

COMPLEX POPULATION DYNAMICS IN THE REAL WORLD: MODELING THE INFLUENCE OF TIME-VARYING PARAMETERS AND TIME LAGS

ZHENG ZENG,¹ ROBERT M. NOWIERSKI,¹ MARK L. TAPER,² BRIAN DENNIS,³ AND WILLIAM P. KEMP⁴

¹Department of Entomology, Montana State University, Bozeman, Montana 59717 USA

²Department of Biology, Montana State University, Bozeman, Montana 59717 USA

³Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho 83844 USA

⁴USDA/ARS, Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah 84322-5310 USA

Abstract. We propose a class of complex population dynamic models that combines new time-varying parameters and second-order time lags for describing univariate ecological time series data. The Kalman filter and likelihood function were used to estimate parameters of all models in the class for 31 data sets, and Schwarz's information criterion (SIC) was used to select the best model for each data set. Using the SIC method, models containing density-dependent processes were selected for 23 of the 31 cases examined, while models containing complex density-dependent processes were selected in 19 of these 23 density dependence cases. The density-dependent models identified by SIC had various linear or nonlinear forms, suggesting variable patterns of population regulation in nature. Population dynamics may combine density-dependent, inversely density-dependent, and density-independent processes, which may operate at different times and under different density ranges. These results suggest that our approach offers an advance for modeling complex population dynamics, discovering complex regulation processes, and estimating the distribution of extinction times in changing environments.

Key words: complex population dynamics; density dependence; Gompertz model; information criterion; Kalman filter; maximum-likelihood function; nonlinear density dependence; nonlinear time series; population regulation; Ricker model; second order model; time-varying parameters.

INTRODUCTION

Various methods for testing density dependence and direct testing for population regulation have been proposed over the last 20 years, including the reciprocal of von Neumann's ratio test (Bulmer 1975), the major axis test (Slade 1977), the randomization test (Pollard et al. 1987), the permutation test (Reddingius and Den Boer 1989), Crowley's test of attraction (Crowley 1992), the parametric bootstrap likelihood ratio test (PBLR test, Dennis and Taper 1994), and a delayed density dependence test (Turchin 1990). Many of these tests have been widely used in density dependence studies of field populations (e.g., Gaston and Lawton 1987, Den Boer and Reddingius 1989, Turchin 1990, Vickery and Nudds 1991, Woiwod and Hanski 1992, Holyoak 1993a, b, Kemp and Dennis 1993, Wolda and Dennis 1993, Rotella et al. 1996).

None of the various density dependence tests proposed over the past two decades has been identified as being more powerful and consistent than all others under all conditions in detecting density dependence in the field. Simulation results from Pollard et al. (1987) suggested that the randomization test may be an effective tool in testing for density dependence, but Dennis and Taper (1994) found that this distribution-free

test has low power when the alternative hypothesis is a stochastic Ricker model. They also found that Turchin's (1990) method of detecting second-order lags would cause an excessive type I error rate. Holyoak (1994) found that Turchin's (1990) method was not capable of reliably distinguishing between delayed and nondelayed density dependence. Holyoak and Lawton (1993) and Holyoak (1994) found that the PBLR test identified density dependence less frequently in some insect time series data than using the randomization test of Pollard et al. (1987). However, the PBLR testing approach is not limited to the Ricker model, but may be applied to other dynamic models if diagnostics or prior evidence indicate the Ricker model is not appropriate (Dennis and Taper 1994, Rotella et al. 1996). Moreover, inconsistent results have been frequently reported if more than one density dependence test was used (e.g., Den Boer and Reddingius 1989, Woiwod and Hanski 1992, Holyoak 1993a, b). For a more detailed review and comparison of density dependence test methods refer to Holyoak (1993a, b), Dennis and Taper (1994), and Fox and Ridsdill-Smith (1995).

Using simple modeling approaches and test techniques, early studies rarely found density-dependent processes in the field (e.g., Stiling 1987, 1988, 1989, Den Boer and Reddingius 1989, Murdoch 1994). This has stirred considerable controversy (Dempster and Pollard 1986, Brown 1989, Hassell et al. 1989). As a

consequence of the infrequent detection of density-dependent processes, some authors have questioned equilibrium theory (Strong 1986, Wolda 1989, 1991, Krebs 1992). Krebs (1992) declared that "it is clear that only after you reject such a paradigm (density dependence) can much progress be expected." Others supported the concept as a logical necessity (Royama 1977, 1992, Berryman 1991, Murdoch 1994). Long-term persistence of populations was asserted by Royama (1977, 1992) to necessarily imply a negative correlation between per unit abundance growth rate (per capita growth rate) and population size. Thus, the persistence of many populations and species is taken by some as evidence of population regulation (Royama 1977, 1992, Berryman 1991, Murdoch 1994). Some have blamed spatial heterogeneity for the inability to detect density dependence in intergeneration data (Hassell 1985, 1987, Hassell et al. 1987), or use of short time series for the failures to detect population regulation (Turchin 1995). Others argued that statistical estimation and model evaluation of the complex dynamics should be emphasized to solve the problem of low power, which has been an inherent problem with many of these tests (Hanski et al. 1993, Dennis and Taper 1994, Wolda et al. 1994, Turchin 1995). In fact, recent and extensive analyses of ecological time series based on improved statistical techniques are now finding density dependence in substantial proportions of the cases investigated (Woiwod and Hanski 1992, Holyoak 1993a, b, Kemp and Dennis 1993, Wolda and Dennis 1993, Dennis and Taper 1994).

However, the utility of such results is limited. First of all, there are inherent problems in the interpretation of statistical tests of density dependence, due to the lack of tight correspondence between the scientific hypothesis and the statistical hypothesis (Royama 1977, Wolda and Dennis 1993, Wolda et al. 1994). Second there are potential problems with model misspecification. Density dependence is a complex phenomenon that may involve consumer–resource, predator–prey, pathogen–host, intra- and interspecific interference, and other ecological interactions. Such relationships may not be well described by simple models.

Most statistical tests of density dependence were designed to test simple correlation, simple dependence, or the effect of dependence between per unit abundance growth rate and population density, with less focus on the dynamics (e. g. Bulmer's test, Bulmer 1975; major axis test, Slade 1977; randomization test, Pollard et al. 1987; permutation test, Reddingius and Den Boer 1989; Crowley's test of attraction, Crowley 1992; PBLR test, Dennis and Taper 1994). The key problem in density dependence tests may be that the density-dependent model in many statistical test methods is far too simple and removed from biological reality to cover the various complex population dynamics encountered in the field (Turchin 1990, Hanski et al. 1993, Wolda et al. 1994, Zeng 1996). The diversity in patterns of natural

population regulation also poses a problem for the classical hypothesis-testing framework used in these tests, where a single null model is contrasted with a single alternative model, and the alternative model may not indicate how the population is regulated in the field (Hanski et al. 1993, Zeng 1996). Because our intention is to detect the population regulation patterns in the field, hypothesis testing can at best convey only limited information.

Recently, Hooten (1995) explored the use of information criteria to select the best population dynamic model of six constant-parameter models (zero- and first-order lag), rather than pairwise hypothesis testing. Among other things, this procedure determines whether the best model selected using information criteria incorporates density dependence. Such an approach offers greater flexibility and provides additional information beyond what can be obtained from traditional statistical tests of density dependence based on ecological time series data. The information criterion approach will be emphasized and improved in this study.

Our purpose in this paper is to develop procedures that more effectively characterize the dynamics of a natural population. To do this we fit a broad suite of population dynamic models, some with great flexibility, to univariate time series of field populations. We select a "best model" from amongst these models using Schwarz's information criterion (SIC, Schwarz 1978). One of the major advances we make is the introduction of the Kalman filter to the study of time-varying parameters in population dynamics. A substantial proportion of the population dynamic models we studied were identified as showing time-varying parameters. By including time-varying-parameter models as well as other linear and nonlinear models of complex population dynamics, such as delayed density dependence, we increase our understanding of the biological system and our ability to predict its further behavior.

MODEL DESCRIPTION

Theoretically, the simple population dynamics of an organism can be characterized by an intrinsic growth rate and a density-mediated effect. The parameters corresponding to these can be used to express the interactions between an organism and its environment. Two stochastic models that have incorporated similar parameters in modeling animal population dynamics include the stochastic Ricker model (Ricker 1954; also referred to as a discrete time stochastic exponential logistic model, Dennis and Taper 1994) and the stochastic Gompertz model (Dennis and Taper 1994). The general form of both types of models can be represented as follows:

$$N_t = N_{t-1} \exp[a + bf(N_{t-1}) + \varepsilon_t]. \quad (1)$$

If we let $X_t = \ln(N_t)$, then Eq. 1 becomes

$$X_t = X_{t-1} + a + bf(N_{t-1}) + \varepsilon_t \quad (2)$$

or

$$R_t = X_t - X_{t-1} = a + bf(N_{t-1}) + \varepsilon_t. \quad (3)$$

Here, N_t is population density at time t ($t = 1, 2, \dots, T$; T is the number of the observations), R_t is the realized per unit abundance growth rate, and ε_t is a normally and independently distributed (NID) random variable with mean zero and variance σ^2 , which we term system noise. Parameter a is the population growth rate related to the intrinsic growth rate of deterministic models (see Dennis and Taper 1994), and b is the density dependence parameter. A stochastic Ricker model can be obtained from Eq. 1 by applying a Ricker transformation ($f(N_t) = N_t$), while the Gompertz model can be obtained from Eq. 1 by applying a Gompertz transformation ($f(N_t) = \ln(N_t)$). According to Dennis and Taper (1994), when $b < 0$ or $b > 0$, density-dependent or inversely density-dependent processes are implied, respectively. When $b = 0$, a density-independent population process is implied.

