of the process) *does* depend on any and all values of the process prior to time $t-1$. The pdf for Y_t, given $Y_{t-1} = y_{t-1}$, $Y_{t-2} = y_{t-2}$, ..., $Y_0 = y_0$ is that of a normal distribution with mean m_t and variance ${v_t}^2$ that are computed recursively using the history of the observations:

$$f(y_t \,|\, y_0, y_1, ..., y_{t-1})$$

$$= \left({v_t}^2 2\pi\right)^{-1/2} \exp\left[-\frac{(y_t - m_t)^2}{2{v_t}^2}\right].$$

The recursion relationships for m_t and ${v_t}^2$ are

$$m_t = a + c\left[m_{t-1} + \frac{v_{t-1}^2 - \tau^2}{v_{t-1}^2}(y_{t-1} - m_{t-1})\right],$$

$${v_t}^2 = c^2 \frac{v_{t-1}^2 - \tau^2}{v_{t-1}^2}\tau^2 + \sigma^2 + \tau^2 .$$

If the initial population is assumed to arise from the stationary distribution, the recursions are initiated at the stationary mean and variance: $m_0 = a/(1-c)$, ${v_0}^2 = [\sigma^2/(1-c^2)] + \tau^2$. The pdf for Y_0 is that of the stationary normal distribution:

$$f(y_0) = \left({v_0}^2 2\pi\right) \exp\left[-\frac{(y_0 - m_0)^2}{2{v_0}^2}\right].$$

The recursion expressions for m_t and ${v_t}^2$ are contained in a set of general equations known as the *Kalman filter*. Derivation of the expressions is straightforward; the derivation uses repeated applications of properties of the bivariate normal distribution.

With the conditional normal pdfs in hand, the likelihood function is thus

$$L(a, c, \sigma^2, \tau^2) =$$

$$f(y_0)f(y_1 \mid y_0)f(y_2 \mid y_0, y_1) \cdots f(y_q \mid y_0, y_1, ..., y_{q-1})$$

$$= (2\pi)^{-(q+1)/2}\left(v_0^{\,2} v_1^{\,2} \cdots v_q^{\,2}\right)^{-1/2} \times$$

$$\exp\left[-\frac{1}{2}\sum_{t=0}^{q} \frac{(y_t - m_t)^2}{v_t^{\,2}} \right].$$

4. REML ESTIMATION USING FIRST DIFFERENCES (*RE*STRICTED *M*AXIMUM *L*IKELIHOOD)

A. First differences

First differences are defined as:

$$W_t \;=\; Y_t \;-\; Y_{t-1}$$

for $t = 1, 2, ..., q$. Then $W_1, W_2, ..., W_q$ have a joint multivariate normal distribution with

$$\mathrm{E}(W_t) \;=\; 0$$

$$\mathrm{V}(W_t) \;=\; \frac{2\sigma^2}{1-c^2}(1-c) \;+\; 2\tau^2$$

$$\mathrm{Cov}(W_t, W_{t+1}) \;=\; -\,\frac{\sigma^2}{1-c^2}(1-c)^2 \;-\; \tau^2$$

$$\mathrm{Cov}(W_t, W_{t+s}) \;=\; -\,\frac{\sigma^2}{1-c^2}(1-c)^2 c^{|s|-1}$$

B. Likelihood function for REML

The data are $w_1 = y_1 - y_0$, $w_2 = y_2 - y_1$, ..., $w_q = y_q - y_{q-1}$. The unknown parameters are c, σ^2, τ^2 (a is eliminated in the distribution of the differences). The likelihood function is denoted $L(c, \sigma^2, \tau^2)$:

$$\mathbf{w} = [w_1, w_2, ..., w_q]'$$

$$L(c, \sigma^2, \tau^2) =$$

$$\left(\frac{1}{(2\pi)^{q/2} |\mathbf{\Phi}|^{1/2}} \right) \exp\left(-\frac{1}{2} \mathbf{w'} \mathbf{\Phi}^{-1} \mathbf{w} \right)$$

C. ML estimate of a, with the elements of V known (i.e fixed at REML values):

$$\widehat{a} = (1-c)\,\frac{\mathbf{j}'\mathbf{V}^{-1}\mathbf{y}}{\mathbf{j}'\mathbf{V}^{-1}\mathbf{j}}\,.$$

