Analysis of ecological time series with ARMA(p,q) models

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Abstract. Autoregressive moving average (ARMA) models are useful statistical tools to examine the dynamical characteristics of ecological time-series data. Here, we illustrate the utility and challenges of applying ARMA(p,q) models, where p is the dimension of the autoregressive component of the model, and q is the dimension of the moving average component. We focus on parameter estimation and model selection, comparing both maximum likelihood (ML) and restricted maximum likelihood (REML) parameter estimation. While REML estimation performs better (has less bias) than ML estimation for ARMA(p,q) models with p=1 (as has been found previously), for models with p>1 the performance of the estimators is complicated by multimodal likelihood functions. The resulting difficulties in estimation lead to our recommendation that likelihood functions be routinely investigated when applying ARMA(p,q) models. To aid this investigation, we provide MATLAB and R code for the ML and REML likelihood functions. We further explore the consequences of measurement error, showing how it can be explicitly and implicitly incorporated into estimation. In addition to parameter estimation, we also examine model selection for identifying the correct model dimensions (p and q). Finally, we estimate the characteristic return rate of the stochastic process to its stationary distribution, a quantity that describes a key property of population dynamics, and investigate bias that results from both estimation and model selection. While fitting ARMA models to ecological time series with complex dynamics has challenges, these challenges can be surmounted, making ARMA a useful and broadly applicable approach.

Key words: autoregressive moving average (ARMA) models; estimation bias; model selection; restricted maximum likelihood (REML) parameter estimation; return time; stability.

Introduction

Studies of time-series data have been increasing in both frequency and sophistication in the ecological literature, and are used to address diverse ecological questions. In conservation and stock management, timeseries analyses are used to assess population sizes and whether these sizes are declining (Dennis et al. 1991, Dennis and Taper 1994, Hilborn and Mangel 1997, Fagan 2001, Mullon et al. 2005). Time-series analyses are also used to quantify the strength of population regulation, or the stability of natural population dynamics (e.g., Kendall et al. 1999, Ives et al. 2003, Sæther et al. 2005, Brook and Bradshaw 2006, Sibly et al. 2007). Sophisticated techniques are available to search for evidence of complex population dynamics such as chaos or alternative states (Ellner and Turchin 1995, Bjornstad and Grenfell 2001, Dennis et al. 2001, de Valpine and Hastings 2002), or to anticipate incipient regime shifts in the dynamical character of ecological systems (Scheffer and Carpenter 2003, Biggs et al. 2009).

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Finally, time-series analyses using models tailored to specific species or communities have been used to extract demographic information such as reproduction rates, strengths of interaction between species, and impacts of environmental factors (Zeng et al. 1998, Coulson et al. 2001, Gross et al. 2005).

Here, we discuss statistical approaches and challenges for fitting autoregressive moving average (ARMA) models to ecological time series. The ARMA(p,q) model (where p is the dimension of the autoregressive component of the model, and q is the dimension of the moving average component) is as follows (Box et al. 1994):

$$(x_t - \mu) = \sum_{i=1}^p \beta_i (x_{t-i} - \mu) + \sum_{j=0}^q \alpha_j \varepsilon_{t-j}$$
 (1)

where x_t is a measure of population density at sample t, μ is a parameter giving the mean of the stationary process, β_i are the autoregressive coefficients, ϵ_t is a temporally independent random variable, and α_j are the moving average coefficients. Generally, population densities are log-transformed for analyses, so that Eq. 1 can be applied as a loglinear model of dynamics.

The autoregressive (AR) component of the model $(x_{t-i} \text{ terms})$ can arise ecologically from delayed effects of densities x_{t-i} on per capita population growth rates.

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These can occur, for example, in age- or stage-structured populations in which juveniles born in one year do not reproduce until several years in the future (Fromentin et al. 2001, Lande 2002, Murdoch et al. 2002). Delayed density dependence may also occur as the result of interactions among species (Turchin 1990, Turchin and Taylor 1992). For example, in simple predator-prey models that generate population cycles, the time series of prey (or predator) density exhibits a lagged density dependence, because prey born in year t-2 increase the predator density in year t-1, which in turn decreases the prey density in year t. In fact, for any nonlinear deterministic population model, Takens' theorem states that the dynamics of an n-dimensional system (e.g., n interacting species) are completely captured by a singledimensional model (e.g., for the dynamics of a single species) that includes no more than p = 2n + 1 lags (Takens 1981). For linear models, it is easy to show that only p = n lags are needed (Royama 1992).

The moving average (MA) component of the model (ε_{t-j}) terms) can arise from interactions among multiple species in a similar manner as the delayed density dependence in the AR component of the model. In fact, for any nonlinear stochastic population model, Stark and colleagues (Stark 1999, Stark et al. 2003) demonstrated that an n-dimensional system is completely captured by a single-dimensional model that includes no more than p = 2n + 1 lags in density and q = 2n lags in the process error ε_t . For linear models, this reduces to p = n AR lags and q = n - 1 MA lags.

ARMA models have at least three general, possibly overlapping uses in ecology. First, they can be used when a researcher has one or a few time series in hand and wants to investigate potential processes underlying their dynamics. When performing detailed analyses on the dynamics of a particular system, we generally advocate for a research approach involving mechanistic models tailored specifically for the system (Kendall et al. 1999). Nonetheless, fitting a simple ARMA model might be useful as a first step, for example, identifying the lagged structure of the data (i.e., values of p and q). Because it is linear, the ARMA model is the simplest model that includes lagged effects in both densities and environmental (random) fluctuations. Although ecological time series are unlikely to be linear, by the Wold representation theorem (Wold 1938) any stochastic process can be represented by a MA process that has identical statistical moments, and under mild restrictions a pure MA process can be written as an ARMA process (Box et al. 1994). Therefore, although equation 1 is linear, it can nonetheless be used to approximate any nonlinear stochastic process. In practice, this might not be a useful result, because the MA process representation may be infinite $(q = \infty)$ and the number of lags required to well-approximate the dynamics with an ARMA process may be too large to allow practical model fitting. Even in situations of strongly nonlinear dynamics, however, fitting a linear ARMA model to the data may be valuable. For example, in a study investigating nonlinear dynamical phenomena such as chaos or alternative states, a best-fitting linear model can serve as a null hypothesis against which to compare the fits of nonlinear models. This provides a test for the existence of complex dynamics that cannot be well-explained by linear processes (e.g., Ives et al. 2008).