Models explicitly incorporating more than one time lag and/or parameters that change through time are referred to as complex population dynamic models in this study. Such population dynamic processes are not represented well by the stochastic Ricker or Gompertz models. When the information on fluctuations in resource availability, dynamics of natural enemies and other density-dependent factors is unavailable, models with time-varying parameters and high-order lags can be used to describe the influence from these unknown density-dependent factors on population dynamics (Zeng 1996). Mathematically, a time series with dynamics described by a nonlinear stochastic dynamic function with autoregressive moving average terms can, under certain assumptions, be approximated by a linear time-varying-parameter model via standard Taylor series linearization techniques (Young 1994).

The structural population dynamic process developed in our study incorporates time-varying growth rate and density dependence parameters. This process also incorporates population dynamics as a function of these parameters and previous population density. A fourth class of models arises when time-varying density dependence parameters are considered. The population dynamics are termed indeterminate if the density dependence parameters take on values during the time from two or more of the following categories: $b < 0$, $b > 0$, and $b = 0$ (Strong 1986, Brown 1989). Little attention has been paid in the literature to the formulation of models for indeterminate density dependence.

The first-order time-varying parameter process is a modification of Eq. 2 obtained by allowing the parameters a and b to follow the first-order autoregressive models:

$$X_t = X_{t-1} + a_t + b_t f(N_{t-1}) + \varepsilon_t \quad (4)$$

$$a_t = a + \phi_a(a_{t-1} - a) + \omega_{a,t} \quad (5)$$

$$b_t = b + \phi_b(b_{t-1} - b) + \omega_{b,t}. \quad (6)$$

TABLE 1. Time-varying parameter structure of population-dynamic models used in this study (Ar = First-order autoregressive; Rw = Random walk; Rc = Random coefficient; Cp = Constant parameter; P = Presence of system noise; A = Absence of system noise).

a_t	b_t	ε_t	a_t	b_t	ε_t	a_t	b_t	ε_t
Ar	Ar	P	Rw	Ar	P	Cp	Ar	P†
Ar	Ar	A	Rw	Ar	A	Cp	Ar	A
Ar	Rc	P	Rw	Rc	P	Cp	Rc	P
Ar	Rc	A	Rw	Rc	A	Cp	Rc	A
Ar	Rw	P	Rw	Rw	P	Cp	Rw	P
Ar	Rw	A	Rw	Rw	A	Cp	Rw	A
Ar	Cp	P	Rw	Cp	P	Cp	Cp	P‡
Ar	Cp	A	Rw	Cp	A	Cp	...	P§
...	...	P						

† Constant-growth-parameter models can be considered as random-coefficient models (e.g., CpArP = RcArA). The system noise ε_t and parameter noise $\omega_{a,t}$ might be mixed and considered as a single noise term in the model, when the growth rate is considered as a random coefficient.

‡ Ricker or Gompertz model.

§ Exponential-growth model.

|| Random-walk model.

Here a and b are central values (i.e., the unconditional mean) of the growth and density dependence parameters, respectively (the parameters a and b in Eqs. 2 and 3 can be considered central values of the stationary processes). Parameters ϕ_a and ϕ_b are autocorrelation coefficients of parameters a and b , respectively. Also, $\omega_{a,t}$ and $\omega_{b,t}$ are NID random variables with mean zero and variance σ_a^2 , σ_b^2 , respectively, and refer to parameter noise. Special cases of the first-order autoregressive parameter model include random-coefficient models (Rc; $b_t = b + \omega_{b,t}$), parameter-random-walk models (Rw; $a_t = a_{t-1} + \omega_{a,t}$, $b_t = b_{t-1} + \omega_{b,t}$), and constant-parameter models (Cp; $a_t = a$, $b_t = b$). Twenty-five different model structures were obtained by combinations of various parameter changes of a_t and b_t (Table 1). The letters A and P are used after the codes for growth rate and density dependence parameters to indicate whether the system noise is absent ($\sigma^2 = 0$) or present ($\sigma^2 > 0$). For all models, except for the random-walk and exponential-growth models, a code of R or G was used in the classification to indicate whether a Ricker or Gompertz transformation was used. The CpRcP-G model (i.e., constant-growth-rate parameter (Cp) and random-coefficient density dependence parameter (Rc) model with the Gompertz transformation (G) and the system noise present (P)) is the same as that presented by Royama (1977).

To expand the class of models to cover more complex dynamics, second-order stochastic Ricker and Gompertz models were included. The constant-parameter, second-order Ricker, and Gompertz models can be expressed as follows (Moran 1953, Royama 1977, 1981, 1992, Berryman 1978, Turchin 1990, Turchin et al. 1991, Dennis and Taper 1994):

$$X_t = X_{t-1} + a + b_1 f(N_{t-1}) + b_2 f(N_{t-2}) + \varepsilon_t. \quad (7)$$

ArCpA models and second-order models can be used

to describe the results of interactions between two species (Royama 1977, 1981, 1992, Berryman 1978, Turchin 1990) and internal population biological processes (e.g., the negative effects of high population density on the fecundity of the next generation, Prout and McChesney 1985, Turchin 1990). The ArCpA models in Table 1 can be expressed as either a second-order Gompertz model (i.e., ArCpA-G) or in a form similar to the second-order Ricker model (i.e., ArCpA-R, Zeng 1996). A total of 50 models were considered in this study, based on the models in Table 1 and the second-order models. These include: 23 first-order model and one second-order model in Ricker form, 23 first-order models and one second-order model in Gompertz form, one random-walk model, and one exponential-growth model. For more about considering the parameters b_1 and b_2 in second-order models as random coefficients, refer to Zeng (1996).

PARAMETER ESTIMATION

All models except for random-walk and exponential-growth models were expressed in state space form to take advantage of Kalman filter techniques. The state space form contains the system and one step transition state equations. The system equation in this study describes the dynamics where the observable variable (X_t) at time t is determined by the state vector at time $t - 1$ and the lag variables related to X_{t-1} , or to X_{t-1} and X_{t-2} . The state equation represents the dynamics of the various unobserved components (i.e., the state vector) at time t , determined by the state vector at time $t - 1$ and noise at time t . The state space model represents the most efficient condensation of information contained in the past and present about the future (Tong 1990). However, population dynamics expressed in state space form are nothing more than linear or nonlinear autoregressive models in which the parameters change over time. Based on state space form, the Kalman filter provides the means to predict, update, and smooth the state vector. As an example, the state space form for model ArArP, where both growth and density dependence parameters follow the first autoregressive model and where system noise is present, is

$$X_t = \mathbf{Z}_t \mathbf{A}_t + X_{t-1} + \varepsilon_t, \tag{8}$$

$$\mathbf{A}_t = \Phi \mathbf{A}_{t-1} + (\mathbf{I} - \Phi) \mathbf{B} + \Omega_t \tag{9}$$

where $\mathbf{Z}_t = [1, f(N_t)]$, $\mathbf{A}_t = [a_t, b_t]^T$, $\Phi = [(\phi_a, 0); (0, \phi_b)]$, $\mathbf{B} = [a, b]^T$, $\mathbf{I} = [(1, 0); (0, 1)]$ and $\Omega_t = [\omega_{a,t}, \omega_{b,t}]^T$. \mathbf{A}_t is called the state vector at time t , and Eqs. 8 and 9 are called the system equation and state equation, respectively. Other types of time-varying-parameter models can easily be obtained by changing the parameter values. For example, if we let $\phi_a = 1$ and $\phi_b = 1$, the above model will become RWRWP. This structural population dynamic model (Eqs. 8 and 9) is known as a conditionally Gaussian model. Kalman filter analysis

can be used to estimate parameters in this nonlinear population dynamic model.

When all parameter values in the state space model are known, the Kalman filter uses a recursive algorithm for estimating the conditional mean and covariance of the state vector based on the information available at time $t - 1$, and updating related estimates, when the information at time t is available. The Kalman filter finally smooths the estimates of conditional mean and covariance to utilize all information in the time series data (Kalman 1960, Harvey 1989a). The prediction, updating, and smoothing equations represent three parts of the Kalman filter (Eqs. A.1 and A.2, A.3 and A.4, and A.5 and A.6, respectively, in the Appendix).

SAS PROC IML (SAS 1988) was used to program the Kalman filter, and a trust region nonlinear optimization method (NLPTR, starting with release 6.08, Hartmann 1994) in the NLP subroutines in SAS IML was used to maximize the likelihood function. The approximate derivatives for the gradient vector and Hessian matrix used for some nonlinear optimization methods can be automatically calculated by built in functions, using finite differences. SAS IML provides an efficient way to program the Kalman filter and maximum-likelihood function because of the great flexibility of various nonlinear subroutines. The execution of the program usually takes <2 min with a PC 486/DX2-66 computer to finish the optimization for one model. However, it is important to note that sometimes the optimization may fail due to lack of convergence in parameter estimation.

MODEL SELECTION

In order to identify the best density-dependent-model form for the given ecological time series, we need to use goodness-of-fit statistics to select a model form among alternative models that either best approximates the generating mechanisms, or offers the best prediction of the data. The value of the maximized log-likelihood function (Eq. A.9) is a measure of the goodness-of-fit statistic. Generally, models with more parameters have higher maximized likelihood values. However, this by itself may not determine which is the most appropriate model, because excessively large confidence and prediction intervals may occur in overparameterized models. Information criteria are model selection methods that adjust the value of the maximized likelihood function for the number of parameters, for the sample size, or for both, to select the best model among alternative models. Information criteria take the form of the negative log-likelihood plus some penalty terms, which increase with the number of parameters and the sample size (Scllove 1987). One of the advantages of using information criteria is their computational simplicity for comparing different models. Additionally, the models compared can be nested or non-nested (Takane 1987, Harvey 1989b).