5. EXAMPLES

A. Data sets

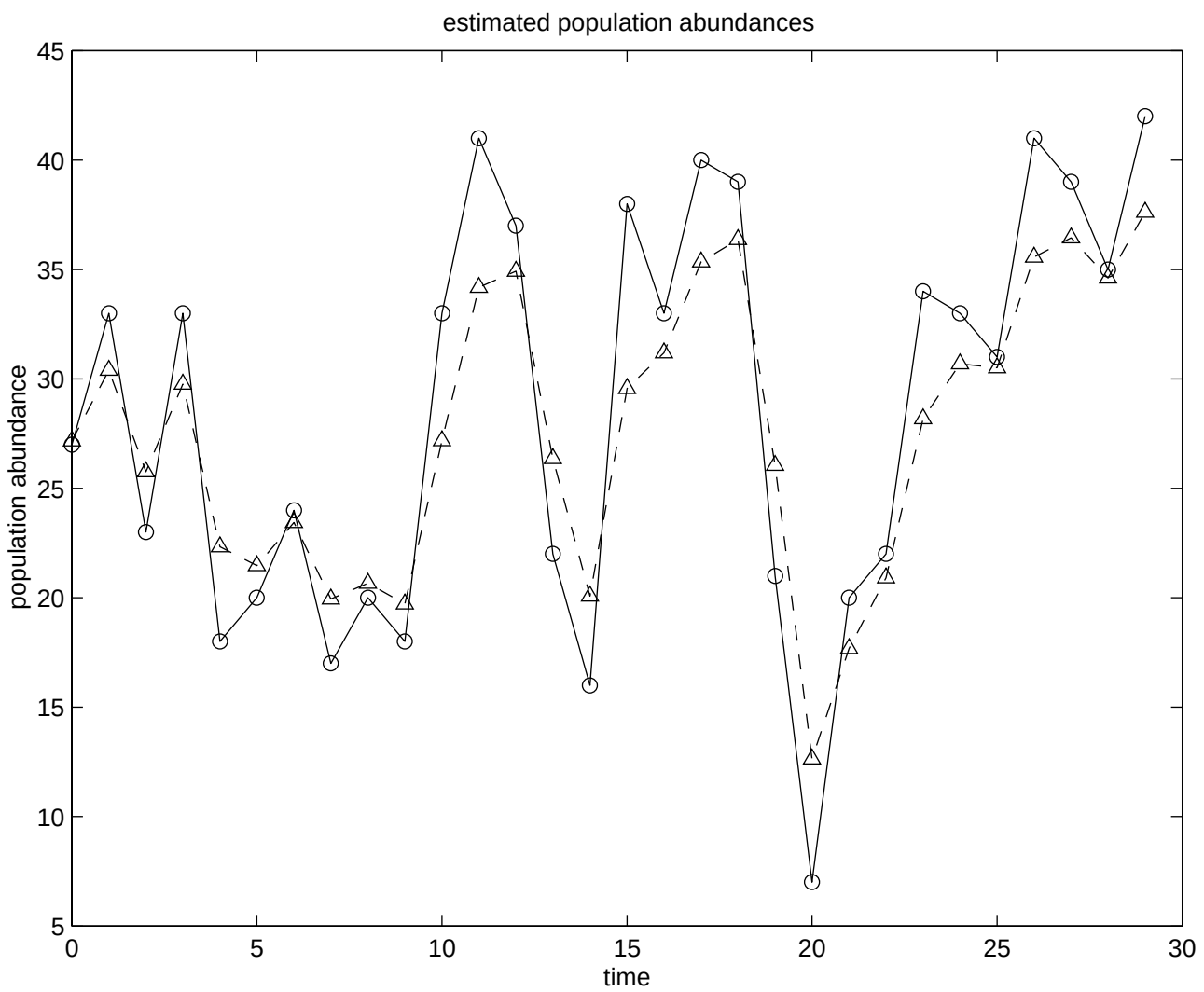
Breeding Bird Survey: American Redstart (2 locations)

