Oikos 118: 1940–1946, 2009
doi: 10.1111/j.1600-0706.2009.17839.x,

Subject Editor: John Vucetich. Accepted 15 June 2009

Research

A better way to estimate population trends

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Estimation of a population trend from a time series of abundance data is an important task in ecology, yet such estimation remains logistically and conceptually challenging in practice. First, the extent to which unequal intervals in the time series, due to missing observations or irregular sampling, compromise trend estimation is not well-known. Furthermore, the predominant trend estimation method (loglinear regression of abundance data against time) ignores the possibility of process noise, while an alternative method (the 'diffusion approximation') ignores observation error in the abundance data. State-space models that account for both process noise and observation error exist but have been little used. We study an adaptation of the exponential growth state-space (EGSS) model for use with missing data in the time series, and we compare its trend estimation to the status quo methods. The EGSS model provides superior estimates of trend across wide ranges of time series length and sources of variation. The performance of the EGSS model even with half of the counts in the time series missing implies that trend estimates may be improved by diverting effort away from annual monitoring and towards increasing time series length or improving precision of the abundance estimates for years that data are collected.

Estimating a population's rate of change, or trend, is a fundamental challenge in basic and applied ecology. Population trend can be defined as the average change in log-abundance per unit of time (Dennis et al. 1991, Link and Sauer 1998). Although trend can be estimated from age or stage-specific vital rates, it is commonly estimated from abundance data collected over time via enumeration, abundance estimates or abundance indices (Morris et al. 2002, Marsh and Trenham 2008). Ecological time series models, derived from abundance data over time for single populations, can incorporate additional factors such as environmental covariates (Dennis and Otten 2000), observer-related covariates (Link and Sauer 1997), and density dependence (James et al. 1996, Brook and Bradshaw 2006, Dennis et al. 2006). However, data to support such analyses are often not readily available (e.g. covariates are mostly absent in the nearly 5000 population time series maintained by the Global Population Dynamics Database; see Fagan et al. (2001), Inchausti and Halley (2001) and Brook et al. (2006)). Therefore, exponential growth models lacking covariates are most commonly used for trend estimation in applications (Sabo et al. 2004).

Ecologists interested in estimating simple exponential trend from abundance data typically face four primary challenges. First, the lengths of time series are short, often consisting of only 5–10 time steps (e.g. years) and seldom more than 30. Second, time series often have unequal time intervals, arising from observations missing due to funding, logistical or personnel constraints. Third, variance in the abundance data arises from an often unknown combination of environmental noise and observation or estimation error in the abundance data themselves. Finally, different statistical methods exist to estimate trend for time series abundance data, with little guidance as to relative performance.

At present two methods that accommodate unequal intervals in the time series are most commonly used to estimate trend (Table 1). The oldest, and predominant, method is a log-linear regression of counts against time, where the slope of the regression gives the population trend (Caughley 1977, Gerrodette 1987, Eberhardt and Simmons 1992). We refer to this as the exponential growth observation error (EGOE) model, because it tacitly assumes that variability in the data arises purely as sampling or 'observation error', with the population itself governed by deterministic exponential growth (Supplementary material Appendix 1).

A second method for estimating exponential trend parameters assumes that the population is censused (i.e. no observation error), and that variability in abundances is entirely due to growth rate fluctuations caused by environmental variability or 'process noise' (Dennis et al. 1991, Lande et al. 2003). The method takes abundance on the logarithmic scale to be described by a Brownian motion diffusion process with a constant drift rate. We refer to this as the exponential growth process noise (EGPN) model.

Table 1. Examples of typical applications of EGOE (exponential growth observation error), EGPN (exponential growth process noise), and EGSS (exponential growth state space) methods to estimate trend parameters for animal populations.

Application	Taxa	Citation
EGOE (log-linear approach)		
Determine contemporary declines	koala	Phillips 2000
Assess declines	common frog	Meyer et al. 1998
Determine population growth rate	wildebeest, buffalo, zebra	Grange et al. 2004
Estimate growth rate for an endangered species	wallaby	Fisher et al. 2000
Estimate population growth rate	ibex	Largo et al. 2008
EGPN (diffusion approximation approach)		
Predict extinction probabilities	35 rare breeding bird species	Gaston and Nicholls 1995
Predict extinction probabilities	mount Graham red squirrel	Buenau and Gerber 2004
Predict extinction probabilities	cape mountain zebra	Watson et al. 2005
EGSS (state-space approach)		
Estimate population growth and extinction parameters	can. sea otter and Yellowstone grizzly bear	Lindley 2003
Determine how spatial correlations affect PVA	chinook salmon	Hinrichsen 2009

Interestingly, EGPN estimates have been used widely to estimate the trend parameter for population viability analysis (PVA) but rarely for simply describing the trend of populations (Table 1).

