Stochastic modeling of ecological time series : animal population dynamics, complex regulation and structural changes

by Zheng Zeng

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
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Abstract:
Modeling complex population dynamics, discovering complex population regulation processes, and assessing structural changes in the population dynamics in changing environments are of great importance in ecology. Using simple modeling approaches and testing techniques, many studies have failed to find density dependent population regulation, and decades of controversy have been caused by weak support for density dependence from field studies. Considerable debate continues regarding the theory and appropriate methodology for evaluating population regulation. In this study, I proposed a set of complex dynamics models, including new time-varying parameter models, second order and second order random coefficient models, to model the structural population dynamics, and identify complex population regulation processes due to the influences from natural enemies, resource availability, and other environmental factors in changing environments. The Kalman filter and maximum likelihood function were used to estimate the parameters in time-varying parameter models arid second order models. The Akaike's information criterion (AIC), adjusted AIC (AICc), Schwarz's information criterion (SIC) were used to identify the best model. A parametric bootstrap test based on the information criterion was proposed to find the probability value of the model selection. Diagnostic techniques (CUSUM, and CUSUMSQ) were used to identify structural changes in the time series. These models were used to evaluate 20 insect and 11 vertebrate univariate time series using Kalman filter analysis.

Monte Carlo simulation results showed that time-varying parameter models perform well in approximating both systematic and stochastic parameter changes over time. The Kalman filter was found to yield efficient estimates of time-varying parameters for longer time series data, larger variations in the parameters, fewer number of the noise terms and smaller system noise. Density dependent regulation was found in 23 out of 31 cases examined, while complex population regulation was found in 18 out of these 23 density dependence cases using the SIC method. Stronger evidence of density dependent regulation in 17 out 23 cases was found to be statistically different from the density independence process at the 0.05 probability level from the parametric bootstrap test. The complex population dynamic models selected by SIC or the significant probability value were diversified in linear or nonlinear forms, which suggest various complex population regulation patterns in nature. Various topics related to ecological time series modeling are discussed in this thesis.

Population dynamics may combine density dependent, inverse density dependent and density independent processes, which may operate in different times and different density ranges in nature. Models that fail to include important density dependent factors may not be able to detect density dependent regulation and explain population dynamics. This study offers an advance for modeling complex population dynamics, discovering complex regulation patterns, improving tests for density dependence, and assessing structural changes in the population dynamics over time in changing environments using various linear and nonlinear models.

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

May 1996

APPROVAL

of a thesis submitted by

Zheng Zeng

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ACKNOWLEDGMENTS

I would like to thank Dr. Robert M. Nowierski, my major advisor, for his support, advice, and encouragement throughout this research project. Without his help both academically and personally, it would have been impossible for me to finish this study. I wish to express my appreciation to my major advisor, Dr. Daniel Goodman, who first brought the ecological time series modeling to my attention in an individual problem course he taught, thus providing me with the opportunity to explore this wonderful field in ecology.

I would like to thank Dr. Mark L. Taper for valuable discussions, suggestions and questions posed during the course of this study. Appreciation is also extended to graduate committee members: Drs. William P. Kemp, Pat L. Munholland and Matt Lavin for their advice and assistance in this study.

Thanks are also extended to Dr. Mark M. Hooten for his generosity in exchanging of the data and his thoughts on the application of information criteria in the testing density dependence before publishing his results. I also wish to thank the following people: Dr. Brian Dennis, Dr. Subhash R. Lele, Bryan C. FitzGerald, Jorge M. Brito, Robert T. Grubb, and Steven Kearing for informal discussions.

I thank my wife Jiang and my son Li for their support, help and understanding.

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ABSTRACT

Modeling complex population dynamics, discovering complex population regulation processes, and assessing structural changes in the population dynamics in changing environments are of great importance in ecology. Using simple modeling approaches and testing techniques, many studies have failed to find density dependent population regulation, and decades of controversy have been caused by weak support for density dependence from field studies. Considerable debate continues regarding the theory and appropriate methodology for evaluating population regulation. In this study, I proposed a set of complex dynamics models, including new time-varying parameter models, second order and second order random coefficient models, to model the structural population dynamics, and identify complex population regulation processes due to the influences from natural enemies, resource availability, and other environmental factors in changing environments. The Kalman filter and maximum likelihood function were used to estimate the parameters in time-varying parameter models and second order models. The Akaike's information criterion (AIC), adjusted AIC (AICc), Schwarz's information criterion (SIC) were used to identify the best model. A parametric bootstrap test based on the information criterion was proposed to find the probability value of the model selection. Diagnostic techniques (CUSUM, and CUSUMSQ) were used to identify structural changes in the time series. These models were used to evaluate 20 insect and 11 vertebrate univariate time series using Kalman filter analysis.

Monte Carlo simulation results showed that time-varying parameter models perform well in approximating both systematic and stochastic parameter changes over time. The Kalman filter was found to yield efficient estimates of time-varying parameters for longer time series data, larger variations in the parameters, fewer number of the noise terms and smaller system noise. Density dependent regulation was found in 23 out of 31 cases examined, while complex population regulation was found in 18 out of these 23 density dependence cases using the SIC method. Stronger evidence of density dependent regulation in 17 out 23 cases was found to be statistically different from the density independence process at the 0.05 probability level from the parametric bootstrap test. The complex population dynamic models selected by SIC or the significant probability value were diversified in linear or nonlinear forms, which suggest various complex population regulation patterns in nature. Various topics related to ecological time series modeling are discussed in this thesis.

Population dynamics may combine density dependent, inverse density dependent and density independent processes, which may operate in different times and different density ranges in nature. Models that fail to include important density dependent factors may not be able to detect density dependent regulation and explain population dynamics. This study offers an advance for modeling complex population dynamics, discovering complex regulation patterns, improving tests for density dependence, and assessing structural changes in the population dynamics over time in changing environments using various linear and nonlinear models.

I. INTRODUCTION

All animals have the reproductive capacity to increase their populations geometrically, but this does not happen in nature. A logical explanation is that one or more factors in nature limit population growth. In 1798, the Reverend Thomas Malthus pointed out that "a strong and constantly operating check on population from difficulty of subsistence" is necessary to maintain the balance of nature. He thought that mortality from lack of food and disease would prevent the population from further increases. The Malthusian hypothesis provided not only the basis for a portion of Charles Darwin's theory of natural selection, but also greatly influenced ecologists of this century in their studies of population regulation (Sinclair, 1989).

Having studied population dynamics for two hundred years, ecologists today are still struggling to understand and explain which factors influence the regulation and persistence of natural populations, and how these factors operate in the field (Tamarin, 1978; Sinclair, 1989; Cappuccino, 1995). The study of the population regulation progressed considerably through laboratory and field studies, dynamic modeling, and statistical tests, to find the factors that prevent populations from following geometric growth, but strong evidence to support regulation theory was wanting (Wu and Loucks, 1995). Perhaps the field of ecology has not advanced enough to be able to explain what has happened in the past and predict what will happen in the future, which are two criteria that are critical to making ecology a stronger science (Tamarin, 1978; Peters, 1991).

It was not until the early twentieth century that more formal searching and study began to address the mechanisms involved in the natural balance of animal populations. In this section, I will briefly review the literature related to the population regulation theory and the efforts made by biologists in studying population regulation in nature.

Early Work and Debates on Population Regulation

In the study of parasitic control of insect pests, Howard and Fiske (1911), created "facultative" (density dependent) and "catastrophic" (density independent) terms to classify ecological factors that influenced a given population. They thought that natural balance could be maintained only through the operation of at least one or more facultative factors, which apply a relative more severe restraint when the population increases. They believed that parasitism was one of the most effective facultative factors, and starvation was the ultimate facultative factor, which almost never operated.

Thompson (1929) considered that populations are more likely controlled by more than a single factor. He presented a view that animal populations are regulated by the intrinsic limitations of the organisms themselves. His basic idea is that any environmental factor can regulate the population, but whether a population increases or decreases totally depends on a more or less optimal environment based on the complex factors varying in space and in time.

In 1933, Nicholson provided an explanation for the balance found in nature - that the persistence of the population over a long time was regulated by the self governing intensity of intraspecific competition. He stated “Without such balance, population density would be indeterminate, and so could bear a relation to any thing”. Nicholson (1933) used the concept of control factors, including natural enemies and resource availability, to emphasize the intraspecific competition for food and a place to live, and other factors that regulated the population. His ideas were obviously rooted in the thinking of Malthus (1798) and Howard and Fiske (1911).

After Smith (1935) proposed the classification of ecological factors into density dependent and density independent factors - one of the most important concepts put forth in the ecological science, had to do with the notion that the population density regulated by density dependent factors (Nicholson, 1954, 1957, 1958). However, density dependence may not operate all the time - there are times of increase and times when density independent factors cause a decrease without the compensating effects from density dependent factors (Nicholson, 1958; Sinclair, 1989).

The climate school of thought, developed originally from Bodenheimer (1928) and Uvarov (1931), was later proposed again by Andrewartha and Birch (1954) and emphasized the influence of the climate on the population parameter, outbreak, instability, and finally the distribution and abundance of an organism. Andrewartha and Birch (1954) stated "weather is a component of the environment of animals which effectively determines the limits to distribution and the abundance of some species". They thought that all environmental factors are density dependent factors, and denied the usefulness of classifying ecological factors into density dependent and density independent factors. They rejected the balance of nature concept in natural populations for lack of supporting data, which caused a big debate in ecology in the 1950s (Andrewartha and Birch, 1954; Andrewartha, 1957; Nicholson, 1954, 1957). Instead, Andrewartha and Birch (1954) argued that population density was limited by weather, food, other organisms, and a place to live.

Milne (1957, 1962) thought that Nicholson (1933, 1957) over-stressed the effect of intraspecific competition in population regulation. Based on the work of Thompson (1929), Nicholson (1933, 1954), and Andrewartha and Birch (1954), he recognized three kinds of factors: density independent, imperfectly density dependent and perfectly density dependent factors. The first category mainly included most of the abiotic and some biotic factors (e.g., grazing, casual predation and parasitism). The second category included: competitors, predators, parasites and pathogens in general. The third category included "the one and only perfectly density-dependent factor: intraspecific competition (for food, space, etc.). He concluded that intraspecific competition was the ultimate factor in population regulation. However, most of the time, population density was below the competition level, and hence, the population density was regulated by the combined action of imperfectly density dependent and density independent factors. This line of thought can be considered the "comprehensive" school. However, like Nicholson's density dependent school of thought, it has not been tested from field data.

The field population dynamics is influenced by various density dependent and density independent factors. Before the 1960s, no efficient methods were available in ecology to separate the influences from different factors on population dynamics.

Because of the difficulty of testing the regulation hypothesis in the field, some famous experiments were conducted in the laboratory to test the regulation of populations under controlled conditions (e.g., Nicholson, 1957; Utida, 1941, 1957; Huffaker et al., 1963). The results obtained in the laboratory showed that the population could be regulated by either resource availability or natural enemies, or both. However, the laboratory-based studies can only determine whether density dependence is possible, and do not necessarily mean that the population in the field should follow the same type of regulation (Stiling, 1989). Due to the lack of field evidence and an effective measurement of the population equilibrium, Andrewartha (1957) argued that it was useless using the equilibrium as there was no way to measure the equilibrium in the field. The search for the method to detect the existence of density dependence in a field population has become a strong preoccupation of researchers in population ecology in the past forty years (Krebs, 1992).

After many years of controversy, population regulation theory has become concerned with critical persistence and equilibrium concepts in population ecology, even though population regulation has been only infrequently detected in the field data (Murdoch, 1994). Various new views in both theoretical ecology and experimental ecology have been presented to explain the population dynamics. For example, many authors consider population regulation under environmental noise to be a statistical stationary distribution of population size (e.g., May, 1973; Chesson, 1982; Chesson and Case, 1986; Dennis and Taper, 1994; Turchin, 1995). Royama (1977) thought that density independence should be infrequent in nature as density dependence is a necessary condition for population persistence. Berryman (1989, 1993) used the similar concept of negative feedback from systems theory to express the density dependent process. Population regulation, which is believed today by many ecologists to cause population persistence, is the core of modern ecology, and has enormous practical consequences (Krebs, 1978; Murdoch, 1994; Wu and Loucks, 1995).

Recently, due to lack of enough evidence from field population studies to support the equilibrium and regulation theory, some authors (e.g., Wolda, 1989; Krebs, 1992) have argued that it was useless to accept such a concept in ecology, as the existence of an equilibrium and related regulation cannot be tested. This is the same argument made by Andrewartha (1957) nearly forty years ago!

Why density dependence has been found only infrequently in field populations, and the questions of whether or not equilibria exist, what they are, and how to detect them are posed today in the study of the natural populations (May, 1986; Murdoch, 1994). Research efforts by ecologists to address these questions have fostered a never ending debate (Turchin, 1995).

Methods and Problems in Detecting Population Regulation

In this section, I will briefly review some major methods used in the study of the population regulation, current debates and the status of population regulation theory using theoretical and statistical modeling approaches over the past forty years.

Statistical Density Dependence Test of Population Regulation

Morris (1963a, 1963b) proposed a regression method to test for density dependence, on the basis of key factor analysis of a mortality factor to determine if it is responsible for the changes in a population in the next generation (Morris, 1959). The population was considered to have no density dependent process if the slope of the regression of ln(N_t) on ln(N_{t-1}) was equal to one, while a density dependent process was considered to be operating in the population if the slope was found to be less than one (ln(N_t) is the natural logarithm of the population density at time t). This model can be considered as a different form of the Gompertz model or a first order autoregressive model (Royama, 1977; Dennis and Taper, 1994). A few years later, several researchers suggested that this simple regression model was not a good criterion for testing for density dependence, because of problems related to underestimates of the slope and the non-robustness of the model (Maelzer, 1970; St. Amant, 1970; Itô, 1972; Pielou, 1974). When this method is used, it would produce an excessive type I error, because of the underestimate of the slope parameter (Null = no density dependence).

Bulmer (1975) proposed a distribution test of the reciprocal of von Neumann's ratio test using the random walk as the null hypothesis, and the Gompertz model as the alternative model (von Neumann test refers to Harvey, 1989b). This test is almost equivalent to using the first serial correlation coefficient. Bulmer (1975) pointed out that his distribution test was almost equivalent to the use of the likelihood ratio test, and would thus be efficient. Solow (1990) found Bulmer's test to be non-robust and insensitive against an auto-correlated error.

Later, various tests such as the 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), parametric bootstrap likelihood ratio test (PBLR test, Dennis and Taper, 1994) were also used by researchers interested in detecting density dependence in ecological time series data. Of the various density dependence test proposed over the past two decades, no single test has been identified as being more powerful and consistent than the others in detecting density dependence. Simulation results suggested that the randomization test may be an effective tool used in density dependence testing (Pollard el al., 1987), but Dennis and Taper(1994) found that this distribution free test has low power. They also found that a second order model used by Turchin (1990) and Berryman (1991) suffered an excessive type I error. Additionally, inconsistent results often occurred if more than one density dependence test was used (e.g., Den Bore and Reddingius, 1989; Woiwod and Hanski, 1992, 1993a, 1993b). Wolda and Dennis (1993) thought that under these circumstances it is not appropriate to draw any conclusions about density dependence. For a more detailed review and comparison of density dependence test methods refer to Holyoak (1993a, 1993b) and Dennis and Taper (1994).

To date, many parametric and non-parametric test methods have been developed to detect density dependence in field populations. However, all proposed methods appear unsatisfactory even when using census data, because of the low detection ratio of density dependence (Pollard et al., 1987; Sinclair, 1989; Murdoch, 1994).

Evidence of the Density Dependent Process from Field Data

Over the last 20 years, many density dependence test methods, including these mentioned above, have been used to test the hypothesis of population regulation in the field. The infrequent detection of density dependence has been commonly reported in the literature, and hence the regulation hypothesis has not been supported by many studies. Stiling (1987, 1988, 1989) in a review of the life table studies, found a lower frequency of density dependence. Den Boer and Reddingius (1989) rarely found statistically significant density dependence in the 16 data sets examined using the randomization test of Pollard et al. (Pollard et al., 1987). Den Bore (1991) concluded that the hypothesis that populations "exist in a state of balance because densities fluctuate about a relative stable norm" (Nicholson, 1933, p133) is not supported by empirical evidence, and denied the need for regulation, as a random walk model appears to mimic the fluctuation patterns sufficiently in the natural population. Vickery and Nudds (1991) found density dependence in three of 16 populations examined using a major axis test (Slade, 1977), 14 of 59 cases using Bulmer's test (Bulmer, 1975) and 10 of 59 cases using randomization test of Pollard et al. (Pollard et al., 1987). Murdoch (1994) failed to detect density dependence for red scale (*Aonidiella aurantii*) in eight cases which included spatial heterogeneity in attack rates, a refuge, and metapopulation dynamics. He also failed to detect density dependence in parasitoids (*Aphytis melinus*), and only detected low frequency density dependence in bird populations. For more examples in literature in which the researchers failed to detect density dependence refer to the reviews from Sinclair (1989) and Murdoch (1994). In contrast, Woiwod and Hanski (1992) detected density dependence in 79% of the moth time series data and 88% of the aphid time series data, which were longer than 20 years, using Bulmer's test (Bulmer, 1975). Similarly, Turchin (1990) reported on the frequent occurrence of delayed density dependence. However, Turchin's (1990) method was criticized on statistical grounds

(Murdoch, 1994; Dennis and Taper, 1994) and spurious detection of delayed density dependence (Holyoak, 1994).