Many authors (e.g., Koehler and Murphree 1988,

Hooten 1995) have verified that SIC (Schwarz 1978) offers greater consistency than other information criteria in identifying the appropriate model. A number of information criteria were compared by Hooten (1995) for selection of the appropriate model form in studies of density dependence. The SIC method was found to be the most appropriate information criterion for identifying the best model among six alternative models considered. It should be noted that in using SIC, there is a slight tendency to choose lower order models, which makes identification of complex dynamics conservative (Hooten 1995). Based on Monte Carlo simulation, Zeng (1996) also found a conservative model selection among time-varying and constant-parameter models using SIC.

SIC, sometimes called the Bayesian information criterion (BIC), is denoted as follows:

$$\text{SIC} = -2 \ln(L) + k \ln(n - \tau) \quad (10)$$

where $\ln(L)$ is the maximized log-likelihood, k is the number of parameters, n is the number of free observations used in the maximum-likelihood function ($n = T - [\text{no. of terms related to the initial observations dropped in the maximum-likelihood function}]$), and τ is the number of observations missing. In this study, we used SIC to select the best model among the classes of density-dependent and density-independent models.

The model that produces the minimal SIC value is defined as the best model for describing the particular time series data set. The number of free observations for the ecological time series varies with the model, and the value of the information criterion varies with the sample size. For comparative purposes, all SIC values were adjusted by multiplying the value by $(T - 1)/(T - O)$, where O is the order of the model. For example, the order of the NID model is zero, the order of the random-walk model is one, and the order of the second-order model is two. This method is similar to using the mean information criterion value (i.e., the information criterion value divided by the number of free time series observations in the analysis, Tong 1990, Hooten 1995). In this study, a Ljung and Box (1978) Q test statistic was used to test simultaneously if all orders of the autocorrelation of the residuals up to M were zero, where M is the maximum order of the autocorrelation considered in the test (see the Appendix).

DATA SETS

Sixteen insect census data sets were used to test our modeling approach (Table 1 from Den Boer and Reddingius 1989). These included some famous historical examples in population ecology (e.g., pine looper, *Bupalus piniarius*, Klomp 1966; winter moth, *Operophtera brumata*, Varley et al. 1973; viburnum whitefly, *Aleurotrachelus jelinekii*, Southwood and Reader 1976). Current test methods have frequently failed to detect density dependence in these data sets (Den Boer

and Reddingius 1989, Dennis and Taper 1994), and parts of them have been used to address many controversies in population regulation (e.g., Den Boer 1986, 1987, 1988, Gaston and Lawton 1987, Hassell et al. 1987, Latto and Hassell 1987, Southwood and Reader 1988, Vickery and Nudds 1991, Dennis and Taper 1994, Hooten 1995).

In addition, three 60-yr insect census data sets from German forests (Schwerdtfeger 1941), one insect data set from Morris (1959), three vertebrate data sets used in Dennis and Taper (1994), three vertebrate data sets used by Hooten (1995), four vertebrate data sets from Keith (1963), and a *Lynx* data set from Elton and Nicholson (1942) were reanalyzed by this new modeling approach. All data sets and their original sources used in this study are available from the senior author, and these can also be found in Zeng (1996).

RESULTS

Model selection results for the first four best models based on SIC, and the difference of the SIC values between the first best model and additional three best models selected for 31 data sets, are shown in Table 2. The best model for each of the 31 data sets was determined by evaluating the SIC and selecting the model with the minimum information criterion value for each data set. Table 2 indicates the strength of model separation among the first four best models in describing the population dynamics, and the frequency of the particular models occurring among the first four best models. In Table 2, smaller SIC value differences (i.e., those < 1 , as recommended by Sakamoto et al. 1986, page 84 and Burnham and Anderson 1992) between the first best model and any other best model are inexplicable due to uncertainty in the model selection processes, while larger differences in the SIC values are more plausibly attributable to meaningful differences in the applicability of these models to the data (e.g., in density-dependent or density-independent models). The percentage of the examples in which certain models occurred among the best four models were 15% for the random-walk model, 6% for exponential growth, 8% for Ricker, 13% for Gompertz, 9% for second-order Ricker, and 11% for second-order Gompertz. As a group, the 44 time-varying density-dependent models were included in the best four models 38% of the time. Density-independent models were included in the best four models in only 21% of the cases. The results in Table 2 thus suggest that the use of any single density-dependent model form, such as time-varying-parameter models, the Ricker model, Gompertz, or second-order models may not maximize the detection of the density dependence in the field populations using statistical hypothesis testing.

Parameter estimates and model selection results based on SIC for each population are presented in Table 3. Models selected using this criterion included: seven random-walk, two Ricker, two Gompertz, five second-

TABLE 2. The best four models according to the Schwartz information criteria (SIC) and the difference of the SIC (dSIC) between the first best model and other best model selected, based on SIC information criteria.

Species	1st	2nd	dSIC (1st-2nd)	3rd	dSIC (1st-3rd)	4th	dSIC (1st-4th)
1) <i>Operophtera brumata</i> larvae	R(2)	RW	1.613	G(2)	1.943	G(1)	3.354
2) adults	CpRcA-G	CpArA-G	1.745	R(1)	2.886	RW	3.276
3) <i>Bupalus piniarius</i> larvae	CpRcA-R	CpArA-R	1.449	CpRcP-R	2.153	CpRcA-G	2.474
4) larvae (Sept.)	CpRcA-R	CpArA-R	1.130	CpRcP-R	2.385	CpArA-G	3.346
5) pupae	G(1)	RW	0.292	ArCpA-G	2.564	EG	2.856
6) adults	G(1)	G(2)	1.935	ArCpA-G	2.560	R(2)	3.557
7) <i>Bupalus piniarius</i> pupae	R(2)	R(1)	0.310	RW	1.270	ArCpA-R	1.551
8) <i>Phyllopertha horticola</i>	RW	EG	3.277	G(1)	3.842	R(1)	5.724
9) 3rd instar Hawes End Farm	G(2)	ArCpA-R	1.001	CpRcA-R	1.632	ArCpA-G	2.015
10) <i>Zeiraphera diniana</i>	G(2)	ArCpA-G	20.500	R(2)	21.740	RW	22.778
11) <i>Choristoneura fumiferana</i>	RW	G(1)	1.863	R(1)	2.433	EG	2.528
12) 3rd instar larvae	RW	G(1)	0.253	G(2)	0.408	R(1)	0.699
13) <i>Aleurotrachelus jelinekii</i>	R(2)	G(2)	6.990	R(1)	9.401	EG	11.620
14) 4th instar larvae, pop. 2	R(2)	G(2)	0.551	RW	1.094	EG	2.748
15) 4th instar larvae, pop. 3	CpRcA-P	G(1)	1.428	CpArA-G	2.040	RW	2.642
16) <i>Nebria brevicollis</i> adults	RW	G(1)	0.574	ArCpA-R	1.157	ArCpA-G	1.314
17) <i>Acleris variana</i>	G(2)	R(2)	0.193	RW	10.198	ArCpA-G	10.808
18) <i>Panolis flammea</i>	CpRcP-G	CpArA-G	2.909	ArRwA-G	3.123	CpArP-R	3.919
19) <i>Dendrolimus pini</i>	CpRcP-G	RwArA-G	0.404	CpArP-G	2.343	ArCpA-G	4.071
20) <i>Bupalus piniarius</i>	G(2)	ArCpA-R	1.656	G(1)	3.856	ArRcA-R	5.652
21) <i>Ursus arctos horribilis</i>	CpArA-G	ArCpA-G	0.393	ArCpA-R	0.421	G(2)	0.795
22) <i>Cervus elaphus</i>	R(1)	R(2)	2.546	CpRcA-G	2.815	G(1)	3.342
23) <i>Cervus elaphus</i>	R(1)	CpRcA-G	0.868	G(1)	1.021	RW	2.614
24) <i>Cervus elaphus</i>	CpRcA-G	G(1)	0.074	R(1)	0.400	ArCpA-G	3.050
25) <i>Anas strepera</i>	RW	R(1)	0.505	G(1)	1.422	CpRcA-G	2.508
26) <i>Anas platyrhynchos</i>	RW	EG	2.694	G(1)	3.427	CpRcA-G	3.431
27) <i>Vulpes</i> spp.	G(2)	ArCpA-G	2.022	R(2)	4.732	RW	5.348
28) <i>Canis latrans</i>	R(2)	G(2)	0.653	RW	1.193	ArCpA-G	1.371
29) <i>Mustela vison</i>	RW	EG	3.504	CpRcA-G	4.059	G(1)	5.413
30) <i>Ondatra zibethica</i>	G(2)	G(1)	0.269	ArCpA-G	1.561	RW	3.352
31) <i>Lynx canadensis</i>	G(2)	R(2)	2.522	ArCpA-G	38.725	CpArA-G	40.379

Note: Data sets nos. 1-16 were from Den Boer and Reddingius (1989). Data set no. 17 was from Morris (1959). Data sets nos. 18-20 were from Schwerdtfeger (1941). Data sets nos. 21-23 were from Dennis and Taper (1994). Data sets nos. 24-26 were from Hooten (1995). Data sets nos. 25-30 were from Keith (1963). Data set no. 31 was from Elton and Nicholson (1942). G(1) = Gompertz model; R(1) = Ricker model; G(2) = second-order Gompertz model; R(2) = second-order Ricker model; RW = random walk model; EG = exponential growth model.

order Ricker, seven second-order Gompertz, three CpRcA-G, two CpRcA-R, one CpArA-G, and two CpRcP-G models. Data are categorized as density dependent or density independent simply by noting whether the best model is in the family of density-dependent models or in the family of density-independent models (Hooten 1995).

The results from the comparison of the best density-independent and best density-dependent models selected using SIC are also listed in Table 3. For the 31 cases in Table 3, the model yielding the lowest SIC values was density dependent in 23 cases, density independent in seven cases, and inversely density dependent in one case. But invoking the above-mentioned one-unit criterion for distinguishing SIC values (Sakamoto et al. 1986, Burnham and Anderson 1992) resulted in 22 cases of density dependence, only four of density independence, one of inverse density dependence, and four cases that could be either density dependent or density independent (i.e., nos. 5, 12, 16, and 25). Models featuring complex population regu-

lation were selected in 19 of the 22 unambiguous cases of density dependence.