A recently developed third method for estimating trend uses a stochastic 'state-space' exponential growth model that assumes both observation error and environmental process noise (Holmes 2001, Lindley 2003, Staples et al. 2004, Dennis et al. 2006). We term this the exponential growth state space (EGSS) model. Estimation is based on the insight that the EGSS model can be written as a linear mixed model (Staples et al. 2004), thereby making calculations possible through software for analysis of variance with mixed random and fixed effects. The EGOE and EGPN models occur as limiting special cases when the corresponding variance parameters approach zero. More recently, Staudenmayer and Buonaccorsi (2006) scale the observations in the linear mixed model framework to allow for unequally spaced time intervals. That the EGSS model can accommodate missing data is not well known in ecological practice.

In this paper we explain how to obtain maximum likelihood (ML) and restricted maximum likelihood (REML) parameter estimates for the EGSS model based on the scaled observations of Staudenmayer and Buonaccorsi (2006). We then use computer simulations to compare the performance of EGOE, EGPN and EGSS approaches for estimating population trend. We document the statistical properties of point and interval estimates of the trend parameter when each of the three models are applied to data generated by stochastic exponential growth with varying time series lengths, numbers of missing values in the time series, and ratios of observation error versus process noise. In light of our findings of substantial robustness of trend estimates under the EGSS model, we provide recommendations for future biomonitoring study design and analysis.

Methods

We use lower case to denote data as well as constants, and upper case to denote the stochastic process (random variable) that generates data. So, we write $n(0)$, $n(t_1)$, …, $n(t_q)$ for a recorded time series of population abundances at times 0 ($=t_0$), t_1, …, t_q, and $N(t)$ for a random population abundance at time t with some associated probability distribution. 'Abundance' refers to numbers, biomass, or density, and may be determined from a complete census, an estimate, or an index that reliably and proportionally tracks population fluctuations.

The three models we consider are based on familiar deterministic exponential growth:

$$n(t) = n_0\lambda^t \quad (1)$$

Here $n(t)$ is population abundance at time t, with $n_0 = n(0)$, and λ is a positive constant indicating an increasing ($\lambda > 1$) or decreasing ($\lambda < 1$) population. On the logarithmic scale:

$$\ln n_t = \ln n_0 + (\ln \lambda)t \quad (2)$$

A general stochastic version of the exponential growth model with both process noise and observation error takes the form of a state space model with an unobserved population component and a component representing the observed or estimated abundance values. Let $X(t)$ be the unobserved log-abundance of the population (now assumed to be a stochastic process) at time t and $Y(t)$ be the estimated or observed value of $X(t)$. We write the EGSS model as:

$$dX(t) = (\ln \lambda)dt + dB(t) \quad (3)$$

$$Y(t_i) = X(t_i) + F_i \quad (4)$$

Here $dB(t) \sim \text{normal}(0, \sigma^2 dt)$, and $F_i \sim \text{normal}(0, \tau^2)$. The term $dB(t)$ is a random perturbation representing the process noise (environmental variability), and F_i represents the observation error, assumed to have no auto- or cross-correlations. The quantity $\mu = \ln\lambda$ is the expected change of $X(t)$ in one time unit; it is our trend parameter (see Supplementary material Appendix 1 for more details). The model defines $X(t)$ as a Brownian motion process with drift rate μ and represents a generalization of the earlier EGSS version to continuous time. Equation 3 provides a simple recipe for simulating an increment of a population trajectory over a small time interval dt as an increment of deterministic exponential growth on the log scale perturbed by a normal random quantity; an entire population trajectory would be constructed by accumulating such increments. Sampling times

t_0 (=0), t_1, ..., t_q are not necessarily equally spaced. Special cases of the EGSS model are EGOE ($\sigma^2 = 0$) and EGPN ($\tau^2 = 0$). Additional properties of the EGOE, EGPN, and EGSS models, along with details of ML and REML parameter estimation, are given in Supplementary material Appendix 1.