New Controversies

Over the last two decades, ecologists have frequently failed to detect density dependence in animal populations, which contradicts the regulation hypothesis. If the finding of infrequent density dependence in these studies is correct, then what are the implications of this to regulation theory and to the persistence of populations? As a consequence of various failures in detecting density dependence, and in order to avoid problems of applying density dependence tests to inter-generation data, three major controversies developed and were addressed in the literature. These included: population regulation under spatial heterogeneity (Hassell, 1985, 1987; May, 1986; Dempster and Pollard, 1986; Hassell et al., 1987; Mountford, 1988), equilibrium theory (Wolda, 1989; Wolda, 1991; Berryman, 1991; Krebs, 1992; Murdoch, 1994) and the methodology for evaluating population regulation and explaining density dependence test results (Wolda and Dennis, 1993; Hanski et al., 1993; Holyoak and Lawton, 1993; Wolda et al., 1994).

The first controversy is related to the relationship between spatial heterogeneity and temporal density dependence. In order to address the low frequency of density dependence in inter-generation data, Hassell (1985) and May (1986) suggested that population regulation could arise from spatial heterogeneity, although density dependence was not found in the temporal data. Hassell et al. (1987) and Hassell (1987) concluded that a large body of existing life table data is not always a reliable source for revealing the causes of the regulation in natural populations by conventional analyses. Dempster and Pollard (1986) argued that spatial heterogeneity can modify, but cannot replace the role of temporal density dependence in population regulation. They believed that there can be no population regulation if there is no temporal density dependence. Mountford (1988) found the interesting result that spatial heterogeneity enhances the detection of density dependence, and stochastic heterogeneity is neutral in its effect for a given mean size of equilibrium population using a randomization test and data simulated for 50,000 generations.

The second debate concerns about the usefulness of the equilibrium concept. Wolda (1989, 1991) argued that the equilibrium cannot be measured in the field, "as it seems impossible to separate fluctuating equilibrium values from fluctuating deviations from those equilibrium values", and he concluded that "tests for population regulation cannot be expected to produce the expected results, making them next to useless". Wolda (1989) recommended using the stabilization concept, which is defined as "The often supposed (general) tendency for population density to stay for some time between relatively narrow limits" (Reddingius and Den Boer, 1989). Reddingius and Den Boer (1989) considered that "Stabilization may, but need not, result from the influence of 'governing' (density dependent) factors. [...]. Only if in this case, it should be called 'regulation'". Based on systems theory, Berryman (1991) argued that the equilibrium can be obtained from the analyses, and that regulation and stabilization have the same underlying cause - "that at least one component of the system be subjected to negative feedback and that the sum of the negative feedbacks between components be stronger than the sum of the positive feedbacks". Furthermore, both agreed that the equilibrium may not be a point attractor, but may show a dynamic behavior(e.g., some complex attractor, Berryman, 1991).

Krebs (1992) made an even more critical statement about the equilibrium than Wolda (1989) as "Density dependence is still the holy grail of many population ecologists, yet it is clear that only after you reject such a paradigm can much progress be expected". Additionally, some ecologists complained and questioned current ideas on density dependence and how populations were regulated in the field (Strong, 1984, 1986; Murray, 1994). Strong (1986) used "density-vagueness" term to describe high variance in demographic performance of an organism under high population density levels, and lack of density dependence in medial densities, in contrast to the explicit density dependence relationships. In reviewing various density dependence concepts in the literature, Murray (1994) pointed out many density dependence definitions are ambiguous and thus, are untestable. His first two most serious questions were with regards to whether density dependent responses are linear or not, and over what range of population density do density dependent factors act?

The third controversy concerns density dependence test methods and how to explain the density dependence test results. Wolda and Dennis (1993) tested density dependence for non-univoltine (i.e., bi/polyvoltine) species or non-semelparious species using the PBLR test developed by Dennis and Taper (1994). Wolda and Dennis (1993) argued that the PBLR test is the best density dependence test in statistical clarity, and emphasized the difference between causal density dependence and statistical density dependence in testing density dependence. Holyoak and Lawton (1993) questioned the influence of the parameter values and time series length on power using the PBLR test, and reported that the PBLR test identified density dependence less frequently in some insect time series data than using the randomization test of Pollard et al. (Pollard et al., 1987). Holyoak and Lawton (1993) argued that "tests for density dependence give misleading results if sampling is not at generation intervals". If such non inter-generation data was used, "Tests for density dependence cannot reveal the mechanism of regulation, but they do indicate the nature of long-term population dynamics". Regarding how to explain the density dependence test results in Wolda and Dennis (1993), Hanski et al. (1993) questioned "why time series of population abundances of univoltine semelparious insects should be exempt from explanations other than regulation". Hanski et al. (1993) thought that it is extremely unlikely that the alternative mechanisms to density dependent regulation would produce the set of results in their study. However, Hanski et al. (1993) and Wolda et al. (1994) agreed that estimating parameters by flexible population dynamic models, would provide more insight into population dynamics than statistical hypothesis testing. Furthermore, each author agreed that the density dependence test is just a test for a "return tendency", a tendency for population size to return to some intermediate range of value, that results in a long term statistical equilibrium (Hanski et al., 1993; Wolda et al., 1994).

Modeling Complex Population Dynamics

In my view, current reports of infrequent density dependence in field data do not appear to provide any new insights in population regulation theory, but they nonetheless may show serious shortcomings in the simple density dependence test methods themselves. Hence, complex modeling approaches to detect population regulation, instead of statistical hypothesis testing on the ecological time series data, should be developed (Hanski et al., 1993; Wolda et al., 1994; Hooten, 1995).

In this section, I will review the most important features of ecological time series data and the modeling methods used to evaluate such data. Less attention will be given to simple testing methods, which are characterized by simple first order, constant parameter population models. I will argue why it is necessary to model complex population dynamics (Nisbet and Gurney, 1982; Turchin and Taylor, 1992), determine complex population regulation processes (Royama, 1977, 1981; Berryman, 1978; Turchin, 1990; Turchin et al., 1991) and assess structural changes in the population dynamics in changing environments. The complex regulation term (complex density dependence) is preferred to describe the regulation occurring in complex density dependent and density independent conditions. I will also use the complex dynamic model concept defined as a model involving more than one time lag and/or parameters that change through time. These are processes that simple models (i.e., Ricker and Gompertz models) cannot represent.

Does the Theoretical Model Work?

There are lots of theoretical models for describing population dynamics available today. Many of them (e.g., exponential logistic difference model) have been used to understand the mechanisms of population dynamics, infer population biological processes (e.g., detect statistical density dependence and study chaos behavior), and make population predictions (e.g., Ricker, 1954; Logan and Hain, 1990; Logan and Allen, 1992; Kemp and Dennis, 1993; Turchin and Taylor, 1992; Dennis and Taper, 1994). Most statistical tests of density dependence were designed to test the simple correlation or dependence between per capita 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). In modeling population dynamics, estimating the parameters and assessing the goodness of fit may produce more profound ecological results than simple density dependence tests (Hanski et al., 1993; Wolda et el., 1994).

Theoretical modeling may provide qualitative explanations of population dynamics by examining the system behavior of population models, and has the potential to be used in practical applications in the future. However, a considerable gap exists between the theoretical population dynamic models and practical application of those models based on field data (Royama, 1977; Nisbet and Gurney, 1982). One of the first shortcomings of the theoretical models is that they depend on detailed descriptions of many ecological processes. For example, one needs both observations of the host and parasitoid to model a host - parasitoid interaction process. Unfortunately, field observations have generally been always made for single species, and the observations on the associated species are scanty. Furthermore, theoretical population models have not been much help in describing field population dynamics and population regulation processes, when the information for environmental covariates is unavailable (Royama, 1977). A second disadvantage is that many theoretical models place more emphasis on the deterministic part of the model and less on the stochastic part, the latter of which is one of the model's essential features (Schnute, 1991). As field data are full of noise due to environmental factors which are "exogenous" to the community or population and are excluded, the theoretical models have failed to separate the effects of exogenous from endogenous components (Royama, 1977). The third disadvantage is that a theoretical model can be forced to fit the data, if the difficulty in applying it under a changing environment is neglected. The parameter estimation and hypothesis testing may suffer greatly from the bias using the arbitrary model. Unfortunately, in modeling of the ecological time series data, only a few papers have carried out the diagnostic test (e.g., Kemp and Dennis, 1993; Dennis and Taper, 1994; Dennis et al., 1995). The fourth disadvantage is that the population dynamics of many species is discrete in nature, which is characterized as discrete generations or distinct seasonality, and is not conveniently modeled using theoretical models with continuous time (Royama, 1977; Schnute, 1991).

The time series data for a single species can be designated as a univariate ecological time series. Two papers from Royama (1977, 1981) form the basis for a realistically modeling biological population dynamics based on univariate ecological time series data in a changing environment. The univariate ecological time series may include information about the interaction between organisms and the changing environment. A good single population model should be based on biological reality and simplicity in the mathematical form to consider the characteristics of field data. A more realistic mathematical model should include meaningful biological parameters, good approximations of the natural population processes, and good generalization to most of the biological species.

Simple vs.Complex Population Dynamic Models

The assumption that population dynamics in theoretical population models, follows a first order Markov chain has been more widely accepted in density dependence tests (Dennis and Taper, 1994). Royama (1977, 1981) showed that the first order model which is currently being widely used, is just one of many density dependence forms. The first order, constant parameter population models (e.g., Ricker and Gompertz models, Dennis and Taper, 1994) which are based on the laboratory experiments provide an oversimplified view of long term population changes in the field. Hence, they are considered as simple models in my study.

Second order models can be derived from linear dynamic models of two species interactions, when the population dynamics of one species is expressed as a function of its previous density only (Royama, 1977, 1981, 1992). Moran (1953) first used a second order process to model the dynamics of the Canadian *Lynx*. Royama (1977), Berryman (1978), Turchin (1990) and Turchin et al. (1991) applied second order models in either Ricker form or Gompertz form to explore population dynamics and density dependence. However, Hanski and Woiwod (1991) reported that a few density dependent processes were identified from thousands of insect data sets examined using a second order model and a model selection method introduced by Turchin (1990) (also see, Woiwod and Hanski, 1992).

Various complex population dynamic model forms are available in either theoretical ecology and statistical ecology. The time-varying intrinsic growth rate and environmental carrying capacity in either periodic or random fashion were considered in some theoretical models (Roughgarden, 1979; May, 1981; Nisbet and Gurney, 1982). In a stochastic population dynamic model, Royama (1977) considered the model's parameters perturbed by independent random noise due to random exogenous factors, and found stationary conditions for such a random coefficient population model. He concluded that such a model may be realized when the performance of parasitoids or predators is greatly influenced by weather, temperature, etc. Unfortunately, Royama (1977) did not further address the problem how to estimate these random coefficients due to statistical difficulty.

In testing for density dependence, unless a correct model identification technique is utilized, the use of higher order models may overparameterize the model. In recent years, modeling of complex population dynamics using second order models for the field data has not been satisfactory. Dennis and Taper (1994) argued that Turchin's (1990) method would cause an excessive type I error when the second order model was used. Holyoak (1994) found that Turchin's (1990) method was not capable of reliably distinguishing between delayed and non-delayed density dependence.

Recently, Hooten (1995) used information criteria to study density dependence and identify the best model for the population dynamics based on six different models. This approach offers substantial improvement over traditional statistical tests of density dependence, and will be emphasized.

Structural Changes of the Ecological Time Series Data

All models are some kinds of approximations and simplifications of the true natural processes, which are formulated by our knowledge of the system. When we apply any model to the data, some assumptions concerning the data and model necessarily have to be made, such as the noise should be independent, identically distributed (IID) random numbers.

The analysis of time series data is usually based on the assumption that the relationships within the model (i.e., model structure, value of parameters and noise terms) are constant over time. Biologically, the interactions within the biological system should be consistent enough to maintain consistent patterns in the data, which means that the mechanisms responsible for generating the data are invariate through the time period of study. However, biological systems over the long term may not satisfy such assumptions, as great nonlinearity and uncertainty can be associated with biotic and abiotic processes in the ecosystem, and both the data and models do not represent the actual levels of complexity found in nature. For ecological time series data, due to irregular disturbances or different data generating processes from complex interactions in the ecosystem over time, there will usually be some observations that deviate from the current model's predictions, and may not be adequately explained by the current time series model. These phenomena can be considered as structural changes in the population dynamics, which, to my understanding, have been given little attention in the ecological literature, yet have been widely addressed in statistics and econometrics (Brown et al., 1975; Harvey and Durbin, 1986; Harvey, 1989a, 1989b; Bos and

Fetherston, 1992).

Objectives of This Study

The first objective of this study is to formulate a group of population dynamic models to consider the influence of important density dependent factors on field population dynamics. The various linear and nonlinear dynamic models formed should be more realistic than the Ricker model and Gompertz model (first order, constant parameter models) in testing density dependence as well as modeling field population dynamics. Ecological knowledge is critical to the formulation of various alternative models for both population dynamics and regulation processes associated with the field data, and against the function misspecification (i.e., failure to add important biological reality to the models). However, the final appropriate model form among alternative models, and the best estimates of the parameters related to population regulation should be determined by actual field data.

The second objective of this study is to develop a parameter estimation technique, and test the efficiency of the parameter estimation for time-varying parameter models. The last objective is to apply the complete model sets in the analysis of insect and vertebrate population data from the literature, estimate parameters, select the best model and access structural changes in the ecological time series data. It will be expected that this study, by combining both population dynamics and regulation, may help answer questions as to whether a population is regulated, and how the population is regulated in the field.

II. MODEL DESCRIPTIONS

Important Definitions

Turchin (1995) considered a definition of density dependence from Murdoch and Walde as “a dependence of per capita population growth rate on present and/or past population density” as the best (Murdoch and Walde, 1989 in Turchin, 1995). A more causal sense density dependence (population regulation) was defined by Berryman (1987) as that which "occurs when some factor or series factors increase their negative impact on the reproduction and survival of individuals in response to increases in population density." Such factors are called density dependent (endogenous) factors. These definitions based on the effects of the ecological factors can be used as the basis for detecting statistical density dependence on inter-generation data. Population regulation is considered as synonymous with density dependence in most textbooks (Krebs, 1992). Begon et al. (1990) pointed out that "regulation by definition, can only occur as a result of one or more density dependent processes". In the ecology literature, definition of density dependence and population regulation seems accepted by most ecologists (but see Murray, 1994).

Among many extrinsic and intrinsic density dependent factors (see Price, 1984), fluctuations in resource availability and dynamics of the natural enemies should be the most important factors to be considered in identifying factors regulating populations. The resource availability can directly determine the degree of intraspecific competition in the population (Nicholson, 1933), and is considered as the ultimate factor in population regulation (Howard and Fiske, 1911; Milne, 1957, 1962; Huffaker and Messenger, 1964). Natural enemies may indirectly influence intraspecific competition (via removal of individuals in the population or limit the resource availability, Nicholson, 1933) and interact with the host population dynamics, which differs from the influence made by density independent factors (i.e., single direction influence, with generally no feedback mechanisms available).

A density dependent factor not only influences population density, but it should be influenced by population density. Otherwise, it is considered a density independent (exogenous) factor (Royama, 1992). In modeling processes, it is useful to distinguish the total measure of the biological factor, from a proportional measure of the biological factor which actually generates density dependence effects. For example, resources and resource availability are two different concepts for population regulation. The total measure of the resource may not be a density dependent factor, if it is not influenced by the abundance of animals feeding on it. Resource availability, part of the resource, is the actual factor that controls the intensity of intraspecific competition (Nicholson, 1933). Royama (1992) used a conditional density dependence concept to describe density dependence that was affected conditionally by resource availability. It is also possible that the amount of resource is identical to the resource availability such as in the laboratory. For some generalist natural enemies, pressure exerted on the host population may only be partially density dependent, the degree of which will be determined by how much the natural enemy is influenced by the host population.