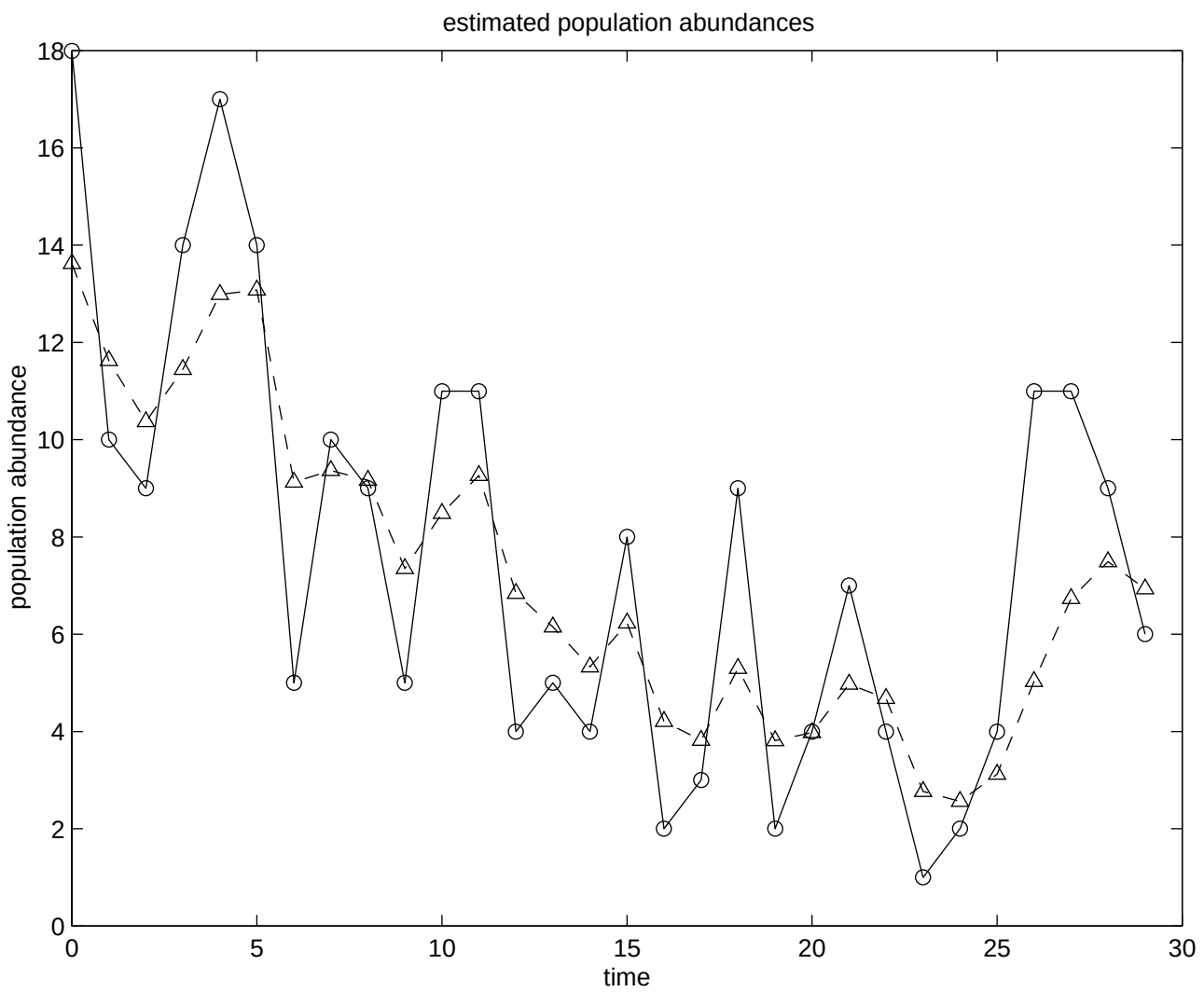
Simulation

B. Simulated properties of parameter estimates

ML

REML


estimated population abundances
population abundance
time
45
40
35
30
25
20
15
10
5
0
5
10
15
20
25
30


estimated population abundances
population abundance
time
0
2
4
6
8
10
12
14
16
18
0
5
10
15
20
25
30