A. jelinekii population one (no. 13 in Table 3) was identified as a second-order inversely density-dependent process, because of the positive coefficients. According to Southwood and Reader (1976), the resources for *A. jelinekii* population one and population two increased considerably during the experimental period. The use of the total count of the population instead of population density per unit resource may obscure possible density-related influences of resource availability and violate some assumptions of the models (Zeng 1996).

One advantage in using dynamic modeling of ecological time series is that one may further improve the SIC and prediction by using a model with fewer parameters based on current modeling results. For example, the estimate of the density dependence parameter for the *B. piniarius* pupal population (no. 5 in Table 3) based on the Gompertz model is close to negative one ($\hat{b} = -0.669$, $SE = 0.258$). We attempted to im-

prove the fit by setting the density dependence parameter value to negative one. This is identical to a model in which log-population size is the NID process ($X_t = a + \varepsilon_t$). Using the NID model, we obtained the adjusted SIC value of 41.382. This SIC value was smaller than the SIC value obtained using the Gompertz model (42.474) in Table 3, which suggests a higher likelihood for the NID model to be the best model, since the model has fewer parameters, and the penalty is less. It should be noted that the difference in the SIC values among random-walk and NID models is larger than one unit compared with the results achieved in Table 3, due to the finding of a more appropriate model form. The mean and variance parameters in the NID model here are based on the maximum-likelihood estimates of the mean and variance (i.e., mean and population variance). The SIC value for the NID model is adjusted to $(T - 1)SIC/T$, because one more observation is considered in computing the maximum-likelihood value for the NID model than for first-order models.

A similar procedure was carried out for *O. brumata* larvae, *B. piniarium* adults, and *C. elaphus* populations (nos. 1, 6, and 24 in Table 3, respectively). By setting $b_1 = 0$ in the second-order Gompertz model and re-estimating parameters for the *O. brumata* larval population, we obtained an adjusted SIC value of 53.972, which is smaller than that from the best model (second-order Ricker model, $SIC = 54.881$) in Table 3, suggesting a better fit of the data. For *B. piniarium* adults, an adjusted SIC value of 40.832 was obtained using the NID model, which is smaller than the SIC value (42.861) in Table 3. This suggests that the *B. piniarium* adult population can be better modeled using the NID model. For the *C. elaphus* population, by setting $b = -1$, for both Gompertz and CpRcA-G models and re-estimating parameters, we obtained the adjusted SIC value of -36.769 and SIC value of -41.30 , respectively. The smaller SIC value in the latter case suggested that a time-varying noise model ($X_t = a + X_{t-1}\varepsilon_t$) was the more appropriate model form.

A density-dependent model was found to fit the grizzly bear data (*Ursus arctos horribilis*) better than the density-independent models. In order to consider if the central b (i.e., the unconditional mean of the density dependence parameter) is equal to zero in the autoregressive density dependence parameter for the grizzly bear data set, we set $b = 0$ and obtained the following parameter estimates, $\hat{a} = 0.0394$, $\hat{\phi}_b = -0.648$, $\hat{\sigma}_b^2 = 5.65 \times 10^{-4}$, and $SIC = -23.482$. The slightly smaller SIC value compared to the SIC value, -22.429 , in Table 3, suggests that the central b may actually be zero. Because the b_t values range from positive to negative, the population dynamics of the grizzly bear may include density-dependent, inversely density-dependent and density-independent processes. The negative autocorrelation among these b_t values is especially interesting. But certain features of the grizzly bear data, such as the 3-yr moving average and the likelihood that

the same individuals were recounted in subsequent years, make this autocorrelation pattern much more difficult to interpret and suggest that firm conclusions must await more detailed studies of this population.

In the first 16 data sets in Table 3, density-dependent models were selected in 10 out of 16 cases, while one ambiguous case and one case of inverse density dependence were found using SIC. In contrast, Den Boer and Reddingius (1989) detected a density-dependent process in none of 16 using the randomization test of Pollard et al. (1987), 3 of 16 using Bulmer's test, and 1 of 16 using the permutation test of the same data sets. Dennis and Taper (1994) rejected density independence in two of the data sets using the PBLR significance test and using the exponential-growth model as the null model. Using constant-parameter models and a model selection approach based on SIC, Hooten (1995) identified the density-dependent model as the best model in 9 out of 16 cases. Both *B. piniarium* pupae and adults (numbers 5 and 6 in Table 3), were identified as independent, identically distributed (IID) models by Hooten (1995), who applied empirical density distribution estimation techniques to estimate the density distribution. More density-dependent models were selected here by using the time-varying-parameter approach and second-order models than in previous studies.

Four types of complex regulation models (CpRcA, CpArA, CpRcP, and second-order models) were found among 31 data sets (Table 3). Time-varying density dependence parameters were found in 6 out of 20 insect data sets examined, and 2 out of 11 vertebrate data sets using SIC. Among the time-varying-parameter models, the random-coefficient parameter model seemed to be the model selected more frequently in animal populations than other time-varying models. The random-walk-parameter model seemed to be identified less frequently as the best model (Table 2). The advantage of using the random-walk-parameter model is that it can approximate some linear and nonlinear parameter trends (Zeng 1996). Two out of 20 insect data sets, and two out of 11 vertebrate data sets were not categorized as density dependent using one-unit criterion of SIC. This may have been due to small sample size, a specific period of time in the time series where density dependence was absent or weak in the data, or misspecification of the model. Model misspecification may be identified with the Ljung and Box Q test. Results in Table 3 show that the error terms for some of the best models selected were not IID, and further improvement of the population dynamic models is needed.

Time-varying changes in the density dependence parameter might be expected under unstable natural-enemy performance (Royama 1977), and/or fluctuations in resource availability. A combination of density-dependent, inversely density-dependent, and density-independent processes may exist in the populations with a time-varying density dependence parameter, as the \hat{b}_{VT}

TABLE 3. Results of parameter estimation and fit of population time series data.

Species	No. of observations	Density-independent model [†]			Density-dependent model		
		$\hat{\sigma}^2$	$\ln(L(\mathbf{X}, \mathbf{W}))$	SIC	Model type [‡]	\hat{a} (SE)	\hat{b}_1 or \hat{b} (SE)
1	19	1.150	-26.802	56.494	R(2)	0.938 (0.344)	-0.00348 (0.0024)
2	19	0.783	-23.338	49.567	CpRcA-G	1.049 (0.0484)	-0.542 (0.104)
3	15	1.310	-21.757	46.153	CpRcA-R	1.029 (0.105)	-0.084 (0.0269)
4	15	1.800	-23.981	50.601	CpRcA-R	1.148 (0.085)	-0.108 (0.0363)
5	14	1.290	-20.101	42.766	G(1)	0.391 (0.299)	-0.669 (0.258)
6	14	1.720	-21.973	46.510	G(1) [¶]	-0.271 (0.265)	-0.914 (0.260)
7	13	1.430	-19.174	40.834	R(2)	0.741 (0.401)	-0.0279 (0.0101)
8	29	0.747	-35.637	74.606	G(1)	0.876 (0.515)	-0.231 (0.135)
9	18	0.610	-19.929	42.692	G(2)	0.985 (0.518)	-0.746 (0.211)
10	20	6.667 [¶]	-44.983	92.910	G(2)	1.898 (0.364)	0.387 (0.113)
11	15	2.031	-24.825	52.288	G(1)	0.611 (0.420)	-0.285 (0.148)
12	14	2.230	-23.660	49.886	G(1)	0.484 (0.370)	-0.427 (0.179)
13	12	1.217	-16.690	35.777	R(2)	0.360 (0.215)	3.35×10^{-6} (1.035×10^{-5})
14	12	0.643	-13.181	28.760	R(2)	0.582 (0.215)	-4.7×10^{-5} (6.447×10^{-5})
15	12	1.370	-17.340	37.078	CpRcA-G	2.397 (0.743)	-0.598 (0.198)
16	11	0.350	-8.941	20.185	G(1)	3.445 (1.558)	-0.526 (0.0590)
17	12	2.206 [¶]	-19.960	42.318	G(2)	2.538 (0.556)	0.208 (0.148)
18	60	1.502	-95.725	195.527	CpRcP-G	0.264 (0.115)	-0.327 (0.147)
19	60	1.800 [¶]	-101.059	206.196	CpRcP-G	0.201 (0.140)	-0.266 (0.115)
20	60	3.591	-121.431	246.940	G(2)	1.0689 (0.319)	-0.0519 (0.122)
21	17	0.017 [¶]	10.076	-17.379	CpArA-G	-0.377 (0.30)	0.113 (0.0811)
22	12	0.021 [#]	5.753	-6.710	R(1)	0.468 (0.0637)	-4.1×10^{-5} (7×10^{-6})
23	23	0.067	-1.439	5.922	R(1)	0.731 (0.231)	-0.00049 (1.56×10^{-4})
24	25	0.015 [¶]	16.410	-29.643	CpRcA-G	7.317 (1.514)	-0.810 (0.168)
25	31	0.044	4.252	-5.102	R(1)	0.403 (0.154)	-2.64×10^{-4} (1.0012×10^{-4})
26	31	0.019	16.638	-29.874	G(1)	1.858 (1.121)	-0.208 (0.124)
27	44	0.245	-30.788	65.337	R(2)	1.614 (0.739)	0.411 (0.132)
28	44	0.325	-36.839	77.439	R(2)	0.106 (0.162)	-3.7×10^{-6} (1.23×10^{-5})
29	44	0.124	-16.141	36.043	CpRcA-G	1.691 (1.0625)	-0.182 (0.116)
30	44	3.489 [¶]	-87.880	179.522	G(2)	7.404 (1.731)	-0.252 (0.145)
31	114	0.681 [¶]	-138.669	282.065	G(2) [¶]	2.435 (0.277)	0.384 (0.063)