Boundedness regulation is a tendency that population dynamic processes return to the equilibrium density, following departure from that density (Varley et al., 1973). Statistically, boundedness regulation can be considered as a stationary probability distribution, where the population density fluctuates around the mean density level (May, 1973; Chesson, 1986; Kemp and Dennis, 1993; Dennis and Taper, 1994). In ecology, boundedness regulation is mainly related to the resource availability or the combined effects of resource availability and other density dependent factors. Under an ideal situation, resources and biological factors may be less influenced by the abundance of the animal population, but resource availability might monotonically decrease as the population density increases. Ricker and Gompertz models (first order, constant parameter models, Ricker, 1954; Dennis and Taper, 1994) are considered appropriate to describe such processes, because these two models were formulated based on a simple hypothesis that dynamics of resource availability is linearly decreased as population density increases, without involving the complex dynamics of the resource availability, natural enemies and other density dependent factors. Ricker and Gompertz models are expected to work better under simple laboratory conditions (See various laboratory results from Krebs, 1978). In this study, these two models are classified as simple models, the regulation related to the models will be considered as simple regulation processes, where the overall biological factors may be less or not influenced by population density.

Complex regulation is a process generally involving more than one density dependent factor. In such type of regulation, the dynamics of the biological factors responsible for density dependence are strongly influenced by the abundance of the animal population and other factors, and more and more density dependent factors may become involved in the transient dynamics of population, when the population density is far from its equilibrium points (Berryman, 1993). Because the Ricker and Gompertz models may not be appropriate models to describe various complex regulation processes, alternative models such as those developed by Royama (1977, 1984, 1992) may offer an improvement for assessing such regulation processes. Unfortunately, current field studies of density dependence pay little attention to such interactions in forming tests for density dependence, except for second order models.

Regulation from resource availability, among all density dependent factors, is essential in any population, though it may not operate all the time and all density regions (Nicholson, 1958; Milne, 1958; Huffaker and Messenger, 1964; Dempster, 1983). If without the bounded regulation from resources, a population cannot persist based on the Nicholson - Bailey model (Nicholson and Bailey, 1935; Murdoch, 1994).

A Comprehensive Model of Population Dynamics

Although the concepts of density dependence and density independence have been central themes in population ecology and modeling over half a century, the classical density dependence tests have failed to recognize various influences from density dependent factors under density independent environmental conditions. For example, the dynamics of resource availability or the dynamics of natural enemies may be strongly influenced by the population density itself and other ecological factors. The mutual interaction process may generate complex population dynamics as described in classical theoretical population dynamic models and statistical population dynamic models (e.g., Lotka-Volterra model, in Rodzis, 1989; higher order autoregressive models, Royama, 1977, 1981). The limit circle of population dynamics is one of the indications of this strong interaction process.

Density independent factors (e.g., the climate) not only directly influence resource availability and the dynamics of the animal populations by influencing the population parameters (Andrewartha and Birch, 1954), but provide the conditions within which density dependent factors operate (Huffaker, 1984). Density independent factors are considered by some to be the ultimate factors that determine population distribution and dynamics (Nicholson, 1933; Andrewartha and Birch, 1954). In additional to the direct influences, the influences of density independent factors on the animal population dynamic process may be partly included in the influences from density dependent factors, such as resource availability and natural enemies. However, density independent factors are not directly responsible for population persistence and regulation (Nicholson, 1933, 1957, 1958).

The population dynamics of an organism is influenced by / interact with a number of factors including resource availability, natural enemies and other density dependent factors under density independent environmental conditions and noise (chance), that are operating currently or in the past. The log per capita growth rate of the population is defined as, $R_t = \ln(N_t / N_{t-1})$, where R_t is called the log reproductive rate by Royama (1977) and the *K* factor by Varley and Gradwell (1960), N_t is the population density at time t, t = 2,...,T; T is the number of observations. The log per capita growth rate may be determined by population intrinsic growth ability, resource availability, natural enemies, other density dependent factors, density independent factors and noise. It can be represented by the following mathematical equation:

$$R_t = g(N_{t-1}, S_{t-1}, \mathbf{P}_{t-1}, \mathbf{D}_{t-1}, \mathbf{E}_t, \varepsilon_t, \varepsilon_{t-1},\ldots,\varepsilon_{t-m}). \quad (1)$$

Where, $g(.)$ is generally considered linear or nonlinear first order function dependent on the population density and environmental factors in time t or t-1; N, S, $\mathbf{P}$, $\mathbf{D}$ and $\mathbf{E}$ are population density, resource availability, the vector of the density of natural enemies, the vector of other density dependent factors, and the vector of density independent factors measured, respectively. ε_t are IID random numbers, which describe the environmental stochasticity and inherent stochasticity in the population dynamic process.

In equation 1, the information about density dependent factors may be unavailable, and hence some alternative forms of this equation may help resolve this problem. One such alternative method is to consider a model with more than one time lag of the population density as an approximation of equation 1, because interactions between two species (i.e., prey-predator and host-parasitoid) or more species will always generate higher order models due to mutual feedback interactions (Royama, 1977, 1981, 1992). Thus, equation 1 can be approximately expressed by merging the effects from density dependent factors into a higher order form as follows:

$$R_t = y(N_{t-1},N_{t-2},\ldots,N_{t-p},\mathbf{E}_t, \varepsilon_t, \varepsilon_{t-1},\ldots,\varepsilon_{t-m}). \quad (2)$$

Where the function $y(.)$ can be represented in various linear and nonlinear forms. Higher order population dynamic models can be derived by various linear population dynamic models (Royama, 1977, 1981, 1992). Furthermore, density independent factors in equation 2 also can be assimilated into the noise term, unless the assumption of IID random numbers does not apply for them over a long period (see discussion).

The influences from density independent factors can be achieved by evaluating the relationships between the residuals from density dependent factors and density independent factors (Royama, 1977), or directly achieved by using multiple linear and nonlinear regressions based on equations 1 or 2. In general, we cannot evaluate the influences from density independent factors only, without considering the influences from density dependent factors in the model. For example, it is invalid to use the direct correlation between the population density and the climate to detect the climate's influence on the population dynamics, unless population dynamics is an IID process. Because density dependent factors may consistently operate on the population dynamics, and the observations of population density may be correlated together, one generally cannot drop all density dependent factors in equations 1 or 2, and evaluate the influences from density independent factors only. In the following section, I will show how theoretical and statistical population dynamic models are developed compared to equations 1 and 2.

Deterministic Population Dynamic Models

Based on equation 2, when the regulation from density dependent factors and noise terms do not exist, the simple model for population dynamics is to include an intrinsic population growth parameter only, to describe the population growth. A simple discrete deterministic population model for density independent growth can be described as follows (May, 1981):

$$N_t = N_{t-1}\exp(r). \tag{3}$$

Where N_t is defined as before, r is the intrinsic population growth rate. In this model, the population will continue growing without limits.

Under limited resource conditions, the rate of the increase of the population may be reduced as the population increases. Assuming that the relationship between the rate of increase and population density decreases linearly, a stable age distribution, and the density is measured in appropriate units (Krebs, 1978), the constraint $(1\text{-}f(N_{t-1})/K)$ can be used to measure the availability of the resource and to produce a density dependent growth process by modifying r as below ($f(N_t)$ is some transformation of N_t, K is the environmental carrying capacity, $K = f(N^*)$, where N^* is the equilibrium density):

$$N_t = N_{t-1}\exp(r(1\text{-}f(N_{t-1})/K)) = N_{t-1}\exp(r+bf(N_{t-1})), \tag{4}$$

where $b = -r/K$. The Ricker model can be derived from equation 4 by applying an $f(N_t) = N_t$ transformation (Ricker, 1954), while the Gompertz model can be derived from equation 4 by applying an $f(N_t) = \ln(N_t)$ transformation (Dennis and Taper, 1994).

Simple Stochastic Population Dynamic Models

Equation 4 is a simple equation considering a constant growth rate and an environmental carrying capacity to describe the population dynamics and its interaction with the biological and physical environment (May, 1981). Under both field and laboratory conditions, because of the environmental stochasticity and the inherent uncertainty of the population systems (e.g., chance related to individuals), stochastic population models should be developed that consider such effects by adding simple or complex noise terms.

A simple form of a general stochastic model can be written as follows:

$$N_t = N_{t-1}\exp(a + bf(N_{t-1})) + \varepsilon_t, \tag{5}$$

letting $X_t = \ln(N_t)$,

$$X_t = X_{t-1} + a + bf(N_{t-1}) + \varepsilon_t, \tag{6}$$

or $$R_t = a + bf(N_{t-1}) + \varepsilon_t, \quad (R_t = X_t - X_{t-1}). \tag{7}$$

Where ε_t (i.e., system noise) are IID random variables with a mean zero and variance σ^2. Parameter a is hereafter defined as the population growth parameter, and b, the density dependence parameter. The noise ε_t can be considered as the random disturbance on growth parameter a. According to Dennis and Taper (1994), when $b<0$, density dependent population regulation is evident. When $b = 0$, a density independent population process is implied, and this form of the equation is called a stochastic exponential growth model. When both $a = 0$ and $b = 0$, equation 6 is called a random walk model. Inverse density dependence is implied when $b > 0$. In the deterministic Ricker model, the environmental carrying capacity is expressed as $-r/b$, and the intrinsic growth rate as $r = a+\sigma^2/2$ by a deterministic analogue to equation 5 (Dennis and Taper, 1994; Note: this result also can apply to the Gompertz model).

The influence from density independent factors and noise can be combined into one noise term as in equation 6 by simply assuming that the noise term satisfies the IID conditions. If such an assumption is not met, we may need additional environmental density independent covariates or assumptions to improve the parameter estimation. It should be noted that this assumption may be violated if systematic behavior exists among any density independent factors and noise. For example, many polyvoltine insects have a distinct seasonality, and hence care should be taken in analyzing such population dynamics.

Ricker and Gompertz models, and others with simpler forms have been widely used to model population dynamics under controlled experimental conditions. In addition, they also have been used as the basis for the population dynamic modeling and statistical density dependence tests for field populations (see reviews by Dennis and Taper, 1994). In the field, the strict assumptions about noise and constant resources can be rarely fulfilled (Krebs, 1978). As mentioned before, density dependent factors may have their own dynamic processes which depend on current or past population density, and which have a systematic influence on the population dynamics. The influence from density dependent factors cannot be treated in similar fashion as density independent factors by integrating them into the noise term, and may not be characterized by these two models with constant growth rate and density dependence parameters (Royama, 1977). Because of this, Ricker and Gompertz models do not have the capacity to recognize more complex regulation. Furthermore, little attention has been paid in the literature regarding the formulation of a dynamic model for indeterminate density dependence, in which a population may combine two or more of following parameter values: $b < 0$, $b > 0$ and $b = 0$ in equation 6 or 7 (Strong, 1986; Brown, 1989).

If some important density dependent factors are missing in the models, or if we consider all density dependent factors are combined and represented by the density dependence parameter and/or the noise term, and Gompertz or Ricker models are used to estimate the parameters, some serious statistical problems may occur (e.g., autocorrelation, heteroscedacity of the noise, and misspecification of the model), and which may result in unreliable parameter estimation (see discussion). In the following sections, the models will be formed by considering the influence of fluctuations in resource availability, dynamics of natural enemies and other density dependent factors, when the information related those factors is unavailable.

Complex Population Dynamic Models

A consideration of the mutual interactions between density dependent factors and animal populations is the key to formulation of the population dynamic models under a changing environment. In theoretical modeling, many population models can be found to describe such interactions. The population may show some theoretical dynamics as circle, chaos, multiple equilibrium points, etc. (e.g., Rodzis, 1989). In the statistical population dynamics area, Royama (1977, 1981, 1992) found that second order population dynamic models can be used to approximately describe the linear dynamics of two species. He found that higher order time series models are appropriate to describe univariate ecological time series for more complex systems, such as three species interaction systems. It is convenient to use more time lag equations to model the univariate population dynamics to consider the influence from resources, natural enemies or competitors, when such information is unavailable. Royama even expanded the population dynamic models into whole autoregressive and moving average (ARMA) family (Royama, 1992; Box and Jenkins, 1976), and developed a random coefficient population dynamic model (Royama, 1977). In this study, I will modify first order models, combine them with second order models, and will then build a group of models in linear and nonlinear forms.

Time-Varying Parameter First Order Population Dynamic Models

The population process can be considered as a structural process, which combines the time-varying parameters (i.e., a_t and b_t) and noise by a transformation (i.e., $X_t = X_{t-1} + a_t + b_t f(N_{t-1}) + \varepsilon_t$), to consider the influence of external environmental factors (e.g., resource availability and natural enemies) and internal population characteristics on parameters in first order models. In theoretical population dynamic modeling, several methods have been used to describe the time variable intrinsic growth rate and environmental carrying capacity in either deterministic or stochastic fashion in fluctuating environments (Roughgarden, 1979; May, 1981; Nisbet and Gurney, 1982), however, the practical application or testing these models seems very difficult (Royama, 1977; Nisbet and Gurney, 1982).

Considering a time series which can be described by a nonlinear stochastic, dynamic function such as equation 2, under certain assumptions and using standard Taylor series linearization techniques, this nonlinear stochastic system can be approximated by a linear time-varying parameter model (Young, 1994).

Time-varying parameter and higher order models are two basic approaches that can be used to describe the influence of resource variability, dynamics of the natural enemies and other density dependent factors on population dynamics, when the information on fluctuations in resource availability, dynamics of natural enemies and other density dependent factors is unavailable.

Modeling time-varying growth and density dependence parameters are essential for interpreting the structural population dynamic process under unavailable quantitative environmental information. However, the time-varying parameters a_t and b_t are not true biological entities, and therefore cannot be observed. Deterministic functions of time (e.g., sine wave functions) used to describe time-varying changes in the parameters are inflexible for general modeling purposes, as knowledge for the parameter changes is not always available. The stochastic parameters seem appropriate to describe some systematic and stochastic changes in parameters because of the great flexibility associated with stochastic processes. In this study, in addition to modeling population dynamics, the time-varying parameter changes in changing environments were also considered, based on a simple first order autoregressive model, a random coefficient model and a random walk model. Changes in parameters are based on the following assumptions:

a). One or both parameters follow the first order autoregressive model (Ar; a_t-a = $\phi_a(a_{t-1}-a) + \omega_{a,t}$, b_t-b = $\phi_b(b_{t-1}-b) + \omega_{b,t}$; $\omega_{a,t}$, $\omega_{b,t}$ are noise terms that are IID random variables with mean zero and variance σ_a^2, σ_b^2, respectively; all the noise terms below will follow the same assumptions. a and b here are central values of the growth and density dependence parameters, respectively).

b). The density dependence parameter is considered as a random coefficient (Rc; $b_t = b + \omega_{b,t}$) (Note: the system noise ε_t and $\omega_{a,t}$ might be mixed and considered as a single noise term in the model, when the growth rate parameter is considered as a random coefficient).

c). One or both parameters follow a random walk process

(Rw; $a_t = a_{t-1} + \omega_{a,t}$, $b_t = b_{t-1} + \omega_{b,t}$).

d). One or both parameters are constant parameters

(Cp; $a_t = a$, $b_t = b$).

e). Any combinations of time-varying parameter and constant parameter changes above may be considered in the modeling process, unless the combination already exists.

Parameters found in sections b) - d) can be considered as a specific case of the time-varying parameter found in section a). Twenty-five different models were obtained using the process outlined above, including random walk, exponential growth and constant parameter population dynamic models (Table 1). For all models, except random walk and exponential growth models, a code R or G was used in the classification to indicate whether an $f(N_t) = N_t$ or $f(N_t) = \ln(N_t)$ transformation was used.

The following general time-varying parameter population dynamic model was used to describe the population and parameter dynamics:

$$X_t = X_{t-1} + a_t + b_t f(N_{t-1}) + \varepsilon_t, \tag{8}$$

$$a_t - a = \phi_a(a_{t-1} - a) + \omega_{a,t}, \tag{9}$$

$$b_t - b = \phi_b(b_{t-1} - b) + \omega_{b,t}. \tag{10}$$

When $\phi_a = 0$ and $\phi_b = 0$, the model is considered as a random coefficient model ($b_t = b + \omega_{b,t}$). When $\phi_a = 1$ and $\phi_b = 1$, both parameters follow a random walk process ($a_t = a_{t-1} + \omega_{a,t}$, $b_t = b_{t-1} + \omega_{b,t}$). If the $\omega_{a,t}$ and $\omega_{b,t} = 0$, then Ricker or Gompertz models can be derived based on either a random coefficient model or a random walk model.

Second Order and Second Order Random Coefficient Models

In order to identify the best model for modeling time series data, the second order Ricker model ($f(N_t) = N_t$) and Gompertz model ($f(N_t) = \ln(N_t)$) were used as competitive models (Royama, 1977; Turchin, 1990; Dennis and Taper, 1994), resulting in a total of 50 models considered (24 of the Ricker form, 24 of the Gompertz form, one random walk model, and one exponential growth model). The general form of the second order model can be expressed as follows (Royama, 1977, 1981):

$$X_t = X_{t-1} + a + b_1 f(N_{t-1}) - b_2 f(N_{t-2}) + \varepsilon_t \qquad (11)$$

This model can be used to describe the strong influences from natural enemies, fluctuations in resource availability or other density dependent factors on the population dynamics (Royama, 1977).