A second use for ARMA models is to give a quantitative estimate of some qualitative descriptor of dynamics. For example, an ARMA model could be used to estimate the mean and variance of the stationary distribution of a stochastic process, or some measure of the "stability" of the process. In this case, the quantity in question is a function of the ARMA coefficients β_i and/or α_i , and we are more interested in this function than the actual coefficients. We then judge our ability to fit the ARMA model to data based on the bias and precision of the estimates of this function rather than the bias and precision of the estimates of the specific coefficients. An informative summary measure of the dynamics of a system is its characteristic return time, or more precisely, the rate at which the stochastic process approaches its stationary distribution (i.e., the distribution that a process settles to after sufficient time). The characteristic return time gives a measure of the stability of the stochastic process, with greater stability corresponding to more rapid return to stationarity.

A third use for ARMA models is to conduct broad surveys of multiple time-series data sets (e.g., Fagan 2001, Brook and Bradshaw 2006, Sibly et al. 2007, Ziebarth et al. 2009). When analyzing large numbers of time series from different sources and possibly heterogeneous systems (e.g., taxonomically diverse species), it is not practical to construct separate mechanistic, nonlinear models appropriate for each system. Instead, ARMA models can be fit to all time series, and the resulting fitted models used to compare them. In broad surveys, we are likely to be interested in functions of ARMA coefficients, like the characteristic return time discussed above, rather than the coefficients themselves. When comparing multiple data sets, the sample size is the number of data sets (rather than the number of points in any one data set). Therefore, we are more concerned about bias than precision. While we would like high precision in the individual estimates for each time series, any imprecision will merely make it harder to statistically infer patterns. Bias, on the other hand, could give us false results. The importance of bias over precision separates the use of ARMA models for broad surveys from the other two uses of ARMA models that we described above for which both bias and precision are important.

Of the three general uses we just outlined, we will focus primarily on the second and third in this paper. Therefore, we will de-emphasize estimating the values of coefficients relative to a function of the coefficients, the characteristic return time of a stochastic process. Furthermore, we will focus more on bias than precision.

Our leaning in part reflects our pragmatic assessment of available ecological time series. While a time series covering 40 years might represent an ecologist's entire career, such time series are short for statistical purposes. With short data sets, the precision of the estimates of ARMA coefficients may be sufficiently poor that the estimates are of little value. Nonetheless, estimates of functions of the coefficients may be much more precise, and comparisons among numerous data sets for which precision is less important may still be insightful. Finally, by restricting ourselves to ARMA models, we will in general only consider stationary stochastic processes, that is, processes that have a finite long-term variance. This excludes the case often investigated in population viability analyses in which populations are possibly decreasing to extinction (Morris and Doak 2002).

Our goal here is to present statistical approaches to fitting ARMA models and describe possible statistical challenges that may be encountered. We first address parameter estimation using both restricted maximum likelihood (REML) and maximum likelihood (ML) techniques. While there are other estimation approaches, for example corrected estimating equations (Staudenmayer and Buonaccorsi 2005) and the Whittle estimator (Hauser 1999), ML and REML techniques are more widely used and available in standard statistical software packages. Downward (towards zero) bias in the estimates of the AR coefficients is a well-known problem for AR(1) (Quenouille 1949, Kendall 1954), AR(p) (Cheang and Reinsel 2000), and ARMA (McGilchrist 1989) models, and theoretical and simulation studies (McGilchrist 1989, Cheang and Reinsel 2000, 2003, Kang et al. 2003) generally show that REML estimates are less biased than ML estimates. In addition to exploring bias, we also illustrate difficulties with ML and REML estimation caused when the likelihood and restricted likelihood functions are multimodal. Multimodality may cause standard statistical software to fail to find the ML and REML parameter estimates, and it may introduce a particular type of bias as the global maximum of the likelihood or restricted likelihood functions jumps among local maxima. We have not found a discussion of multimodal likelihood functions for ARMA models in the literature, possibly because attention has been focused on models with few lags ($p \le 2$, $q \le 1$) and/or longer time series.

Second, we address the issue of measurement error. Measurement error may contaminate time-series data, generating lags in the MA component of a fitted model and causing bias in the coefficient estimates (Shenk et al. 1998, Ives et al. 2003, Staples 2004, Staudenmayer and Buonaccorsi 2005, Dennis et al. 2006, Buonaccorsi and Staudenmayer 2009). Here, we investigate two approaches to incorporating measurement error into ARMA models. First, we use the well-known result that measurement error in an ARMA(p,q) model gives rise or contributes to the first p MA coefficients (Box et

al. 1994:126). Therefore, if interest is in the AR components of an ARMA model, an ARMA(p,p) (or an ARMA(p,q) if q > p) will implicitly absorb the measurement error into the MA component, leaving the AR coefficients (at least in principle) uncontaminated by measurement error (Staudenmayer and Buonaccorsi 2005, Dennis et al. 2006). Second, we incorporate measurement error explicitly by assuming that the standard error of the point estimates in a time series is known and equal for all points (homoscedastic). For this case, we use "pseudo-ML" and "pseudo-REML" estimators (Bell and Wilcox 1993, Staudenmayer and Buonaccorsi 2005) to fit the ARMA model. We treat the second approach with pseudo-ML and -REML estimators as the standard against which we judge the first, implicit, and easier approach to account for measurement error. While Staudenmayer and Buonaccorsi (2005) also make this comparison (and also consider a corrected estimating equation approach), they do this only for AR(p) models and only in detail for AR(1) and AR(2) models.

Finally, we investigate order selection (the values of pand q) for ARMA models. Generally, the order of an appropriate ARMA model is not known for a given data set, and there are several methods of model selection that have been used to estimate p and q (Shibata 1976, Liang et al. 1993, Potscher and Srinivasan 1994, Galeano and Pena 2007). We focus here on order selection using Akaike's information criterion corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989), which has been shown with simulation studies to give relatively good estimates of ARMA model order (Malgras and Debouzie 1997). Functions of coefficients, such as the characteristic return time, are defined for ARMA models of arbitrary order. Because we do not know the true order of the model, estimating the characteristic return time has to be performed in conjunction with model selection; the characteristic return time might be estimated as some value for one ARMA model but another value for an ARMA model of different order. Here, we explore two procedures, estimating the characteristic return time for the bestfitting model and using model averaging (Burnham and Anderson 2002), and determine how well they perform in estimating the true characteristic return time.

We illustrate these approaches first using three example data sets of grouse populations and then using simulations based on models fitted to the grouse data. We focus on the challenges faced when fitting ARMA models; we selected these grouse data sets specifically because they present statistical challenges, and we focus the simulations on detailing causes of the challenges.

