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Statistical methods to correct for observation error in a density-independent population model

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Abstract. The problem of observation error in assessing the dynamics of populations over time has received increasing attention of late. Of particular interest has been a density-independent dynamic model, which allows a trend and is commonly employed in population viability analysis (PVA). Most of the recent work in this area has focused on assessing the impact of the observation error and on finding corrected estimators, primarily under normal models with the observation errors assumed to have a constant variance. This paper provides a comprehensive overview of statistical methods for this problem and evaluates them through simulations. This includes the development and assessment of simple and practical ways to obtain standard errors and confidence intervals for the basic parameters in the model and functions of them, such as the intrinsic rate of increase or the probability of eventual extinction. We allow for unequally spaced data and possibly changing observation error variances, and we also discuss how to employ standard errors that often accompany the estimated abundances. Both likelihood techniques under normality and methods allowing non-normal observation errors are discussed, and we describe how the various likelihood-based techniques can be implemented using standard mixed-model software, such as PROC MIXED in SAS. The projection technique we use to handle functions of the basic parameters is also valuable when there is no observation error. The methods are motivated and illustrated using data for grizzly bears, Whooping Cranes, California Condors, and Puerto Rican Parrots. We present a simulation experiment to evaluate the performance of some of the methods.

Key words: confidence intervals; dynamic; measurement error; mixed models; observation error; population viability analysis; random walk; standard errors; time series.

INTRODUCTION

The role of observation/measurement error in the modeling of population dynamics has attracted considerable attention of late (e.g., de Valpine and Hastings 2002, Calder et al. 2003, de Valpine 2003, Clark and Bjornstad 2005) with the random walk with drift model being of particular interest. The random walk model, commonly employed in population viability analysis, allows for a trend in the population over time resulting from a density-independent dynamic model. More precisely with N_t denoting population abundance at time t and $X_t = \log(N_t)$, the model assumes that $X_t - X_{t-1} = \mu + \varepsilon_t$ where ε_t is normally distributed with mean 0 and variance σ^2 . This corresponds to a model for the abundance with growth parameter $r = \mu + \sigma^2/2$ and “finite rate of increase” or trend parameter $\lambda = e^r$. This model has also been referred to as the diffusion approximation model (Dennis et al. 1991, Holmes 2004, Staples et al. 2004) and is a stochastic Malthusian model. The goal in these problems is estimation of the basic parameters, μ and σ^2 , and functions of them based

on a series of observed/estimated abundances. Of particular interest are the growth parameter, the trend, the probability of eventual extinction and probabilities about abundance at future points in time. The conclusions of such an analysis can carry important implications for management policies, especially in the case of endangered species. Dennis et al. (1991) and Morris and Doak (2002), among others, provide extensive discussion of this model and treat many of the statistical issues in the absence of observation error.

With observation error, only an estimate of the abundance rather than the abundance itself is available. The effects of observation error on analyses which ignore it are now fairly well understood (e.g., Ludwig 1999, Meier and Fagan 2000, Holmes 2001, 2004, Holmes and Fagan 2002, Parysow and Tazik 2002, Buonaccorsi et al. 2006). There has been recent progress in developing and comparing different estimators that correct for observation error, but techniques for inference (i.e., standard errors, confidence intervals, and so on) have not been fully developed. This paper provides a comprehensive discussion of inferential issues under a fairly rich class of models, including allowance for the fact that the observation error variances can be changing over time. We examine in detail both likelihood and moment-based methods for inference, address ways in

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which to make use of estimated standard errors that often accompany the estimated abundances, illustrate the methods using data from four species, and evaluate the techniques via simulations.

The predominant approach to correct for observation error has been to assume that the errors on estimated log-abundance are normal with mean 0 and constant variance, in which case all of the parameters can be estimated from the estimated log abundances. Staples et al. (2004) and Dennis et al. (2006) apply likelihood methods for estimation and inference and demonstrate how, for equally spaced data, estimation can be carried out with mixed-models software (e.g., PROC MIXED in SAS). In their examples, however, confidence limits were only provided for the mean parameter μ . Building from developments in Staudenmayer and Buonaccorsi (2006), we extend these methods in a number of ways. First, we show that in the likelihood setting one can make use of a mixed-model approach, and related software, even if the data are unequally spaced. We demonstrate how to obtain confidence intervals for the main parameters μ , σ^2 , and the observation error variance via this mixed-model approach. Moment-based estimators, which can be computed in closed form and allow for more general assumptions than strict normality, are also developed. We then propose a simple but powerful technique for computing confidence intervals for other quantities, such as the finite rate of increase or the probability of extinction, which are functions of the primary parameters μ and σ^2 . A Bayesian approach to this problem is also possible, as described by Lindley (2003), who combined a state-space formulation with Bayesian techniques for inferences; see Calder et al. (2003) and Clark and Bjornstad (2004) for more general treatments on Bayesian methods in treating observation error in population dynamic models. We do not consider the Bayesian approach further for reasons given in the discussion.

The other important area we explore is the use of so-called “pseudo methods” which exploit standard errors which might accompany the estimated abundances or log-abundances. (Here we use the term pseudo as it is used in reference to first estimating “nuisance parameter,” in this case the observation error variances; see for example Gong and Samaniego [1981].) Such standard errors come from direct estimates of sampling error at each time, such as if there are counts from several locations that are averaged to estimate abundance, but can also be used to give an estimate of sampling variance. There are two benefits to not throwing away that information. First, it can lead to more efficient and stable estimators (i.e., generally narrower confidence intervals). In addition, this approach also easily allows the observation error variance to realistically change over time, which commonly occurs as a result of either changing sampling effort or dependence of the variability on the underlying abundance. This problem has received limited attention. Inferential techniques paralleling those described in the preceding paragraph are

presented for the pseudo-estimators, and we discuss the challenges and limitations in handling unequal observation error variances.

We begin with a description of the models for the true values and the observation errors. A brief summary is then given of methods which ignore observation error followed by detailed developments of likelihood and moment-based techniques for inference when correcting for observation error. Methods for getting confidence intervals on important functions of the basic parameters (e.g., intrinsic rate of increase) are then described. The methods are illustrated using data on grizzly bear, Whooping Cranes, California Condors, and the Puerto Rican Parrot, all of which were presented and discussed by Staples et al. (2004). These are displayed in Fig. 1, which shows estimated log-abundance and difference in log-abundances. See *Examples* for further discussion. Simulations are presented followed by general discussion.

MODELS

Following up on notation presented at the start of the paper, the model can be written in terms of true log-abundance values as

$$X_t|x_{t-1} = x_{t-1} + \mu + \varepsilon_t \quad (1)$$

where the notation $|x_{t-1}$ means “given $X_{t-1} = x_{t-1}$.” This distinguishes the actual value of log-abundance which occurs, x_t , from the random variable X_t (with a similar distinction for n_t and N_t). In terms of abundance $N_t|n_{t-1} = e^{\mu}n_{t-1}\delta_t$, where $\delta_t = e^{\varepsilon_t}$ is distributed lognormal, so with E denoting expected value,

$$E(N_t|n_{t-1}) = \lambda n_{t-1} \quad (2)$$

where $\lambda = e^{\mu+(\sigma^2/2)}$ is the “finite rate of increase” or trend.

As in Dennis et al. (1991), we allow data to be collected at possibly unequally spaced time points $t_0 < t_1 < t_2 < \dots < t_q$. With X_i denoting the random abundance at time t_i , Eq. 1 leads to

$$W_i = X_i - X_{i-1} = \tau_i\mu + \varepsilon_i \quad (3)$$

for $i = 1, \dots, q$, where $\tau_i = t_i - t_{i-1}$ is the time between observations $i - 1$ and i . The ε_i , referred to as process errors, are assumed to be independent and normally distributed with mean 0 and variance $V(\varepsilon_i) = \tau_i\sigma^2$.

Observation error models

Observation, or measurement, error arises from estimation of abundance through some type of sampling. The estimated abundance at time t_i is denoted by $\hat{N}_i$ and the estimated log-abundance by $\hat{X}_i$. Specification of an observation error model raises a number of questions, including: Is the model specified in terms of the estimated abundance or log-abundance? Does the observation error variance change over time? This can happen for at least two reasons; due to dependence of the variance on the underlying but unobserved true

FIG. 1. Plot of estimated log abundance and differences in estimated log abundance over time for four species. For the grizzly bears, the error bars are ± 2 estimated standard deviations of the observation error.

abundance or due to changes in sampling effort over time. Are the observation errors correlated? This correlation could result from the use of common sampling units at different time points, or result from observation errors depending on the underlying true abundances, which are themselves correlated over time.

A full discussion of the nature of the observation errors, which is both longer and more technical than is needed here, can be found in Buonaccorsi et al. (2006) and Staudenmayer and Buonaccorsi (2006). We refer the interested reader to those papers for complete details. Here, we will work under the assumptions that

$$\hat{X}_i = m + X_i + u_i \quad (4)$$

where $\hat{X}_i$ is the estimator of log-abundance at time t_i and, with Cov denoting covariance,

$$\begin{aligned} E(u_i) &= 0 & V(u_i) &= \sigma_{u(i)}^2 \\ \text{Cov}(u_i, u_j) &= 0 & \text{for } i \neq j. \end{aligned} \quad (5)$$

The quantity m represents bias in $\hat{X}_i$ as an estimator of the true log-abundance x_i and the last assumption assumes that the observation errors are uncorrelated. The assumptions of constant bias and uncorrelated observation errors can be relaxed (see Staudenmayer and Buonaccorsi 2006), but we will not do so here.

Almost all of the applications and methodological developments for this problem to date have made these simplifying assumptions. This will allow us to focus the discussion as changing bias and correlated observation errors introduce a suite of additional considerations that are beyond the scope of this paper.