Based on equation 11, a second order random coefficient model can be represented as below:

$$X_t = X_{t-1} + a + b_{1,t} f(N_{t-1}) + b_{2,t} f(N_{t-2}) + \varepsilon_t, \qquad (12)$$

and $b_{1,t} = b_1 + \omega_{1,t}$, $b_{2,t} = b_2 + \omega_{2,t}$. $\omega_{1,t}$ and $\omega_{2,t}$ are IID random numbers, but may be correlated together (i.e., $E(\omega_{1,t}, \omega_{2,t}) \neq 0$). The Gompertz form of this model, is also called as the second order autoregressive model with random coefficients, which was first used by Nicholls and Qiunn (1982) for modeling *Lynx* data based on the de-meaned data set. This nonlinear model will be considered as a competitive model for second order models in this study in order to demonstrate complex dynamics.

State Space Form of Stochastic Population Dynamics

Except for the random walk model, exponential growth model, and second order random coefficient models with correlation between noises $\omega_{1,t}$ and $\omega_{2,t}$ (equation 12), all models were transformed into state space form to take advantage of Kalman filter techniques (the Kalman filter will be described later). Although random walk and exponential growth models also can be transformed into state space form, it is not necessary as the parameter estimation is simple. The general state space form for model ArArP (equations 8, 9 and 10), which implies that both growth and density dependence parameters follow the first autoregressive model and system noise is present, is:

$$X_t = \mathbf{Z}_{t-1}\mathbf{A}_t + X_{t-1} + \varepsilon_t \tag{13}$$

$$\mathbf{A}_t = \mathbf{A}_{t-1} + (\mathbf{I} - \mathbf{\Phi})\mathbf{B} + \mathbf{\Omega}_t, \tag{14}$$

where $\mathbf{Z}_t = [1\ f(N_t)]$, $\mathbf{A}_t = [a_t\ b_t]^{\mathrm{T}}$, $\mathbf{\Phi} = [(\phi_a\ 0);\ (0\ \phi_b)]$, $\mathbf{B} = [a\ b]^{\mathrm{T}}$, $\mathbf{I} = [(1\ 0);\ (0\ 1)]$ and $\mathbf{\Omega}_t = [\omega_{a,t}\ \omega_{b,t}]^{\mathrm{T}}$. $\mathbf{A}_t$ is called the state vector at time t, and equation 14 is called the state equation. The state equation describes the dynamics (i.e., dynamics of the parameter) in which the state vector at time t ($\mathbf{A}_t$) is determined from the state vector at time t-1 ($\mathbf{A}_{t-1}$). Equation 13 can be called as the system equation which describes the dynamics in which the system variable (X_t) at time t is determined by the state vector at time t-1 and the variables related to X_{t-1}. This model (equations 13 and 14) actually is known as a conditionally Gaussian model (i.e., a nonlinear model, or is called as a linear time-varying parameter model), because of internal dependence of the state variable X_t on X_{t-1}, and $f(N_{t-1})$. Other types of time-varying parameter models can be easily obtained by changing the parameter values (e.g., let $\phi_a = 1$, $\phi_b = 1$, the above model will be RwRwP). Model ArCpA-G can be rewritten in the second order model form as (see appendix C):

$$X_t = X_{t-1} + c + (b + \phi_a)X_{t-1} - (b+1)\phi_a X_{t-2} + \varepsilon_t. \quad (15)$$

This model will be identical to the second order Gompertz model if $b + \phi_a = b_1$, and $(b+1)\phi_a = - b_2$. When b_1 and b_2 are given, one may not find correspondent real values for b and ϕ_a, thus, the second order Gompertz model is the super model set which includes the Gompertz model with an autoregressive error term. It should be noted that switching b and ϕ_a does not change the dynamic properties of the model ArCpA-G. In contrast, ArCpA-R and second order Ricker models are two different models (appendix C). Model ArRcA and second order models can be used to describe the results of interactions between two species (e.g., predator-prey, and host-parasitoid; Royama, 1977, 1981; Berryman, 1978), internal population biological population processes (Prout and McChesney, 1985) and inconsistent measurement errors associated with the data (see discussion). The CpRcA-G model is the same as that presented by Royama (1977), who also provided the stationary conditions (also see Nicholls and Pagan, 1985).

III. PARAMETER ESTIMATION AND MODEL SELECTION

Generally, ordinary least squares or maximum likelihood function can be used to estimate the parameters in constant parameter models (Dennis and Taper, 1994). For the time-varying parameter model expressed in a state space form as in equations 13 and 14, the system variable X_t (equation 13) depends on the observations up to and including X_{t-1}, and the X_{t-1} may be regarded as a fixed term once we are at time t-1 (Harvey, 1984, 1989a). Hence the general Kalman filter can be used to analyze such nonlinear structural population dynamics (Kalman, 1963; Harvey, 1989a). The parameter estimating techniques for second order random coefficient models with correlated noise terms will be introduced in the final section.

Kalman Filter

For a state space model with IID normal noise terms, the Kalman filter is a recursive procedure for computing the linear estimator of the state vector at time t, based on the information available at time t-1. When the information at time t is available, the filter can update related parameters in the model and yield the conditional mean and covariance estimates of state variables (Harvey, 1989a). The prediction and updating equations of the univariate time series are main parts of the Kalman filter described below.

Let the vector, $\mathbf{A}_{t-1/t-1}$ denote the conditional mean estimator of $\mathbf{A}_{t-1}$ based on the observations up to and including X_{t-1}. Let $\mathbf{P}_{t-1/t-1}$ denote the p by p conditional covariance matrix of the estimation error (p is the number of variables in the state vector). The prediction equation is as (see appendix D):

$$\mathbf{A}_{t/t-1} = \Phi\mathbf{A}_{t-1/t-1} + (\mathbf{I} - \Phi)\mathbf{B} \tag{16}$$

$$\mathbf{P}_{t/t-1} = \Phi\mathbf{P}_{t-1/t-1}\Phi^T + \mathbf{Q}. \tag{17}$$

When a new observation X_t is available, the updating equations are expressed as:

$$\mathbf{A}_{t/t} = \mathbf{A}_{t/t-1} + \mathbf{P}_{t/t-1}\mathbf{Z}_{t-1}^T f_t^{-1} v_t \tag{18}$$

$$\mathbf{P}_{t/t} = \mathbf{P}_{t/t-1} - \mathbf{P}_{t/t-1}\mathbf{Z}_{t-1}^T f_t^{-1}\mathbf{Z}_{t-1}\mathbf{P}_{t/t-1}, \tag{19}$$

where, the one step ahead prediction residual and variance are:

$$v_t = X_t - \mathbf{Z}_{t-1}\mathbf{A}_t - X_{t-1} \tag{20}$$

$$f_t = \mathbf{Z}_{t-1}\mathbf{P}_{t/t-1}\mathbf{Z}_{t-1}^T + \sigma^2. \tag{21}$$

The estimators $\mathbf{A}_{t/t}$, $\mathbf{P}_{t/t}$ yield conditional estimates of the state vector 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 state variables, the recursive smoothing techniques were used to estimate the conditional mean ($\mathbf{A}_{t/T}$) and the conditional variance ($\mathbf{P}_{t/T}$), which start with the final quantities $\mathbf{A}_{T/T}$ and $\mathbf{P}_{T/T}$ and work backwards (Harvey, 1989a).

$$\mathbf{A}_{t/T} = \mathbf{A}_{t/t} - \mathbf{P}_t^*(\mathbf{A}_{t+1/T} - \mathbf{A}_{t+1/t}) \tag{22}$$

$$\mathbf{P}_{t/T} = \mathbf{P}_{t/t} + \mathbf{P}_t^*(\mathbf{P}_{t+1/T} - \mathbf{P}_{t+1/t})(\mathbf{P}_t^*)^T, \tag{23}$$

where

$$\mathbf{P}_t^* = \mathbf{P}_{t/t}\Phi^T\mathbf{P}_{t+1/t}^{-1}, \qquad t = T-1, T-2, \ldots, 2. \tag{24}$$

When $\mathbf{Q} = \mathbf{0}$ ($\mathbf{Q} = [(\sigma_a^2\ 0);\ (0\ \sigma_b^2)]$) in the RwRwA model, the smoothed estimates $\mathbf{A}_{t/T}$ and $\mathbf{P}_{t/T}$ are independent of time t, and identical to ordinary least squares estimates, which is a specific case of the Kalman filter (Otter, 1978). However, a slight difference may exist between the estimates from the Kalman filter and ordinary least squares due to the uncertainty of the starting values provided for the Kalman filter. In this study, the final parameters for the constant parameter model were estimated by applying the Kalman filter five times and adjusting the initial values each time, to eliminate bias in the estimates of the parameters caused by inappropriate initial values.

Maximum Likelihood Function for the State Space Model

In statistical applications, the Kalman filer, which is a recursive algorithm, cannot give the estimates of the time-varying parameters, and hence it must be combined with the maximum likelihood function to estimate the parameters (Harvey, 1989a). For the structural time series model as in equations 13 and 14, the maximum likelihood function is defined as:

$$L(\mathbf{X},\mathbf{W}) = \prod_{t=1}^{T} p(X_t|\mathbf{X}_{t-1}) = p(X_t|\mathbf{X}_{t-1})p(X_{t-1}|\mathbf{X}_{t-2})\dots p(X_1), \tag{25}$$

where $\mathbf{X} = (X_1, X_2,\dots,X_T)$, $\mathbf{W}$ is the parameter set in the likelihood function (e.g., $\mathbf{W} = [a, b, \phi_a, \phi_b, \sigma_a^2, \sigma_b^2, \sigma^2]$ for equations 13 and 14), the $p(X_t|\mathbf{X}_{t-1})$ is the distribution of X_t conditional on the $\mathbf{X}_{t-1}$ values up to date at time t-1, which is considered the normal distribution density function, with the prediction residual v_t, and the prediction variance f_t associated with v_t based on information at time t-1, and can be expressed as:

$$p(X_t|\mathbf{X}_{t-1}) = \frac{1}{\sqrt{2\pi f_t}} \exp(-\frac{v_t^2}{2f_t}) \tag{26}$$

Thus, the complete log-likelihood function for a univariate time series can be expressed as (Schweppe, 1965; Nicholls and Pagan, 1985; Harvey, 1989a):

$$\ln(L(\mathbf{X},\mathbf{W})) = -\frac{T-1}{2}\ln(2\pi) - \frac{1}{2}\sum_{t=2}^{T}\ln(f_t) - \frac{1}{2}\sum_{t=2}^{T}\frac{v_t^2}{f_t} + \ln(p(X_1)). \tag{27}$$

The v_t and f_t can be calculated from the Kalman filter. $\ln(p(X_1))$ can be considered a fixed term and dropped from the likelihood function, since prior knowledge of the variation associated with X_1 is not always available. For similar reasons, $\ln(p(X_1))$ and $\ln(p(X_2|X_1))$ were also dropped from the likelihood function in second order models, and the likelihood function only needed miner modification about the time index t. Dropping a few initial data points will not affect the parameter estimation for a longer time series (Harvey, 1989b; Tong, 1990). It should be noted that a different state space form is available for first order models and second order models. The details for the derivation of the concentrated likelihood function can be found in the literature, which would eliminate parameter σ^2 from likelihood function (Harvey, 1984, 1989a).

The Kalman filter was used to do the recursion, and the maximum likelihood function was used to estimate parameters σ_a^2, σ_b^2, σ^2, a, b, etc. All models used in this study were analyzed by the Kalman filter and maximum likelihood functions, except for the maximum likelihood estimates of the parameters in random walk and exponential population growth models, which were obtained directly as follows (Dennis and Taper, 1994):

for the random walk model, $\sigma^2 = \frac{1}{T-1}\sum_{t=2}^{T}(X_t - X_{t-1})^2$, (28)

for the exponential model, $a = \frac{1}{T-1}\sum_{t=2}^{T}(X_t - X_{t-1})$, (29)

and $\sigma^2 = \frac{1}{T-1}\sum_{t=2}^{T}(X_t - a)^2$. (30)

The complete (or full) likelihood function value can be achieved using equation 27, 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 $f_t = \sigma^2$.

Initialization of the Kalman Filter

The unconditional mean and covariance of the parameters a_t and b_t were used to initialize the Kalman filter (e.g., $\mathbf{A}_{1/1,}$ and $\mathbf{P}_{1/1}$ for state space model from equations 13 and 14), when they were available. For the first order autoregressive parameter model (equations 8 and 9), the unconditional mean is the central value a and b, respectively, and the unconditional variance for a_t and b_t 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.

The unconditional mean and variance for the random walk parameters does not exist. Harvey (1989a) suggested that a small value (e.g., 0) and a large value (e.g., 1000) be used to initialize the mean vector and covariance matrix in the Kalman filter, respectively, this procedure were followed in my study. The covariance matrix of the estimated parameters was approximately estimated from the Kalman filter by inversing the Hessian of the log likelihood (Nicholls and Pagan, 1985). The parameter estimates from constant parameter models were used as the initial parameters for optimization, when they are available. For the parameters without the initial knowledge, any value within the reasonable range was used to as the initial try value (such as ϕ_a and ϕ_b should be set between -1 to 1). Missing observations in the time series can be easily treated using predicted value from the Kalman filter to replace missing observations, then the Kalman filter will not update parameter estimation related to them.

Test of the Independent, Identically Distribution of the Noise

Assuming that the noise term ε_t is IID noise, then the autocorrelation function of the noise $r(m)$ (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 until M is zero. The Q statistic is expressed as follow:

$$Q(M) = T_n(T_n+2)\sum_{m=1}^{M}(T_n-m)^{-1}(r(m))^2 \qquad m=1,2,\ldots,M. \tag{31}$$

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 $r(m)$ is the estimated sample autocorrelation at time lag m (Shumway, 1988).

Model Selection Tool: Information Criteria

In this study, I assume that the model which best fits and predicts the data should best approximate the generating mechanisms for the data among alternative models. In the selection of the best model, a direct test of the parameters for statistical significance using a subjective arbitrary critical value is not appropriate, simply because significance of the parameters may not suggest the best model. For time series modeling, it is not difficult to find a model with parameters that are statistically significant, however, it may not help in the inference of underlying mechanisms of the data. For example, data from a random walk process can be easily fit by a first order autoregressive model with a statistically significant parameter. Here, a model selection method is required to determine the best model, which best fits data, infers parameter values and predicts future values of the time series. Whether a population is judged statistically regulated or not, depends on the final model selected, then distribution of "true" parameter values, such as the density dependence parameter, can be determined from the best model.

Regarding goodness of fit statistics, the prediction residual variance which can be obtained from the Kalman filter are basic measures of goodness of fit in the time series model (Harvey, 1989a). The value of the maximized likelihood function is another goodness of fit statistic and will be emphasized in this study. Generally, a model with more parameters is associated with a higher maximized likelihood value, but may not suggest the appropriate model because of less information gain. Information criteria are popular model selection methods which adjust the values of the maximized likelihood functions by the number of parameters or samples size, or both to generate an appropriate model selection among alternative models. They generally take the form of a penalized likelihood function value with the negative log likelihood plus a penalty term, which increases with the number of parameters and often the number of observations (Sclove, 1987). Information criteria are of importance in modern statistical data modeling and statistical model identification. One of the advantages of using information criteria is their computational simplicity for comparing different models. The models compared can be nested or non-nested (Takane, 1987; Harvey, 1989b). In this study, I will use three information criteria to select the best model among a group of density dependence and density independence models, including Akaike's Information Criterion (AIC; Akaike, 1974), adjusted AIC (AICc; Hurvich and Tsai, 1989) and Schwarz's Information Criterion (SIC; Schwarz, 1978).

AIC is defined as (Akaike, 1974):

$$\text{AIC} = -2\ln(L)+2k, \tag{32}$$

where $\ln(L)$ is the log-likelihood, k is number of the parameters.

AICc is defined as (AICc; Hurvich and Tsai, 1989):

$$\text{AICc} = -2\ln(L)+2k+2(k+1)(k+2)/(n\text{-}k\text{-}2\text{-}\tau), \tag{33}$$

where $n = T\text{-}1$ except $n = T\text{-}2$ for second order models ($n = T$ - number of observations dropped in maximum likelihood estimation), τ is number of the missing observations.