For each set of conditions evaluated, we simulated 5000 replicate time series from the EGSS model with specified μ (from -0.2 to 0.2) and variance parameters (from 0 to 0.25 for both σ^2 = process noise and τ^2 = observation error). The duration of the simulated time series ranged from 5 to 50, bracketing from well below the minimum duration deemed acceptable for estimating population trend to approximately the longest time series currently available (Bence 1995, Holmes 2004).

The log-population abundances X(t), (t = 1, 2, ...) were generated with the discrete time autoregressive model:

$$X(t) = X(t-1) + \mu + E_t \tag{5}$$

where $E_t \sim \text{normal}(0, \sigma^2)$. The autoregressive model has statistical properties identical to the continuous time model (Eq. 3) evaluated at discrete times. Observation errors were then added to each X(t):

$$Y(t) = X(t) + F_t \tag{6}$$

where $F_t \sim \text{normal}(0, \tau^2)$. The simulated population values were calculated as exp(Y(t)). Also, if a simulated population decreased to ≤ 2, it was deleted and simulated again in order to limit estimation to populations that do not become extinct before the requisite number of observations were obtained. The size of X(0) was always ln(1000), and the initial value of Y(t) was randomly chosen by $Y(0) = \ln(1000) + F_0$. (Results were insensitive to changes in X(0); Supplementary material Appendix 2). To explore the effects of missing observations in the time series, we removed randomly a fixed number of the abundance data from each simulated time series (the first and last observations were not allowed to be removed to keep the length of the survey constant). Comparing the estimates of trend from the same time series under complete and missing data isolates the effect of missing observations from other effects such as process stochasticity.

To each simulated time series, we fitted the EGOE and EGPN models using ML and the EGSS model using REML. We created box plots of point estimates of μ across the 5000 replicates for each of the three methods (EGOE, EGPN, and EGSS). We also explored the coverage of the interval estimators of μ by plotting the percent of 5000 replicates whose confidence intervals (CI) actually included μ. (See Supplementary material Appendix 1 for details on confidence interval construction). Because it may be equally problematic, in an applied context, for a CI of $\hat{\mu}$ to either over- or under- include the true μ, we use a 50% CI to provide symmetry for assessing over and underestimation. For example, a model reaching 40% coverage can be interpreted as equally biased to another model with 60% coverage. By contrast, a more traditional 90% or 95% CI would obscure comparisons because of the asymmetry of over- and under-inclusion. All simulations and computations were performed with R 2.8.1 for Windows (code available in Supplementary material Appendix 1).

Results

The same general patterns were found for all combinations of input trend parameters (positive, zero, or negative μ, with a range of process noise and observation error). Therefore, we only present detailed results for one scenario, a small true population decline with comparatively large process and sampling variance ($\mu = -0.02$, $\sigma^2 = 0.01$, $\tau^2 = 0.01$). (Results of other combinations of input parameters can be found in Supplementary material Appendix 2).

All three models provided relatively unbiased estimates of μ regardless of the ratio of process noise (σ^2) to observation error (τ^2) (Fig. 1A). Additionally, estimates of μ were robust to time series lengths from 5 to 50 years (Fig. 1B) and the number of missing observations in the time series (Fig. 1C). Although the additional parameter in the EGSS model might lead to an expectation of higher variability in the estimate of μ compared to the EGOE and EGPN models, we found no evidence for this under any conditions. For all 3 methods, variability increased with the ratio of process variation to observation error (Fig. 1A) and as the time series length decreased (Fig. 1B), but was mostly unaffected by missing observations (Fig. 1C).

While performance of the three models was good relative to bias in the estimates of μ, there were substantial differences in confidence interval coverage (Fig. 2). Confidence intervals constructed using the EGOE model were good (i.e. μ was contained in about 50% of the intervals) only when process noise was absent or small in relation to observation error (σ^2/τ^2 ratio near 0; Fig. 2A). However, as the σ^2/τ^2 ratio increased, confidence interval coverage became $<50\%$ indicating that the intervals were too narrow. The coverage was improved by decreasing the time series length (Fig. 2B). Similarly, coverage also improved as the time series became less complete (i.e. more missing values; Fig. 2C). Improved coverage for smaller samples often happens when estimates are statistically inconsistent (i.e. converge to the wrong values asymptotically).

Confidence intervals constructed using the EGPN model had excellent coverage when process noise overwhelmed observation error (e.g. $\sigma^2/\tau^2 > \sim 5$; Fig. 2A). However, when process noise was minimal relative to observation error ($\sigma^2/\tau^2 < \sim 1$), confidence intervals constructed using the EGPN model became too wide ($>>50\%$). As with the EGOE model, coverage improved (slightly) with decreased time series length (Fig. 2B) and more missing data (Fig. 2C).