STATISTICAL METHODS

Both REML and ML estimation for time-series data can be implemented in standard statistical packages, although for more complicated models (with p > 1 and q > 1), these may have difficulties. We used the lme()

function in R with corARMA() to structure the covariances to perform REML estimation (R Development Core Team 2008). While this performed well when p = 1, it often failed for higher-order models for two reasons. First, it often failed to converge, making it necessary to attempt different starting values for the likelihood maximization. Second, the REML likelihood functions were often not unimodal, and there is no guarantee that lme() will find the global maximum. Searching for the global maximum was hampered by the restriction for lme() that initial values for coefficients be bounded between -1 and 1, even though the true coefficient values may have considerably larger magnitude. For ML estimation we used the arima() function in R. While this did not have the convergence problems of lme(), it often did not find the global maximum likelihood when the likelihood function was multimodal. Despite these problems, lme() and arima() are useful as a first place to start analyses; example code using both lme() and arima() is given in the Appendix.

To overcome these problems of standard software routines, and to allow us to explore in more detail the difficulties of fitting ARMA models, we wrote our own code for the ARMA likelihood and restricted likelihood functions that can be used for ML and REML estimation; the derivation is given in the Appendix, along with code for both MATLAB (MathWorks 2005) and R. Although our code implements estimation differently from arima() and lme(), we confirmed that it gives identical estimates when used for ML and REML, respectively, in the cases where arima() and lme() converged on the global maximum. Because the code gives the likelihood and restricted likelihood functions, it can be used with any maximization routine that can overcome problems with finding a global maximum when there are multiple local maxima, such as simulated annealing (Kirkpatrick et al. 1983). Furthermore, while ML estimation for ARMA models generally uses a Kalman filter, as in arima() in R, and REML estimation generally uses a linear mixed model approach, as in lme() in R (although REML can be performed with a Kalman filter; Tsimikas and Ledolter 1994, 1998), our implementation uses a linear mixed model approach for both. For long time series this is not as efficient as a Kalman filter for ML estimation, but for short time series it may be faster due to the ability to condense out two parameters that hence do not need to be considered during maximization. Our code for ML and REML estimation is almost identical, differing in a single term in one line of code, making it clear how ML and REML estimation differ.

In addition to estimating coefficients of ARMA models, we also estimated a measure of the characteristic return time of the stochastic process (Ives et al. 2003). The characteristic return time is determined by $||\lambda||$ (Appendix), the magnitude of the inverse of the minimum root of the characteristic equation (Box et al. 1994). This value depends only on the AR coefficients

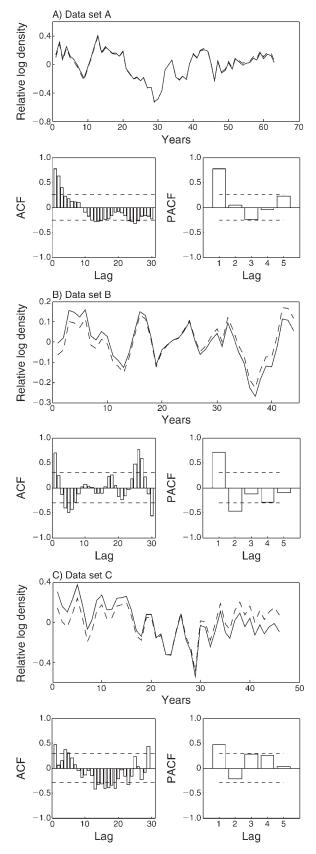
of an ARMA model. To illustrate this measure, consider the transition distribution, that is, the time-dependent distribution of x_t if the process is perturbed from the stationary distribution. Letting \bar{x}_t denote the timedependent mean of the transition distribution, the asymptotic return rate of \bar{x}_t to the mean of the stationary distribution \bar{x}_{∞} is given by $|\bar{x}_t - \bar{x}_{\infty}| = ||\lambda|| |\bar{x}_{t-1} - \bar{x}_{\infty}|$; thus, the larger the magnitude of $||\lambda||$, the slower the asymptotic rate of return. As the process approaches nonstationarity, $||\lambda||$ approaches 1 (although the estimation methods we use assume stationarity, and therefore estimates of $||\lambda||$ will always be less than 1). For models for which λ is complex, $\lambda = \gamma_r \pm \gamma_i i$, the AR components of the model generate quasi-cyclic dynamics whose characteristic period is given by $2\pi/\gamma_i$. Even though the estimates of the AR coefficients (β_i) of an ARMA model might be poor, the estimates of $||\lambda||$ might be good; this situation might arise if different sets of coefficients produce similar $||\lambda||$ values, so the statistical determination of a general feature of the dynamics (the characteristic return time) might be "easier" than the estimation of the actual coefficients.

Data sets are often contaminated with measurement error, and ignoring measurement error can lead to incorrect inferences about the dynamical properties of time series (Fuller 1996, Ives et al. 2003, Staudenmayer and Buonaccorsi 2005, Dennis et al. 2006). The ARMA(p,q) model modified to include measurement error is

$$(x_{t} - \mu) = \sum_{i=1}^{p} \beta_{i}(x_{t-i} - \mu) + \sum_{j=0}^{q} \alpha_{j} \varepsilon_{t-j} \qquad x_{t}^{*} = x_{t} + m \phi_{t}$$
(2)

where x_t is the "true" population density, and x_t^* is the observed value with measurement error given by the normal (0,1) random variable ϕ_t multiplied by m so that the measurement error has standard deviation m. The inclusion of measurement error adds MA components for lags $1, \ldots, p$ to the time series (Box et al. 1994:126). For example, if the biological processes are given by an ARMA(3,0) process, contamination with measurement error will make the time series an ARMA(3,3) process. If the biological processes are given by an ARMA(1,2) process, then measurement error will not change the order of the process, although it will contribute to the MA(1) component.

This result gives a strategy for implicitly incorporating measurement error when interest is limited to the AR components of an ARMA model; fit models with $q \ge p$ and let the MA(p) components absorb the measurement error (Staudenmayer and Buonaccorsi 2005). To assess this approach, we compared it to an alternative method (Appendix) for explicitly incorporating measurement error using pseudo-ML and pseudo-REML estimation (Bell and Wilcox 1993, Staudenmayer and Buonaccorsi 2005). To explicitly incorporate measurement error, we assume that we know the standard error m of the



measurement error term $m\phi_i$; this is equivalent to assuming that all measurements in the time series have the same standard error (for a full discussion of measurement error, see Staudenmayer and Buonaccorsi [2005]). To compare approaches, we assume that the main goal of an analysis is to assess the characteristic return time of an ARMA process, as determined by $||\lambda||$. We know measurement error in a model with AR lags up to order p will cause MA lags up to p. Therefore, if we fit an ARMA(p,p) model to the data set, are the estimates of β_i and $||\lambda||$ improved? If the implicit incorporation of measurement error by using an ARMA(p,p) performs nearly as well as the model explicitly incorporating measurement error, this shows the utility of the ARMA(p,p).