The variance of u_i , denoted $\sigma_{u(i)}^2$, can contain components due to sampling error and, if present, variability due to dependence of the observation error variance on the underlying log-abundance X_i . The difference in estimated log abundances at time t_i is

$$\hat{W}_i = \hat{X}_i - \hat{X}_{i-1} \quad (6)$$

and from the preceding discussion,

$$\begin{aligned} E(\hat{W}_i) &= \tau_i \mu & V(\hat{W}_i) &= \tau_i \sigma^2 + \sigma_{u(i)}^2 + \sigma_{u(i-1)}^2 \\ \text{Cov}(\hat{W}_i, \hat{W}_{i+1}) &= -\sigma_{u(i)}^2 \end{aligned} \quad (7)$$

and $\text{Cov}(\hat{W}_i, \hat{W}_j) = 0$, if $|i - j| > 1$. These moments are the key for assessing the properties of naive estimators that ignore observation error and for developing correction techniques.

NAIVE ANALYSES

“Naive” approaches use the estimated log-abundances as if they were the true log-abundances, that is, as if

there were no observation errors. This leads to a standard linear model (see Dennis et al. 1991 and Morris and Doak 2002 for details) and the naive estimators of μ and σ^2 are

$$\hat{\mu}_{\text{naive}} = \sum_{i=1}^q \hat{W}_i / (t_q - t_0)$$

and

$$\hat{\sigma}_{\text{naive}}^2 = \sum_{i=1}^q (\hat{W}_i \tau_i^{-1/2} - \tau_i^{1/2} \hat{\mu}_{\text{naive}})^2 / (q - 1). \quad (8)$$

With equally spaced data, these are just the sample mean and sample variance of the W_i 's respectively.

Naive confidence intervals for μ and σ^2 (which are exact with no observation error and under normality) are

$$\hat{\mu}_{\text{naive}} \pm t_{1-\alpha/2, q-1} \text{SE}(\hat{\mu}_{\text{naive}}) \quad (9)$$

where

$$\text{SE}(\hat{\mu}_{\text{naive}}) = \hat{\sigma}_{\text{naive}} / q^{1/2}$$

and

$$\left[\frac{(q-1)\hat{\sigma}_{\text{naive}}^2}{\chi_{1-\alpha/2, q-1}^2}, \frac{(q-1)\hat{\sigma}_{\text{naive}}^2}{\chi_{\alpha/2, q-1}^2} \right] \quad (10)$$

respectively, where $t_{1-\alpha/2, q-1}$ is the 100(1 - $\alpha/2$)th percentile of the t -distribution with $q - 1$ degrees of freedom with a similar interpretation for $\chi_{1-\alpha/2, q-1}^2$ based on the chi-square distribution with $q - 1$ degrees of freedom.

Numerous authors have documented the impacts of observation errors on naive analyses which ignore it, either through simulations or analytically (see Meier and Fagan 2000, Holmes 2001, Buonaccorsi et al. 2006, Staudenmayer and Buonaccorsi 2006). Buonaccorsi et al. (2006) show that the observation error here generally leads to overestimation of λ in Eq. 2, the result of overestimation of σ^2 . This is in sharp contrast to simple linear regression where measurement error in the predictor usually leads to underestimation of the slope (see Carroll et al. 2006).

CORRECTING FOR OBSERVATION ERROR

Here we describe two general approaches to correcting for observation error. The first, which has dominated much of the literature uses only the estimated differences in log abundances; the $\hat{W}_1, \dots, \hat{W}_q$. The second technique comes under the general heading of pseudo methods, and utilizes the estimated standard errors which accompany the estimated abundances. Within each of these approaches either likelihood methods based on distributional assumptions or moment-based techniques can be employed.

Using the estimated log abundances only

Interestingly and unlike many other measurement error problems, it has been recognized that if the

observation error variance is constant, the parameters μ , σ^2 , and σ_u^2 can be estimated simultaneously from the estimated log-abundances alone with no further information about the observation errors. This is the result of correlations arising from the underlying dynamic model; see Eq. 7. Both likelihood- and moment-based approaches can be used.

Likelihood methods.—Suppose the W_i 's are normally distributed and that the observation errors are uncorrelated and normally distributed with constant observation error variance σ_u^2 . This leads to the $\hat{W}_i$'s being normally distributed, with mean, variance and covariances as given in Eq. 7 but with all $\sigma_{u(i)}^2$ equal to σ_u^2 . Using this model, in which μ , σ^2 , and σ_u^2 are all identifiable. Lindley (2003), Holmes (2004), and Staples et al. (2004) use either maximum likelihood (ML) or restricted maximum likelihood (REML) estimators for equally spaced data. We will utilize REML estimators, as Staples et al. did, since they generally lead to less biased estimates of variance components. For equally spaced data, Staples et al. (2004) recognized the advantage of a linear mixed-model formulation and used proc MIXED in SAS to obtain REML estimators for their examples. In their implementation of MIXED the two variance related parameters that are directly estimated are $-\sigma_u^2$ (the covariance of adjacent estimated differences) and $\sigma^2 + 2\sigma_u^2$ (the variance of an estimated difference). These estimates must be converted to get estimates of σ^2 and σ_u^2 and to get standard errors associated with the estimates of the variance components. This is easy since the conversions are linear, but it will be easier to directly parameterize in terms of the variances as we do below. Notice also that with this parameterization when converting one can get negative estimate of the variances components, which is not allowable. We also note that Staples et al. (2004) provided estimates but no standard errors or confidence intervals for the variance parameters, which is one of our main objectives.

The linear mixed-model approach can be extended to accommodate unequally spaced time points as shown by Staudenmayer and Buonaccorsi (2006) and discussed further in Appendix A. Further, as shown in Appendix C, PROC MIXED in SAS can be implemented to provide direct estimates and confidence intervals for the two variances. In addition since we parameterize directly in terms of the variances of interest we can (using suitable options) require nonnegative estimates of variances beforehand.

The REML estimators of the variance components will be denoted $\hat{\sigma}_{\text{REML}}^2$ and $\hat{\sigma}_{u, \text{REML}}^2$. The associated estimator of the mean, $\hat{\mu}_{\text{REML}}$, produced by most mixed-models software, is a generalized least squares (GLS) estimator (e.g., Eq. 12 in Staples et al. 2004 or Eq. 2.26 in Demidenko 2004) that uses estimates of the two variance components. Approximate standard errors of these REML estimators are based on the large sample theory for maximum likelihood estimates and can be

obtained from mixed-model software; see for example SAS Institute (1995) or Demidenko (2004) for analytical details on computation of the standard errors.

An approximate confidence interval for μ is given by

$$\hat{\mu}_{\text{REML}} \pm t(1 - \alpha/2, d) \text{SE}(\hat{\mu}_{\text{REML}}) \quad (11)$$

where d is an approximate degrees of freedom and $\text{SE}(\hat{\mu}_{\text{REML}})$ is the estimated standard error of $\hat{\mu}_{\text{REML}}$. There are various options for obtaining d . We use the Satterthwaite approach in our examples, although other choices can be made. An alternative for estimating μ is to use the naive estimator

$$\sum_{i=1}^q \hat{W}_i / (t_q - t_0)$$

which we now denote $\hat{\mu}_{\text{mom}}$ (since it is a moment estimator). While asymptotically it may be less efficient than the weighted REML estimator, it has the advantage of being exactly unbiased for any sample size (the REML estimator is not). Using Eq. 9 in Staudenmayer and Buonaccorsi (2006) the estimated standard error of $\hat{\mu}_{\text{mom}}$ is

$$\text{SE}(\hat{\mu}_{\text{mom}}) = \left[\frac{\hat{\sigma}_{\text{REML}}^2}{t_q - t_0} + \frac{2\hat{\sigma}_{u, \text{REML}}^2}{(t_q - t_0)^2} \right]^{1/2} \quad (12)$$

and the associated Wald confidence interval is $\hat{\mu}_{\text{mom}} \pm z_{1-\alpha/2} \text{SE}(\hat{\mu}_{\text{mom}})$.

There are multiple approaches available for obtaining confidence intervals on the variance components. Two, the Wald and chi-square-based intervals, are usually available from standard mixed-model analyses. To illustrate consider intervals for σ^2 , with parallel results for σ_u^2 . The first technique uses the Wald interval of the form

$$\hat{\sigma}_{\text{REML}}^2 \pm z_{1-\alpha/2} \text{SE}(\hat{\sigma}_{\text{REML}}^2). \quad (13)$$

The second approach utilizes a chi-square approximation for the estimated variance leading to the interval

$$\left[\frac{v\hat{\sigma}_{\text{REML}}^2}{\chi_{1-\alpha/2, v}^2}, \frac{v\hat{\sigma}_{\text{REML}}^2}{\chi_{\alpha/2, v}^2} \right] \quad (14)$$

where $v = 2\hat{\sigma}^4 / (\text{SE}(\hat{\sigma}^2))^2$ is an approximate degrees of freedom. Most of these intervals are produced by mixed-model software (e.g., SAS PROC MIXED). We will see in our examples, however, that the chi-square approach can produce odd results when the approximate degrees of freedom are small.

Under the assumptions of normality and constant observation error variance, one can also obtain confidence intervals using two more computationally intensive techniques; the parametric bootstrap or a profile-likelihood method.

For a general discussion of bootstrapping see Efron and Tibshirani (1993) and Manly (1997). Dennis et al. (1991) utilize the bootstrap in the random walk model

with no observation error. For $b = 1$ to B (large), the b th bootstrap sample, indexed by b , is generated as follows:

1) Generate true values. First set $X_{b0} = \hat{X}_0$ which uses the estimated log abundance at time 0 as the starting point for each bootstrap sample. The remaining true values are generated by $X_{bi} = X_{b,i-1} + \varepsilon_{bi}$ for $i = 1$ to q , where the ε_{bi} are independent and identically distributed as normal (i.i.d.) with mean 0 and variance $\hat{\sigma}^2$.