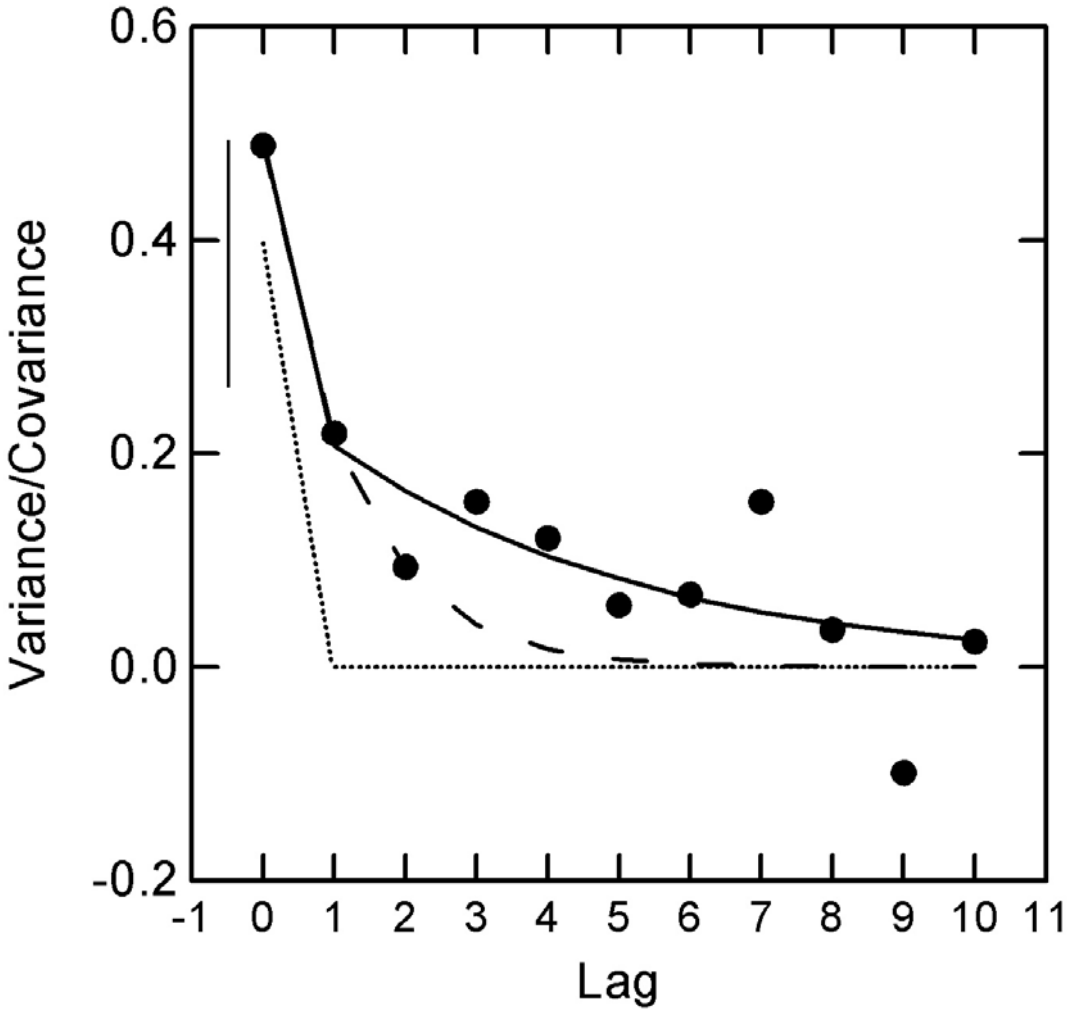


Figure 2.