To identify the best-fitting ARMA(p,q) model (i.e., the best choices of p and q), we used Akaike's information criterion corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989, Malgras and Debouzie 1997, Burnham and Anderson 2002). We also estimated $||\lambda||$ in two ways. First, we estimated $||\lambda||$ from the single AIC_c best-fitting model. Second, we took the average of the estimates of $||\lambda||$ for all models, weighting these estimates by their AIC_c weights (Burnham and Anderson 2002). This gives a weighted consensus among models of the estimate of $||\lambda||$.

DATA SETS

To illustrate ARMA model estimation and selection, we chose three time series of grouse dynamics from 27 data sets analyzed in Williams et al. (2004). We initially selected this grouse database because we knew the time series showed cyclic dynamics, and we chose three of these specifically because they presented statistical challenges. Therefore, while these data sets serve to illustrate the strengths and limitations of different methods, they are not representative of data sets that are generally available in the literature. Data set A is from a Prairie Chicken population in Wisconsin, USA (see Plate 1); data set B is from a Ruffed Grouse population in the Upper Peninsula of Michigan; and data set C is from a Sharp-tailed Grouse population in South Dakota.

Fig. 1 presents the data, along with autoregression functions (ACFs) and partial autoregression functions (PACFs). Because researchers often detrend their data before analyses, we also present the data after simple, linear detrending (Fig. 1, dashed lines). To identify the best-fitting model (the best lag structure p and q), we

Fig. 1. Three grouse data sets. In the panels showing the time series, dashed lines give the detrended data. In panel (A), the dashed and solid lines are almost coincident. In plots of autoregression functions (ACFs) and partial autoregression functions (PACFs), the dashed lines give approximate 95% confidence bounds. Mean log densities were subtracted from log densities to give relative log densities.

Table 1. Analyses of three grouse data sets with and without linear detrending using REML estimation.

Data set	Not detrended						Detrended					
	ΔAIC_c	p	q	\lambda	Period	λ	ΔAIC_c	p	q	\lambda	Period	$ \lambda $
A	0	1	2	0.67	†	0.71	0	1	2	0.79	†	0.70
	1.07	1	0	0.80	÷		1.13	1	0	0.79	÷	
	2.13	3	0	0.61	35.9		2.13	3	0	0.60	34.7	
В	0	2	0	0.62	18.7	0.63	0	2	1	0.89	15.2	0.79
	0.46	1	1	0.59	†		0.89	2	0	0.66	14.6	
	2.53	2	1	0.68	17.1		1.30	2	2	0.84	16.2	
С	0	3	2	0.95	8.7	0.92	0	3	2	0.86	8.7	0.71
	1.04	3	1	0.99	9.4		1.69	3	3	0.80	9.3	
	2.12	3	3	0.91	9.0		1.69	3	1	0.91	9.4	

Notes: The best three ARMA(p,q) models (where p is the dimension of the autoregressive component of the model, and q is the dimension of the moving average component), as determined by AIC_c, are included. The magnitude of the dominant eigenvalue, $||\lambda||$, and the period of cyclicity are given. The symbol $||\lambda||$ denotes the AIC_c model-averaged estimate of $||\lambda||$ using all models (not just those listed).

computed AIC_cs for both raw data and detrended data using REML estimation (Table 1). For data sets A and C, detrending did not greatly change the conclusions of model fitting. For data set B the detrended data were best-fit by an ARMA(2,1) model, in contrast to the nondetrended data that were best fit by an ARMA(2,0). Furthermore, $||\lambda|| = 0.62$ for the best-fitting model of the non-detrended data, whereas $||\lambda|| = 0.89$ for the bestfitting model of the detrended data, suggesting very different characteristic return times. Given that the visual differences between the non-detrended and detrended data set B are not great (Fig. 1B), this illustrates a caution about detrending. Even simple linear detrending can change inferences about the dynamics of a data set and should be avoided unless there is clear evidence that some external condition affecting a population has changed over the course of the data collection.

Overall, model selection and the (P)ACFs give the following impression of the data sets. Data set A has a strong lag-1 AR component, although there is some ambiguity about assigning p=1 vs. p=3; this distinction in part depends on whether the lagged structure is captured by the MA component (the best-fitting model) or the AR component (the third-best model). Data set B could have p=1 or 2, whereas data set C is more securely an ARMA(3,q) process. Data set C in particular seems to have slow characteristic return rates (large values of $||\lambda||$), suggesting it is nearer to being nonstationary (i.e., showing nearly correlated random walk behavior).

SIMULATIONS

We performed simulations first to investigate the statistical properties of parameter estimation and estimation of $||\lambda||$ under the assumption that we know the true model underlying the data (i.e., the true values of p and q). For the simulations we used parameter values that are similar to those obtained by fitting the three data sets after linear detrending. Although we do not recommend detrending these data sets for analyses,

we based simulations on the detrended data because this produced parameter values giving interesting and contrasting statistical challenges for the different sets of simulations. Furthermore, we used the second-best model for data set A to give an example of a simple AR process. The simulated models are ARMA(1,0), ARMA(2,1) and ARMA(3,2) processes, and we made slight changes in coefficient values so all have $||\lambda|| = 0.85$. All simulated data sets had length 40.

Estimation

Overall, both REML and ML gave coefficient estimates that were biased towards zero (Table 2: Simulations without ME). For simulation set A (p = 1, q = 0), REML outperformed ML estimation, giving less-biased estimates of $||\lambda||$, which for an AR(1) process is identical to the absolute value of the coefficient β_1 . In contrast, for simulation set B (p = 2, q = 1), ML outperformed REML estimation, giving less-biased estimates of the coefficients and slightly less-biased estimates of $||\lambda||$. Finally, for simulation set C (p = 3, q = 2), REML provided better coefficient estimates yet more severe bias in its estimates of $||\lambda||$.

We also performed simulations with contaminating measurement error (Eq. 2) in which the standard deviation of the measurement error, m, was set equal to the standard deviation of ε_t , σ . Here, for brevity we present the results of pseudo-REML estimation, although similar conclusions were found for pseudo-ML estimation. The pseudo-REML approach (Table 2: $ARMA_ME(p,q)$) performed almost as well as fitting the ARMA(p,q) model to simulated data without measurement error contamination, illustrating the relatively good performance of ARMA_ME(p,q) in terms of bias. Fitting an ARMA(p,p) model to the data contaminated with measurement error did almost as well as ARMA ME(p,q) at estimating the AR components of the models (β_i) . In contrast, fitting an ARMA(p,q)that in no way accounts for measurement error performed much worse. These results suggest that, while explicit incorporation of measurement error can im-

[†] These cases that are not cyclic and hence do not have a period.