Empirical coverage of confidence intervals constructed using the EGSS model tended to be less than 50% (CIs too narrow) but only slightly so as coverage rarely strayed more than 10% from the nominal value (Fig. 2). Coverage was consistently better than EGOE and EGPN models across all combinations of process noise and observation error, time series lengths, and number of missing observations. Unlike EGOE and EGPN, coverage improved

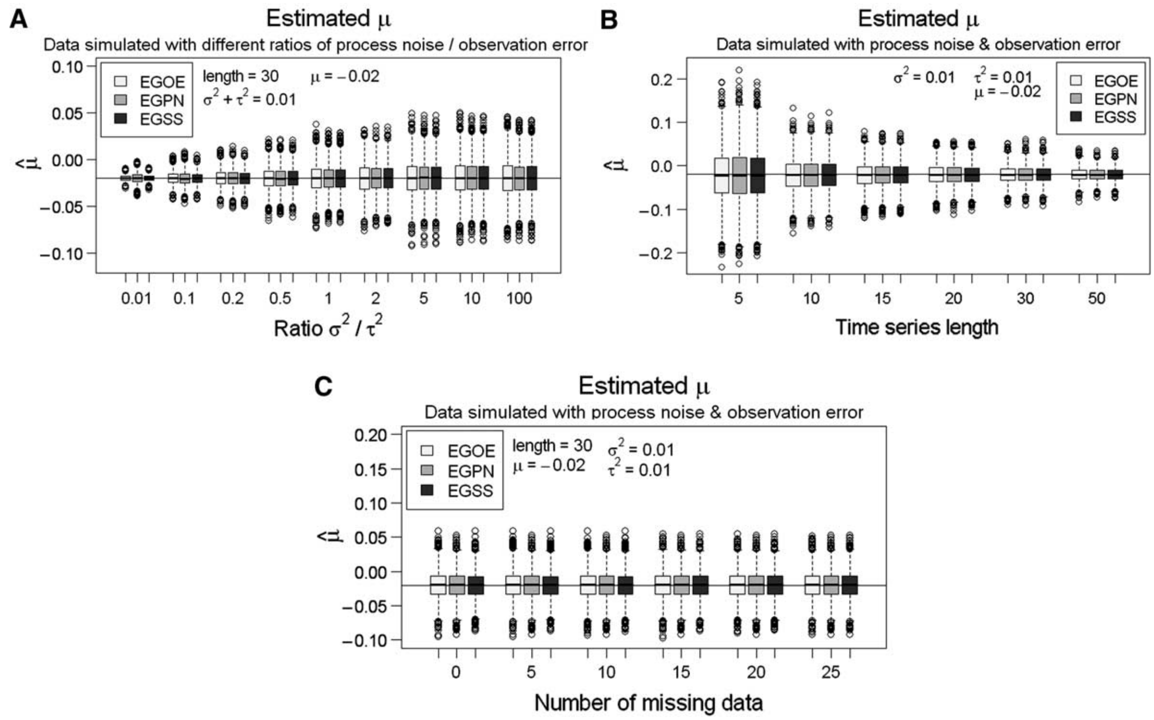

Figure 1. Estimation of trend (μ) using three estimators of exponential growth from time series of abundance data: EGOE (exponential growth with observation error), EGPN (exponential growth with process noise), EGSS (exponential growth state space). The horizontal line shows the true $\mu = -0.02$ (error bars extend to the most extreme data point in 5000 simulations which is no more than 1.5 times the interquartile range from the box). Performance is evaluated under varying conditions: (A) ratio of process (σ^2) to sampling (τ^2) variance ranging from 0.01 (trivial process variance) to 100 (trivial sampling variance); (B) time series length from 5 to 50 time steps; (C) for a time series of 30 time steps, missing abundance data ranging from none to 25 missing out of 30. Results here are typical of a range of values of μ, σ^2, τ^2 and time series lengths (Supplementary material Appendix 2).

with increasing time series length (Fig. 2B) and decreased number of missing values (Fig. 2C).