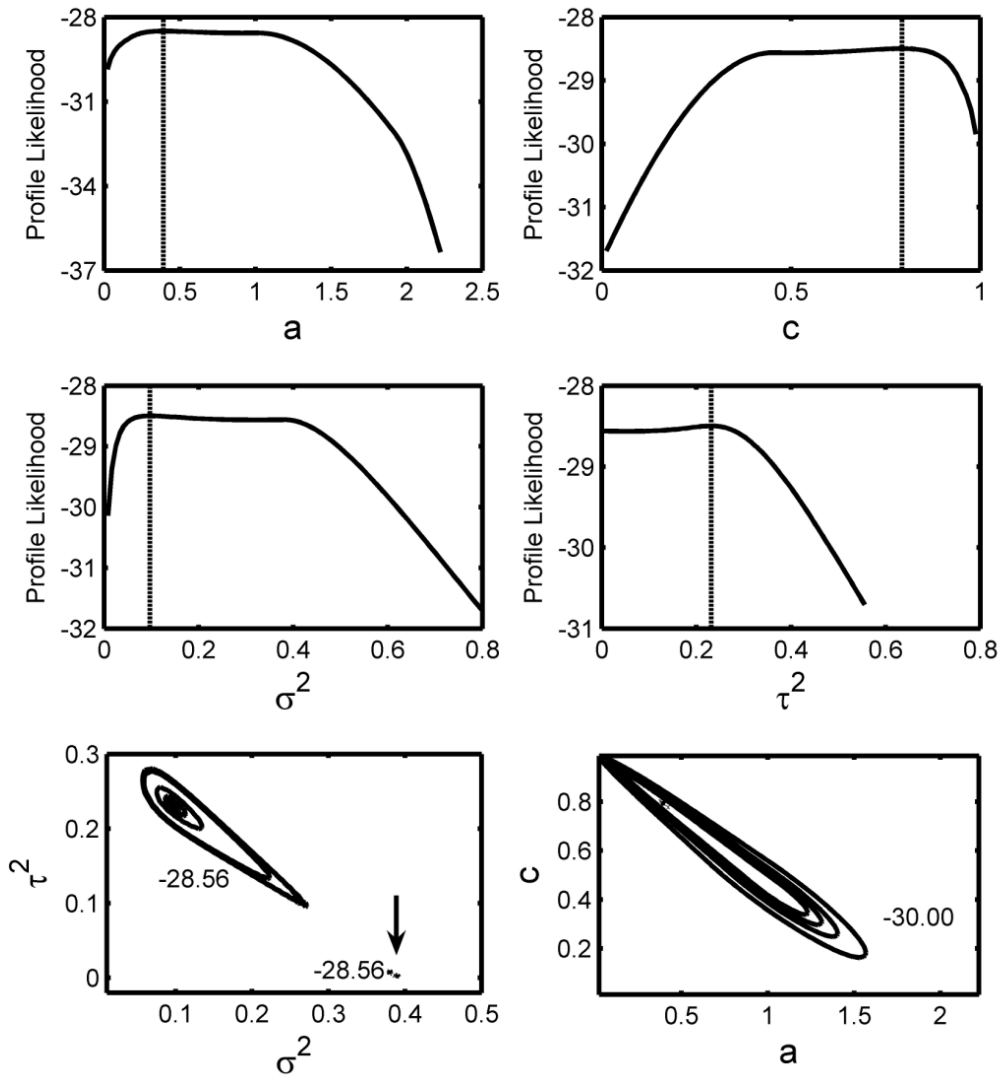


Figure 3.