Table 2. Average of parameter estimates and $||\lambda||$ from 1000 simulated data sets of length 40 based on the models fitted to the detrended grouse data sets.

Model	β_1	β_2	β_3	α_1
Simulation set A				
True values Simulations without ME	0.85			
REML	0.81 (0.52, 0.98)			
ML	0.76 (0.48, 0.92)			
Simulations with ME				
REML ARMA_ME(p , q)	0.78 (0.36, 1.0)			
REML ARMA(p,p)	0.73 (-0.19, 1.0)			-0.25 $(-0.72, 0.64)$
REML ARMA(p,q)	0.56 (0.15, 0.86)			, , ,
Simulation set B				
True values Simulations without ME	1.58	-0.72		-1.00
REML	$ \begin{array}{c} 1.32 \\ (-0.17, 1.71) \end{array} $	-0.58 $(-0.87, 0.41)$		-0.83 (-2.27, 0.89)
ML	1.46 (0.34, 1.71)	-0.68 (-0.87, 0.00)		-0.90 $(-1.00, 0.51)$
Simulations with ME				
$REML\;ARMA_ME(\mathit{p},\!q)$	1.28 (-0.32, 1.82)	-0.62 (1.00, 0.42)		-0.46 (-1.54, 1.00)
REML ARMA(p,p)	1.00 (-0.86, 1.87)	-0.56 $(-1.00, 0.54)$		-0.73 (-1.99, 1.44)
REML ARMA(p,q)	0.84 (-0.57, 1.59)	-0.24 $(-0.74, 0.56)$		(-1.91, 1.00)
Simulation set C				
True values Simulations without ME	1.77	-1.5	0.6	-1.47
REML	1.48	-1.26	0.51	-1.23
ML	(-0.45, 1.96) 1.37	(-1.76, 0.22) -1.20	(-0.17, 0.81) 0.44	(-1.75, 0.96) -1.12
IVIL	(-0.56, 1.92)	(-1.71, 0.13)	(-0.24, 0.77)	(-1.77, 1.10)
Simulations with ME				
REML ARMA_ME(p , q)	1.10 (-0.92, 2.14)	-1.02 (-2.04, 0.64)	0.48 (-0.54, 0.98)	-0.63 (-1.96, 1.73)
REML ARMA(p,p)	0.97 (-0.98, 2.27)	(-2.04, 0.04) -0.74 $(-2.03, 0.73)$	0.28 (-0.81, 0.95)	-0.83 (-2.45, 1.35)
REML ARMA(p,q)	1.01 (-1.12, 1.95)	-0.83 (-1.59, 0.69)	0.25 (-0.29, 0.68)	(-2.07, 1.53) -0.90 (-2.07, 1.52)

Notes: For simulations with measurement error (ME), the standard deviation of measurement error, m, was set equal to σ , the standard deviation of the process error ε_t . The columns for β_i and α_i give coefficients for, respectively, the autoregressive and moving average components of the ARMA model (Eq. 1). Values in parentheses are 95% inclusion intervals (0.025 and 0.975 percentiles). Values of α_0 are set to 1 without loss of generality. Abbreviations are: ML, maximum likelihood; REML, restricted maximum likelihood; ARMA, autoregressive moving average.

prove estimation of the AR component of a model, simply using an ARMA(p,p) model with extended MA lags is a good strategy, especially in comparison to ignoring the effects of measurement error.

In presenting these results and making this recommendation, we have focused on bias in estimation rather than precision (variance of the estimator). The intrusion of measurement error noticeably decreased the precision of estimates of $||\lambda||$ for simulation sets A and B. For the case of the AR(1) process (simulation set A), inclusion of known measurement error (Table 2: ARMA_ME(p,q)) allowed more precise estimates of

 $||\lambda||$ in comparison to implicitly absorbing the measurement error in the MA component of the ARMA(1,1) model, as found by Staudenmayer and Buonaccorsis (2005) in a more extensive set of simulations. This phenomenon was investigated in detail by Knape (2008) who demonstrated the identifiability problem of estimating both measurement error and the autoregression coefficient β_1 of an AR(1) model. Somewhat surprisingly, the precision of the estimates of $||\lambda||$ for simulation sets B and C, ARMA(2,1) and ARMA(3,2) models, both with and without measurement error contamination is greater than for the AR(1) models of simulation

Table 2. Extended.

		112.11
α_2	α_3	λ
		0.85
		0.83
		0.81
		(0.52, 0.98) 0.76
		(0.48, 0.92)
		, , ,
		0.79
		(0.36, 1.00)
		0.76 (0.18, 1.00)
		0.56
		(0.15, 0.86)
		0.85
		0.80
		(0.46, 0.94)
		0.83 (0.58, 0.94)
		(0.36, 0.34)
		0.82
		(0.39, 1.00)
0.52		0.83
(-6.7, 1.00)		(0.38, 1.00) 0.72
		(0.35, 0.99)
1		0.85
0.93		0.89
-0.31, 1.16)		(0.70, 1.00)
0.90		0.88
-0.12, 1.00)		(0.70, 1.00)
0.85		0.95
-0.68, 1.29		(0.75, 1.00)
0.72	-0.07	0.91
-0.81, 2.32) 0.84	(-1.00, 1.00)	(0.75, 1.00) 0.88
-0.72, 1.54		(0.64, 1.00)

set A. While imprecision may make the estimate of $||\lambda||$ for a single data set uninformative, the relative lack of bias means that this approach is still useful to make comparisons among large numbers of data sets. Several studies have investigated the dynamics of a large collection of data sets (Fagan 2001, Brook and Bradshaw 2006, Sibly et al. 2007, Ziebarth et al. 2009), and for these studies the precision of the estimates is less important when questions focus on the average dynamics of the collections as a whole.

These estimation results are underlain by some unpleasant statistical features. For simulation sets B and C the likelihood functions were often multimodal (Figs. 2 and 3). To find the global maximum for the estimates in Table 2, we used both simulated annealing (a maximization approach that is suitable for multimodal functions [Kirkpatrick et al. 1983]) and knowl-

edge of the true parameter values (the values of β_i and α_j used to simulate the data). The existence of multimodal likelihood functions makes application of standard routines to fit time-series data (such as lme() and arima() in R) problematic.