SIC, sometimes called the Bayesian information criterion, is defined as (Schwarz, 1978):

$$\mathrm{SIC} = -2\ln(L) + k\ln(n-\tau). \tag{34}$$

Using any one of the three information criteria, the model that generates the minimal information criterion value is herein defined as the best model for fitting and predicting time series data. Because of the limited number of the observations for the ecological time series, and the value of the information criterion (IC) varies with sample size, the information criterion for the second order was adjusted by adding a positive term $|\mathrm{IC}|/(T\text{-}2)$ in this study. This method is similar to using the mean information criterion value from the actual number of the time series observations in the analysis (Tong, 1990; Hooten, 1995).

Many authors (e.g., Koehler and Murphree, 1988; Hooten, 1995) have verified that the AIC will favor the selection of higher order models compared to those chosen using SIC, although the more sophisticated models may not necessarily improve the fit of the time series data. Furthermore, the SIC method offers more consistency in identifying the appropriate model compared to the AIC method, which suggests that the SIC may be a more reliable model selection criterion. AICc is designed to improve the model selection under small sample size (Hurvich and Tsai, 1989). However, for data sets of small sample size, the AICc method tends to favor lower order models (Hooten, 1995). A number of information criteria (including the three identified above) were compared by Hooten (1995) for selection of the appropriate model form in study 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. In this study, the SIC method will be emphasized when inconsistencies occur among the three information criteria used to select the best model. This model selection method actually is identical to the use of the SIC method only.

Parametric Bootstrap of the Ecological Time Series.

A difference between the null and alternative models is considered significant, if the difference value in the AIC between two models is at least 1 to 2 (Sakamoto et al., 1986). If several models have almost equal AIC values, and hence the information criterion provides insufficient evidence for identifying the best model, Akaike (1979) suggested considering the average models using the AIC value as the likelihood of each model based on Bayesian statistics. Because the AIC, AICc and SIC do not imply any probability value in the selection of the best model, the meaning of the word "significant" used by Sakamoto et al. (1986) is not clear. I believe that the probability level associated with the model selection would enable density dependence test results to be more fairly compared between statistical significance test and model selection using information criteria, and evaluate uncertainty in model selection. In this study, I used a parametric bootstrap test of the ecological time series data based on information criteria, to find the probability value associated with the model selection. The basic idea of the current test is from the PBLR test proposed by Dennis and Taper (1994). Unlike the likelihood ratio test, the models used in this test are not necessarily restricted to the nested models here, thus maintaining the advantage of using the information criteria. The parametric bootstrap test procedure is described below.

1). On the bases of parameter estimation and model selection results from the original time series data, the difference of the information criterion value between two models is calculated. These two models are the null and the alternative models. For the density dependence test, generally, either a random walk or an exponential model is considered as the null model, and the best model among the density dependence models should be considered as the alternative model. Assume that the difference in the information criterion value between the null model and the alternative model is D.

2). Based on original time series data and estimated parameters for the null model, generate a larger number of bootstrap data (e.g., 1000) using Monte Carlo simulations, and each should be the same length as original data. The starting value of each of the bootstrap time series data sets will be randomly drawn from the original time series.

3). Estimate the parameter values and the information criterion value based on bootstrap data using the null model and alternative model, and calculate the difference in the information criterion value between them. The latter is denoted as D^*.

4). The p-value can be estimated from the proportion that D^* is larger than D. Generally, reject the null model in favor of the alternative if $\hat{p} < 0.05$.

Actually, this test method is identical to the use of the likelihood ratio test in testing non-nested models, as the penalty terms in the information criterion will be canceled, thus, there is no difference using any information criterion in the parametric bootstrap test (see appendix E). Compared to the PBLR test in Dennis and Taper (1994), this method also differs in using any observation in the time series instead of only the first observation, as they used. It seems that the parametric bootstrap tests, including the likelihood ratio test make sense in comparing either nested or non-nested models, as no assumptions regarding the type of distribution for either the likelihood ratio or the information criterion values are required in the test. In this study, the parametric bootstrap test were only applied for the population, where density dependence model was selected as the best model using the SIC method.

Structural Changes and Misspecification of the Model

The cumulative sum (CUSUM) and cumulative sum of squares (CUSUMSQ) are two general test methods used to detect structural changes in the model over time, misspecification of model form, and nonstationarity of the time series, based on recursive residuals from ordinary least square estimation (Brown, Durbin and Evans, 1975). For time series data analysis using the Kalman filter, the prediction residual (v_t) and variance (f_t) can be used to form two diagnostic tests in structural time series analysis (Harvey and Durbin, 1986; Harvey, 1989a). The recursive residuals are IID normal variables with mean zero and variance f_t, and can be standardized by the prediction residuals from the Kalman filter (Harvey, 1989a).

$$w_t = v_t / \sqrt{f}_t \qquad t = k + d + 1,..,T. \qquad (35)$$

Where w_t is the standardized recursive residual, k is number of the parameters, and d = number of the initial observations dropped in the maximum likelihood estimation (e.g., $d = 1$ for random walk and time-varying parameter first order model).

These two tests can be considered post sample predictive tests, which test the model's ability to make accurate predictions outside of the sample period. The procedures used to form the two test statistics are as follows (Brown, Durbin and Evans, 1975; Harvey, 1989b):

$$\text{CUSUM}(t) = \sigma^{-1} \sum_{j=k+d+1}^{t} w_j, \qquad t = k+d+1,\ldots,T, \tag{36}$$

where $\sigma^2 = \sum(w_t - \overline{w})^2 / (T-k-d-1)$, $\overline{w} = \sum w_t / (T-k-d)$.

The two predefined significance lines are:

$$\text{CUSUMSL}(t) = \pm\alpha(\sqrt{T-k-d} + 2\alpha(t-k-d)/\sqrt{(T-k-d)}), \tag{37}$$

where $\alpha = 0.948$ for a 0.05 probability significant level.

$$\text{CUSUMSQ}(t) = \sum_{j=k+d+1}^{t} w_j^2 \Big/ \sum_{t=k+d+1}^{T} w_t^2, \qquad t = k+d+1,\ldots,T. \tag{38}$$

The two predefined significance lines for CUSUMSQ are:

$$\text{CUSUMSQSL}(t) = \pm c_0 + (t-k-d)/(T-k-d), \tag{39}$$

where value of c_0 can be found in the Table C given by Harvey (1989b, p365). Harvey (1989b) suggested that the significance lines are best regarded as yardsticks against which to assess the observed plots rather than as formal tests of significance.

Structural changes are indicated where the CUSUM or CUSUMSQ lines show an irregular increase or decrease, approaching the upper or lower significance lines (Harvey, 1989b). Structural changes indicate that the current best model, identified by the information criteria, is not capable of modeling certain parts of time series data, which may have resulted from irregular events or any unusual environmental changes based on the current model. CUSUM and CUSUMSQ tests indicate the misspecification of the model when the CUSUM and CUSUMSQ lines are found on one side of the central line due to many recursive residuals which have the same sign (Harvey, 1989a). Based on CUSUM and CUSUMSQ equations, it seems that CUSUM test may be more sensitive to the changes of the mean than the changes of variance in the time series, and the CUSUMSQ test may be sensitive to the changes of both. This may be the reason that some authors found that the CUSUMSQ test is more powerful than the CUSUM test in detecting structure changes (e.g., Bos and Fetherston, 1992). Sometimes, the difference between moderate model misspecification and structural changes is not clear in the figures produced for these two test methods.

Performance of the Parameter Estimation Using Monte Carlo Simulations

Kalman filter analysis has many advantages over classical Box-Jenken's methods in that the Kalman filter can deal with multiple noise terms (e.g., parameter noise, observation noise and system noise) and time series components (e.g., trend, circle) in a state space form (Harvey, 1989a). However, for conditionally Gaussian models, the efficiency of parameter estimation regarding the given parameter values, the number of parameter noise terms and length of the time series under small sample size (<50) is not known. In contrast, parameter estimation for a simple regression model with an autoregressive parameter can be found in Harvey and Phillips (1982).

In order to demonstrate the ability of time-varying parameter population dynamic models for modeling both systematic and stochastic changes in the parameters, I will use the time-varying Gompertz population dynamic model in Monte Carlo simulations. This model is identical to the first order autoregressive model (AR(1)) with the time-varying parameter below:

$$X_t = a + (1+b_t)X_{t-1} + \varepsilon_t = a + \beta_t X_{t-1} + \varepsilon_t, \quad (\beta_t = 1+b_t). \tag{40}$$

Three systematic parameter changes (a linear, a sigmoid and a sine wave function) were used to evaluate the performance of the time-varying parameter model.

For stochastic parameter changes, the dynamics of β_t is defined as:

$$\beta_t - \beta = \phi(\beta_{t-1} - \beta) + \omega_t. \tag{41}$$

Where ω_t are IID random numbers with mean zero and variance σ_β^2. In this study, three types of time-varying parameter models (first order autoregressive parameter, random coefficient and random walk processes) were considered under different parameter values and lengths of the time series to evaluate the parameter estimate property for time-varying parameter autoregressive models using the Kalman filter.

The time series **X** was simulated using the predefined parameters a, β, σ_β^2 and σ^2, the initial value of the time series X_1 (from a (-1,1) uniform distribution), and β_1 (from a normal distribution with the unconditional mean and variance, if available). After the parameters were estimated based on this simulated time series using the maximized likelihood function, the information criteria were used to identify best model between time-varying parameter and constant parameter models. CUSUM and CUSUMSQ statistics were used to check misspecification of the models.

In the section above, the potential of the Kalman filter for estimating the time-varying parameter, and in identifying the dynamics of the unknown factors that generate the time series, can be evaluated. However, a few simulations are certainly not enough to show the efficiency of the parameter estimate made by the Kalman filter. In order to test the performance of the Kalman filter for parameter estimation under a larger number of Monte Carlo simulations, the autoregressive, random coefficient, and random walk parameter models were used. The efficiency of parameter estimation was tested under different values of noises and length of the time series, which were compared with the estimates from the constant parameter model. Three information criteria (AIC, AICc and SIC) were used to evaluate the model selection.

A total of 400 simulations was carried out for each given parameter set. Eleven, 10 and 8 different given parameter sets were used for the autoregressive, random coefficient, and random walk parameter models, respectively. It is important to note that, under some conditions, the Kalman filter may fail to achieve optimization in estimating the parameters.

Parameter Estimation for the Second Order Random Coefficient Model

The Kalman filter and maximum likelihood function described above can be directly used to estimate parameters in the random coefficient model with independent parameter noise terms. If the parameter noises are dependent, a two-step procedure based on least squares proposed by Rosenberg (1973) and maximum likelihood function methods proposed by Nicholls and Quinn (1982) can be used to estimate the parameters.

Based on the convention used in many time series analyses, the parameter a in the time series model can be dropped from the time series using the de-meaned series (e.g., Nicholls and Quinn, 1982). The second order random coefficient model (equation 12) can be rewritten as

$$X'_t = X'_{t-1} + b_{1,t}f(N_{t-1}) + b_{2,t}f(N_{t-2}) + \varepsilon_t$$

$$= b_1 f(N_{t-1}) + b_2 f(N_{t-2}) + \omega_{b,1} f(N_{t-1}) + \omega_{b,2} f(N_{t-2}) + \varepsilon_t$$

$$= b_1 f(N_{t-1}) + b_2 f(N_{t-2}) + u_t. \quad (42)$$

Where $X'_t = X_t - \overline{X}$, and $u_t = \omega_{b,1} f(N_{t-1}) + \omega_{b,2} f(N_{t-2}) + \varepsilon_t$. The idea in a two-step procedure is to estimate the central value (i.e., b_1 and b_2) using ordinary least squares and finding the residuals first. The squared residuals are then used to regress on the squares of the lag variables and all the cross product terms of the lag variables to get the estimate of variance and covariance of the parameter noises, and variance of system noise. These are obtained by squaring both sides of this equation and using mathematical expectation operators as follow,

$$\mathrm{E}(u_t^2) = \mathrm{E}(\varepsilon_t^2) + \mathrm{E}(\omega_{1,t}^2 f^2(N_{t-1})) + \mathrm{E}(\omega_{2,t}^2 f^2(N_{t-2})) + \mathrm{E}(2\omega_{1,t}\omega_{2,t} f(N_{t-1}) f(N_{t-2}))$$

$$= \sigma^2 + f^2(N_{t-1})\mathrm{E}(\omega_{1,t}^2) + f^2(N_{t-2})\mathrm{E}(\omega_{2,t}^2) + 2f(N_{t-1})f(N_{t-2})\mathrm{E}(\omega_{1,t}\omega_{2,t}). \quad (43)$$

Based on the conditional expectations of the mean and variance for equation 42, the log likelihood function equation is the same as equation 27 and can be rewritten (Nicholls and Quinn, 1982) as:

$$\ln(L(\mathbf{X},\mathbf{W})) = -\frac{T-2}{2}\ln(2\pi) - \frac{1}{2}\sum_{t=3}^{T}\ln(h_t)$$

$$-\frac{1}{2}\sum_{t=3}^{T}\frac{(X_t - b_1 f(N_{t-1}) - b_2 f(N_{t-2}))^2}{h_t} + \ln(p(X_2|X_1)) + \ln(p(X_1)). \qquad (44)$$

Where, h_t is the conditional variance dependent on $\mathbf{X}_{t-1}$, which is equal to $E(u_t^2 \mid \mathbf{X}_{t-1})$ (i.e., equation 43). This modeling approach will be applied for the lengthy data sets (>30) in this study only.

In order for the information criteria to be directly compared, all modeling processes must use the same adjusted or unadjusted data. For example, because the mean of the natural logarithm of the population density is subtracted first, the information criterion value cannot be directly compared with such analysis without subtracting the mean.

Data Sets

Sixteen insect census data sets were used as major data to test my modeling approach (Table 1 from Den Bore and Reddingius, 1989). These included some famous historical examples in population ecology (e.g., winter moth, *Operophtera brumata*, Varley et al., 1973; pine looper, *Bupalus piniarius*, Klomp, 1966; viburnum whitefly, *Aleurotrachelus jelinekii*, Southwood and Reader, 1976). These data sets appear to show frequent density independence behavior according to test methods currently available (Den Bore and Reddingius, 1989, Dennis and Taper, 1994; Hanski et al., 1993). These data sets are considered as the benchmark for various density dependence tests. Parts of them have been studied by many authors. These data sets have been used in various density dependence test methods, and have been used to address many controversies in population regulation (e.g., Den Boer, 1986, 1987, 1988; Southwood and Reader, 1988, Latto and Hassell, 1987; Hassell et al., 1987; Vickery and Nudds, 1991; Gaston and Lawton, 1987; Dennis and Taper, 1994; Hooten, 1995).

Three 60-year insect census data sets from German forests (Schwerdtfeger, 1941), one data set from Morris (1959), three vertebrate data sets used in Dennis and Taper (1994) and three vertebrate data sets used by Hooten (1995) were re-analyzed by this new modeling approach. An additional four vertebrate data sets from Keith (1963), and a *Lynx* data set from Elton and Nicholson (1942) were also used. All data sets and their original sources used in this study are listed in appendix F.

IV. RESULTS

The Performance of the Kalman Filter

Some examples for the Monte Carlo simulations and parameter estimates are shown in Figs.1-7. The time series data generated from simulation, and the fit made by the time-varying parameter and constant parameter models are listed in graphic A in each figure. CUSUM and CUSUMSQ tests for both the time-varying parameter and constant parameter models are listed graphics B and C, respectively. The true time-varying parameter changes and the estimates are shown in graphic D. All initial parameter values and estimated parameters were listed in the text of each figure. The time-varying parameter model was identified using information criteria. It may take a few trials until the time-varying parameter model is selected as the best model, because the potential to detect the time-varying parameter model by the Kalman filter varies with the model, given parameter values and sample size (see results below).

In Figs. 1-6, models with the time-varying parameter seem to fit time series data better than constant parameter time series models visually (Figs. 1A-6A). CUSUM and CUSUMSQ lines for time-varying parameter models, which occur more towards the central line compared those generated from constant parameter models, suggest a better fit of the data (Figs. 1B-6B and Figs. 1C-6C). In Figs. 1D-6D, the estimated parameters approximate the time-varying systematic parameter changes and stochastic parameter changes well. A simple regression model with a time-varying parameter is shown in Fig. 7, which shows that the Kalman filter produced a good fit of the time series data, and good estimates of the given time-varying parameter.

When the true mechanisms to mix various noises (e.g., parameter and system noises) was known, the results above showed that the Kalman filter can be used to separate the parameter and system noises, and estimate the dynamic changes of the parameters, based on a single output - univariate time series. For an AR(1) model, the true mechanism generating the time series (X_t) is a linear combination of the previous time series data (X_{t-1}) and a random noise (ε_t). Unfortunately, the true mechanisms for generating the data may be not known in many biological studies. The best way is to use statistical modeling and knowledge to find a model, which can approximate the true mechanisms in a stochastic world. Then, this model is assumed to be responsible for generating the ecological data. The assumption can be called the true model assumption. Finding a good approximated model is the key in searching the generating mechanisms. If this assumption does not hold at all, one generally cannot use the Kalman filter or statistical models to search for the truth of nature. More about how to formulate the alternative models and improve the true model assumption is addressed in the discussion part.