Note: DD = density dependence; ID = inverse density dependence; DI = no density dependence was detected.
[†] The best model between random walk and exponential growth models.
[‡] The best model among all density dependence models in this study (except models which failed in nonlinear optimization).
[§] SIC for the best model between Ricker and Gompertz models. SIC is not listed for models where either the Ricker or Gompertz model is the best model among all density-dependent models.
[¶] Nonindependent, identically distributed residuals were detected by a Ljung and Box (1978) *Q* test at the 5% probability level.
[#] Exponential growth model, $\hat{a} = 0.111$.

may be smaller than, larger than, or close to zero in different time periods and under different density ranges. Finding occasional periods of positive density dependence in these populations was not surprising, and could be expected when outbreak-prone insect populations overwhelm their predators' or their hosts' resistance mechanisms (Dennis 1989). These features are also demonstrated in the notable time series of *P. flammea* and *D. pini* reported by Schwerdtfeger (1941). The population densities, the estimated density dependence parameters and the fit (i.e., conditional expected mean) from the time-varying-parameter model are presented in Fig. 1A ($\hat{b} = -0.327$, no. 18 in Table 3) and 1B ($\hat{b} = -0.266$, no. 19 in Table 3), respectively. It can be seen that the density dependence parameter ($\hat{b}_{i/T}$) from the Kalman-filter smoothing procedure closely follows the population dynamic trends of the *P. flammea* and *D. pini* populations, respectively.

DISCUSSION

In this section, we elaborate on the general statistical and ecological advantages of our current modeling ap-

proach over tests of density dependence that invoke only simple models. We focus on the ability of our methods to categorize density-dependent processes in natural populations and gain biological insights into the intricacies of complex population regulation associated with the ecological time series data.

The advantage of using the Kalman filter in ecological time series analyses

The Kalman filter is a series of recursive equations that are capable of analyzing structural time series models represented in state space form. The structural time series modeling method using the Kalman filter shown in Harvey (1989a) has many advantages over classical Box-Jenkins methods (Box and Jenkins 1976), in that the model can contain multiple noise terms (e.g., parameter noise, observation noise and system noise) and deterministic or stochastic components of the time series (e.g., linear-trend, circular, seasonal, or autoregressive processes) (Harvey 1989a). Unlike Box-Jenkins methods, it is not necessary to assume stationarity

TABLE 3. Extended.

Density-dependent model						
\hat{b}_2 (SE)	$\hat{\sigma}_a^2, \hat{\sigma}_b^2,$ or $\hat{\sigma}^2$	$\ln(L(\mathbf{X}, \mathbf{W}))$	SIC	Density dependence?	SIC§	
-0.00761 (0.00248)	0.634	-20.250	54.881	DD	58.235G(1)¶	
	0.154	-18.810	46.291	DD	49.177R(1)	
	0.005	-13.260	34.436	DD	43.019R(1)	
	0.011	-15.796	39.51	DD	47.737R(1)	
	0.850	-17.389	42.474	DD	...	
-0.0146 (0.0102)	0.876	-17.583	42.861	DD	...	
	0.662	-13.337	39.563	DD	39.873R(1)	
	0.675	-34.226	78.448	DI	...	
0.295 (0.218)	0.312	-13.373	40.201	DD	42.373G(1)	
-0.983 (0.121)	1.248	-27.532	70.326	DD	95.212G(1)¶	
	1.591	-21.222	54.152	DI	...	
	1.533	-13.105	50.139	DI	...	
3.504×10^{-6} (1.99×10^{-5})	0.207	-6.305	24.003	ID	33.403R(1)	
-3×10^{-5} (6.762×10^{-5})	0.288	-7.970	27.666	DD	32.349R(1)	
	0.041	-13.621	34.436	DD	35.863G(1)	
	0.234	-6.925	20.759	DI	...	
	0.432	-9.995	32.120	DD	44.188R(1)¶	
$\hat{\sigma}_a^2 = 0.44$ (0.178)	0.472	-81.938	180.185	DD	189.959G(1)	
$\hat{\sigma}_b^2 = 0.212$ (0.105)	0.738	-90.766	197.842	DD	206.353G(1)	
-0.369 (0.121)	2.642	-110.469	241.269	DD	245.125G(1)	
$\hat{\phi}_b = -0.712$ (0.158)	5.0×10^{-4}	16.760	-22.429	DD	-13.987R(1)¶	
	0.00489	13.654	-20.115	DD	...	
	0.044	2.913	3.266	DD	...	
	9.4×10^{-5}	24.454	-39.374	DD	-39.300G(1)	
	0.0357	7.400	-4.597	ID	...	
	0.017	18.326	-26.447	ID	...	
-0.605 (0.142)	0.166	-21.821	59.989	DD	70.521R(1)¶	
-1.4×10^{-5} (1.236×10^{-5})	0.242	-29.761	76.246	DD	82.868G(1)	
	0.0014	-14.409	40.102	ID	41.456G(1)	
-0.335 (0.145)	2.467	-78.561	176.171	DD	176.440G(1)¶	
-0.748 (0.063)	0.274	-86.359	193.303	DD	279.315G(1)¶	

of the time series in structural time series modeling, because the nonstationarity of the time series can be embedded directly into the model. These advantages are also very useful in the analysis of shorter ecological time series data where the nonstationarity of the time series is not easy to determine. In the structural time series model, it is easy to include and estimate unobserved components. In our study, the unobserved components are parameters a_t and b_t . Because the Kalman filter uses recursive algorithms, it can easily deal with missing data.

The Kalman filter provides a powerful mechanism for estimating the parameters and detecting various sources of noise, such as parameter and system noise from density-dependent and density-independent factors, if the model is clearly specified. As we have shown, increasing the complexity of the models may help in more realistically describing density dependence. However, because of the limited information in many data sets, one may not arbitrarily raise the complexity of models by increasing the number of parameters or noise terms to be estimated. For a relatively short time series such as one with <20 observations, higher power can be expected when only one noise term is considered in the system equation, growth rate,

or density dependence parameters (Zeng 1996). Furthermore, the set of models that we used should not be considered definitive. Researchers could reasonably use a subset of the models presented in this study or include others, depending on their prior knowledge of the particular biological system and on the length of the time series.

Study of the performance of the Kalman filter in estimating the time-varying Gompertz model can be found in Zeng (1996). Using Monte Carlo simulations, the Kalman filter, and information criteria, Zeng (1996) explored the parameter-estimation efficiency of time-varying-parameter models and model identification (with respect to different strengths in parameter and system noise, the number of the noise terms, and length of the time series). Based on three information criteria (including SIC) used to identify the best model between constant-parameter and time-varying-parameter models, Zeng (1996) found that greater parameter noise relative to system noise, fewer noise terms, reduced system noise, and a longer time series will consistently increase the parameter estimation efficiency and the percentage of time-varying-parameter models that are correctly identified.

For more general results and discussion about the

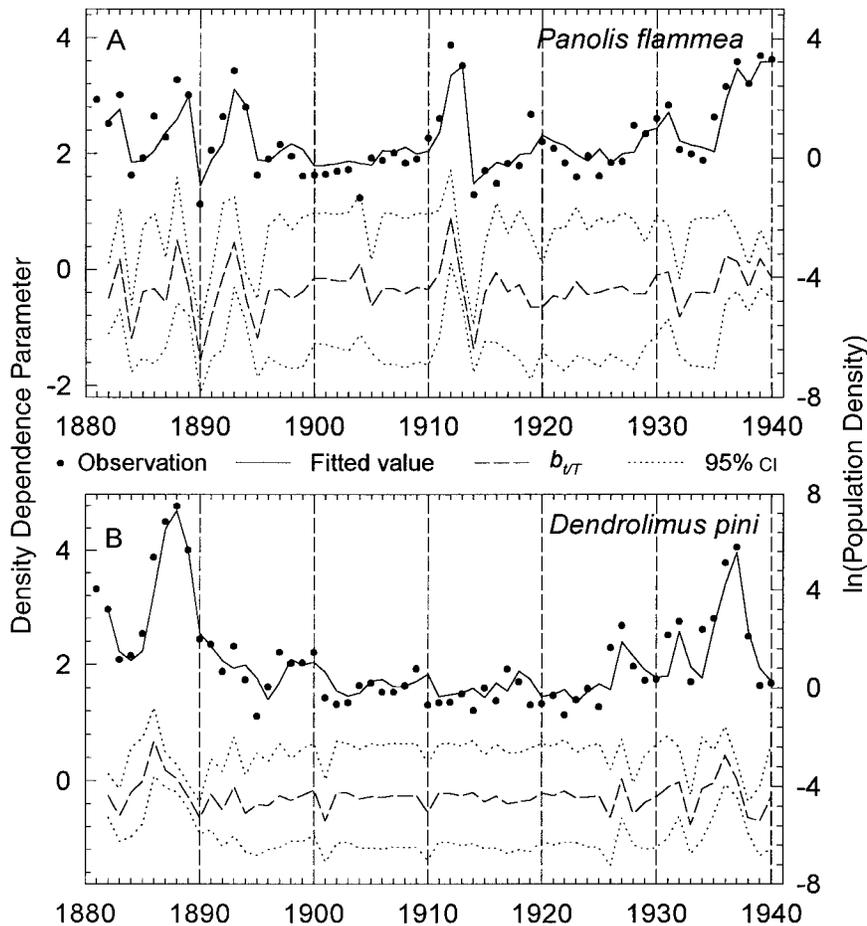


FIG. 1. Natural logarithm of population density (census counts of pupae/m²) of *P. flammea* (Fig. 1A) and *D. pini* (Fig. 1B) reported by Schwerdtfeger (1941), the fit from the time-varying parameter model (i.e., conditional expected mean) and estimated time-varying density dependence parameters.