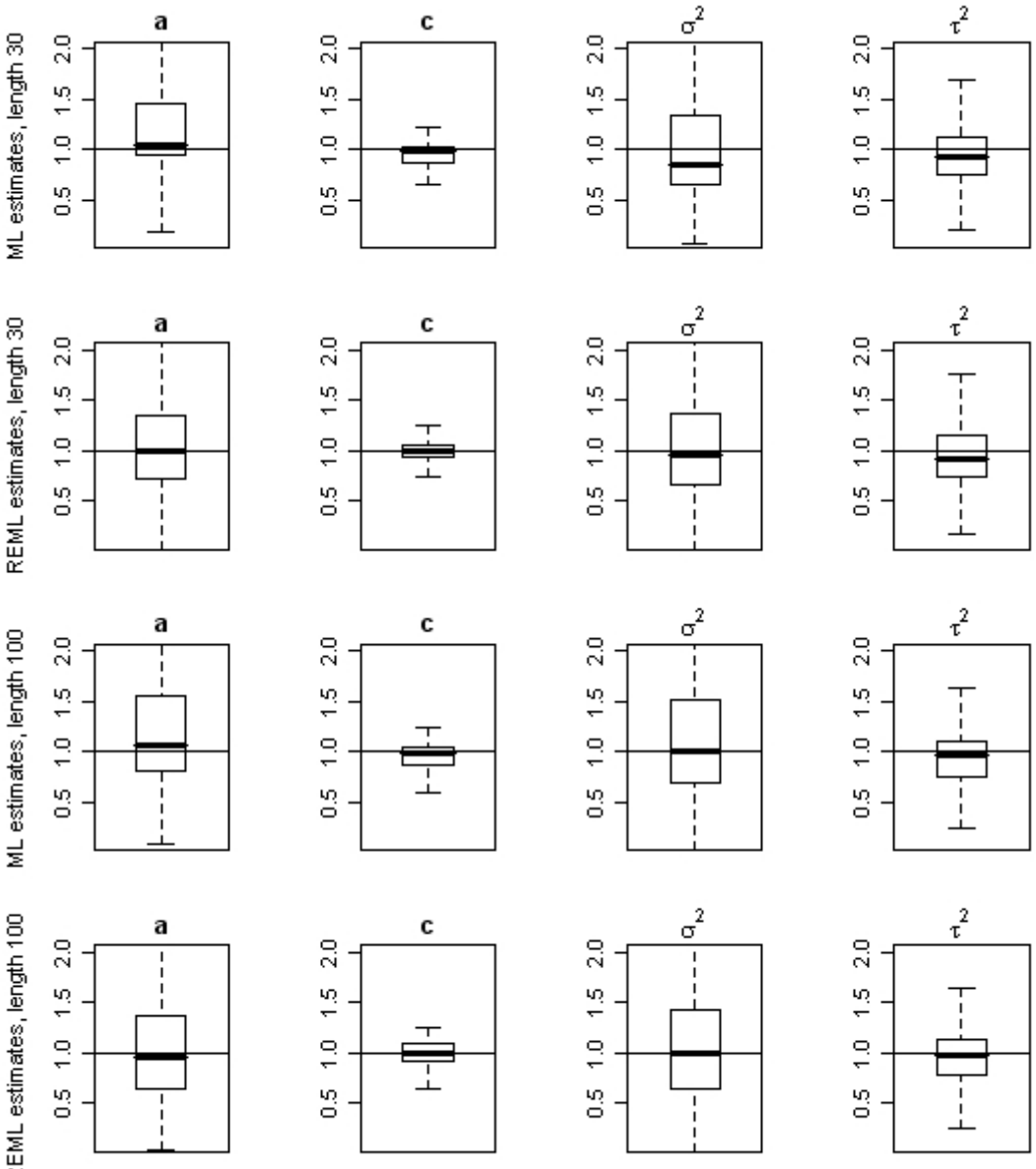

ML estimates, length 30
REML estimates, length 30
ML estimates, length 100
REML estimates, length 100
a
c
σ^2
τ^2
0.5
1.0
1.5
2.0

Figure 4.

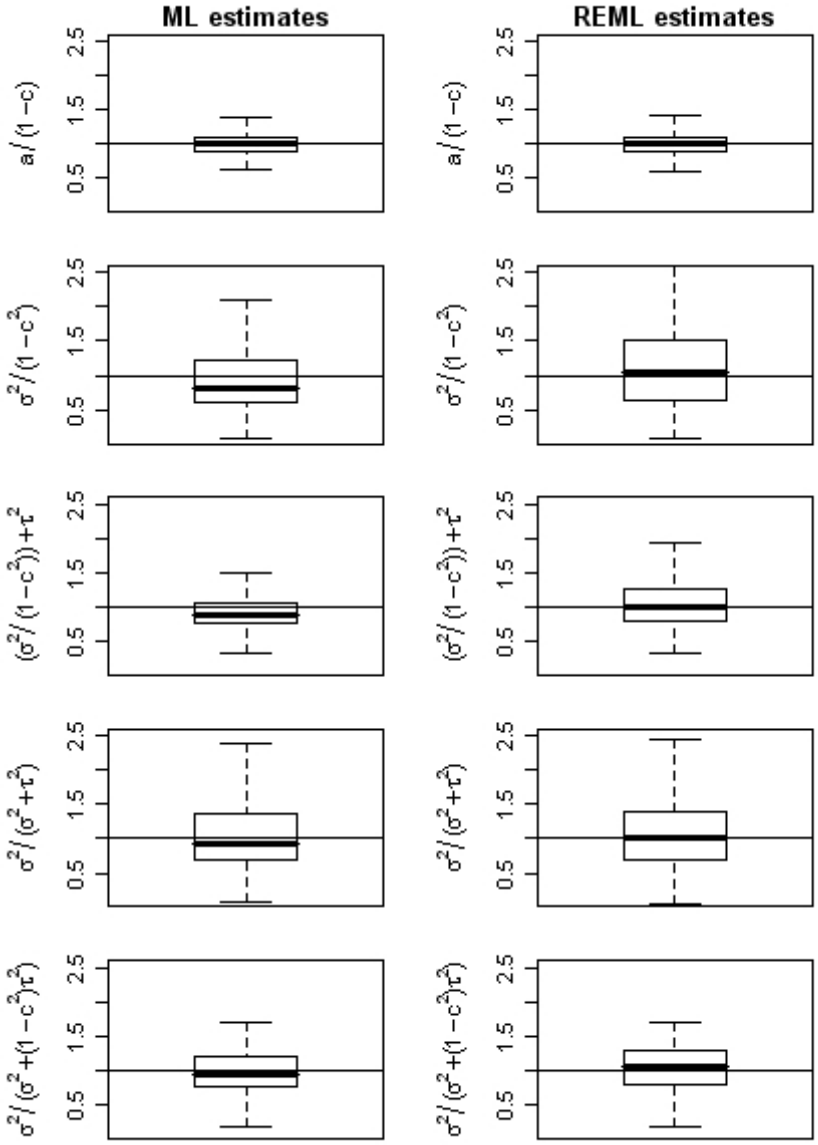

ML estimates
REML estimates
a/(1−c)
σ²/(1−c²)
(σ²/(1−c²))+τ²
σ²/(σ²+τ²)
σ²/(σ²+(1−c²)τ²)
0.5
1.5
2.5

Figure 5.