2) Generate error-prone measures. For $i = 0$ to q , $\hat{X}_{bi} = X_{bi} + u_{bi}$, where the u_{bi} are i.i.d. normal with mean 0 and variance $\hat{\sigma}_u^2$ and $\hat{W}_{bi} = \hat{X}_{bi} - \hat{X}_{b,i-1}$, for $i = 1$ to q .

Estimates are obtained for each of the B bootstrap samples, from which standard errors and confidence intervals can be obtained in standard ways. In our examples, we will use bootstrap confidence intervals based on the percentile method; for example, a 95% confidence interval uses the 2.5th and 97.5th percentiles. While BC_a (bias corrected and accelerated) bootstrap intervals are often preferred, further investigation is needed to address how to jackknife to obtain the acceleration constant in this setting.

We also obtain profile-likelihood confidence intervals under the normality assumptions; see, for example, Section 3.4 of Demidenko (2004) for details. For the variance components, we use the restricted log-likelihood, $l(\sigma^2, \sigma_u^2)$ and let $\hat{l}$ denote its maximized value, maximized under the constraint that the variance estimates are nonnegative. The profile likelihood confidence interval for σ_u^2 is $C_{\text{PL}}(\sigma_u^2) = \{c: -2P(c) \leq -2\hat{l} + z_{1-\alpha/2}^2\}$, where $P(c) = \max_{\sigma^2} l(\sigma^2, c)$, which is referred to as the profile-likelihood for σ_u^2 . We have expressed the interval in terms of $-2 \log(\text{likelihood})$ since this is the quantity reported in most mixed-models procedures. A profile likelihood confidence interval for σ^2 is obtained in a similar manner by swapping the roles of σ^2 and σ_u^2 . This method could also be used to get an interval for μ , but it would utilize the full likelihood (which is a function of μ , σ^2 , and σ_u^2) rather than the restricted likelihood.

Moment-based methods.—The likelihood approach described above depends on the assumed normality of the estimated difference in log-abundances. While the assumption of normality of the X_i (and hence the W_i) is required for the expressions used for the finite rate of increase, the probability of extinction and other quantities, the observation errors may or may not be normally distributed. If they are not normal then neither are the $\hat{W}_i$'s. In addition, even if the observation error is normally distributed if its variance is a function of the true value, then unconditionally, $\hat{W}_i$ is not normally distributed. One could build likelihood methods assuming some other distribution for the observation error but it may be difficult to specify a suitable distribution and even if one could do so, customized programming would be needed for the analysis (as opposed to the normal-based analysis from mixed-model software). It is useful therefore to have a method of estimation that does not depend on normality. Even if normality did hold, the likelihood estimators and associated inferences of the

TABLE 1. Parameter combinations used in simulation for mean parameter μ and variance parameter σ^2 along with corresponding trend parameter λ and the expected abundance, $E(N)$, at time $t = 11$ and $t = 21$ for the given parameters.

μ	σ^2	λ	$E(N_{11})$	$E(N_{21})$
-0.1	0.01	0.909	58.0	22.4
-0.1	0.04	0.923	67.4	30.3
-0.1	0.09	0.946	86.5	49.9
0.1	0.01	1.111	428.6	1224.9
0.1	0.04	1.127	498.0	1653.5
0.1	0.09	1.156	639.5	2726.1

previous section depend on the availability of mixed-model software, while moment estimators and associated standard errors can be obtained using explicit expressions and are easily programmed.

In simpler mixed models, moment and REML estimators essentially coincide. In more complex models, as here, differences can emerge. The REML estimators are generally known to be robust to the normality assumption, in the sense of producing consistent estimators, but the standard errors produced by most mixed-models software are not, as they do depend on the use of an information matrix based on the normality assumption; see Searle et al. (1992:64) and the reference there. The closed form of the moment estimators simplifies the derivation of the standard errors for the estimated variances when normality is not present.

For estimating the mean the naive estimator, now denoted $\hat{\mu}_{\text{mom}}$ can be used. This is an unbiased estimator and under the assumption of constant observation error variance has an estimated standard error of

$$\text{SE}(\hat{\mu}_{\text{mom}}) = \left[\frac{\hat{\sigma}_{\text{mom}}^2}{t_q - t_0} + \frac{2\hat{\sigma}_{u,\text{mom}}^2}{(t_q - t_0)^2} \right]^{1/2}. \quad (15)$$

Using the properties in Eq. 7 along with the expected value of the naive estimator of σ^2 , Staudenmayer and Buonaccorsi (2006) developed consistent moment-based estimators of the variance components given by

$$\hat{\sigma}_{u,\text{mom}}^2 = \hat{\mu}_{\text{mom}}^2 \frac{\sum_{i=1}^{q-1} \tau_i \tau_{i+1}}{q-1} - \frac{\sum_{i=1}^{q-1} \hat{W}_i \hat{W}_{i+1}}{q-1} \quad (16)$$

and

$$\hat{\sigma}_{\text{mom}}^2 = \hat{\sigma}_{\text{naive}}^2 - \frac{2\hat{\sigma}_{u,\text{mom}}^2}{q-1} \left[\left(\sum_{i=1}^q \tau_i^{-1} \right) - \frac{1}{t_q - t_0} \right] \quad (17)$$

where recall τ_i is the elapsed time between the $(i-1)$ st and i th observations (and so all $\tau_i = 1$ with equally spaced data). Section 5.1 of Staudenmayer and Buonaccorsi (2006) also provides expressions for the approximate variances of $\hat{\sigma}_{\text{mom}}^2$ and $\hat{\sigma}_{u,\text{mom}}^2$ as well as for the covariance among them and $\hat{\mu}_{\text{mom}}$. While the analytical expressions for the true standard errors of the variance estimators do not depend on normality, obtaining estimated standard errors without assuming normality is general challenging, and fully robust methods need further development; see the Appendix of Staudenmayer and Buonaccorsi (2006) for some discussion. One approach, implemented in the examples, is to estimate the standard errors based on the normality assumption. The procedure then is only partly distribution free; the estimators and their properties do not depend on the normality assumption but the estimation of standard errors and associated confidence intervals do.

Once the standard errors for the moment estimators are obtained, Wald and chi-square confidence intervals can be obtained in the same manner as with the REML estimators of the preceding section, except that the Wald interval for μ will use a z rather than a t value. If we assumed normality but used the moment estimators for computational convenience, we can bootstrap them in the same manner as we did the REML estimators. Without normality of the observation errors one cannot easily apply the bootstrap in a nonparametric manner. The difficulty is the need for a nonparametric estimate of the distribution of the observation error, a challenging problem which has not been attacked in this context.

TABLE 2. Average performance of estimators of μ .

Observation error	Parameter	M	PRC	PRI	R
Normal-equal	$\sqrt{\text{mse}}$	0.0734	0.0703	0.0703	0.0685
Normal-unequal	$\sqrt{\text{mse}}$	0.0762	0.0715	0.0710	0.0703
Uniform-equal	$\sqrt{\text{mse}}$	0.0742	0.0698	0.0698	0.0685
Normal-equal	$ \text{bias} $	0.0733	0.0691	0.069	0.0685
Normal-unequal	$ \text{bias} $	0.0762	0.0702	0.0698	0.0702
Uniform-equal	$ \text{bias} $	0.0741	0.0688	0.0687	0.0685
Normal-equal	SD	0.0027	0.0131	0.0132	0.0024
Normal-unequal	SD	0.0025	0.0137	0.0129	0.0022
Uniform-equal	SD	0.0026	0.0118	0.012	0.0024

Note: Variables and abbreviations are: M , moment estimator; R , restricted maximum likelihood (REML) estimator; PRC, pseudo-REML estimator assuming constant variance; PRI, pseudo-REML estimator using individual variances; SD, standard deviation; $|\text{bias}|$, absolute bias; mse, mean squared error.

TABLE 3. Average performance of estimators of σ^2 .

Observation error	Parameter	M	N	PMC	PMI	PRC	PRI	R
Normal-equal	$\sqrt{\text{mse}}$	0.1943	0.646	0.2541	0.254	0.1623	0.1641	0.1773
Normal-unequal	$\sqrt{\text{mse}}$	0.2215	0.8012	0.3018	0.3028	0.1754	0.168	0.1923
Uniform-equal	$\sqrt{\text{mse}}$	0.1955	0.6285	0.2131	0.2131	0.142	0.1431	0.179
Normal-equal	$ \text{bias} $	0.1323	0.2693	0.1973	0.1973	0.1051	0.107	0.1217
Normal-unequal	$ \text{bias} $	0.168	0.3966	0.2535	0.2541	0.1253	0.1151	0.1435
Uniform-equal	$ \text{bias} $	0.1311	0.2164	0.1526	0.1526	0.0752	0.0765	0.1215
Normal-equal	SD	0.1422	0.5872	0.16	0.16	0.1236	0.1244	0.1288
Normal-unequal	SD	0.1444	0.6962	0.1639	0.1646	0.1228	0.1224	0.128
Uniform-equal	SD	0.145	0.5901	0.1487	0.1487	0.1205	0.121	0.1315

Notes: Variables and abbreviations are as in Table 2. In addition, N , naive estimator; PMC, pseudo-moment estimator assuming constant variance; PMI, pseudo-moment estimator using individual variances.