Kalman filter, parameter estimation efficiency, alternative models, true model assumptions, number of noise terms, and omitting variables in statistical population dynamic modeling, we refer the reader to Zeng (1996).

Detecting density dependence: hypothesis testing vs. model selection

In this study, some complex form of density dependence was suggested in 23 out of 31 cases classified as density dependent. In such a situation, hypothesis-based tests designed to detect simple correlations or simple dependence between growth rate and population density may frequently fail because of the poor match between the implied dynamic model and underlying natural processes. Furthermore, in most density dependence tests, only one alternative density-dependent model form (usually, Ricker and Gompertz models) has been compared against either a random-walk model or an exponential-growth model. We have seen that these alternative models often present an over-simplified picture of population dynamics in a changing environ-

ment. It is important to note that forcing complex dynamics to fit the simple alternative models may generate serious statistical and ecological problems (Guckenheimer et al. 1977, Schaffer and Kot 1985, Turchin and Taylor 1992, Zeng 1996).

Our approach provides less opportunity to misspecify the models compared with hypothesis testing and other modeling approaches using single null and alternative models (e.g., constant-parameter, first-order, or second-order models). While the use of a broad array of candidate models also increases the likelihood that one of our models will approximate the underlying process, the use of the SIC model selection criterion protects against the perils of overfitting the data. The statistically rigorous selection of models has not received sufficient attention in previous work on complex population dynamics in natural populations (Schaffer 1985, Schaffer and Kot 1985, Turchin 1990, Turchin and Taylor 1992).

Results from hypothesis testing and model selection are not directly comparable, and hence it is necessary to address the difference between these two approach-

es. One advantage of using hypothesis testing is that the Type I and Type II error rates associated with a hypothesis test can be explicitly explored, once the basic assumptions of the test are satisfied. Hypothesis testing is best suited for problems in a closed world: a world in which the truth lies in either the null or alternative hypothesis (Oreskes et al. 1994). However, in the real world, a number of problems arise when attempting to use the hypothesis-testing framework to detect density dependence. First, as we have shown, it is difficult to find a few models associated with null and alternative hypotheses which are general enough to describe the full range of population dynamic patterns observed in field populations. Dennis and Taper (1994) used the term "Type III error" to describe the error associated with fitting the wrong model. Chatfield (1995) expressed the belief that model misspecification is the dominant source of error for many problems. When the Type III error rate is high, the Type I and Type II error rates are meaningless in hypothesis testing. Second, because there are two possible null models (random-walk model and exponential-growth model), many possible alternative models (e.g., Ricker model, Gompertz model, time-varying-parameter models, second-order models, etc.), and different test methods (e.g., linear regression, Morris 1959; test of correlation, Bulmer 1975; test of the density dependence parameter, Pollard et al. 1987, Dennis and Taper 1994; test limit, Reddingius and Den Boer 1989), different researchers may produce different and incomparable density dependence test results (Wolda and Dennis 1993).

Model selection simultaneously takes account of the goodness-of-fit of a model, the number of model parameters, and the sample size used to achieve that fit (Sclove 1987). Model selection invites the use of multiple models and thus can make full use of modern nonlinear modeling techniques without abandoning classical simple models. Hence, it is better suited for problems in an open world. Hooten (1995) found that even when failing to select the true model, the use of information criteria will tend to select a similar model form, and increasing the number of models under consideration seems to increase the likelihood of correctly identifying a class of models such as density-dependent models. One disadvantage of using model selection is that it is difficult to determine statistical significance levels among a group of nested and nonnested models.

Different information criteria in use today might give slightly different rankings to a set of tested models. The best model among a group of models can be selected based on its prediction ability or the ability to approximate the data-generating mechanism. The most popular information criteria are the AIC (Akaike, 1974) and the SIC (Schwarz 1978). The AIC attempts to choose the model that will minimize the prediction error (Shibata 1981, Reschenhofer 1996) and is asymptotically equivalent to model selection by cross-validation (Stone 1977). On the other hand, the SIC and

other consistent information criteria asymptotically select the model that generated the data (Reschenhofer 1996). Simulations (Hooten 1995, Zeng 1996) have shown that the SIC identifies the order of the generating model more consistently than does the AIC, and further that the AIC tends to suggest the use of models with more parameters. In this paper, we are more concerned with identifying the form of "density dependence" than with immediate predictions and, thus, have opted to use SIC as a model-selection criterion.

Hypothesis testing in the context of population dynamic time series has some additional difficulties. It is well known that allowing inspection of the data to affect selection of the alternative model biases hypothesis testing by producing unrealistically low probability values (Chatfield 1995). This study (see Table 2) and that of Hooten (1995) indicates that no single model represents the real world well in even a majority of cases. Thus, the researcher interested in hypothesis testing is faced with the choice of either consistently using a single generic test such as the parametric bootstrap test of Dennis and Taper (1994) or randomization test of Pollard et al. (1987) and accepting the loss of power and biological insight due to common model misspecification, or to select an alternative model after viewing the data and compromising any meaning the probability value may have. We believe that the model selection approach is a viable way to avoid this quandary. However, because there are no probability values directly associated with model selection, the model selection itself cannot reject or accept a hypothesis of density dependence, but can only indicate that data are more consistent with density dependence or density independence. If a researcher wishes to combine model identification and hypothesis testing for density dependence, a legitimate probability value can be obtained by performing a parametric bootstrap (Dennis and Taper 1994) of the entire model identification process. This topic will be considered in a subsequent paper.

Biological insight

Detecting density dependence in natural populations is an important first step in ecological studies. However, of far greater ecological interest is explaining what actually happens in the field. Thus, determining, or closely approximating, the actual form and pattern of natural population regulation surpasses in interest the detection of density dependence. Here again our approach represents a major advance.

Ecological factors such as the dynamics of natural enemies and fluctuations in resource availability are considered by many authors to be important factors in animal population regulation (e.g., Dempster and Pollard 1981, Turchin 1990). Models that fail to include such important regulation factors or their various influences on population dynamics may not be able to detect different types of density dependence, such as

indeterminate density dependence, which may contain density-dependent, inversely density-dependent, and density-independent processes (Strong 1986, Brown 1989). These various types of density dependence may operate at different times and under different density ranges in nature (Nicholson 1958, Strong 1986, Sinclair 1989). In this study, we combined time-varying-parameter and second-order modeling approaches, and selected the best model using the SIC information criterion. When information on the dynamics of natural enemies, fluctuations in resource availability, and other density-dependent factors, as well as density-independent factors is not available in a changing environment, this approach has great potential and flexibility for approximating the underlying mechanisms of ecological time series data and for modeling various population dynamics.

The dynamic modeling of time series also provides the means for inferring the importance of changes in environmental factors that occur over greater than yearly or generational time scales. Heretofore, the best approach available was to divide the time series into different segments and fit different models to each segment (Rotella et al. 1996; M. L. Taper and P. Gogan, *unpublished manuscript*). This piecewise approach is, at best, an awkward method for studying populations whose parameters have changed gradually over a long time period.

The comparison between density-dependent models and density-independent models is not the only comparison of interest. Because the models are able to describe various density-dependent influences inherent in the time series data, and because different density-dependent models may indicate different strengths in interaction among groups of density-dependent and density-independent factors on the population dynamics, identifying certain density-dependent model forms may help in inferring the importance of certain environmental factors. For example, if the second-order model is identified as the best model, one may infer strong interaction between population density and density-dependent factors. Ricker and Gompertz models, if identified as the best models, may suggest that the conditional density dependence concept would tend to be supported, in which the influences of the density-dependent factors increase conditionally on the increase of the population density, and overall density-dependent factors are less influenced or not affected by population density (Royama 1992, Zeng 1996). In our study, we found only four cases where the Ricker and Gompertz models provided the best fit of the time series data, and one of these was not unequivocally superior to the random-walk model (Table 3). In some cases as shown in Table 3, the differences between the SIC values for the complex model and simple model are negligible, and statistically indistinguishable. A long time series data set may be helpful in discriminating between different density-dependent model forms, as well as

between density-dependent and density-independent models. However, once the best model is found for an ecological time series data set, the importance of acquiring additional biological information and the need for further experimentation to test the hypotheses regarding the mechanism of population dynamics cannot be overemphasized, as the statistical approaches used cannot guarantee that the density dependence detected is from the density-dependent factors.

Long-term ecological studies and field experimental studies are two important complementary approaches that have been used to address various issues in ecology (Krebs 1991). Under a stochastic population system, replication, or the like, is the only way to isolate trends or deterministic dynamics from the noise in a given system. In practice, it may be difficult to carry out many independent field experiments, because of the correlation of density-independent factors in some large geographical regions (Royama 1992). Long-term studies have a number of advantages that enable the study of population and community dynamics over temporal and/or spatial scales that are often difficult, if not impossible, to consider in experimental studies. Such study may allow one to detect dynamic patterns (e.g., trends) under equilibrium and nonequilibrium ecological paradigms, monitor environment changes, and test ecological hypotheses related to the past and present. In contrast, it is not easy to conduct experimental studies sufficiently comprehensive to obviate the need for long-term data, which have inherent historical characteristics (Zeng 1996).