6. DISCUSSION POINTS

• There *is* information in population time-series data for jointly estimating density dependence, process noise, and observation error, and a variety of modeling approaches (of varying computational complexity). Estimation is tricky and needs hands-on attention. Linear Gaussian model can be *adapted*, via transforming to logarithmic scale, for more realistic ecological uses.

• ML estimation for the linear Gaussian model (= Kalman filter) requires care but works reasonably well (simulations). Likelihood is *routinely* ridge-shaped & multimodal. The proper solution of the likelihood equation (giving statistically consistent estimates) frequently is *not* the *global* likelihood maximum. Published ML simulations for other models which did not accomodate multimodality are suspect.

• REML works reasonably well (preliminary simulations); seems to fix the some of the ML bias problems.

- Lognormal sampling model is a realistic model of ecological sampling under heterogeneous conditions: Poisson “mixture” models typically have *constant coefficients of variation* (as a function of size of population being sampled).

- Gompertz process model has held its own in comparative density dependence model-fitting studies (usually fits as well as logistic/Ricker/Bev-Holt).

- SAS program!

Supplement: SAS program for calculating parameter estimates for the Gompertz state space model.

Dennis et al.: Estimating density dependence, process noise, and observation error. Ecology.

```
/*---------------------------------------------------------------------------*/
/*       PARAMETER ESTIMATES FOR THE GOMPERTZ STATE SPACE MODEL              */
/*  SAS program to calculate parameter estimates for the Gompertz state-     */
/*  space model, using time series population abundance estimates.  The      */
/*  GSS model is given by                                                    */
/*        X(t) = a + cX(t-1) + E(t)                                          */
/*        Y(t) = X(t) + F(t)                                                 */
/*  where X(t) is the natural logarithm of population abundance N(t)         */
/*  (assumed unknown), Y(t) is the observed value of X(t), E(t) has a        */
/*  normal distribution with mean 0 and variance sigmasquared, F(t) has      */
/*  a normal distribution with mean 0 and variance tausquared (with no       */
/*  auto- or cross-correlations in E(t) and F(t)), and t is time.  Unknown   */
/*  model parameters are a, c, sigmasquared, tausquared.  Data to be         */
/*  input into the program consist of observed or estimated population       */
/*  abundances O(0), O(1), O(2), .., O(q) (estimates of N(0), N(1), etc.),   */
/*  along with the values of t.  The program currently does not accomodate   */
/*  missing observations.                                                    */
/*                                                                           */
/*  Program transforms data to logarithmic scale:  Y(t) = ln[O(t)].  The     */
/*  program recasts the model as a linear mixed model with:  (1)  repeated   */
/*  measures on one subject having an AR(1) covariance structure, and (2)    */
/*  a random effect due to time (considered as a categorical variable).      */
/*  The random effect represents the extra variance component due to ob-     */
/*  servation error and produces a "nugget" (augmented main diagonal) in     */
/*  the var-cov matrix for the observations.                                 */
/*                                                                           */
/*  The example data are from the North American Breeding Bird Survey        */
/*  (record # 0214332808636, American Redstart), and correspond to Table 1   */
/*  and Figure 1 of Dennis et al. (200X).                                    */

options nocenter;
data in;
input observed time;
y = log(observed);
cards;
 18 0
 10 1
  9 2
 14 3
 17 4
 14 5
  5 6
 10 7
  9 8
  5 9
11 10
11 11
 4 12
 5 13
```

```
 4 14
 8 15
 2 16
 3 17
 9 18
 2 19
 4 20
 7 21
 4 22
 1 23
 2 24
 4 25
11 26
11 27
 9 28
 6 29
;
proc mixed  method=ml alpha=.05 noitprint noinfo data = in;

/*  Restricted maximum likelihood (REML) is the default estimation method  */
/*  in PROC MIXED (SAS System for Windows Version 9.1).  Delete "method=   */
/*  ml" (or substitute "method=reml") in list of options in the above      */
/*  "proc mixed" statement for REML estimation if desired.  Also, the      */
/*  value of alpha, for asymptotic 100(1-alpha)% confidence intervals for  */
/*  parameters, can be changed in the option list.                         */


class time;
model y= ;
random time;
repeated / type=ar(1) subject=intercept;
estimate 'intercept' intercept 1;

run;
quit;
/*---------------------------------------------------------------------------*/



/*---------------------------------------------------------------------------*/
/*           ANNOTATED OUTPUT OF THE GSS ESTIMATION PROGRAM                  */
/*                                                                           */