“Pseudo” methods using estimated observation error variances

The estimate of x_i is often accompanied by an estimated standard error, $\hat{\sigma}_{u(i)}$. While these were not given for the data used in our examples, such standard errors usually follow from the same sampling procedure (subsampling, and so on) that produced the estimated log-abundance $\hat{x}_i$. For illustration, standard errors were generated for the grizzly bear data; see Fig. 1 and the *Examples* section. Here we present “pseudo approaches” in which the $\hat{\sigma}_{u(i)}^2$ are substituted for the observation error variances in Eq. 7, treated as known and then μ and σ^2 are estimated using either likelihood or moment techniques. If the observation error variance can be assumed to be constant, then instead of using the individual $\hat{\sigma}_{u(i)}^2$, the pseudo estimators can be obtained after setting each $\sigma_{u(i)}^2$ to the common

$$\hat{\sigma}_u^2 = \sum_{i=0}^q \hat{\sigma}_{u(i)}^2 / (q+1) \quad (18)$$

which is simply the mean of the estimated observation error variances. The pseudo approach has been employed in other dynamic models (Williams et al. 2003, Staudenmayer and Buonaccorsi 2005) and has been developed for the random walk model by Staudenmayer and Buonaccorsi (2006).

As discussed in Appendix C, the pseudo-REML estimators can be obtained directly with the appropriate implementation of mixed-model software, whether we use the individual observation error variances or the mean $\hat{\sigma}_u^2$. The pseudo-MOM estimator of σ^2 , which

arises by a direct, explicit correction for the bias of the naive estimator (see Section 5.2 of Staudenmayer and Buonaccorsi 2006) is

$$\hat{\sigma}_{pmom}^2 = \hat{\sigma}_{naive}^2 - \frac{1}{q-1} \left[\left(\sum_{i=1}^q \frac{\hat{\sigma}_{u(i-1)}^2 + \hat{\sigma}_{u(i)}^2}{\tau_i} \right) - \frac{\hat{\sigma}_{u0}^2 + \hat{\sigma}_{uq}^2}{t_q - t_0} \right] \quad (19)$$

in general, and $\hat{\sigma}_{naive}^2 - 2\hat{\sigma}_u^2(\sum_{i=1}^q \tau_i^{-1} - (t_q - t_0)^{-1})/(q-1)$ under the assumption of constant observation error variance.

If we treat the estimated observation error variances as known, then standard error and associated chi-square or Wald confidence intervals can be easily obtained for either the pseudo-REML estimators using output from mixed-model software or the pseudo-moment estimators using the first three terms in Eq. 13 of Staudenmayer and Buonaccorsi (2006). Under normality assumptions, one can also obtain profile-likelihood confidence intervals or use the bootstrap as described earlier (with the obvious modifications when allowing unequal observation error variances). Again, direct implementation of these approaches assumes the observation error variances are fixed and known.

One should account for the uncertainty due to estimating the observation error variances if possible. The standard error associated with $\hat{\mu}_{mom}$ does not need any adjustment since $\hat{\mu}_{mom}$ does not involve the $\sigma_{u(i)}^2$'s, but the standard error for a pseudo estimate of σ^2 does need modification. Staudenmayer and Buonaccorsi

TABLE 4. Average performance of estimators of λ .

Observation error	Parameter	M	N	PMC	PMI	PRC	PRI	R
Normal-equal	$\sqrt{\text{mse}}$	1.0592	1.355	1.0806	1.0806	1.0456	1.0463	1.0507
Normal-unequal	$\sqrt{\text{mse}}$	1.0781	2.6072	1.1455	1.1466	1.0525	1.0494	1.0589
Uniform-equal	$\sqrt{\text{mse}}$	1.061	1.3326	1.0675	1.0675	1.0409	1.0415	1.0518
Normal-equal	$ \text{bias} $	0.1152	0.3225	0.1725	0.1724	0.1027	0.1035	0.1089
Normal-unequal	$ \text{bias} $	0.175	2.0579	0.3621	0.3639	0.1416	0.1249	0.1401
Uniform-equal	$ \text{bias} $	0.1147	0.2424	0.1303	0.1303	0.0854	0.0858	0.1077
Normal-equal	SD	1.0529	1.3161	1.0668	1.0668	1.0405	1.0412	1.0451
Normal-unequal	SD	1.0638	1.6007	1.0867	1.0873	1.0429	1.042	1.0496
Uniform-equal	SD	1.0548	1.3104	1.0595	1.0595	1.0374	1.038	1.0462

FIG. 2. Root mean squared error of estimators of μ under normal observation error with constant variance. M = moment estimator; R = REML estimator; PRC = pseudo-REML estimator assuming constant variance. Observation error variance is σ_u^2 , and sample size is q .

(2005) discuss modifications of this type in some density-dependent dynamic models and contains general references to adjusting standard errors with the use of pseudo estimators. For the model under consideration here, we briefly summarize the results from Staudenmayer and Buonaccorsi (2006). Suppose SE_F denotes the standard error obtained assuming the observation error variances are fixed and known. The corrected standard error is of the form

$$SE = (SE_F^2 + Q)^{1/2} \quad (20)$$

where Q is an additional piece based on the uncertainty in the estimated observation error variances. In the case where the observation error variances are assumed constant and the pseudo estimator uses $\hat{\sigma}_u^2$ in Eq. 18, then the additional term is

$$Q = c\hat{V}(\hat{\sigma}_u^2) \quad (21)$$

where $\hat{V}(\hat{\sigma}_u^2) = S^2/(q+1)$, $S^2 = \sum_{i=1}^q (\hat{\sigma}_{u(i)}^2 - \hat{\sigma}_u^2)^2/q$ is the sample variance of $\hat{\sigma}_{u0}^2, \hat{\sigma}_{u1}^2, \dots, \hat{\sigma}_{uq}^2$, and c is a constant which differs depending on whether the REML or MOM estimator is being used (see Appendix B). There are some results for allowance of unequal observation error variances but work is ongoing on handling the most general setting where the observation error variances are not modeled in some fashion. Fortunately in the examples and in the simulations, these correction terms play a minor role since they are small relative to the other term entering into the standard error.

Negative estimates of variances

Special attention needs to be given to the problem of negative estimates of one of the variance components. This is a problem that arises in many mixed models (see Searle et al. 1992) if the problem is fit in an unconstrained manner, as occurs in our analysis of the

FIG. 2. Continued.

Parrot data. Most mixed-model software will have an option to constrain the estimates of the variance components to be nonnegative, and for moment estimators, this can be done by rounding to 0 where necessary. However, problems remain in obtaining confidence intervals. The chi-square intervals for variances cannot be calculated as the estimated degrees of freedom will be 0. For the Wald intervals, the standard errors of the estimators will be off since they are computed based on setting a variance to 0. Finally, the parametric bootstrap would have to be carried out using 0 for one of the variances. None of these approaches are satisfactory. With normality assumptions the best option from the relative frequency perspective is to use profile-likelihood confidence intervals. We do note that if a variance is actually equal to 0 the usual asymptotic results do not hold (Self and Liang 1987) but in practice it is usually reasonable to assume that both the process or observation variance are nonnegative.

The problem surrounding the confidence intervals in the presence of negative variance estimates is alleviated if one is willing to adopt a Bayesian approach and calculate a “Bayesian credible interval.” This is relatively straightforward, in principle, with the use of standard priors, but gets more complicated if nonstandard priors allowing a nonzero prior probability of a zero value for the variance are used.

CONFIDENCE INTERVALS FOR FUNCTIONS OF μ AND σ^2

It is usually functions of μ and σ^2 that are of primary interest. In general, suppose we are interested in $\theta = g(\mu, \sigma^2)$ for some function g , such as the growth rate $r = g(\mu, \sigma^2) = \mu + \sigma^2/2$ or the finite rate of increase $\lambda = g(\mu, \sigma^2) = e^{\mu + \sigma^2/2}$.

In those cases where the bootstrap can be used (see earlier discussions), bootstrap standard errors and confidence intervals can be obtained for θ directly, but some care must be exercised. The bootstrap is not a panacea and special attention needs to be given to

FIG. 3. Root mean squared error of estimators of σ^2 under normal observation error with constant variance. Abbreviations are as in Fig. 2 plus N = naive; PMC = pseudo-moment estimator with constant variance.

problems where one or more values of an estimate repeatedly occur in the bootstrap sample (as can happen when estimating the probability of extinction).

One of the most commonly used techniques for getting a confidence interval on θ is to use the Wald interval of the form $\hat{\theta} \pm z_{1-\alpha/2} \text{SE}(\hat{\theta})$, where $\text{SE}(\hat{\theta})$ is an estimated standard error for $\hat{\theta}$. To employ this one needs the variance of $\hat{\theta}$ and then $\text{SE}(\hat{\theta})$ is computed as the square root of the estimated variance. For nonlinear functions, the variance of $\hat{\theta}$ must be approximated, usually done via the “delta/Taylor series method” (see Casella and Berger 2002:242). In general, the smaller the sample sizes, the less accurate the approximation to the variance is. In addition, the Wald method relies on approximate normality of the estimator, which can come into question for short series.

Another approach is what we will refer to here as the *projection method*. This is an established, but often under

used, statistical technique. It has not been previously applied to PVA analyses except as suggested by Ludwig (1999). Here, it starts with a joint two-dimensional confidence region for μ and σ^2 , which we will denote by **R**. For our purposes, **R** will be a rectangle obtained by combining individual confidence intervals for μ and σ^2 ; say $[L_\mu, U_\mu]$ and $[L_{\sigma^2}, U_{\sigma^2}]$, respectively. [In the case with no observation error, it is better to use a non-rectangular confidence region for μ and σ^2 ; see Mood et al. (1974:384).] In the current case with observation error one could also develop an elliptical region for **R**. However, we will not pursue that approach here since it depends on a number of assumptions and the resulting intervals for the functions of interest are both harder to obtain and do not utilize the previously developed intervals for μ and σ^2 . The two individual confidence intervals leading to **R**, can be obtained using any of the

FIG. 3. Continued.

methods described earlier. From this region a confidence set for θ is constructed via

$$C_0 = [g(\mu, \sigma^2), (\mu, \sigma^2) \in \mathbf{R}]. \quad (22)$$

The confidence region for θ is simply the set of values that result by calculating the function of interest over all values of μ and σ^2 in $\mathbf{R}$. In most cases, the confidence set $C(\theta)$ is an interval obtained by finding the min and max of the function of interest over values in $\mathbf{R}$. An advantage of the projection approach is that we have a bound on the confidence coefficient. If the confidence coefficient of the region $\mathbf{R}$ is $\geq 1 - \alpha$ then the same is true for the confidence coefficient for $C(\theta)$. Using Bonferroni's inequality we can achieve this overall coverage of at least $1 - \alpha$ by computing each of the intervals for μ and σ^2 with a confidence level of $1 - \alpha^*$, where $\alpha^* = \alpha/2$.