Discussion

The status quo for monitoring simple exponential trend in wild populations is to analyze the time series data with methods that assume either no process noise (EGOE model) or no observation error (EGPN), and to strive to collect abundance data each year. We recommend two fundamental shifts to this paradigm. First, we encourage the use of the EGSS model, extended to accommodate missing values (Supplementary material Appendix 1). Secondly, we suggest that researchers need not be reluctant to skip sampling in some years if the saved sampling effort could be focused on improving the remaining abundance estimates or on increasing time series length.

For a wide range of realistic conditions we found EGSS to be a superior estimator, performing well even with short time series, missing data, and a range of process and sampling variance. The most popular method for estimating exponential trend (i.e. EGOE) performed the worst of the three methods evaluated, with strongly biased small confidence intervals when process noise became even 1/10 as large as observation error. From an applied perspective this means that using EGOE will impart false confidence in what could be a qualitatively wrong trend, inferring for example that a population is declining when it is actually increasing or stationary. This underscores the fact that the exponential growth model underlying EGOE is deterministic, assuming that none of the variance arises from environmental noise, so CIs will only attain the claimed coverage when process variance is lacking. Also disturbing was our finding that increasing the time series length or ensuring that no abundances are missing from the time series did not improve coverage of the EGOE estimate of trend; in fact the coverage only got worse.

The EGPN, commonly called the diffusion approximation, has received critical evaluation as an estimator of exponential trend parameters in PVA predictions based on abundance data (Holmes and Fagan 2002, Elderd et al. 2003, Holmes 2004). We find that the EGPN performs reasonably well in estimating trend as long as the ratio of process to observation variance is greater than 5. However, because the EGPN model assumes that all variation in the time series comes from process noise (Supplementary material Appendix 1), the presence of substantial observation error leads to confidence intervals of trend that are too wide. The resulting management inferences would too often include 0 and thereby miss actual increases or decreases. Like EGOE, coverage of trend estimates with EGPN becomes worse (although only slightly) with longer or more complete time series.

In most cases a time series will be influenced by both process and observation error. The EGSS both estimates