/*  The following output was generated using SAS/STAT software, Version    */
/*  9.1 of the SAS System for Windows. Copyright (c) 2002-2003 SAS         */
/*  Institute Inc.  SAS and all other SAS Institute Inc. product or        */
/*  service names are registered trademarks or trademarks of SAS Institute */
/*  Inc., Cary, NC, USA.                                                   */

The SAS System

The Mixed Procedure

             Class Level Information

Class    Levels    Values

time         30    0 1 2 3 4 5 6 7 8 9 10 11 12
```

```
                  13 14 15 16 17 18 19 20 21 22
                  23 24 25 26 27 28 29


                  Covariance Parameter Estimates

Cov Parm     Subject      Estimate     Alpha       Lower       Upper

time                        0.2315      0.05     0.08439      1.7944
AR(1)        Intercept      0.7934      0.05      0.1859      1.4010
Residual                    0.2625      0.05     0.08314      3.9119

/*  In the "Estimate" column, the value listed for "time" is the estimate  */
/*  of tausquared, for "AR(1)" is c, and for "residual" is                 */
/*  sigmasquared/(1 - c*c) (the stationary variance of X(t)).  "Lower"     */
/*  and "Upper" columns give boundaries of asymptotic 95% confidence       */
/*  intervals for the parameters, based on inversion of the information    */
/*  matrix (Hessian of the log-likelihood).  The CIs have unknown coverage */
/*  properties for small- and moderate-lengthed time series.  The CI for   */
/*  c, along with the large value of the stationary variance upper bound,  */
/*  might suggest that the density independent model (c=1) is a viable     */
/*  model for the data.  A SAS program to fit the density independent      */
/*  state space model was provided as a supplement to Staples et al.       */
/*  (2004).                                                                */


           Fit Statistics

-2 Log Likelihood               57.0
AIC (smaller is better)         65.0
AICC (smaller is better)        66.6
BIC (smaller is better)         70.6

/*  These "fit statistics" can be used for model selection, in comparison  */
/*  to other models fitted to the data.                                    */

                          Estimates

                        Standard
Label        Estimate       Error      DF    t Value    Pr > |t|

intercept      1.9021      0.2645      29       7.19      <.0001

/*  The estimate listed for "intercept" is the estimate of a/(1-c), the    */
/*  stationary mean of X(t).  The "Standard Error" is an asymptotic        */
/*  estimate based on the information matrix.  The t-test for the null     */
/*  hypothesis that a/(1-c)=0 is nonsensical in the context of the model.  */
/*                                                                         */
/*  Thus for the example BBS data, the ML parameter estimates are:         */
/*                                                                         */
/*            tausquared = 0.2315                                          */
/*            c = 0.7934                                                   */
/*            sigmasquared = 0.2625*(1 - c*c) = 0.09726                    */
/*            a = 1.9021*(1-c) = 0.3930                                    */
/*                                                                         */
/*  Compare with ML estimates, Table 1, Dennis et al. (200X).  Small       */
/*  numerical differences are due to roundoff error in SAS.                */
```

```
/*------------------------------------------------------------------------*/


/*------------------------------------------------------------------------*/
/*                          REFERENCES                                    */
/*                                                                        */
/*  Dennis, B., J. M. Ponciano, S. R. Lele, M. L. Taper, and D. F.        */
/*    Staples.  200X.  Estimating density dependence, process noise, and  */
/*    observation error.  Ecology XX:XXX-XXX, with supplement in          */
/*    Ecological Archives XXXX-XXX-XX.                                    */
/*                                                                        */
/*                                                                        */
/*  Staples, D. F., M. L. Taper, and B. Dennis.  2004.  Estimating        */
/*    population trend and process variation for PVA in the presence of   */
/*    sampling error.  Ecology 85:923-929, with supplement in Ecological  */
/*    Archives E085-025-S1.                                               */
/*                                                                        */
/*------------------------------------------------------------------------*/
```

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http://www.cnrhome.uidaho.edu/fishwild/dennis

This presentation:
http://www.webpages.uidaho.edu/~brian/reprints/kalmanESA2006.pdf

The paper:
Dennis, B., J.M. Ponciano, S.R. Lele, M.L. Taper, D.R. Staples. 2006. Estimating density dependence, process noise, and observation error. *Ecological Monographs*, in press