Following are details for getting confidence intervals for some specific quantities of interest.

Confidence intervals for r .—The growth parameter r is the most easily handled since the variance of $\hat{r}$ can be obtained exactly with $V(\hat{r}) = V(\hat{\mu}) + (V(\hat{\sigma}^2)/4) + \text{Cov}(\hat{\mu}, \hat{\sigma}^2)$. In the naive analysis and the likelihood approach, the Cov term is zero but the moment approach allows for a nonzero value. The Wald interval for r is $\text{CI}_r(W) = \hat{r} \pm z_{1-\alpha/2} \text{SE}(\hat{r})$, where $\text{SE}(\hat{r})$ is the square root of the estimate of $V(\hat{r})$; see also Eq. 61 in Dennis et al. (1991) and Morris and Doak (2002). The projection interval for r is

$$\text{CI}_r(P) = [L_\mu + L_{\sigma^2}/2, U_\mu + U_{\sigma^2}/2]. \quad (23)$$

Notice that the projection technique bypasses the need to worry about the covariance in the estimators of μ and σ^2 since it works from the individual intervals.

Confidence intervals for λ .—The Wald interval is $\text{CI}_\lambda(W) = \hat{\lambda} \pm z_{1-\alpha/2} \text{SE}(\hat{\lambda})$, where $\text{SE}(\hat{\lambda}) = (\hat{\lambda}^2 \hat{V}(\hat{r}))^{1/2}$ and the projection interval is

FIG. 4. Root mean squared error of estimators of λ under normal observation error with constant variance. Abbreviations are as in Fig. 3.

$$CI_{\lambda}(P) = [e^{L_{\mu} + L_{\sigma^2}/2}, e^{U_{\mu} + U_{\sigma^2}/2}]. \quad (24)$$

Since λ is a monotonic function of r , there is a third approach here, namely to just transform the interval for r . Suppose the Wald interval for r , call it $[L_r(W), U_r(W)]$, then the transformed interval for λ would be $CI_{\lambda}(TrW) = [e^{L_r(W)}, e^{U_r(W)}]$, where TrW indicates transforming the Wald interval for r . Notice that if we transform the projection interval for r we just get the projection interval for λ .

Confidence intervals for the probability of extinction π .—Estimation of the probability of extinction has proved to be notoriously difficult, both with respect to bias of the point estimator and deriving standard errors and confidence intervals in some traditional ways. There are good arguments to be made for abandoning trying to estimate the probability of eventual extinction or the expected time to extinction given not only the statistical issues, but also because it is unclear how useful these quantities really are from an ecological perspective; see

Ludwig (1999) for example. However, since the estimation of the probability of extinction continues to draw attention, we will address it briefly. It also serves to illustrate the advantage of the projection method for situations where the Wald approach may encounter difficulty. Estimating π is especially difficult when μ is less than or equal to 0 or close to 0. In particular, there are problems with bias and with getting a standard error for the estimate and associated confidence intervals when there is sufficient probability of an estimated mean less than 0 which leads to a significant point mass associated with an estimated extinction of 1. Many of these issues can be resolved through the projection method which bypasses the issue of bias and the need for a standard error by going directly to interval estimation.

Let

$$\pi(x_*) = e^{-2\mu x_*/\sigma^2} \quad \text{if } \mu > 0$$

and

FIG. 4. Continued.

$$\pi(x_*) = 1 \quad \text{if } \mu \leq 0 \quad (25)$$

where $x_* = \log(n) - \log(n_c) > 0$. This is the probability of the population size eventually crossing the threshold n_c starting from population of size n . The n_c may represent a threshold for true extinction or some other important critical value, sometimes referred to as “pseudo-extinction.”

The typical estimator of $\pi(x_*)$ is $\hat{\pi}(x_*) = e^{-2\hat{\mu}x_*/\hat{\sigma}^2}$ if $\hat{\mu} > 0$ and 1 otherwise, but this estimator is plagued by bias issues.

The projection confidence “interval” for π is easily obtained via

$$\text{CI}_\pi(P) = 1 \quad \text{if } U_\mu \leq 0$$

(i.e., the interval for μ contains all negative values)

$$\text{CI}_\pi(P) = \begin{cases} [e^{-2U_\mu/L_{\sigma^2}}, 1] & \text{if } L_\mu < 0 < U_\mu \\ [e^{-2U_\mu/L_{\sigma^2}}, e^{-2L_\mu/U_{\sigma^2}}] & \text{if } 0 < L_\mu. \end{cases}$$

Other probabilities.—Instead of estimating the probability of extinction a more reasonable objective may be to

estimate probabilities concerning abundance at a future point in time, say at the next time point $t_q + 1$, for illustration. If the interest is in the probability that the population at the next time point is less than or equal to a certain proportion of the current abundance, that is in $P(N_{q+1} \leq pN_q)$, then Buonaccorsi et al. (2006) show that under normality this is a function of μ and σ^2 , namely $\Phi((\log(p) - \mu)/\sigma)$. The projection technique can be applied immediately for these quantities. On the other hand, inferences for the probabilities about absolute abundance are more challenging since these probabilities also depend on the current, but unobserved abundance. See the discussion in Staudenmayer and Buonaccorsi (2006).

SIMULATIONS

Here we present the results of a simulation experiment to compare the performance of estimators and confidence interval construction methods across a variety of parameter combinations and observation error models. We simulated series with $q = 21$ and 11 years of data (corresponding to 20 and 10 differences, respectively) all

TABLE 5. Average coverage for 95% confidence intervals for μ .

Method	Normal-equal	Normal-unequal	Uniform-equal
NAIVE-T	0.9936	0.9935	0.9938
MOM-W	0.8933	0.8938	0.8911
PMOM-C-W	0.8819	0.8821	0.8846
PREML-C-T	0.8763	0.8969	0.8958
REML-T	0.8299	0.8490	0.8496

Notes: Key to methods: NAIVE-T, naive interval using t value; MOM-W, moment method using Wald interval; PMOM-C-W, pseudo-moment method with constant variance, Wald interval; REML-T, REML method using t value; PREML-C-T, pseudo-REML method under constant variance using t value.

with a starting abundance of $N_1 = 150$. Table 1 displays the combinations of μ and σ^2 we used to generate the data, along with related quantities of interest. For constant observation error variances we used $\sigma_u^2 = 0.01, 0.04, 0.09$, and 0.50 . The first three values are based on Staples et al. (2004) reflecting what they called small, medium, and large observation error variance, and 0.50 is the “very large” observation error variance used in Holmes (2004). Three types of observation error are considered: normal errors with constant variance, uniform observation errors with constant variance, and normal errors with unequal variances. For the unequal variances, the observation error variance at the first time point is σ_u^2 as above, and at subsequent time points $\sigma_{u(i)}^2 = \sigma_u^2(N_i/N_1)^{1/2}$, where N_i is the abundance at time i . This third model allows the observation error variance in the estimated log-abundance to depend on abundance. The $\sigma_{u(i)}^2$ we used arises (approximately) from assuming that the variance of i is proportional to $N_i^{5/2}$ (note that if the variance were proportional to N_i^2 the variance of $\hat{X}_i$ is approximately a constant).

In summary, for each of three settings (constant variance with normal observation errors, constant variance with uniform observation errors, and normal observation errors with unequal variances) there are 48 combinations arising from two sample sizes, two values of μ , three values of σ^2 and four values of σ_u^2 .

With $\mu = -0.1$ (declining trend) there were some cases where the simulated population went extinct (i.e., $X_t < 0$ implying $N_t < 1$) before reaching q and in those cases additional simulations were run to get 1000 simulations where extinction was not reached.

Estimation

We discuss the estimators first. For μ , we consider four estimators: the method of moments/naive (M) estimator, the REML (R) estimator and pseudo-REML estimators assuming constant (PRC) or unequal (PRI) observation error variances. For σ^2 and λ we have seven estimators: naive (N), method of moments (M) and pseudo methods of moments assuming constant (PMC) or unequal (PMI) observation error variances, along with R, PRC, and PRI as defined above. The pseudo estimators are based on estimated observation error

variances $\hat{\sigma}_{u(i)}^2$, generated so that $d\hat{\sigma}_{u(i)}^2/\sigma_{u(i)}^2$ was distributed chi-square with d degrees of freedom. This results in $\hat{\sigma}_{u(i)}^2$ being unbiased for $\sigma_{u(i)}^2$, and we chose the degrees of freedom so that the coefficient of variation of $\hat{\sigma}_{u(i)}^2$ as an estimator of σ_u^2 is 0.10 (10%).

In general, we note that there were cases where the REML or pseudo-REML estimators could not be obtained. This could have been due to nonexistence of the estimators or because of lack of convergence in PROC MIXED. With equal observation error variances, this was not much of an issue for the pseudo methods but the REML estimates could not be obtained in upwards of 5% of the cases. With unequal variances, all three methods had similar problems, with up to 10% of the cases not having estimates. In general, the worse case scenarios were with the larger observation error variances and the small process variance of 0.01.