For simulation set B, the likelihood functions were often bimodal. Sometimes (e.g., Fig. 2A) the restricted likelihood function was maximized at one of the local peaks while the likelihood function was maximized at the other. This led to very different REML and ML parameter estimates even though the respective likelihood functions were similar. Most of the differences in REML and ML estimates observed in Table 2 were caused by this type of phenomenon. Of 1000 simulations 37% had unimodal REML and ML likelihoods; for 35% both REML and ML were bimodal; and for the remainder only one was bimodal. The REML and ML estimates differed due to the selection of different local maxima in 6.3% of the simulations; roughly half of these resulted when one likelihood function was bimodal and

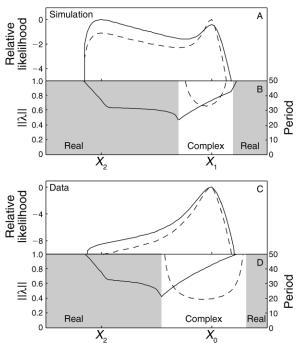


Fig. 2. Restricted likelihood (solid line) and likelihood (dashed line) functions for (A) a simulated data set and (C) data set B. Both likelihood functions are scaled to have a global maximum of 0 and therefore give relative likelihoods. Panels (B) and (D) give corresponding values of $||\lambda||$ (solid line) and the approximate period of oscillatory dynamics (dashed line). In panels (A) and (B), the points $X_1 = (1.44, -0.56, -1.00)$ and $X_2 = (-0.10, 0.49, 0.56)$ are the parameter values ($\beta_1, \beta_2, \alpha_1$) giving the local maxima of the restricted likelihood function. The likelihood functions are plotted along the line between X_1 and X_2 . In panels (C) and (D) $X_0 = (1.58, -0.72, -1)$ is the restricted maximum likelihood (REML) estimate of parameter values ($\beta_1, \beta_2, \alpha_1$) for data set B, and X_2 is the same as in panel (A). Parameter values used to generate the simulated data set are given by X_0 .

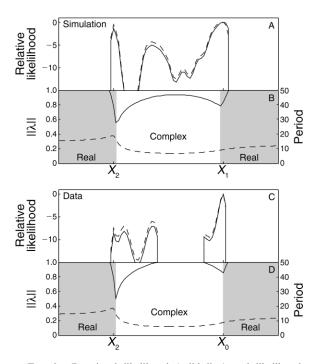


Fig. 3. Restricted likelihood (solid line) and likelihood (dashed line) functions for (A) a simulated data set and (C) data set C. Both likelihood functions are scaled to have a global maximum of 0 and therefore give relative likelihoods. Panels (B) and (D) give corresponding values of $||\lambda||$ (solid line) and the approximate period of oscillatory dynamics (dashed line). The white and gray regions show where λ (the minimum root of the characteristic equation) is complex or real. In panels (A) and (B), the points $X_1 = (1.48, -1.13, 0.49, -1.76, 1.24)$ and X_2 =(-1.29, -0.58, -0.14, 1.77, 1.00) are the parameter values (β_1 , β_2 , β_2 , α_1 , α_2) giving the locally maximum values of the restricted likelihood function. The likelihood functions are plotted along the line between X_1 and X_2 . In panels (C) and (D), $X_0 = (1.77, -1.52, 0.62, -1.47, 1.00)$ is the REML estimate of parameter values (β_1 , β_2 , β_2 , α_1 , α_2) from data set C, and X_2 is the same as in panel (A). Parameter values used to generate the simulated data set are given by X_0 .

the global maximum did not match the location of the single maximum in the other likelihood function, and the other half occurred (as in Fig. 2A) when both likelihood functions were bimodal with a mismatch between their global maxima. While mismatches between REML and ML maxima were not common (6.3%), the resulting estimates from REML and ML were so different that they caused REML and ML coefficient estimates to have differing degrees of bias (Table 2).

For comparison, we also present the restricted likelihood and likelihood functions for the actual data set B (Fig. 2C). Both likelihood functions are very similar, leading to similar REML and ML parameter estimates. Thus, the analysis of the real data set B did not suffer from the difficulties of the simulation data set we selected for illustration (Fig. 2A).

It is important to ask what attributes of time series cause these mismatches between REML and ML by

creating bimodal likelihood functions. In the vicinity of the true parameter values (X_1 in Fig. 2B), λ is complex with imaginary parts of ± 0.19 i, implying quasi-cyclic population dynamics with a period of 34 ($=2\pi/0.19$). At the alternative peak (X_2) λ is real, implying non-cyclic dynamics. The simulated data set had 40 data points, and therefore it is not surprising that support for a cycle of period 34 can only be weak. In contrast, the real data set B had coefficients corresponding to cycles of period 20 (Fig. 2D), and these were sufficiently well supported to give unimodal likelihood functions.

The likelihood functions for simulation set C are considerably more complex, having numerous local maxima (Fig. 3); there are also regions of parameter combinations for which the likelihood functions are not defined, because the AR coefficients give nonstationary dynamics (i.e., $||\lambda|| > 1$). We selected a single simulation data set (Fig. 3A, B) to show an example in which REML and ML estimation give very different parameter estimates, corresponding to points X_1 and X_2 , respectively. Despite large differences in the parameter estimates, however, the dynamics at parameter combinations X_1 and X_2 are not strikingly different. At X_1 the characteristic roots of the ARMA model are 0.84 and 0.32 ± 0.70 i, and at X_2 they are -0.78 and -0.26 ± 0.34 i. The values of $||\lambda||$ are similar, 0.83 and 0.78, respectively, and they show oscillations of period 9 and 19 years, respectively. The most striking difference is the positive real eigenvalue at point X_1 and the negative real eigenvalue at X_2 . These are coupled, however, with values of $\alpha_1 = -1.76$ at X_1 and $\alpha_1 = 1.77$ at X_2 . Thus, at X_1 the dynamics have a strong positive lag-1 autocorrelation coupled with a strong negative lag-1 MA coefficient, and at X_2 there is a strong negative lag-1 autocorrelation coupled with a strong positive lag-1 MA coefficient. The difference between the parameter sets is in how they attribute strong lag-1 effects between AR and MA processes. This illustrates how parameter estimation will be difficult when very different parameter sets nonetheless give similar dynamical characteristics of a stochastic process.

For the real data set C (Fig. 3C, D), we see that although the REML and ML likelihood functions were not unimodal, they nonetheless give very similar parameter estimates.