Population viability analysis

The ability to classify and characterize complex population regulation should have important practical applications. The model selection and parameter estimation techniques we have demonstrated can be used to develop population management models and generate more realistic estimates of extinction time distributions in population viability analysis. For example, we investigated the extinction time distributions for two of the populations analyzed in this study. In Fig. 2, a Monte Carlo simulation was conducted to study the number of generations needed to reach a minimum population density (arbitrarily set at $0.01/m^2$) based on three time series models and corresponding estimated parameter values. The time to reach the minimum population density was recorded for 1000 simulations for each model. Simulations were carried out for the random-walk, constant-parameter, and time-varying-parameter models. The cumulative frequency of extinction times to reach the minimum population density for *O. brumata* (no. 2, in Table 3) and *B. pinarius* (no. 3, in Table 3) is presented in Figs. 2A and 2B, respectively, and varied among the three models. A rapidly rising curve indicates a propensity for reaching the minimum density quickly (i.e., rapid extinction), while a shallow curve indicates greater persistence. The cu-

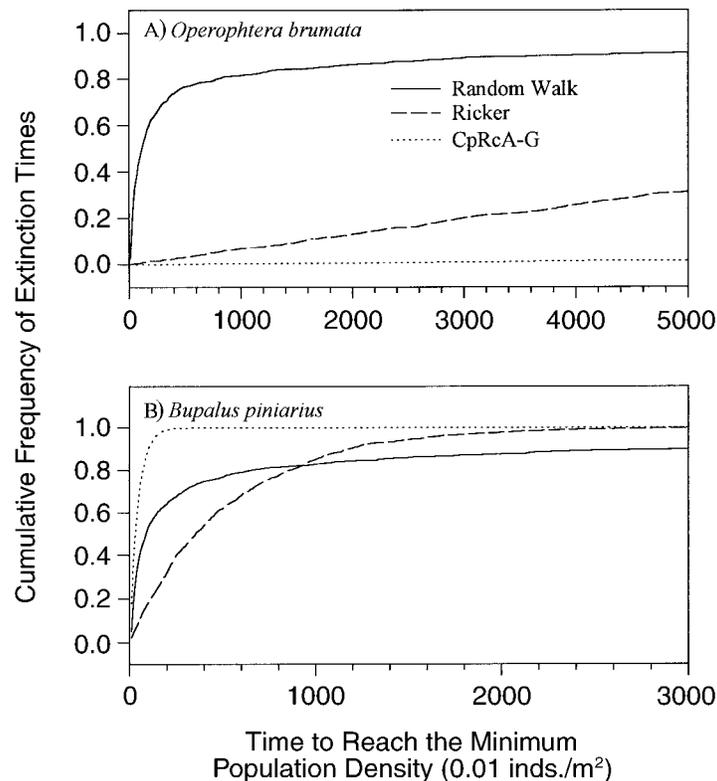


FIG. 2. The cumulative frequency of extinction times (i.e., number of generations) of *O. brumata* larvae (Fig. 2A), and *B. piniarius* larvae (Fig. 2B) to reach the minimum population density ($0.01/\text{m}^2$) based on the estimated parameters in Table 3.

mulative frequency from the time-varying model, which was the best model among all alternative models, indicated a longer persistence time than that from random-walk and constant-parameter models for *O. brumata*. However, the simulation results for *B. piniarius* indicated that the time-varying-parameter model generated a shorter persistence time than the other two models. A time-varying coefficient density-dependent model may not always generate a longer persistence time prediction for a regulated population and, as Figs. 2A and 2B indicate, the differences may be dramatic.

CONCLUSION

We believe that the approach we have developed and demonstrated in this paper represents a major advance in the ecological statistics of modeling population dynamics and in the characterization of population regulation patterns. We see three major advantages:

1) By using a broad array of models (some of which exhibit a great deal of flexibility), it is more likely that one of them will closely approximate the true population dynamics of a population than if a researcher confined his or herself to a single null and alternative model. This increases the likelihood that complex density dependence, if it exists, will be recognized as such, in contrast to procedures using standard hypothesis tests with simple models, where complex population

dynamics will decrease the power for detecting density dependence.

2) This ability to recognize and identify a broad array of density dependence forms increases the biological insight derivable from the statistical analysis.

3) The increased ability to characterize complex population regulation may have profound effects on our ability to predict the fate of populations. Our examples show that for populations exhibiting complex population regulation, a population viability analysis that takes this into consideration may predict population survival times that are either shorter or longer than those predicted by simple population dynamic models. These differences can be quite large.

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APPENDIX

PARAMETER ESTIMATION PROCEDURE

Kalman filter

Based on the state representation of the population dynamic model (Eqs. 8 and 9), let the vector, $\mathbf{A}_{t-1/t-1}$, denote the conditional mean estimator of state vector \mathbf{A}_{t-1} based on the observations up to and including X_{t-1} ($\mathbf{X}_t = [X_1, X_2, \dots, X_t]$). Let $\mathbf{P}_{t-1/t-1}$ denote the $p \times p$ conditional covariance matrix of \mathbf{A}_{t-1} , based on the observations up to and including X_{t-1} , where p is the number of variables in the state vector. In this study, $p = 2$ and $p = 3$ for first-order and second-order models, respectively. The one-step ahead prediction equations of the conditional mean ($\mathbf{A}_{t/t-1}$) and variance ($\mathbf{P}_{t-1/t-1}$) at time $t - 1$ are as follows:

$$\begin{aligned} \mathbf{A}_{t/t-1} &= E(\mathbf{A}_t | \mathbf{X}_{t-1}) \\ &= E\{[\Phi \mathbf{A}_{t-1} + (\mathbf{I} - \Phi)\mathbf{B} + \Omega_t] | \mathbf{X}_{t-1}\} \\ &= \Phi \mathbf{A}_{t-1/t-1} + (\mathbf{I} - \Phi)\mathbf{B} \end{aligned} \tag{A.1}$$

$$\begin{aligned} \mathbf{P}_{t/t-1} &= \text{Var}(\mathbf{A}_t | \mathbf{X}_{t-1}) \\ &= \text{Var}\{[\Phi \mathbf{A}_{t-1} + (\mathbf{I} - \Phi)\mathbf{B} + \Omega_t] | \mathbf{X}_{t-1}\} \\ &= \Phi \text{Var}(\mathbf{A}_{t-1} | \mathbf{X}_{t-1}) \Phi^T + \text{Var}(\Omega_t) \\ &= \Phi \mathbf{P}_{t-1/t-1} \Phi^T + \mathbf{Q} \end{aligned} \tag{A.2}$$

where $\mathbf{Q} = [(\sigma_a^2 \ 0); (0 \ \sigma_b^2)]$.

The mean and variance of the one-step ahead prediction at time $t - 1$ for the system equation are as follows:

$$\begin{aligned} E(X_t | \mathbf{X}_{t-1}) &= E[(\mathbf{Z}_{t-1} \mathbf{A}_t + X_{t-1} + \varepsilon_t) | \mathbf{X}_{t-1}] \\ &= \mathbf{Z}_{t-1} \mathbf{A}_t + X_{t-1}, \\ \text{Var}(X_t | \mathbf{X}_{t-1}) &= \text{Var}[(\mathbf{Z}_{t-1} \mathbf{A}_t + X_{t-1} + \varepsilon_t) | \mathbf{X}_{t-1}] \\ &= \text{Var}(\mathbf{Z}_{t-1} \mathbf{A}_t | \mathbf{X}_{t-1}) + \text{Var}(X_{t-1} | \mathbf{X}_{t-1}) \\ &\quad + \text{Var}(\varepsilon_t | \mathbf{X}_{t-1}) \\ &= \mathbf{Z}_{t-1} \text{Var}(\mathbf{A}_t | \mathbf{X}_{t-1}) \mathbf{Z}_{t-1}^T + \sigma^2 \\ &= \mathbf{Z}_{t-1} \mathbf{P}_{t/t-1} \mathbf{Z}_{t-1}^T + \sigma^2. \end{aligned}$$

The covariance between X_t and \mathbf{A}_t based on information available at time $t - 1$ is

$$\begin{aligned} \text{Cov}(\mathbf{X}_t, \mathbf{A}_t | \mathbf{X}_{t-1}) &= \text{Cov}(\mathbf{Z}_{t-1} \mathbf{A}_t, \mathbf{A}_t | \mathbf{X}_{t-1}) \\ &= \mathbf{Z}_{t-1} \text{Cov}(\mathbf{A}_t, \mathbf{A}_t | \mathbf{X}_{t-1}) \\ &= \mathbf{Z}_{t-1} \text{Var}(\mathbf{A}_t | \mathbf{X}_{t-1}) = \mathbf{Z}_{t-1} \mathbf{P}_{t/t-1}. \end{aligned}$$

$[\mathbf{A}_t, \mathbf{X}_t]^T$ has a multivariate conditional normal distribution, mean is

$$\begin{bmatrix} \mathbf{A}_{t/t-1} \\ \mathbf{Z}_{t-1} \mathbf{A}_t + X_{t-1} \end{bmatrix},$$

covariance is

$$\begin{bmatrix} \mathbf{P}_{t/t-1} & \mathbf{P}_{t/t-1} \mathbf{Z}_{t-1}^T \\ \mathbf{Z}_{t-1} \mathbf{P}_{t/t-1} & \mathbf{Z}_{t-1} \mathbf{P}_{t/t-1} \mathbf{Z}_{t-1}^T + \sigma^2 \end{bmatrix}.$$

Based on the properties of the multivariate normal distribution (Harvey 1989a), when the information at time t is available, the updating equations are:

$$\mathbf{A}_{t/t} = E(\mathbf{A}_t | \mathbf{X}_t) = \mathbf{A}_{t/t-1} + \mathbf{P}_{t/t-1} \mathbf{Z}_{t-1}^T f_t^{-1} v_t, \tag{A.3}$$

$$\mathbf{P}_{t/t} = \text{Var}(\mathbf{A}_t | \mathbf{X}_t) = \mathbf{P}_{t/t-1} - \mathbf{P}_{t/t-1} \mathbf{Z}_{t-1}^T f_t^{-1} \mathbf{Z}_{t-1} \mathbf{P}_{t/t-1}, \tag{A.4}$$

and

$$v_t = X_t - \mathbf{Z}_{t-1} \mathbf{A}_t - X_{t-1},$$

$$f_t = \mathbf{Z}_{t-1} \mathbf{P}_{t/t-1} \mathbf{Z}_{t-1}^T + \sigma^2.$$

v_t is the prediction error, and f_t is the prediction error variance. $v_t \sim N(0, f_t)$.