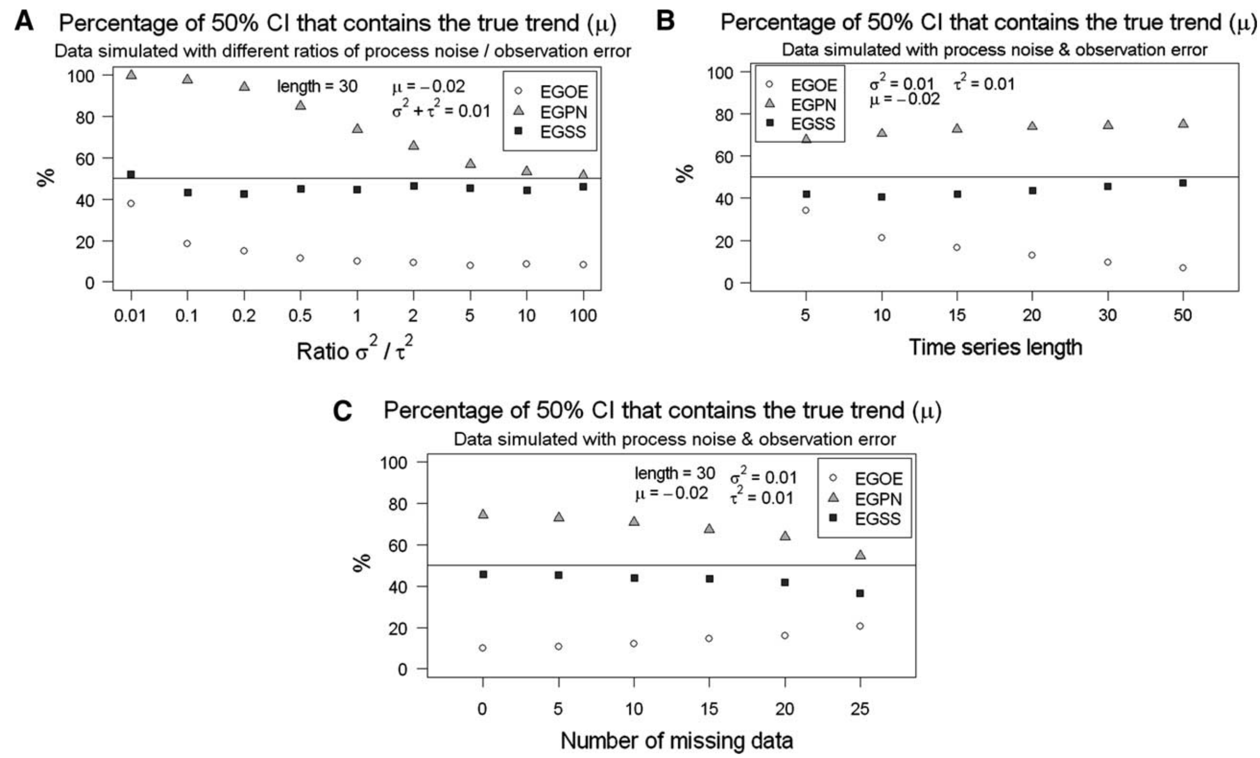

Figure 2. Estimation of coverage of confidence intervals of trend (μ). Scenarios are similar to Fig. 1, except that dependent variable is the percentage (of 5000 simulations) of trend 50% CI's that contains the true trend. The horizontal line shows the expected 50% coverage.

and incorporates both forms of variation. If observation error predominates, EGSS performs only slightly worse than EGOE, and if process noise predominates, EGSS is only slightly worse than EGPN. Except for those rare cases where an investigator knew for certain that a time series was entirely dominated by either process noise or observation error, the EGSS should be used to estimate trend. Furthermore, coverage of the CI for trend under the EGSS model improves with time series length. It also improves with fewer missing observations in the time series.

The EGSS model, as adapted for missing data, performed well for trend estimation even with approximately half of the abundance estimates missing from the time series. This implies that in some cases the collection of data every time step (e.g. year) may be less important than the quality of abundance estimates and length of time series. In other words, exponential trend estimation may well be improved if the money spent on data collection each consecutive year could instead be used to collect fewer, better estimates of abundance over the same total time duration, or to extend the time duration of the monitoring farther. Such a strategy is in stark contrast to many monitoring programs in management agencies, which strive to collect data every year to keep the time series complete, even if the data are poor (Hauser et al. 2006).

As for the chronic question of 'How much data is enough?', the minimum data requirements for trend parameter estimation are four data points for the EGSS and three for the EGPN and EGOE. Our simulations showed that the EGSS performed well (i.e. unbiased estimate of μ and proper confidence intervals) with as short a time series as 10 and approximately half of the abundances missing; this implies that a 10-year time series with five data points could be considered a minimum for trend estimation using EGSS under the conditions we considered, and assuming that the density independent model is adequate. However, a better approach to determining sample design would calculate confidence intervals for μ for data simulated with trial parameter values under different time series lengths.

We emphasize that we were by no means comprehensive in our assessment of various ways that exponential population growth rate or trend might be estimated from count data (Pradel 1996, Clark and Bjornstad 2004, Ryding et al. 2007). For example, much more detailed trend analyses derived from log-linear models exist (Thomas and Martin 1996, Link and Sauer 1998, Bart et al. 2003, Sæther and Engen 2004), and for linear state-space models in the presence of autocorrelated environmental variables in density dependent populations (Lindén and Knape 2009). Our goal was to focus on the simple case where a series of abundance data without covariates for a single location are assessed for estimating trend and calculating an associated CI. This scenario is widely used for introducing students to the practice of estimating growth rate from field data, and is also applicable to many surveillance monitoring programs and population assessments (Table 1).

Trend analyses of monitoring data will likely proliferate with continued human-caused stresses on plants and animals (Balmford et al. 2003, Marsh and Trenham 2008), and yet both our review of first principles of model construction and our simulations indicate that the most widely used method of log-linear regression of abundance data against time (i.e. EGOE) performs poorly if variance in the time series includes meaningful amounts of process variation. We find that a state space model (EGSS) was superior to either the EGOE or EGPN for the same length of sampling. The robustness of the EGSS model to the absence of more than half of the counts in the time series implies that in some cases improved estimates of trend and its variance may be obtained by skipping some consecutive years in a monitoring program and putting the money saved into extending the time series or improving estimates for each year that data are collected.

Acknowledgements – We thank the SERDP Program (D.o.D.) for funding; LSM thanks NSF (DEB-0415604). We appreciate reviews of various drafts of this ms by Elizabeth Crone, Dan Doak, Oz Garton, Justin Gude, Cynthia Hartway and Matthew Kauffman.

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Supplementary material (available online as Appendix O17839 at www.oikos.ekol.lu.se/appendix). Appendix 1. Description of three exponential growth models allowing unequal intervals in the time series, with computer program in R. Appendix 2. Results from some other parameter combinations.