Estimation with model selection

In the preceding discussion, we have focused on estimation of coefficients while assuming that we know the correct model (i.e., p and q). This is generally not the case for real data. To investigate model selection, we performed similar simulations to those above but fit them to ARMA(p,q) models with p=1 to 3, and q=0 to 3 (Table 3). We assessed the fit of the models based on their abilities to estimate $||\lambda||$. We compared $||\lambda||$ estimated from (1) the AIC $_c$ best-fitting model, (2) the AIC $_c$ weighted model average, and (3) the "true" model that has the same order (p and q) as the model used to

TABLE 3. Simulation study of model selection without and with measurement error (ME).

Simulation set	Mean p	Mean q	% Correct	Best-fit $ \lambda $	λ	True model $ \lambda $
Without ME						
A $(p = 1, q = 0)$	1.19	0.20	77	0.81 (0.46, 1.00)	0.82 (0.54, 0.99)	0.81 (0.53, 0.98)
B $(p = 2, q = 1)$	1.66	0.63	29	0.73 (0.28, 0.99)	0.72 (0.42, 0.94)	0.78 (0.39, 0.94)
C $(p = 3, q = 2)$	1.9	1.01	26	0.69 (0.08, 1.00)	0.70 (0.31, 0.97)	0.90 (0.65, 1.00)
With ME						
A $(p = 1, q = 0)$						
Best-fit q	1.36	0.43	53	0.72 (0.26, 1.00)	0.74 (0.40, 0.97)	0.57 (0.16, 0.85)
q = p	1.2		84	0.78 (0.22, 1.00)	0.80 (0.33, 1.00)	
B $(p = 2, q = 1)$						
Best-fit q	1.42	1.45	3	0.63 (0.17, 1.00)	0.64 (0.39, 0.95)	0.68 (0.3, 0.98)
q = p	1.43		37	0.62 (0.12, 1.00)	0.65 (0.22, 0.98)	(,)
C(p = 3, q = 2)						
Best-fit q	1.42	0.54	5	0.52 (0.02, 1.00)	0.59 (0.28, 0.94)	0.88 (0.62, 1.00)
q = p	1.32		6	0.68 (0.03, 1.00)	0.71 (0.20, 1.00)	(1112)

Notes: Order of simulations were: A, p=1, q=0; B, p=2, q=1; and C, p=3, q=2. Four hundred simulated data sets were analyzed for each model, each with 40 points. Parameter values were from the fits to data sets A, B, and C after linear detrending, modified slightly so $||\lambda|| = 0.85$. Measurement error was simulated as a zero-mean normal random variable with standard deviation $m=\sigma$, the standard deviation of processes error ε_t . Models of order p=1 to 3 and q=0 to 3 (12 total) were fitted to each simulation except for those in which p=q (3 total). The average orders p and q were calculated from the best-fitting model for each simulation, and "% Correct" gives the percent of simulations for which the best-fitting model was the correct model (used to simulate data); for cases in which 12 (3, when p=q) models were considered, this percentage would be 8% (33%) if all models were equally likely to be selected. "Best-fit $||\lambda||$ " is the estimate from the best-fitting model, $||\lambda||$ is the AIC_c model-averaged estimate of $||\lambda||$, and "True model $||\lambda||$ " is the estimate of $||\lambda||$ from the model of correct order. For simulations with measurement error, we also performed model selection restricting models to have q=p to capture measurement error in the moving-average (MA) component of the model.

simulate the data. Although researchers will not know the true model for a given data set, we use the third estimate of $||\lambda||$ to compare with the first two estimates in order to assess the effects of uncertainty in model selection on the estimates of $||\lambda||$.

For simulation set A, AICc selected the true model 77% of the time, and the estimates of $||\lambda||$ from the bestfitting model and from model averaging were similar to those from the true model (with the correct p and q); therefore, model selection added little bias to the estimates of $||\lambda||$. In contrast, for simulation sets B and C, model selection contributed downward bias to the estimates of $||\lambda||$ when using both the best-fitting model and model averaging. The proportion of simulations in which the true model was selected was 29% and 26% for simulation sets B and C, and the estimates of $||\lambda||$ for the best-fitting model (B, 0.73; C, 0.69) and from model averaging (B, 0.72; C, 0.70) were lower than those values estimated using the true model (B, 0.78; C, 0.90). For simulation set C in particular, the imprecision in the estimates of $||\lambda||$ was increased due to model selection, with 95% inclusion intervals for estimates from the bestfitting model and model averaging of (0.08, 1.00) and (0.31, 0.97), in comparison to (0.65, 1.00) from the fitted true model

To investigate the effects of measurement error, we contaminated the simulation sets by setting $m = \sigma$ as above. We then performed model selection, first by considering all models with p = 1 to 3 and q = 0 to 3, and then by considering only those models with p = q = 1 to 3. The latter group of models implicitly incorporates measurement error since measurement error will manifest as q = p lags in the MA component of the model; here, we assume that the underlying biological process has order $q \leq p$, as is the case for our models used for simulations. For simulation set A, model selection led to less-biased estimates of $||\lambda||$ than those obtained from the "true" ARMA(1,0) model; a greater fraction of models was selected with q > 0 in the presence of measurement error, and the MA components of these models apparently absorbed some of the measurement error. For models forced to have q = p and thereby conform to the stochastic process created by measurement error, model selection added no bias to the estimates of $||\lambda||$ (compare to Table 2, Simulation set A). In contrast to simulation set A, model selection failed to compensate well for measurement error for



PLATE 1. Greater Prairie Chicken female courted by, but ignoring, a booming male. Photo credit: Roger D. Applegate.

simulation set B, giving more severely downward biased estimates of $||\lambda||$ than in the absence of measurement error. Finally, for simulation set C, only limiting model selection to ARMA(p,p) models provided some improvement in estimates of $||\lambda||$.

DISCUSSION

Time-series analyses of our three example data sets using ARMA models were valuable, identifying contrasting dynamics among data sets and giving insight into the contrasts. A single best-fitting structure for data set A (Fig. 1A) could not be identified unequivocally; models with AR lags of p = 1 and 3 were well-supported (Table 1). Data set B (Fig. 1B) appeared to have either an ARMA(2,0) or an ARMA(1,1) structure; there is a lag structure to the data, although this could be either in the AR component (p = 2) or MA component (q = 1). For data set C (Fig. 1C) all of the best models had p = 3, indicating an AR structure with relatively long lags. Even though these ARMA models are not mechanistic and therefore give no detailed insight into the biological processes generating the dynamics, they are nonetheless useful for identifying contrasting patterns; they quantify in a statistically rigorous fashion patterns that are visible yet difficult to assuredly discern among data sets.