The given conditions for the parameter values, the length of the time series, the results for parameter estimation, model selection and the percentage of models that were correctly identified (i.e., AR(1) with the AR(1) slope) are listed in Table 2. By comparing the given a, β, ϕ_β, σ_β^2 and σ^2 with the estimates from constant parameter and autoregressive parameter models, and their related mean square error(MSE) values, the parameter estimates from the constant parameter models given by the Kalman filter always differ more from the given parameter values than the time-varying parameter model does. In row 1, the estimated parameters $\hat{a}$, $\hat{\beta}$ and their MSE seem not to differ much between constant and time-varying parameter models. A probable explanation is that the percentage of models correctly identified is low (13.78%), and most of the constant parameter models are considered as the best model. However, due to the variation of the parameter β_t, the estimates of the system noise from the constant parameter model always have a much larger $\hat{\sigma}^2$ and MSE$\hat{\sigma}^2$, which will decrease the prediction ability of the model. Based on the estimates for both parameter noise and system noise terms (ω_t and ε_t), from time series length 25 to 50, the bias related to overestimates of parameter a, and underestimates of central β and ϕ_β decreased under the same given parameter values (row 1 vs. row 3, row 2 vs. row 4, row 5 vs. row 7 and row 6 vs. 8). As the length of the time series increased, the bias in the estimate for σ_β^2 and σ^2 decreased, and the percentage of models correctly identified increased. For example, when the given conditions for σ_β^2 and σ^2 are 0.16 and 0.64, respectively, in the first row, the percentage of the correct identification of the first order autoregressive parameter model based on the SIC is 13.78% for 25 observations, and the percentage increased to 33.42% for 50 observations (row 3). The correlation coefficient for the slope parameter is always underestimated. As the parameter noise increased, the bias in the parameter estimates would decrease, and percentage of models that correctly identified would increase (row 1 vs. row 2, row 3 vs. row 4, row 5 vs. row 6, row 7 vs. row 8 and row 10 vs. row 11). This similar trend was found for the correlation coefficient ϕ_β increased (row 1. vs row 9), which generated larger variation in the slope parameter. However, as the system noise decreased, the bias in parameter estimation decreased, and the percentage of models that were correctly identified increased (row 1 vs. row 5, row 2 vs. row 6, row 3 vs. row 7, row 4 vs. row 8, and all vs. rows 10 or 11). A higher percentage of models correctly identified (79.75 and 93.20 by the SIC method in rows 10 and 11, respectively) was achieved by setting the system noise to zero. This makes sense as this Monte Carlo simulation and model selection were designed for detection of time-varying parameter models.

The given conditions for the parameter values, length of the time series, the results for parameter estimation, model selection, and the percentage of models correctly identified for an AR(1) with the random coefficient slope are listed in Table 3. For the given conditions, the estimated parameters $\hat{\alpha}$, $\hat{\beta}$ and $\hat{\sigma}^2$ from random coefficient models tend to approximate the true values, and have smaller MSE values than those from constant parameter models. The percentage of models correctly identified varies with the number of noise terms, the strength of the noise, and length of the time series in a similar way as shown in Table 2. When the parameter noise is smaller (rows 1, 3, 5 and 7), the percentage of models correctly identified is lower than 15%. As the variation of the parameter noise and the length of time series increased, the percentage of models correctly identified increased. The last two rows in Table 3, showed that the percentage of models correctly identified will greatly increase, if only one random coefficient noise term is included in the true model.

The given conditions for the parameter values, the length of the time series, the results for parameter estimation, model selection and percentage of models correctly identified for an AR(1) with a random walk slope are listed in Table 4. The unconditional mean for the random walk slope does not exist, and hence is not included in Table 4. By comparing the estimated noises, and their related MSE values, with the given parameters, it seems that the model with a random walk parameter gives a quite good estimation of the parameter noise and system noise terms. However, the percentage of models correctly identified is still not high for lower parameter noise (rows 1 and 3). Like the parameter estimates above, a high percentage of models correctly identified is associated with larger parameter noise or a longer time series.

In general, higher parameter noise (i.e., a higher correlation coefficient and larger parameter noise), fewer noise terms, lower system noise, and a longer time series will consistently increase the parameter estimation efficiency, and the percentage of the time-varying parameter models that are correctly identified. If this was not the case, it would be difficult to identify the correct model form. It seems that the likelihood of being able to identify two noise terms, one from parameter and one from system equations, generally is not high, when length of the time series is less than 25. If the length of time series is about 50, the percentage of models that are correctly identified will be increased considerably. However, whether the length of the time series is sufficient to be able to identify the correct model also depends on the complexity of the time series and the model.

Model selection made by using a test of the significance of the parameter based on either 0.05 or 0.10 probability levels generally performed worse than that using information criteria in Tables 2, 3, and 4. Comparing three information criteria used to identify the correct model, AIC always does better that AICc and SIC, and AICc does better than SIC. It should be noted that the results obtained here do not be necessarily mean that AIC is a better model identification criterion than AICc or SIC. When a model with fewer parameters is chosen as the null model, and a model with more parameters is chosen as the alternative model in a general statistical test, the percentage of models correctly identified is identical to the power of the test, which is the probability of accepting the alternative hypothesis (i.e., reject the null) when the alternative model is true. Because of the internal overfit feature of the AIC for data obtained from a smaller sample size, higher power is to be expected. SIC still provides a conservative method of model selection for better control of type I error.

Population Regulation in Animal Population Dynamics

Parameter estimates and model selection results based on three information selection criteria for each population are presented in Table 5. The best model for each of the 31 data sets was determined by evaluating three information criteria and selecting the model which contained the minimum information criteria for each data set. Models that met this criterion included: seven random walk, two Ricker, two Gompertz, five second order Ricker, five second order Gompertz, four CpRcA-G, two CpRcA-R, one CpArA-G, one ArCpA-G and two CpRcP-G models. The density dependence test can be achieved by comparing the SIC value from the best model among the density independence models, and the best model from density dependence models. The model selection made by AIC and AICc may be different from that made by SIC, the latter of which provided more conservative model selection.

The parametric bootstrap test results for the comparison of the null and alternative models are listed in Table 5. Fifteen and 20 out of 23 density dependence models, whose selection was based on information criteria, were statistically different from the null model (either random walk model or exponential growth model) at the 0.05 and 0.10 probability level, respectively. *A. jelinekii* population 1 (No. 13 in Table 5) was identified as a second order inverse density dependent regulation ($\hat{p}$ = 0.008), because of the positive coefficients. The evidence of density dependence for *A. jelinekii* population 2 and 3 is also not strong based on relatively larger estimated probability values. From Southwood and Reader (1976), the resource for *A. jelinekii* population 1 and population 2 increased a lot during the experimental period, which may cause some problems in detecting density dependence, when the total count data instead of density data is used (see discussion).

One advantage in using dynamic modeling is that one may further improve the fit of a model with fewer parameters and decrease the SIC value based on current modeling results. For example, the estimate of the density dependence parameter for the *B. piniarius* pupal population (No. 5 in Table 5) based on the Gompertz model is close to negative one (-0.669 (0.258)). The Gompertz model with the negative one value of the density dependence parameter is identical to an IID model ($X_t = a + \varepsilon_t$). I fit the data this IID model, and I obtained an adjusted SIC value, 41.382. This SIC value was smaller than the SIC value (42.474) obtaining using the Gompertz model in Table 5, which suggests a higher likelihood for the IID model to be considered as the best model. The estimated probability value from 1000 parametric bootstrap data is 0.083, which suggested that the likelihood to accept the random walk model decreased compared to the estimated probability 0.268 in Table 5. The mean and variance parameters in the IID model here are estimated based on the maximum likelihood estimates of the mean and variance (i.e., mean and population variance), and the IC value is adjusted by subtracting $| \text{IC} | / T$.

A similar procedure was carried out for *O. brumata* larvae, *B. piniarius* adults and *C. elaphus* population (No.1, 6 and 24 in Table 5, respectively). By setting b_1 to zero in the second order Gompertz model and re-estimating parameters for the *O. brumata* larval population, I 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 5. The estimated probability value for rejecting the null random walk model when it is true from 1000 parametric bootstrap data was 0.049. For *B. piniarius* adults, an adjusted SIC value of 40.832 was obtained using the IID model, which is smaller than the SIC value (42.861) in Table 5. The estimated parametric bootstrap probability value was 0.019. This suggests that the *B. piniarius* adult population can be better modeled using the IID model. For the *C. elaphus* population, by setting b = -1, for both Gompertz and CpRcA-G models and re-estimating parameters, I obtained the adjusted SIC value, -36.769 and SIC value of -41.30, respectively. The smaller SIC value in the latter case suggested a time-varying noise model ($X_t = a + X_{t-1}\varepsilon_t$) was the more appropriate model form. This additional analysis of modeling results in Table 5 yielded two more populations identified as regulated populations at the 0.05 statistically significant level (No. 1 and No. 6).

Density dependent regulation of grizzly bear data (*Ursus arctos horribilis*) was also detected, in contrast to Dennis and Taper (1994), who failed to detect density dependence using the PBLR test. In order to test if central $b = 0$ for the grizzly bear data set, I set $b = 0$ and obtained the following parameter estimates, $\hat{\phi}_b$ = -0.648, $\hat{a}$ = 0.0394, $\hat{\sigma}_b^2$ = 5.65e-4, AIC = -25.799, AICc = -22.163 and SIC = -23.482. This is an interesting phenomenon that the density dependence parameter tends to return a zero central value with a negative correlation on the density dependence ability. Because the actual b_t may be smaller, larger than, or close to zero, the population dynamics of grizzly bear may include statistically density dependent, inverse density dependent and density independent processes. Since the grizzly bear data is three-year moving average sum data, the biological factor responsible for the correlation of the density dependence parameter needs to be examined in the future.

In the first sixteen data sets in Table 5, density dependent regulation was detected in 11 out of 16 cases, while one case of inverse density dependence was found using information criteria. Seven out of 11 density dependent and one case of inverse density dependent regulation were detected at the 0.05 probability level using the parametric bootstrap test (including No. 1 and No. 6). In contrast, Den Boer and Reddingius (1989) detected density dependent regulation in none of 16 using the randomization test of Pollard et al., three of 16 using Bulmer's test and one of 16 using the permutation test at the 0.05 probability level by 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 dependence model as the best model in nine out of sixteen cases. Both *B. piniarius* pupae and adults (No. 5 and No. 6 in Table 5), were identified as IID models by Hooten (1995), who applied an empirical density distribution estimation technique to estimate the parameters related to the IID distribution and carried out the model selection by SIC.

Five types of complex regulation models (CpRcA, CpArA, ArRcA, CpRcP and second order model) were found among 31 data sets. Time-varying density dependence parameters were found in seven out of 20 insect data sets examined, and two out of 11 vertebrate data sets using information criteria. Density dependence was not detected in four out of 20 insect data sets, and three out of 11 invertebrate data sets using information criteria. Failure in detecting density dependence may have been due to small sample size, a specific period of time in the time series which density dependence is not present, misspecification of the model, or sampling error in the estimates of vertebrate population density.

The population dynamic trends for *P. flammea* and *D. pini* reported by Schwerdtfeger (1941), estimated density dependence parameters and fit of the model from smoothed parameters are presented in Fig. 8A ($\hat{b}$ = -0.327) and 8B ($\hat{b}$ = -0.266), respectively. The density dependence parameter ($\hat{b}_{t/T}$) from the Kalman filter smoothing procedure was found to closely follow the population dynamic trends of *P. flammea* and

D. pini population, respectively. Time-varying changes in the density dependence parameter might be expected under unstable natural enemy performance (Royama, 1977), and/or fluctuation in resource availability. In these two graphics, it should be noted that a combination of density dependent, inverse density dependent, and density independent processes may exist in these two populations, as well as in other populations with a time-varying density dependence parameter, as the $\hat{b}_{t/T}$ may be smaller, larger than, or close to zero during different times periods and different density ranges.

Structural Changes in the Ecological Time Series

CUSUM and CUSUMSQ statistics based on the best model selected by information criteria, and the natural logarithm of population density are presented in Figs. 9-24 for each of the 31 data sets using the best model in Table 5. The order of populations in Figs. 9-24 is the same as the order of populations listed in Table 5. Structural changes are indicated in the following data sets: *P. horticula* (B1, B2 in Fig. 12; A1, A2 in Fig. 13), *C. fumiferana* (B1, B2 in Fig. 14), *A. jelinekii* (A1, A2 in Fig. 15), *A. strepera* (A1, A2 in Fig. 21), *C. latrans* (B1, B2 in Fig. 22) and *O. zibethica* (B1, B2 in Fig. 23) as 95% confidence limits were reached in either the CUSUM or the CUSUMSQ lines. Weak structural changes were indicated in some populations: *O. brumata* (A1, A2 in Fig. 9), *B. piniarius* (A1, A2 in Fig. 11), *Z. diniana* (B1, B2 in Fig. 13), *N. brevicollis* (B1, B2 in Fig. 16), *P. flammea* (B1, B2 in Fig. 17), *D. pini* (A1, A2 in Fig. 18), *A. platyrhynchos* (B1, B2 in Fig. 21) and *Vulpes* spp. (A1, A2 in Fig. 22) as the 95% confidence limits for either the CUSUM or the CUSUMSQ were nearly reached. In some figures, the CUSUM and CUSUMSQ lines were found only on one side of the central line, indicating moderate misspecification of the model (e.g., *A. jelinekii* [B1, B2 in Fig. 15] and *Lynx* [A1, A2 in Fig. 24]).

Discontinuous Density Dependence

In Fig. 8A, during years 1915-1940, the value of the density dependence parameter seems very close to zero, and the population dynamics of *P. flammea* looks like a random walk process visually. In order to test if part of the time series data can be modeled by a random walk process, I remodeled the data of *P. flammea* between 1915-1940 using all 50 alternative models, and found that the random walk was the best model for time series data evaluated for this period based on the smallest information criterion value (SIC = 62.420, 66.738, 70.221 for random walk, first order Gompertz and second order Gompertz models, respectively), which indicates a discontinuous density dependence during the 1915-1940 year period. However, year 1914 may not be the best year to separate two dynamic processes in the time series. In order to achieve the best fit of *P. flammea* time series by two different processes, I tried to separate the data into two parts by each year from 1906 to 1926, and estimate parameters for these two parts independently. I found that year 1913 is the best year to generate the minimum sum of the SIC values of two parts. The first part of the data (years 1881-1913) can be best modeled by an ArRcA-G model, and last part (years 1914-1940) can be best modeled by the random walk model (Fig. 25A). From the minimum sum of the SIC values, year 1918 is the second best year to separate the data into two parts (Fig. 25A).

The parameter estimates and information criterion values are listed in Table 6.

It is interesting to know which year the ArRcA-G model will evolve into the CpRcP-G model as the observations from the random walk process were continuously added into the first part of the time series. Based on the change in the SIC value for fitting ArRcA-G and CpRcP-G, year 1918 is the turning point that model CpRcP-G would replace model ArRcA-G as the best model, when observations from the random walk process were gradually added (Fig. 25A and B). The AIC and AICc in Fig. 25B also showed similar changes as the SIC did when the length of time series gradually increased. Figs. 26 and 27 showed the improved estimates for the growth parameter a_t and the density dependence parameter b_t when data from years1881-1918 or years 1881-1913 was used. The smaller estimate value of σ_b^2 (0.188, 0.179) in Table 6 compared to the value (0.44) in Table 5 suggests a better estimate of density dependence parameters using either of the shorter data sets. Autoregressive growth rate changes were also identified, which may suggest the existence of delayed density dependent population dynamics. CUSUM and CUSUMSQ tests (Figs. 28 and 29) showed no apparent structural changes for both ArRcA-G and random walk processes, and an improvement in fit compared to B1-B2 in Fig. 17.

Complex Population Regulation Patterns in Nature

In this study, various complex dynamics includes time-varying parameter and second order models were found. What does the time-varying coefficient parameter model mean? Statistically, the time-varying parameters introduced additional dynamic noise terms, which were always associated with density dependence parameters (e.g., $X_{t-1}\varepsilon_t$) and which generated nonlinear effects on population dynamics in this study. The strength of density dependence noise (e.g., $X_{t-1}\varepsilon_t$) affecting the population dynamics (X_t) depends on the population density (X_{t-1}), where the combined effects from time-varying parameter and population density (i.e., b_tX_{t-1}) would generate different regulation patterns compared to the first order, constant parameter models. In Fig 30, I plotted the distribution of density dependence parameters using estimated parameters for four cases, which are adults of *O. brumata* (No. 2 in Table 5), *P. flammea* (No. 18 in Table 5), *P. flammea* for years 1881-1913 (Table 6), and *Ursus arctos horribilis* (No. 21 in Table 5, with $b = 0$). The distributions of four density dependence parameters suggest that the population dynamic process might contain density dependent, inverse density dependent and density independent processes.