The estimators $\mathbf{A}_{t/t}$ and $\mathbf{P}_{t/t}$ yield conditional estimates of the mean and covariance of state vector \mathbf{A}_t for the time series through time t , but only the last estimators ($\mathbf{A}_{T/T}$, $\mathbf{P}_{T/T}$) use all information in the data. In order to consider all available information to estimate the state variables (e.g., a_t and b_t in the state vector for first-order models), recursive smoothing techniques were used to estimate the conditional mean ($\mathbf{A}_{t/T}$) and the conditional covariance ($\mathbf{P}_{t/T}$), which start with the final quantities $\mathbf{A}_{T/T}$ and $\mathbf{P}_{T/T}$ and work backwards as follows (Harvey 1989a):

$$\mathbf{A}_{t/T} = \mathbf{A}_{t/t} - \mathbf{P}_t^* (\mathbf{A}_{t+1/T} - \mathbf{A}_{t+1/t}), \tag{A.5}$$

$$\mathbf{P}_{t/T} = \mathbf{P}_{t/t} + \mathbf{P}_t^* (\mathbf{P}_{t+1/T} - \mathbf{P}_{t+1/t}) (\mathbf{P}_t^*)^T, \tag{A.6}$$

where

$$\mathbf{P}_t^* = \mathbf{P}_{t/t} \Phi^T \mathbf{P}_{t+1/t}^{-1}, \quad t = T - 1, T - 2, \dots, 2.$$

Eqs. A.1–A.4 are recursive. They cannot be implemented without initial values for $\mathbf{A}_{1/1}$, $\mathbf{P}_{1/1}$, Φ , and \mathbf{B} ($t = 1$ and $t = 2$ for first-order and second-order models, respectively). These initial values will influence the estimates of the conditional mean and variance based on the Kalman filter. This influence diminishes with time series length. Fortunately, dependence on initial guess values is lost in the maximum-likelihood optimization process, provided that a solution is found. Initialization and optimization of the maximum-likelihood function are described in the next section.

Maximum-likelihood function and initialization of the Kalman filter

In statistical applications, the Kalman filter, which is a recursive algorithm for computing the state vector based on known parameter values, cannot give the estimates of the parameters in the state space model by itself. Hence, the Kalman filter must be combined with the likelihood function to estimate the parameters (Harvey 1989a). For a structural time series model as in Eqs. 8 and 9, the likelihood function is defined as

$$\begin{aligned} L(\mathbf{X}_T, \Theta) &= \prod_{t=1}^T p(X_t | \mathbf{X}_{t-1}) \\ &= p(X_1) p(X_2 | X_1) \cdots p(X_T | \mathbf{X}_{T-1}), \end{aligned} \tag{A.7}$$

where $\mathbf{X}_T = (X_1, X_2, \dots, X_T)$, Θ is the parameter set in the likelihood function (e.g., $\Theta = [a, b, \phi_a, \phi_b, \sigma_a^2, \sigma_b^2, \sigma^2]$ for Eqs. 4, 5 and 6), and the $p(X_t | \mathbf{X}_{t-1})$ is the probability density function of X_t conditional on the \mathbf{X}_{t-1} values up to time $t - 1$. Under the state space model assumption, $p(X_t | \mathbf{X}_{t-1})$ is a density function of the normal distribution with the prediction error v_t , and the prediction error variance f_t as follows (Harvey 1989a):

$$p(X_t | \mathbf{X}_{t-1}) = \frac{1}{\sqrt{2\pi f_t}} \exp\left(-\frac{v_t^2}{2f_t}\right). \tag{A.8}$$

Thus, the complete log-likelihood function for fitting the model to a univariate time series can be expressed in prediction error decomposition form (Schweppe 1965, Nicholls and Pagan 1985, Harvey 1989a) as

$$\begin{aligned} \ln[L(\mathbf{X}_T, \Theta)] &= -\frac{T-1}{2} \ln(2\pi) - \frac{1}{2} \sum_{t=2}^T \ln(f_t) \\ &\quad - \frac{1}{2} \sum_{t=2}^T \frac{v_t^2}{f_t} + \ln[p(X_1)]. \end{aligned} \tag{A.9}$$

The v_t and f_t can be calculated from the Kalman filter (Eqs. A.1–A.4). In our analysis, $\ln(p(X_1))$ is considered a fixed term

and can be dropped from the likelihood function. Thus, the likelihood used is not the full likelihood of X_1, X_2, \dots, X_T , but is instead the likelihood of X_2, X_3, \dots, X_T conditional on the realized initial value of the population size X_1 . In certain special cases of stationary time series with well characterized distributions, term $\ln(p(X_1))$ can be included to give the full likelihood, but in general this is not possible. The influence of the initial condition diminishes as the length of the time series increases. The likelihood function for the second-order models can be formulated in a fashion similar to Eq. A.9. For similar reasons, terms $\ln(p(X_1))$ and $\ln(p(X_2 | X_1))$ were also dropped from the likelihood function in the second-order models. Dropping these terms is common practice and affects parameter estimation negligibly (Harvey 1989b, Tong 1990). Setting $\mathbf{Q} = \mathbf{0}$ ($\mathbf{Q} = [(\sigma_a^2, 0); (0, \sigma_b^2)]$) in the CpRcP model, ordinary least squares estimates can be achieved using the Kalman filter and the maximum-likelihood process for the constant-parameter models. The ordinary least squares estimates for the first-order models can also be directly achieved by using the Kalman filter based on the RWRWP model when $\mathbf{Q} = \mathbf{0}$ (Otter 1978, Zeng 1996). The close connection between the Kalman filter and recursive weighted least squares regression is discussed by Diderrich (1985).

For a given model, the Kalman filter is used to do the recursion for $\mathbf{A}_{i|i-1}$, $\mathbf{P}_{i|i-1}$, $\mathbf{A}_{i/i}$, $\mathbf{P}_{i/i}$, v_i and f_i based on a given parameter vector Θ and a data vector \mathbf{X}_T ; the log-likelihood of the parameter vector Θ given data \mathbf{X}_T is evaluated by Eq. A.9. The estimates of the parameter vector Θ are the vector that maximizes the log-likelihood function, and the optimization is done numerically. The parameters in all models considered in our study were estimated using the Kalman filter and likelihood function, except for the parameters in random-walk and exponential-growth models. For these models, parameter estimates were calculated from the following explicit formulas given by Dennis and Taper (1994):

$$\sigma^2 = \frac{1}{T-1} \sum_{t=2}^T (X_t - X_{t-1})^2, \tag{A.10}$$

random walk

$$a = \frac{1}{T-1} \sum_{t=2}^T (X_t - X_{t-1}), \tag{A.11}$$

exponential growth model,

$$\sigma^2 = \frac{1}{T-1} \sum_{t=2}^T (X_t - a)^2. \tag{A.12}$$

and

The value of the maximized likelihood function can be calculated using Eq. A.9, where $v_t = X_t - X_{t-1}$, $v_t = X_t - X_{t-1} - a$ for random-walk and exponential-growth models, respectively; and $f_t = \sigma^2$.

The unconditional mean and covariance of the parameters

a_i and b_i were used to initialize $\mathbf{A}_{1/1}$ and $\mathbf{P}_{1/1}$ (for first-order models) or $\mathbf{A}_{2/2}$ and $\mathbf{P}_{2/2}$ (for the second-order models) for the recursion of the Kalman filter, when they were available. For the first-order autoregressive parameter model, the unconditional mean is the central value a and b , respectively, and the unconditional variance for a_i and b_i is $\sigma_a^2/(1 - \phi_a^2)$ and $\sigma_b^2/(1 - \phi_b^2)$, respectively. The initial conditions of the variance for random-coefficient parameters can be achieved by setting $\phi_a = 0$ and $\phi_b = 0$ in the above equations. Parameter estimates from constant-parameter models were used as the initial parameters \mathbf{B} (e.g., a and b) in the Kalman filter except for random-walk-parameter models. For the parameters without initial knowledge, arbitrary values within the reasonable ranges were used for initialization (such as ϕ_a and ϕ_b which should be set between -1 to 1). The off-diagonal elements in the covariance matrix are initialized with zero.

The unconditional mean and covariance for the random-walk parameters do not exist. Harvey (1989a) suggested a small value (e.g., 0) and large value (e.g., 1000) be used to initialize the elements in the mean vector and the diagonal in the covariance matrix in the Kalman filter, respectively.

The covariance matrix of the estimated parameters was approximately estimated from the Kalman filter by inverting the Hessian of the log-likelihood (Nicholls and Pagan 1985). Missing observations in the time series were treated by using a one-step ahead prediction value from the Kalman filter to replace missing observations, and by letting the Kalman filter skip updating equations related to them (Harvey 1989a). Missing observations should also be skipped in the log-likelihood function, and the term $(T - 1)/2$ in Eq. A.9 needs to be modified to $(T - \tau - 1)/2$, where τ is the number of observations missing.

Test of independent, identically distributed noise

Assuming that the noise term ε_t is IID noise, then the autocorrelation function of the noise $T(m)$ (m is the order of the autocorrelation) is approximately normal with mean zero and variance $1/T_n$, where T_n is the length of the noise term (Shumway 1988). This approximate variance can be used to test if an autoregression of the residual is zero for a specific order M . Ljung and Box (1978) proposed a Q test statistic, which can be used to simultaneously test the order of the autocorrelation of the residuals until M is zero. The Q statistic is expressed as follows:

$$Q(M) = T_n(T_n + 2) \sum_{m=1}^M (T_n - m)^{-1} (r(m))^2, \tag{A.13}$$

where M is the order to be tested, Q is distributed as a chi-square random variable with $M - K$ degrees of freedom, K is the number of parameters in the model, and $T(m)$ is the estimated sample autocorrelation at time lag m (Shumway 1988).