Despite these contrasts in lagged structures among models fit to the data sets, all had values of $||\lambda||$ closer to one than zero. This implies that the dynamics were weakly determined; populations are not brought rapidly back to the mean of their stationary distribution following a perturbation. The model averaged estimates of $||\lambda||$, $||\lambda||$, were 0.74, 0.63, and 0.92 for the non-detrended data sets A, B, and C. When translated into the half-life of a disturbance, the time required for the expectation of the population density to traverse half the distance to the mean of the stationary distribution, these correspond to 2.3, 1.5, and 8.3 years, respectively.

A biologically important conclusion from these analyses is that the populations have dynamics with lagged structure. The study from which these data sets were taken demonstrated a latitudinal gradient in the cyclicity of grouse population dynamics, with populations at higher latitudes showing strong cyclicity and populations at lower latitudes lacking cyclicity (Williams et al. 2004). The three data sets we selected were all from middle latitudes. Our present analyses show strong cyclicity of period roughly 9 years for data set C, and cyclicity of period 14–19 years for data set B; if data set A is cyclic at all, the cycle period is longer than 30 years. The lagged structure in the data sets strongly suggests that there are underlying mechanisms such as interactions with other species that are driving the observed dynamics. The greater the number of lags, the more key interacting species there are likely to be (Royama 1992, Abbott et al. 2009). Our time-series analyses, or any time-series analyses, cannot identify what mechanisms generate the dynamics, but they do demonstrate that something interesting underlies the dynamics.

We have shown the need for caution when applying standard estimation techniques for ARMA models. Our simulations showed that the likelihood functions of higher-order ARMA models applied to "short" data sets (40 years) are likely to be multimodal. Dennis et al. (2006: Fig. 3) showed that likelihood functions for AR(1) models that simultaneously estimate process and measurement error can be bimodal; this occurs as the likelihood "trades off" process error against measurement error. In our case, the likelihoods for dynamically similar ARMA models are similar, and multimodality arises as the lagged structure in the data is assigned to either AR or MA components of the model. Multimodality means that the naïve application of estimation techniques may lead to mistakes, identifying

the incorrect parameter estimates that do not give the global maximum of the likelihood function. Thus, there is no substitute for investigating likelihood functions themselves; this can be done using code such as we provide in the Appendix. In addition to reducing mistakes, this also can give useful information about the data. For example, if the likelihood functions are bimodal (Fig. 2A), comparing the parameter combinations at the local maxima can identify what characteristics of the dynamics (e.g., cyclicity) are supported with high likelihoods (Fig. 2B).

Our main message is that any analysis with ARMA models should include an investigation of the likelihood functions. We have several additional recommendations and observations. First, even though ML estimation outperformed REML estimation for higher-order models, we nonetheless recommend using REML during model selection because it performed better for our firstorder (p = 1) models; for low-order ARMA models, REML generally has lower bias and higher precision than ML estimation (McGilchrist 1989, Cheang and Reinsel 2000, 2003, Kang et al. 2003). The better performance we found for ML appeared to involve cases with multimodal likelihood functions that do not occur with low-order models. Given the better performance of REML for simpler models, we feel it is reasonable to apply REML in model selection when there is no a priori knowledge of the complexity of the dynamics of a data set. If REML identifies a higherorder model, then ML estimation should be explored.

Our simulations showed that model selection often contributed to downward bias in estimates of $||\lambda||$. This bias is distinct from the bias in $||\lambda||$ during parameter estimation. The bias generated by model selection implies that model selection favors models that describe the data as being less dynamically active, with more rapid characteristic return rates, than the stochastic process generating the data. For higher-order stochastic processes ($p \ge 2$ and $q \ge 1$), AICc also tended to select models of lower order (see also Abbott et al. 2009). These results are not surprising since we investigated relatively short data sets for which identifying the true dynamical structure with longer lags might be expected to be hard. In applying the methods we developed here to 1583 time series of different lengths (Ziebarth et al. 2009), we found empirically that estimates of $||\lambda||$ with model selection increased continuously with the length of the data set, with no apparent plateau for even the longest data sets (>60).

As with other studies, we found that measurement error contaminating data sets introduces bias for parameter estimation and model selection (Shenk et al. 1998, Staudenmayer and Buonaccorsi 2005, Dennis et al. 2006, Buonaccorsi and Staudenmayer 2009). While measurement error can be explicitly incorporated into models for estimation (Bell and Wilcox 1993, Staudenmayer and Buonaccorsi 2005), we found that using the simpler approach of fitting ARMA(p,p)

models worked reasonably well to estimate the AR coefficients of the model with little excess bias. This works because measurement errors in an ARMA(p,q < p) model will produce non-zero MA coefficients of order up to p. Of course, this approach does not help to estimate the true (uncontaminated) MA coefficients of the model. Nonetheless, questions regarding the dynamical characteristics of a stochastic process center on AR coefficients, so estimates of AR coefficients may be sufficient. While the approach of fitting only ARMA(p,p) models might reduce the bias in estimates of AR coefficients and $||\lambda||$, measurement error may nonetheless decrease the precision of the estimates, leading to estimates with higher uncertainty (Staudenmayer and Buonaccorsi 2005).

Using ARMA(p,p) models to implicitly account for measurement error brings up the question of whether only ARMA(p,p) models should be considered during model selection, or whether model selection should be used to select the MA lag order (q). In our simulation study (Table 3), we found that confining the selection to ARMA(p,p) models could perform better than selection over all models when we knew measurement error was present. Nonetheless, these simulations involved large amounts of measurement error $(m = \sigma)$. With smaller amounts of measurement error, or when the true MA dimension exceeds p, restricting selection to ARMA(p,p) models may be too limiting. Overall, measurement error presented a serious challenge during model selection when the process generating data was higher order ($p \ge 2$), with the resulting estimates of $||\lambda||$ considerably biased.

In summary, fitting ARMA models to time-series data will likely give valuable information about the structure of the stochastic process generating the data. ARMA models can also be used to compare data sets; model selection and estimation can be automated, making it possible to submit a large number of data sets to the same analyses and using this to compare, for example, the characteristic return time ($||\lambda||$) among them. Fitting ARMA models needs to be done cautiously, however. We have outlined many of the challenges of fitting ARMA models. Simulations (not presented) showed that these challenges largely evaporate for data sets with 250 or more points. Unfortunately, many ecological time series do not offer the luxury of such length, so ecologists are stuck with facing these difficult, but not insurmountable, challenges.

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APPENDIX

Descriptions of the derivation of likelihood and restricted likelihood functions for an ARMA(p,q) process, including the incorporation of measurement error (*Ecological Archives* E091-062-A1).

SUPPLEMENT

MATLAB and R code for performing ARMA(p,q) model fitting (Ecological Archives E091-062-S1).