In order to ensure a fair comparison of two different stochastic dynamic models in modeling the same data set, I assume that the correlation coefficient between the noise terms of two different models is one. An advantage in doing this is to show how this random sequence operates, and how the population dynamic synchronizes among two or more models using a few simulations. These two sequences, with one correlation coefficient value between them and with different standard errors were used to simulate different population dynamics using their estimated parameters shown in either Table 5 or Table 6. The first one or two observations of the original data were used as starting values for the simulation. The relationships between per capita growth rate and population density are shown in Figs. 31A-36A and Figs. 31B-36B based on simulations from different models, and the true relationships are shown in Figs. 31D-36D based on original data. In Figs. 31C-33C, 35C-36C, two simulated population dynamics are generally synchronized except for the random walk model (Fig. 34C). The Gompertz model and random walk model describing the linear relationship between per capita growth rate and population density ($\ln(N_t)$) are shown in Figs. 31A-36A. In contrast, time-varying parameter models (Figs. 31B-34B) or second order models (Figs. 35B-36B) would have a nonlinear relationship between per capita growth rate and population density - more precisely, an inhomogeneous variance of the population dynamic process. The inhomogeneous variance can be found from either simulated data (Figs. 31B-36B) or field data (Figs. 31D-36D). We might see that the variation of per capita growth rate is small with a small density range, but under a high density range, the variation in per capita growth rate would increase. The relationships between log per capita growth rate and population density (N) in the second order Ricker model have an even bigger variation in two dimensions (Fig. 35D), and a nonlinear relationship between per capita growth rate and population density. Furthermore, Fig. 36D showed delayed density dependence as indicated by an anticlockwise spiraling curve, when the sequential line of the time series data is plotted (Varley et al., 1973).

It is interesting that no examples for the random walk parameter model were found. Population that might be fit by a random walk parameter models do not have a long term statistical stationary distribution because of the instability of parameters (e.g. Fig. 6).

Second Order Random Coefficient Models

The model selection results of the second order random coefficient models for all data sets (>30 observations) based on information criteria found does not identify the random coefficient model as the best model, and hence were not listed except for two populations, *D. pini* (No. 19 in Table 5) and *Lynx* (No. 31 in Table 5).

The estimated parameters and information criterion values using second order random coefficient models for the *D. pini* population are shown in Table 7, where the parameter estimates are very close to the parameter estimates listed in Table 5. The three relatively larger information criterion values (compared to those in Table 5) suggest that the CpRcP-G is the better model, the relatively larger standard error of $\hat{b}_1$ compared to the $\hat{b}_1$ value suggests that b_1 is not statistically different from zero.

The *Lynx* data set used in this study, also been represented in most famous examples in modern linear and nonlinear time series modeling, and has allowed many topics to be addressed by statisticians (see review from Tong, 1990) and ecologists (Royama, 1977; Turchin, 1990; Turchin and Taylor, 1992). In statistical modeling, Moran (1953) first applied a second order autoregressive model for *Lynx* using a common logarithm transformation, which resulted in almost the same parameter estimates as those obtained in Table 5. Nicholls and Quinn (1982) applied the second order autoregressive model with random coefficients for *Lynx* to demonstrate the random coefficient modeling approach, and found that the random coefficient autoregressive model made better predictions than those obtained from both Moran's (1953) and Tong's (1977) models.

The parameter estimates and information criterion values for the *Lynx* population based on the de-meaned data sets are listed in Table 8. For the second order random coefficient model, I obtained the same results as Nicholls and Quinn (1982) except for the estimates of the system noise $\hat{\sigma}^2$ and the intercept, because the natural logarithm transformation used here differs from the common logarithm transformation they used. By comparing three information criterion values of Nicholls and Quinn's (1982) model with those from the second order Gompertz model in Table 8, it seems that Nicholls and Quinn (1982)'s model is less desirable than the second order, constant parameter model due to relatively larger information criterion values. The fact that the estimated standard error of the random coefficient noise terms and the covariance term are relatively bigger, does not suggest any significant parameter noise terms in statistics. By setting the covariance between two noises to zero, both the maximum likelihood function (equation 44) and the Kalman filter yielded the same parameter estimates (Table 8). However, this second order random coefficient parameter model still appears to be inferior to the second order, constant parameter model because of relatively larger information criterion values.

V. DISCUSSION

In this chapter, I will discuss various topics in population dynamic modeling - problems with density dependence tests, detecting regulation using inter-generation data, true model assumptions, alternative models used in the searching for the truth of nature, number of noise terms in the models, omitting ecological factors, explanations of test results and regulation theory based on the results of this study.

Why We Failed in Detecting Population Regulation?

The Markov chain was considered as a realistic assumption in modeling population dynamics, and in tests for density dependence in field data including tests using Ricker and Gompertz models (Bulmer, 1975; Holyoak and Lawton, 1993; Wolda et al., 1994; Dennis and Taper, 1994). Only when such simple resource limitation regulation operates in the field as it does in the laboratory, or when overall effects from density dependent factors tend to be conditionally density dependent, can the Ricker and Gompertz models be considered as the appropriate test of the direct density dependence - boundedness. Density dependence test methods based on a first order linear Markov chain cannot be used to describe various mutual interactions between population and density dependent factors, such as changes in the resources and natural enemies formulated by equations 1 and 2. In biology, if important density dependent factors are missing, one will not be able to explain the systematic behavior of the population dynamics (e.g., miss all density dependent factors). Furthermore, serious statistical problems would occur and will be discussed in latter sections.

This study showed that detecting population regulation is more probable if the correct model is used. If a single model is used to detect density dependence, significant statistical density dependence based on the null random walk model and one alternative density dependence model, does not help much towards an understanding of the population dynamics of natural populations (Royama, 1977; Hanski et al., 1993), and it cannot reveal more about what happened in the field and infer which density dependent factor may be responsible for the regulation. Furthermore, if one uses a model to test population regulation without considering the influence from other density dependent factors, one may not find regulation, as the model underfits the data, or, is slightly or highly misspecified. For example, delayed density dependence general cannot be detected by Ricker and Gompertz models (Turchin, 1990). The stronger the influence of the natural enemies, fluctuation in resource availability or other density dependent factors on the population dynamics, the less chance that population regulation was found, as the population dynamics may become more complex, and simple models cannot describe them. On the other hand, some insect pests, which are considered to have weak regulation ability and relatively simple dynamics, may have more chance showing evidence of regulation by using the simple test (e.g., Woiwod and Hanski, 1992).

When density dependent factors constantly operate or temporally operate on the population dynamics in a complex ecosystem, the nonlinear dynamics, the inhomogeneous variance of the disturbance, autocorrelated parameter and system noise, dynamic circle, etc. may emerge. Most current density dependence test methods cannot detect and model such phenomena, and cannot deal with the variation in population regulation ability over time and over a range of densities. Frequent density dependence should not be expected using Ricker and Gompertz models under this situation, where the ideal assumptions of the model are rooted in the results obtained in laboratory studies, and may not be realistically applied for some complex dynamic systems in the field. The frequent failure to detect density dependence may also be explained by the possibility that wrong assumptions and wrong models were used.

The randomization test, is a special approach among classical density dependence tests, and may work better than others, because it depends on fewer assumptions of the models (Pollard et al., 1987). It should be a powerful tool for detecting density dependence if long time series data is available. However, for shorter time series data, it may perform poorly because of the associated low power as in any non-parametric test. The randomization test, like other density dependence test methods, can only identify the dependence of sequence time series data, but not various regulation patterns in the field.

Can Population Regulation Be Identified by the Inter-Generation Data?

Here I would like to reconsider the debate between Hassell (1985, 1987) and Dempster and Pollard (1986) within the framework of this study. Hassell (1985) used the key factor analysis method to test density dependence in the host as influence by the parasitoid. The key factor method used to detect density dependence is identical to the

Gompertz model in this study (Varley and Gradwell, 1960, 1963; also see Holyoak, 1993a, 1993b). Based on my current study, this test method generally may not work under the condition that other density dependent factors have a big influence on the host. On the contrary, the conclusion that spatial heterogeneity can modify, but cannot replace the role of temporal density dependence in population regulation made by Dempster and Pollard (1986) may be more reasonable. Dempster and Pollard (1986) mentioned that a correct method should be used to detect the delay density dependence in Hassell's (1985) examples. In Hassell's (1985) paper, it seems that he did not mention how to deal with the anticlockwise spiraling in the $\ln(N_t/N_{t-1})$ vs. $\ln(N_t)$ figures for the host (Hassell, 1985; Dempster and Pollard, 1986). However, Dempster and Pollard (1986) did not provide an appropriate method for testing for delayed density dependence either.

If a particular mechanism was used to generate the data, I believe that only the model approximating the original model, would possibly be the best to identify the generating mechanisms. Hassell (1985) did not follow this rule, as the Gompertz model generally may not be used to model the data generated by a host - parasite model, because of great difference of the dynamics between two models. A second order model may be a more appropriate alternative model for their studies.

Hassell et al. (1987) detected density dependence in eight of the nine generations from the egg stage to adult for *A. jelinekii* populations on a leaf to leaf basis. The reason that density dependence was detected in small patches probably was due to their method eliminating the influence of increasing trends in resources during the experimental period. I think that population density data, instead of total count data may be more appropriate to test density dependence for *A. jelinekii* populations to eliminate the influence of an increasing trend of resources in inter-generation data. In this study, the time-varying parameter models failed to detect changes in the density dependence parameter as well. Thus, the conclusion related to more evidence of density dependence at the metapopulation level is questionable, because at any level, the correct methods such as dynamic modeling in this study should be used in considering various influences from different density dependent factors.

The True Model Assumptions

In dynamic modeling, the true model assumption is important in parameter estimation, model selection and prediction in both statistics and biology. Strictly speaking, only when the true model (i.e., the exact copy of nature) is used, can one explain the underlying mechanisms. However, this kind of true model does not exist, the best thing that the ecologists can do is to find a model, which may best approximate nature. The true model assumptions implies that a model can approximate truth of nature enough in many aspects interested by the biologists, and thus the model can be used to estimate biological parameters and test some hypotheses based on the field data. The quality of the model used would determine the power in searching the truth in nature. Due to the complexity and diversity of an open system in the real world, many or unlimited alternative models may exist partly as shown in this study. We cannot guarantee that any model used will satisfy the true model assumptions or approximate the truth enough (Oreskes et al., 1994). When a statistical test based on a specific model (e.g., Gompertz model) is used to model the field population dynamics and infer the generating mechanisms, the risk of the violating model's assumptions may be high.

It should be emphasized that efforts in the past to improve the density dependence tests made are always related to building new and better test statistics or modeling approaches based on simple population models, rather than improving the true model assumptions in the test. Authors like Hanski et al. (1993) and Wolda et al. (1994) have emphasized the need to focus on modeling the population dynamics instead of trying to detect density dependence using simple tests. Hanski et al. (1993) argued that the statistical test for detecting density dependence is not flexible or appropriate for describing complex population dynamics. It does not work well nor does it provide any protection, when assumptions of the model are violated or the model is misspecified. The results obtained by Maelzer (1970) and Solow (1990), based on different assumptions of the system noise, actually showed how the assumption of a model could be violated. Failure to test if the model's assumptions are true or violated is another reason that ecologists cannot improve the density dependence tests of the past.

Many statistical tests might be helpful in identifying misspecification to improve the true model assumption (see Harvey, 1989a, 1989b). In the literature, only a few authors (e.g., Kemp and Dennis, 1993; Dennis and Taper, 1994; Dennis et al., 1995) tested the residuals of the fit of the data by the model they used. If one just picks a density dependence test method, passes the data in and gets the conclusion, it would be a highly questionable use of statistics, especially in time series (Harvey, 1989b). Before and after use of any statistics, we need to check if the data satisfies the assumptions that the statistics require.

Alternative Models

It is difficult to know if the model's assumptions are true enough in both ecology and statistics by our current knowledge. Strictly speaking, a true model in ecology is impossible, as the generating mechanisms are more complex than any sophisticated model. However, an ecological time series can be potentially approximated by many statistical models with dynamic properties (such as the models used by Morris (1963a, 1963b), Den Boer (1991), Turchin (1990), Turchin and Taylor (1992), Dennis and Taper (1994), and in this study). The alternative models formulated by our knowledge in ecology and statistics are very important for approximating the generating mechanisms. They can be used to avoid misspecification of the model, identify data patterns and help understand the mechanisms of the population dynamics statistically. The various alternative models formulated by Royama (1977) for density dependence are good examples of the use of alternative models in population dynamics. Without alternative models, studying mechanisms of the population dynamic process in the field is impossible.

Generally, a statistical test can be designed for some specific data generating mechanisms, but it may not cover various mechanisms that operate in different times and different density ranges of the time series, and in different species. Because of this, it will likely be necessary to use a number of statistical tests to identify various complex patterns of population regulation in the field. Compared to the modeling approach using a single model, a number of the alternative models, provide more chance to approximate the mechanisms of the data generated and less chance for the best model to be misspecified. In biology, in order to improve the assumptions of a true model regarding the influence from nature enemies and resource availability in the changing environment, alternative models are important to cover the great diversity of the animal population dynamics in nature. Failure to consider many alternative processes is one reason for the low frequency of density dependence detected in field populations using statistical approaches in the past.

In most statistical density dependence tests, only one alternative density dependence model form has been compared against either the random walk model or the exponential growth model. The density dependence test was usually considered as the test of the random walk vs. one alternative density dependence form (Wolda and Dennis, 1993). The hypothesis formed works only under a closed system when the true model assumptions hold (Oreskes et al., 1994). However, in the real world, as the great variation in the natural processes, we cannot always expect that the population dynamics should follow either a random walk, or the first order density dependence model. We cannot guarantee that the one model used will approximate the generating mechanisms of the data well. Statistical tests of the goodness of fit help, but may not be able to check various potential misspecifications of the model. A given model may always force the model to fit the data. For example, Den Boer (1991) found that the random walk process provided a good approximation of the population dynamics. However, without sufficient number of alternative models, misspecifications of the model may not be identified.

Some authors (e.g., Holyoak and Lawton, 1992; Holyoak, 1993a, 1993b) used many tests currently available to test density dependence. Many of these models were based on the same first order Markov chain assumption. However, using more than one density dependence test is not identical to the use of alternative models mentioned here. Furthermore, many density dependence tests do not address questions as to whether and how the models fit and predict the data, thus it becomes impossible to evaluate the goodness of fit by comparing several tests. It is difficult to explain the controversial results among different tests, different authors and different organisms (Wolda and Dennis, 1993). The density dependence tests would be the appropriate test, if the generating mechanisms for the data were well approximated by the dynamic model. However, the true model in nature is unknown, and a model may not always be a good approximation of the generating mechanisms for the data as shown in this study. Thus, any conclusion about the best density dependence test in the past may not be reliable. It is also meaningless to argue or test which density dependence test method is the best among simple density dependence tests, because various complex regulation patterns are likely to generally rule in nature.

In order to statistically select the best model among all alternative models, the information criteria used by Hooten (1995) in identifying the appropriate density dependence model form provides an important basis to approximate the generating mechanisms behind the ecological time series data. Therefore, statistically, it is possible to find the best model using alternative models, which approximately describe the pattern of the time series data. The best model achieved may not be the true model, and statistical modeling results regarding the regulation may not reveal any true causal relationship in ecology either (Royama, 1977; Dennis and Taper, 1994; Wolda et al., 1994), but it may help improve our understanding about the generating mechanisms.

A problem in model selection arises when the difference of the information criterion value between the null model and the alternative model is small. The evidence of the best model selected by the relative smaller information criterion value may not be strong enough to support a significant model selection based on a given probability value. From the difference of the information criterion values in Table 5, it is difficult to judge how big a difference is necessary to be considered "big" for shorter time series data. Sakamoto et al. (1986) recommended that significant model selection based on at least 1 to 2 differences of AIC values may work better under larger sample size conditions. In smaller sample size situations, the parametric bootstrap test based on the information criterion may be an alternative way to find the probability value associated with the model selection made by the information criterion. However, without going through the best model selection using information criteria first, it would be difficult to use the parametric bootstrap test, because one does not know which alternative model from the larger number of the alternative models should be used in the parametric bootstrap test.