Tables 2–4 summarize the mean performance of the estimators over all of the parameter settings for each of the three observation error models. There is, obviously, some danger in summarizing in this way. Twenty-seven figures were produced which provide an assessment of the bias (b), standard deviation (SD) and root mean squared error ($b^2 + \text{SD}^2$) for estimators of μ , σ^2 , and λ over each of the three observation error models. Figs. 2–4 show the root mean-squared error for the three estimators for the case where the observation errors are normally distributed with constant variance. The parameter combinations corresponding to the different vertical slices are indicated in the first panel of the figure. In Figs. 3 and 4, the naive estimator is omitted in the cases with large observation error variance (0.05) as the root mean-squared errors were large enough that including it would distort the comparison of the other methods. The remaining figures are available in an electronic appendix. Conclusions from these simulations follow.

Without estimates of observation error variance

Without estimates of the observation error variances, the comparison is only between the naive and REML estimator for μ and the naive, moment, and REML estimators for the process variance σ^2 and the trend λ .

TABLE 6. Average coverage for 95% confidence intervals for σ^2 .

Method	Normal-equal	Normal-unequal	Uniform-equal
NAIVE-C	0.2285	0.2284	0.2184
MOM-W	0.9812	0.9822	0.9824
PMOM-C-W	0.9773	0.9746	0.9786
PREML-C-W	0.6977	0.7015	0.7181
REML-W	0.6289	0.6337	0.6358

Notes: Key to methods: NAIVE-C, naive chi-square-based interval; MOM-W, moment method using Wald interval; PMOM-C-W, pseudo-moment method with constant variance, Wald interval; PREML-C-W, pseudo-REML method under constant variance, Wald interval; REML-W, REML method, Wald interval.

TABLE 7. Average coverage for 95% confidence intervals for λ .

Method	Normal-equal	Normal-unequal	Uniform-equal
NAIVE-W	0.9893	0.9881	0.9896
MOM-W	0.9377	0.9359	0.9381
MOM-P-WW	0.9653	0.9644	0.9646
PMOM-C-P-WW	0.9579	0.9582	0.9604
PREML-C-P-TW	0.9147	0.9370	0.9375
REML-P-TW	0.8702	0.8932	0.8938
REML-W	0.7947	0.8124	0.8158

Notes: Key to methods: MOM-W, moment method, Wald interval; PMOM-C-P-WW, pseudo-moment method with constant variance, projection interval constructed using Wald intervals for μ and σ^2 ; REML-W, REML estimator, Wald interval; PREML-C-P-TW, pseudo-moment method with constant variance, projection interval constructed using t -based interval for μ and Wald interval for σ^2 .

For μ , there is generally little distinction between the moment (naive) and REML estimators, both in terms of global behavior and the correlation between the estimators over individual simulations. At the very high observation error variance, however, there is less agreement and the REML estimator gains an advantage over the moment estimator. But, as noted earlier it is in those setting that some concerns arise about being able to obtain the REML estimator.

For σ^2 and λ , as expected, the naive estimator begins to break down as the observation error variance increases and cannot be recommended. The moment and REML estimators again perform very similarly, and the REML has lower root mean squared error when the observation error variance is larger. Recall, however, that there can be problems with obtaining the REML estimators with large observation error variances. We note that both the MOM and REML estimators of σ^2 are relatively robust to both the normality assumption and the assumption of constant variance.

Using estimated observation error variances

Here, the pseudo estimators now come into consideration.

For estimating μ , the pseudo-REML estimator does not really improve on the moment and REML estimator and is often a bit more variable, even in the case of unequal variances.

For estimating the variance and λ , the figures only present results for the pseudo estimators formed under the constant variance assumption (PMC and PRC) since the performance of the estimators using individual variances (PMI and PRI, respectively) was quite similar. The pseudo-REML estimators are competitive with the REML and moment estimators throughout and are superior as the observation error variances increase, for both unequal variance and non-normal observation errors. The pseudo-moment estimators on the other hand, perform poorly compared to the moment estimators (which make no use of estimated observation error variances) at higher observation error variances

and offer no real advantages over the moment estimators in other cases.

Confidence intervals

Turning our attention to confidence intervals, there are numerous intervals that can be computed as described here. A number of those intervals either used directly, or were based on, a chi-square-based confidence interval for σ^2 ; see Eq. 14. While these intervals may be adequate in some mixed models with sufficient sample sizes, they do not perform here, as will also be seen in our examples. In the simulations there are many cases (often the majority within a particular combination of parameters) where the estimated degrees of freedom is less than 1, leading to a ridiculously large confidence interval. For this reason we have dropped these intervals from consideration in our simulations and generally recommend against their use.

For μ , we consider the Wald-based method of moment and pseudo method of moment intervals (MOMW and PMOMCW), along with REML-based confidence intervals both non-pseudo (REMLT) and pseudo (PREMLCT), where the T indicates the use of a t value with an estimated degrees of freedom (see, for example, Eq. 11). Similar confidence intervals are considered for σ^2 except the REML Wald intervals use a z value rather than a t with adjusted degrees of freedom (see Eq. 13). For λ we consider five intervals. Two use an approximate standard error and form a Wald-type interval using either the moment or REML estimators (MOMW and REMLW). The other four (MOMPWW, PMOMCPWW, PREMLCPTW, and REMLPTW) use the projection technique of creating the confidence interval for λ from simultaneous confidence intervals for μ and σ^2 . The first part of the label indicates the general method (MOM = moment, PMOMC = pseudo method of moments with constant observation error variance, PREMLC = pseudo-REML with constant observation error variance and REML) while the last part of the name Pxy indicates projection of an x interval for μ and a y interval for σ^2 . For example, PWW means a projection using a Wald interval for μ and a Wald interval for σ^2 . The pseudo intervals are given based on assuming constant variance since the performance was similar for the procedure using individual estimated observation error variances.

Overall summaries of the coverage rates is given in Tables 5–7 while Figs. 5–7 show more details over all parameterizations for the case with normal observation errors with constant variance. As with the estimation figures, the parameter combinations corresponding to the different vertical slices are indicated in the first panel of the figure. Other figures are given in the electronic appendix. All intervals were trying to achieve a coverage rate of 0.95.

The conclusions about confidence intervals are relatively complicated.

FIG. 5. Continued.

encounters difficulties in these settings. Somewhat surprisingly in the case of unequal variances, the pseudo methods do not offer any great advantages over the non-pseudo methods, at least with respect to overall coverage.

Finally, note that we did not simulate the performance of the bootstrap or profile likelihood intervals in part due to their large computational requirements and the need for a lot of additional programming. Theoretical and empirical results from related problems suggest that the bootstrap or profile likelihood confidence intervals, or more complicated versions of them which make bias adjustments, will perform better (e.g., Efron 1987), so long as the model assumptions are met. We wanted to concentrate here on those methods that are readily available to experimenters. The moment estimators are easily programmed, and the REML-based procedures are available through mixed-model software. But, certainly further investigation of other interval methods is warranted.

EXAMPLES

We first apply the methods using the four data sets described in the introduction and presented in Fig. 1. All of the original data sets are equally spaced in time, although our methods and programs readily accommodate unequally spaced data sets. A SAS program which combines the use of PROC MIXED with customized IML code was used to provide all of the results presented here except for the profile likelihood intervals. See Appendix C for a detailed description on the use of PROC MIXED.

Table 8 provides estimates, standard errors and confidence intervals for the basic parameters μ , σ^2 , and σ_u^2 using naive, REML and MOM procedures under the assumption of constant observation error variances. Fig. 8 illustrates the construction of a profile likelihood confidence interval for σ^2 with the parrot data. Here are some observations on Table 8:

FIG. 6. Coverage of confidence intervals for σ_u^2 under normal observation error with constant variance. The name of a method is located at a height equal to the coverage rate. Abbreviations are as in Fig. 5.

1) Since the naive estimator of μ is also a moment-based estimator of μ the naive and moment estimators of μ are the same. This estimator is unbiased for μ , but the naive standard error of the estimate of μ is not correct. The corrected standard error is the one attached to the moment estimator in the output.

2) As expected, in all but the parrot data, the corrected estimator of the variance σ^2 is smaller than the naive estimator, which in general overestimates the true value. Correspondingly, the confidence intervals for σ^2 are generally moved towards 0 relative to the naive intervals.

3) The chi-square-based intervals for the variance components, either REML or MOM, are quite inconsistent with the other corrected intervals and not very useful. This is especially true with the condor and bear data. This is due to the degrees of freedom being too small, as a result of the standard error being relatively

close to the estimate. This problem was noted in the simulations.

4) The parrot data illustrate the problem of negative estimates of variance components. If the solutions are not bounded, MOM and unbounded REML estimators of the observation error variance are -0.0020 and -0.0030 , respectively, with corresponding estimates of the process variance of 0.0192 and 0.0215 . If we use the strategy of just setting the observation error variance to 0, then the analysis simply reverts to the naive analysis. As discussed earlier, this is unsatisfactory in several ways. The only alternatives here to the naive methods are the profile likelihood or bootstrap-based confidence intervals. The bootstrap confidence intervals for all of the parameters were computed two ways; with observation error variance set to 0 and to 0.0066 , the latter being the upper bound of the profile likelihood interval for σ_u^2 . A conservative approach would be to use the wider

FIG. 6. Continued.

intervals, labeled REML-CI(B), which use the bootstrap with $\sigma_u^2 = 0$.

5) A different problem occurs with the Condor data where the REML approach results in an estimate of essentially 0 for the process variance σ^2 , with an estimated standard error also essentially 0. This is quite different from the moment estimator of 0.0468 and essentially renders the REML related confidence intervals for all parameters (computed assuming a process variance of 0) useless. The best choice here would be to use the moment-based Wald intervals or the profile likelihood intervals, neither of which set σ^2 to 0. A conservative approach is to use the wider of the two.

6) We next look more closely at the bear and crane data, neither of which have an issue with a zero variance estimate. While there are some differences in the REML and moment estimators of the process variance for the bear data, 0.0082 to 0.0053, respectively, the estimates are almost identical for the crane data. Based on our

simulation results, we tend to favor the moment-based Wald confidence intervals, which for μ and σ^2 both are fairly similar to the profile likelihood intervals. The observation error variance (assumed constant here) is of less interest than the other parameters. We note that there are substantial differences between the profile likelihood and bootstrap intervals, with the former being more similar to the moment-based Wald intervals than the latter. Both methods rely on the assumptions of normality and constant observation error variance which may or may not hold. The profile likelihood intervals are also based on a likelihood ratio test statistic being distributed approximate chi-square, which is an asymptotic result, while the bootstrap intervals are computed using the percentile method, which is not guaranteed to always work. These are the key reasons for potential differences in the two techniques, and, of course, the data analysis itself cannot decide which method is better.

FIG. 7. Continued.

Wald intervals (MOM-CI-PWW) or profile likelihood intervals (P-profile), with the former being a bit wider.

For illustration, the confidence intervals for the probability of extinction were computed using a cut-off point of $N = 1$, except for the cranes where $N = 15$ was used. Confidence intervals based on other cut points can be easily calculated using the intervals for μ and σ^2 and the technique described earlier in the paper. If calculated directly from the 95% intervals in Table 8, they would be 90% confidence intervals rather than 95%. With the Crane data, direct bootstrap percentile intervals for π were not very stable over different runs of 1000 bootstrap samples and cannot be recommended here. This is because of the nature of the empirical bootstrap distribution where we can get a stack of values at 1 or 0. A better option, which we have used here on all datasets, is to project individual 97.5% bootstrap intervals for μ and σ^2 to get a bootstrap related interval for π . It is clear that for all of the data sets, there is very limited information about π . As noted earlier, proba-

bilities about the abundance at a future time point are probably of more practical interest than π .

Pseudo-estimation

For illustration, we attached standard errors to the estimated log abundances with the grizzly bear data in order to demonstrate the pseudo approaches. This was done by generating an estimated $\hat{\sigma}_{u(i)}^2$ which had expected value 0.005, and a distribution that was proportional that of a chi square, with degrees of freedom chosen so that the standard deviation of $\hat{\sigma}_{u(i)}$ is 0.002. The error bars in Fig. 1 correspond to abundance ± 2 SE. Results are given in Table 10. We have only included some of the many possible intervals to give the general feel for the analysis. Note that the standard errors and confidence intervals are often smaller and narrower than in Table 8. This is to be expected since the pseudo approaches use more of the available information. Many of the other calculations are like those used in the preceding examples. The first column provides the

TABLE 8. Examples of estimation of process mean and variance and observation error variance.

Parameter and method	Bear	Condor	Crane	Parrot
μ				
Naive (SE)	0.0213 (0.0185)	-0.0768 (0.0885)	0.0377 (0.0187)	0.0273 (0.0275)
MOM (SE)	0.0213 (0.0120)	-0.0768 (0.0584)	0.0377 (0.0157)	0.0273 (0.0275)
REML (SE)	0.0211 (0.0148)	-0.0948 (0.0131)	0.0372 (0.0158)	0.0273 (0.0275)
REML (BSE)	0.0211 (0.0160)	-0.0948 (0.0621)	0.0372 (0.0176)	0.0273 (0.0326)
Naive, CI(<i>t</i>)	(-0.0162, 0.0589)	(-0.2667, 0.1130)	(0.0001, 0.0753)	(-0.0302, 0.0849)
MOM, CI(W)	(-0.0023, 0.0450)	(-0.1914, 0.0377)	(0.0069, 0.0684)	
REML, CI(<i>t</i>)	(-0.0112, 0.0534)	(-0.1228, -0.0668)	(0.0030, 0.0714)	
REML, CI(B)	(-0.0131, 0.0519)	(-0.2061, 0.0329)	(0.0022, 0.0714)	(-0.0402, 0.0912)
REML, CI(B)*				(-0.035, 0.0926)
Profile, CI	(-0.009, 0.051)	(-0.121, -0.068)	(0.005, 0.069)	(-0.028, -0.082)
σ^2				
Naive (SE)	0.0131 (0.0030)	0.1176 (0.0444)	0.0193 (0.0037)	0.0151 (0.0049)
MOM (SE)	0.0053 (0.0036)	0.0468 (0.0539)	0.0134 (0.0053)	0.0151 (0.0089)
REML (SE)	0.0082 (0.0035)	0.0000 (0.0000)	0.0137 (0.0055)	0.0151 (0.0049)
REML (BSE)	0.0082 (0.0030)	0.0000 (0.0254)	0.0137 (0.0040)	0.0151 (0.0085)
Naive, CI(C)	(0.0087, 0.0218)	(0.0630, 0.2924)	(0.0137, 0.0293)	(0.0087, 0.0322)
MOM, CI(W)	(0.0000, 0.0123)	(0.0000, 0.1525)	(0.0030, 0.0238)	
MOM, CI(C)	(0.0020, 0.0379)	(0.0112, 50.2560)	(0.0070, 0.0351)	
REML, CI(W)	(0.0014, 0.0150)	(0.0000, 0.0000)	(0.0030, 0.0244)	
REML, CI(C)	(0.0041, 0.0234)		(0.0071, 0.0362)	
REML, CI(B)	(0.0035, 0.0153)	(0.0000, 0.0971)	(0.0067, 0.0231)	(0.0007, 0.0357)
REML, CI(B)*				(0.00005, 0.0345)
REML CI(P)	(0.0036, 0.019)	(0.0000, 0.12)	(0.006, 0.027)	(0.0085, 0.0307)
σ_u^2				
MOM (SE)	0.0038 (0.0024)	0.0332 (0.0338)	0.0029 (0.0027)	0.0000 (0.0035)
REML (SE)	0.0022 (0.0018)	0.0580 (0.0219)	0.0028 (0.0028)	0.0000 (0.0038)
REML (BSE)	0.0022 (0.0010)	0.0580 (0.0103)	0.0028 (0.0013)	0.0000 (0.0033)
MOM, CI(W)	(0.0000, 0.0084)	(0.0000, 0.0995)	(0.0000, 0.0082)	
MOM, CI(C)	(0.0015, 0.0223)	(0.0088, 10.4905)	(0.0008, 0.0776)	
REML, CI(W)	(0.0000, 0.0057)	(0.0150, 0.1010)	(0.0000, 0.0082)	
REML, CI(C)	(0.0007, 0.0274)	(0.0311, 0.1443)	(0.0008, 0.1102)	
REML, CI(B)	(0.0000, 0.0036)	(0.0000, 0.0350)	(0.0000, 0.0043)	(0.0000, 0.0113)
REML CI(P)	(0.0000, 0.0069)	(0.030, 0.135)	(0.0000, 0.0094)	(0, 0.0066)

Notes: Key to methods: MOM, moment-based estimates; REML, restricted maximum likelihood estimates; (SE), standard error; (BSE), bootstrap standard error. For confidence intervals: CI(*t*), *t*-based interval; CI(W), Wald interval; CI(C), chi-square-based interval; CI(B), bootstrap percentile interval; CI(P), profile likelihood confidence interval. For the Parrot data, CI(B) is computed with an observation error variance $\sigma_u^2 = 0$, and CI(B)* with $\sigma_u^2 = 0.0066$ (upper bound of the profile likelihood confidence interval for σ_u^2).

analysis using the individual estimated observation error variances while the second assumes constant observation error variances and uses the mean observation error variance. Standard errors and confidence intervals in the first two columns are all calculated treating the observation error variances as known. The last column modifies the standard errors and confidence intervals under the assumption of constant observation error variance in order to account for the uncertainty from estimating these variances. As noted earlier, similar corrections when allowing different observation error variances for each observation require further assumptions and are still under development. This appears to be unimportant here since, as we can see in the constant variance case, use of the additional correction term makes almost no difference as it is small relative to the first component of Eq. 20.

In computing the *t*-based confidence interval for μ using the individual variances, PROC MIXED could not compute the interval using the Satterthwaite degrees of freedom, so an alternative was used. See Appendix C.

DISCUSSION

The main goal here was to provide a discussion of the full range of issues and options for obtaining statistical inferences on the basic parameters and functions of them in the random walk/PVA model in the presence of observation error. A variety of techniques were presented based on either normality or moment assumptions, and either with or without the use of additional information on the observation error variance (but assuming the observation error variance is constant) or by exploiting estimated observation variances. In the latter case, the observation error variances could be changing across observation. Our application of these methods to the bear, condor, crane, and parrot data provides a richer assessment of what is known about the dynamics of these species than was available from previous analyses.

We presented and assessed the best available frequentist methods. While our methodology and illustrations included bootstrap techniques and the use of profile

FIG. 8. Illustration of construction of the profile likelihood confidence interval for the process variance using the parrot data. The y-axis is the maximized value of 2 times the restricted log-likelihood with σ^2 held fixed, $\hat{l}$ is the maximized value over both σ^2 and σ_u^2 , $\hat{\sigma}^2$ is the REML estimate of σ^2 , and $z_{0.975} = 1.96$ is the 97.5th percentile of the standard normal distribution.

likelihood confidence intervals, our simulations were limited to the moment and mixed-model/REML-based techniques that would be readily usable by most applied ecologists. With respect to the methods we examined in detail, a few general recommendations emerged as described in detail in the simulation section. One conclusion is that overall the moment-based estimators and associated Wald type confidence intervals appear to be the most robust and should be used. In the case where estimated observation error variances are available, pseudo methods that incorporate them should generally be used, although they do not provide large gains in all cases. The pseudo methods assuming a constant observation error variance are recommended as they are quite robust to that assumption and are more stable than the pseudo estimators that use individual variances.

The simulations also document the (somewhat unsurprising) fact that separating the dynamic model parameters from the observation error is a challenging problem, especially with short series and/or large process or observation error variances. The estimators can be quite variable and, as seen in the simulations, many of the confidence intervals fail to achieve the desired coverage rate, sometimes by a large amount. This is a problem shared by many statistical methods in complex models when using relatively small sample sizes and the remedies may be limited. From what we know at this point, the confidence intervals based on moment estimators and Wald-type intervals are recommended. Our data analysis of the four animal abundance series and the accompanying discussion also illustrate how we think one should attack these problems given the currently available methods.

As noted in the simulation section, our simulations concentrated on methods that can be easily implemented

using standard software (i.e., the mixed-models techniques) or simple programming (i.e., moment methods). It is worth exploring the performance of the more computationally demanding bootstrap and profile likelihood confidence intervals. These techniques do suffer from some disadvantages however. At this point, both rely on the assumption of normality and constant variance. Extending these methods to accommodate unequal observation errors or non-normal observation errors is an area worthy of future work. We note that a nonparametric bootstrap technique is not readily apparent because of the need to unmix the process error and observation error distributions.

We have focused on non-Bayesian relative frequentist techniques. As mentioned in the introduction, Lindley (2003) presented a Bayesian approach to the random walk model. One general benefit of the Bayesian approach is that it provides a natural way to developing confidence intervals (known as “credible intervals” in Bayesian terminology) that both account for all sources of variability in the model and can be extended to address transformations of the parameters without asymptotic approximation. That said, we have omitted a detailed treatment of Bayesian due to both space constraints and practical and technical concerns. In addition to the usual concerns about Bayesian methods (the need for distributional assumptions throughout and potential sensitivity to the specification of prior distributions), a practical reason for omission is that the programming requirements to implement Bayesian methods present a barrier to their implementation by a large number of ecologists. There is a software package (WinBugs; Medical Research Council Biostatistics Unit, Cambridge, UK) that can reduce the programming burden, but it is still much less prevalent than more

TABLE 9. Examples of estimation of trend λ and probability of eventual extinction π .

Parameter and method	Bear	Condor	Crane	Parrot
λ				
Naive (SE)	1.0283 (0.0191)	0.9821 (0.0896)	1.0484 (0.0197)	1.0355 (0.0286)
MOM (SE)	1.0243 (0.0125)	0.9480 (0.0613)	1.0454 (0.0166)	1.0355 (0.0288)
REML (SE)	1.0255 (0.0153)	0.9095 (0.0119)	1.0450 (0.0168)	1.0388 (0.0287)
REML (BSE)	1.0255 (0.0165)	0.9095 (0.0593)	1.0450 (0.0184)	1.0388 (0.0341)
Naive, CI(W)	(0.9908, 1.0657)	(0.8064, 1.1578)	(1.0098, 1.0872)	(0.9795, 1.0915)
Naive, CI(P, tC)	(0.9823, 1.0794)	(0.7633, 1.3692)	(1.0010, 1.1013)	
MOM, CI(W)	(0.9999, 1.0487)	(0.8277, 1.0682)	(1.0128, 1.0780)	
MOM, CI(P, WW)	(0.9943, 1.0566)	(0.81233, 1.1480)		
REML, CI(W)	(0.9956, 1.0555)	(0.8863, 0.9328)	(1.0121, 1.0780)	
REML, CI(TrW)	(0.9960, 1.0559)	(0.8866, 0.9331)	(1.0126, 1.0785)	
REML, CI(P, tW)	(0.9834, 1.0694)			
REML, CI(B)	(0.9920, 1.0587)	(0.8319, 1.0575)	(1.0097, 1.0816)	(0.9692, 1.1070)
P, Profile	(0.9877, 1.0677)	(0.8816, 1.0248)	(1.0025, 1.0936)	(0.9675, 1.115)
π				
Naive	0.00000340	1.00000000	0.00002879	0.00000193
MOM	0.00000000	1.00000000	0.00000030	0.00000193
REML	0.00000000	1.00000000	0.00000048	0.00009419
Naive, CI(P, tC)	(0.0000, 1.0000)	(0.0000, 1.0000)	(0.0000, 1.000)	(0.0000, 1.0000)
MOM, CI(P, WW)	(0.0000, 1.0000)	(0, 1.0000)	(0.0000, 0.7209)	
REML, CI(P, tW)	(0.0000, 1.0000)		(0.0000, 0.5892)	
REML, CI(P, PP)	(0.0000, 1.0000)	(1.000, 1.0000)	(0.0000, 1.000)	(0.0000, 1.0000)
REML, CI(P, BB)	(0.0000, 1.0000)	(0, 1.0000)	(0.0000, 1.000)	(0.0000, 1.0000)

Notes: Key to parameters: λ , finite rate of increase; π , probability of eventual extinction. CI(P-ab) indicates a projection confidence interval based on a interval for μ and b interval for σ^2 . TrW transforms the Wald interval for r (population growth rate) to get a confidence interval for λ . Other quantities are as defined in Table 8.

TABLE 10. Pseudo-analysis of bear data using generated estimates of observation error variances.

Parameter and method	Ind	Ave	Ave-Adj
μ			
PMOM (SE)	0.0213 (0.0092)	0.0213 (0.0090)	
PREML (SE)	0.0203 (0.0125)	0.0206 (0.0131)	
PMOM, CI(W)	(0.0033, 0.0394)	(0.0036, 0.0390)	
PREML, CI(t)	(-0.0051, 0.0457)	(-0.0075, 0.0486)	
σ^2			
PMOM (SE)	0.0029 (0.0035)	0.0028 (0.0034)	0.0028 (0.0035)
PREML (SE)	0.0058 (0.0023)	0.0063 (0.0024)	0.0063 (0.0024)
PMOM, CI(W)	(0.0000, 0.0098)	(0.0000, 0.0096)	(0.0000, 0.0097)
PMOM, CI(C)	(0.0007, 0.5239)	(0.0007, 0.4850)	(0.0006, 0.5608)
PREML, CI(W)	(0.0014, 0.0102)	(0.0016, 0.0111)	(0.0016, 0.0111)
PREML, CI(C)	(0.0030, 0.0150)	(0.0034, 0.0159)	(0.0034, 0.0160)
λ			
PMOM (SE)	1.0231 (0.0096)	1.0230 (0.0094)	1.0230 (0.0094)
PREML (SE)	1.0235 (0.0129)	1.0240 (0.0135)	1.0240 (0.0135)
PMOM, CI(W)	(1.0043, 1.0418)	(1.0046, 1.0415)	(1.0046, 1.0415)
PMOM, CI(TrP-WW)	(1.0007, 1.0485)	(1.0011, 1.0480)	(1.0011, 1.0480)
PREML, CI(W)	(0.9982, 1.0488)	(0.9976, 1.0504)	(0.9976, 1.0504)
PREML, CI(TrW)	(0.9985, 1.0491)	(0.9980, 1.0508)	(0.9980, 1.0508)
PREML, CI(P-tW)	(0.9892, 1.0590)	(0.9883, 1.0610)	(0.9883, 1.0610)
π			
PMOM	0.0000	0.0000	0.0000
REML	0.0000	0.0000	0.0000
MOM, CI(P-WW)	(0.0000, 0.5068)	(0.0000, 0.4724)	(0.0000, 0.4760)
REML, CI(P-tW)	(0.0000, 1.0000)	(0.0000, 1.0000)	(0.0000, 1.0000)

Notes: Key to methods: PMOM, pseudo-moment estimate; PREML, pseudo-REML estimates. "Ind" uses individual observation error variances; "Ave" uses the average observation error variance; "Ave-adj" uses the average observation error variance with adjusted standard errors. Other notation is as in Tables 8 and 9.

standard statistical software, such as SAS (SAS Institute, Cary, North Carolina, USA), Splus (TIBCO Software, Palo Alto, California, USA), or R (*available online*).⁴ The major technical reason we leave Bayesian methods out of this paper is a bit subtle. Bayesian methods require priors on all parameters, and the posterior is nonzero only in regions where the prior is. In some of the examples we considered though, there was evidence that one of the variances might be zero. As a result, priors on those variances should allow for that possibility. Current Bayesian work in the ecological literature does not. That problem can be addressed with new priors and new ways of sampling from the posterior, but doing so is out of the scope of this paper. In addition, we caution that it can be difficult to find non-informative priors on variances in linear mixed models (Gelman 2006), especially when the sample size is small. These issues warrant separate attention.

The model considered in this paper arises from a density-independent model for abundance. This is a nonstationary model, suitable for allowing drift. A popular generalization is $X_t | x_{t-1} = \phi_0 + \phi_1 x_{t-1} + \varepsilon_t$ which with $\phi_1 = 1$ corresponds to the random walk model. Density-dependent models result from $\phi_1 \neq 1$ with $|\phi_1| < 1$ leading to a stationary model, which is appropriate for some populations in equilibrium. This is a linear autoregressive model on the log-abundance scale. Certain aspects of estimation for this model in the presence of observation error have been addressed in a number of papers including Staudenmayer and Buonaccorsi (2005), Dennis et al. (2006), and de Valpine and Hilborn (2005). The latter paper, which is in the fisheries literature, combines and develops several interesting and sophisticated methodologies (state space and Bayesian modeling and computation and nonparametric smoothing) to address this problem. Their approach can accommodate nonlinear dynamic models, but their primary example is similar to the linear autoregressive model above. The development of a full suite of inferential methods for this model, similar to those introduced here, is ongoing. We note it is technically challenging to accommodate either $\phi_1 = 1$ or $|\phi_1| < 1$ simultaneously since the statistical theory changes depending on whether the resulting model is stationary or not.

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⁴ www.r-project.org

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APPENDIX A

Mixed-model formulation (*Ecological Archives* M079-011-A1).

APPENDIX B

Adjusted standard errors for pseudo estimators (*Ecological Archives* M079-011-A2).

APPENDIX C

Use of SAS PROC MIXED (*Ecological Archives* M079-011-A3).

APPENDIX D

Additional figures showing root mean squared error, bias, standard deviations, and coverage of confidence intervals for μ , σ^2 , and λ with varying assumptions (*Ecological Archives* M079-011-A4).