The Noise in the Population Dynamic Model and Long-Term Studies

In deterministic modeling, the population dynamics is simplified into a mathematical form by some transformation function. Under stochastic conditions, the population dynamic model is considered as a transformation function of the deterministic part and noise terms by various combinations, which determines the dynamic behavior of the model. Usually, one noise term is attached to the deterministic function in an additive form. This additive noise term is often considered as a by-product of deterministic modeling (Schnute, 1991). This study showed that it may be less flexible and desirable to treat the noise term as simply additive form in modeling complex dynamic systems. In this study, the IID noise terms, in the model, are used to describe the influence from density dependent factors and density independent factors. When a single noise term was used in modeling, the noise term can be considered as the stochastic variation in the growth rate independent of density (additive noise), or the variation in the density dependence parameter (multiplicative noise). In multiplicative noise, the strength of noise operated depends on the population density (i.e., $X_{t-1}\varepsilon_t$). For more than one noise term, additive and multiplicative terms can be considered together in the model as in equations 8, 9 and 10.

The Kalman filter provides a powerful mechanism for detecting various sources of noise, if the model is clearly specified. The power to identify different sources of noise will be determined by the length of ecological time series data and the model form specified as shown in this study. For a relative short time series such as less than 20, it would be only expected that one would be able to identify one noise term in the growth rate or density independence parameters with relatively high power. Hooten (1995) found that the power is higher for identifying a model's family, such as the density dependence model's family than the specific density dependence model form. Possession of long time series data is a necessary condition for finding various sources of noise in population dynamics. However, structural changes or multiple processes more likely appear in long time series, which would make the time series modeling difficult using the single dynamic model, such as the *P. flammea* population in this study (Fig. 25 and Table 6). Rotella et al. (1996) also found that the gray partridge population in Eastern Washington during two periods can be better described by a Gompertz model with different growth rate parameters.

In order to find the value in the long-term population dynamics studies, we must address the following questions: Does a population regulation mechanism exist for this population? How does it operate in the field and how has it operated in the past? The first question is about the potential existence of the regulation mechanisms, and we can carry out experiments - either in the field or in the laboratory to test it. Laboratory studies can reveal the potential of the population regulation mechanisms, or the regulation in the laboratory, but do not identify what actually happened, and how regulation operated under the complex field conditions (Stiling, 1989).

The second and third questions are related to the study of ecological time series data. Long-term ecological studies and field experimental studies, which are two major components used to address issues in ecology (Krebs, 1991). Under a stochastic population system, replication or the like is the only way to isolate trends from the noise in the given system. In practice, it may be difficult to carry out many field experiments independently, because of the correlation of density independent factors in some large geographical regions (Royama, 1992). One of the advantages of long-term studies is for one to study the population and community over temporal scale, or on both temporal and spatial scale, detect dynamic patterns (e.g., trends) under equilibrium and nonequilibrium (or stationary and non-stationary) ecological paradigms, monitor environment changes and test any ecological hypothesis related to the past and present. It is not easy for one to carry experimental studies to repeat or replace the long-term data which are inherent in historical characteristics.

Omitting Ecological Factors in Modeling

Omitting some explanatory variables is a natural way to formulate the dynamic models in ecology, as shown in this study. It may not be appropriate to keep a large number of ecological factors in the dynamic models as in equation 1, as data limitations mentioned before are always a major problem. In some cases, it may be advantageous to omit some variables, because sometimes the ecological variables cannot be clearly measured (e.g., the resource and resource availability), it is not known which factor is important and worthy to measure, or we do not have the knowledge about mechanisms of various linear and nonlinear complex interactions in the ecological system when observations of additional ecological factors are available. However, omitting variables such as density dependent and density independent variables, those with / without trends over time, would considerably affect the formulation of the population dynamic models. The direct consequence of omitting variables is that many potential and serious statistical modeling problems such as misspecification of model, autocorrelation residuals, inhomogeneous disturbance, poor fit of the data, etc. would occur, which directly affect our understanding of the population dynamics.

When omitting variables, overall effects of these variables should be considered in modeling. In this study, density independent factors are omitted by using IID assumptions for these factors. If the assumptions hold, the consequence of omitting variables is that the models may lose some predictive power and affect the power of the density dependence test, as the system noise increases due to omitting density independent factors. When density dependent factors are omitted, time-varying parameter models or high order models should be considered to represent the mutual interactions between animal population and density dependent factors. Actually, first order models as in equation 6 can be considered by increasing one order based on an exponential model (zero order) because of the consequence of omitting the resource availability and other density dependent factors (i.e., we may be not able to measure the resource availability too). Equation 6 is the simplest model to omit all true measures of density dependent factors, and use the density dependence parameter to account overall effects from such factors. However, the dangerous in misspecification of the model should not be neglected when omitting factors. In the subsequent discussion, I would like to address the autocorrelation error problem in ecology, which may be related to omitting variables.

Autocorrelated Errors vs. Higher Order Models

Autocorrelation of the residuals is recognized as one of the main problems in tests of density dependence (Royama, 1977, 1992; Maelzer, 1970; Solow, 1990; Hanski et al., 1993; Williams and Liebhold, 1995). Williams and Liebhold (1995) found that the Ricker models with an autocorrelation of the exogenous factor might be identified as delayed density dependence, which is identical to the result obtained in my study (appendix C). From appendix C, the second order Ricker model can be used to approximate the Ricker model with autocorrelated errors. The autocorrelated errors for the Gompertz model will generate second order Gompertz models, which has been reported by many authors in both ecology and econometrics (e.g., Royama, 1977, 1992; Solow, 1990; Harvey, 1989b). I agree that the autocorrelated errors or autocorrelated exogenous factors may generate high order models or the appearance of a high order model. However, I believe some concepts related to the definition of noise, practical use of the models, biological explanations of the autocorrelated errors are not clear and may cause confusion in understanding the population dynamics.

The error terms ε_t in the population model 6 (exogenous factors and random density independent factors called by Williams and Liebhold (1995) and Turchin (1995), respectively) can be simply defined as the density independent terms. However, there may be considerable differences between the models we defined and the true relationships found in the field data. The separation of the endogenous influence from exogenous noise would be correct only if the correct model is used! If one gets an autocorrelated noise from the field using the Gompertz model, term "autocorrelation of exogenous factors" may lead one to the conclusion that autocorrelation noise was from correlated exogenous factors or density independent factors (it may be true). I prefer to call the autocorrelated ε_t as autocorrelated errors, noises or disturbances instead of the term "autocorrelation of exogenous factors" to avoid the confusion regarding the source. These terms can be applied before or after estimates of parameters are achieved.

Because the true model assumption may not hold for the field study, the assumption of noise may be violated not only from the density independent factor, but more probably from density dependent factors. There are three sources which may generate autocorrelated errors statistically. The first may be due to the omission of the important ecological factors. "Exclusion of variables would not of itself impart autocorrelation to the disturbance term unless the excluded variables were autocorrelated" (Johnston, 1984). It is my belief that many density independent factors have shown no, or weak correlation within inter-generation data, and the chance to be statistically identified in a short-time data set is small. Second, misspecification of the model may generate autocorrelation errors (Johnston, 1984), such as using a linear model to fit nonlinear data or using lower order models to fit higher order data. The third source is the measurement errors of population density, which may not be random from time to time for long ecological time series data (Johnston, 1984).

When one obtains autocorrelated errors using population dynamic models, first, one should check to see if chance for the second and third sources of the autocorrelated errors can be excluded, before one examines if any density independent factor is autocorrelated. It should be noted that major sources for autocorrelated errors are from density dependent factors, we know that they may consistently operate in the field, and generate higher order autoregressive models or the like.

As mentioned before, the second order Gompertz model is a super set of the Gompertz model with autoregressive errors. The second order Ricker model is a different model from the Ricker model with autocorrelated errors (appendix C). The second order Ricker model can generally describe a wider variety of population dynamics than the Ricker model with autocorrelated errors does based on this study. The results from appendix C imply that both models may show very similar behavior. For example, using a single second order Ricker model, one may get delayed density dependence, when the true model is the first order model with the correlated noise due to density independent factors or measurement errors (Williams and Liebhold, 1995). However, when the true model is the second order model, we may identify it as the first order model with autocorrelated errors, using a single Ricker model. In practice, for the Gompertz model, there is no advantage to using the first order model with autoregressive errors over the second order Gompertz model, and little advantage to use the Ricker model with correlated errors over the second order Ricker model to infer what happened in the field. Though both autocorrelated density dependent and density independent factors may generate the high order model, it is impossible to distinguish them only based on ecological time series data. Williams and Liebhold (1995) reported that autocorrelated density independent factors in the Ricker model will give the appearance of delayed density dependence. If the single second order Ricker model is used, the reality of such a model and risk to be identified as a delayed density dependence model depend on the strength of the correlation of density independent factors in the real world. Using the alternative modeling techniques of this study, a Ricker model with autocorrelated errors and the second order Ricker model are distinguishable in theory, because they are different dynamic models.

What Should Be Done if Regulation Is Found?

Difficulties in explaining the mechanisms of population dynamics arise after analyzing the data from field experiments, where ecological factors are not always controlled and may be missed. Statistical modeling based on various alternative models does not directly indicate any causal ecological relationship in a strictly scientific sense using inter-generation data, where information about the interaction process between environment and organisms are missed. What should we do if statistical density dependence is found? Does an alternative to causal density dependence exist? (Hanski et al., 1993; Wolda et al., 1994).

Density dependence is called statistical density dependence if a reciprocal connection between population density and the factors determining it is established by the statistical approach (Royama, 1977). It would be unwise to postulate what types of factors regulate populations before a certain statistical density dependence is established (Reddingius (1971) in Royama, 1977). Causal density dependence and statistical density dependence are identical to type A density dependence and type B density dependence, respectively from Royama (1977). Royama (1977) stated clearly that all the factors which are causally density dependent are also statistically density dependent. However, many factors which are statistically density dependent are not causally density dependent. He further considered that the statistical regulation is critical for the population resistance without addressing which factor was actually responsible for it. Based on the reasoning of Royama (1977), it seems logical that populations can persist even without causal density dependence. From previous discussion, we know that some autocorrelated noise and autocorrelated sample errors may be alternative sources that cause statistical density dependence, but not causal density dependence. However, it seems that no evidence has been found that the field population can be regulated by any density independent factors (Hanski et al, 1993). It should be noted that inappropriate statistical test methods may identify some density independent process as statistically density dependent regulation due to an excessive type I error.

Unfortunately, testing for the existence of true density independent processes (i.e., $b = 0$) based on sequential survey data from the field is impossible in theory by any statistical test, as one of the density dependence models must be selected as the best model among an unlimited number of alternative density dependence models. Brown (1989) concluded that it would have been difficult to detect density independence in most studies, if density independence had been tested for as rigorously as density dependence. In fact, true density independence may not exist in nature, because of the continuous nature of the density dependence parameter changes (Subhash Lele, 1995, per. communication). In practice, it is impossible and of no use to distinguish between the weak density dependence (i.e., a negative approaching zero b value) and a true random walk model based on small number of observations available, as the larger variance in the stationary distribution from weak density dependence models will drive the population to extinction. In this case, we might never know the truth from the limited data available. Brown (1989) considered that the density dependence parameter is zero when it is less than the stated minimum absolute value. Statistical modeling of the field data may suggest that the random walk process be the best model among alternative models.

Increasing the length of the time series data and using alternative models as shown in this study may change the results regarding selection of the best model.

The density independence concept in modeling still is valid in practice and can help one measure the strength of density dependent regulation in the data, summarize what happened in the field, and add to our knowledge, though it may not be true. The models here, as in other models, are certainly not a true reflection of the dynamics found in nature. Nevertheless, the density independence concept is useful in modeling, and is considered the ultimate process for the natural population, when one is attempting to approximate the true mechanisms in nature.

The Impacts of Population Regulation Theory from Current Studies

In the introduction, I introduced two questions about linear or nonlinear density dependence, and the range of population density where density dependent factors act from Murray (1994). In the following discussion, I would like to address Murray's questions further as well as other questions posed in the literature. First, it is important to point out that density dependence may not be linear under the conditions that consistent, or inconsistent strong mutual interactions act in the system. Second, the hypothesis from previous authors that density dependence might not operate at all density ranges, and all times in the field, seems supported by current study (Milne, 1957; Nicholson, 1958; Huffaker and Messenger, 1964; Strong, 1986). More conservatively speaking, there are times and population density ranges in which density dependence operates weakly. Furthermore, density dependence may be more active in higher density range, and inverse density dependence may be an important mechanism for quickly increasing population density. Whether the overall population is regulated or not, may depend on the combined effects from density dependent, inverse density dependent and density independent factors affecting the population. Time-varying parameter models provide an approach for modeling the unstable performance (e.g., in high density ranges) and systematic changes of some environmental factors related to the population dynamics. I also agree with Murray (1994) in that assuming density dependence starting at zero density in the logistic model in textbooks may not be a realistic description of population regulation.

Inverse density dependence may be more commonly found in nature than is generally assumed. Walde and Murdoch (1988) found that inverse density dependence is about one third of the times at the smallest spatial scale for parasitoids. In this study, the time-varying density dependence parameter model always included inverse density independence. As density dependence and inverse density dependence may operate under specific conditions such as within certain density ranges, it is not unexpected that outbreak-prone insect populations are able to overwhelm their predators or their hosts resistance mechanisms (Dennis, 1989). Finally, populations should be regulated by density dependent factors. When the equilibrium is broken, inverse density dependence may occur again, and prevent the population from going to extinction from low population density and the pressure from other density dependent factors. Inverse density dependence or other positive feedbacks should be considered as merits from natural selection for the population to actively adapt to changes in its environment. In short, these are stabilizing mechanisms for the persistence of the population.

VI. CONCLUSIONS AND PERSPECTIVE

Conclusions

Various linear and nonlinear alternative models including time-varying parameter models and second order models showed more complex dynamic behaviors compared to first order, constant parameter models. Based on the results in this study, population dynamics may include density dependent, inverse density dependent and density independent processes, which may operate in different times, different density ranges in nature. Time-varying parameter models are expected to work better under weak or infrequent density dependence situations. Stronger and consistent interactions between the animal population and density dependent factors may be better characterized by linear or nonlinear high order models. These simple and complex models are helpful in identifying the patterns of the population dynamics, inferring statistical function of environmental factors on a generation or a yearly basis, because they are able to recognize various biological information or dynamic patterns in the time series data. For example, Ricker and Gompertz models generally suggest overall mutual interactions between the population and the natural enemies or resources may not exist in yearly or generation intervals. That means that the dynamics of the resource, and the dynamics of natural enemies are less influenced by the abundance of the animal population, when density dependence is operating conditionally. In many cases, longer time series may provide more chances for us to significantly discriminate between different type of regulation patterns in statistics.

Natural enemies and resource availability are considered by many authors to be important factors in animal population regulation (Nicholson, 1933; Dempster and Pollard, 1981; Turchin, 1990). The complete set of models in this study provide a powerful and flexible means for modeling population dynamics, which may be driven by nature enemies, resource availability, exogenous environmental factors and other unknown factors in a fluctuating environment. Models that fail to include important regulation factors generally may not be able to detect density dependence. Time-varying parameter models combined with second order models performed better against misspecification of the models in changing environments than any specific model currently used in the literature. This modeling approach does not have an excessive type I error such as the model selection method from Turchin (1990) used in modeling delayed density dependence (Dennis and Taper, 1994; Holyoak, 1994); nor is an excessive type II error found in many density dependence tests based on the constant parameter models, because of the great potential in using 50 alternative models, information criteria for model selection and powerful parametric bootstrap test techniques. Among various time-varying parameter models, the random coefficient parameter model seemed to be the model selected more frequently in animal populations than other time-varying parameter models considered in this study. Furthermore, we can enlarge the current model set to include more alternative models and more ecological factors in the model. From an examination of the current ecological literature, it seems to me that the more alternative nonlinear models in ecology still need to be developed. However, as an unlimited number of alternative models may exist, I am not suggesting that one attempt to exhaust all alternative models. A model with a good approximation of the truth in biology and statistics may be acceptable in many applications. One should also note that not all models in this study are realistic for field population dynamics.

In this study, the argument proposed by Royama (1977) that density dependence should be frequent in animal populations seems to be supported. However, finding the regulation patterns in nature is a more interesting topic in ecology (Hooten, 1995). The results in this study suggest that finding details of complex regulation are possible, and are more important than tests of density dependence in population dynamics studies. It was not unexpected that a longer time series and more ecological factors considered would improve the power in estimating parameters using more alternative models.

Time-varying parameter models and other models can be used to study the mechanisms of the field population dynamics, and to explore whether the growth rate and density dependence parameters are more likely influenced by environmental factors. Furthermore, such models may help improve our understanding about population dynamics, complex regulation and structural changes using ecological time series data. 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 and structural changes in time series data cannot be overemphasized.

Perspectives

This study showed that regulation mechanisms in animal populations are more complex than previously thought. If the data sets in previous density dependence test studies are long enough, it seems appropriate that such data can be re-analyzed using some models presented in this study and perhaps other nonlinear models. Current modeling approaches can also be extended to study multiple species. However, the most difficult thing is to carry out both simple and complex population dynamic modeling for the relatively short ecological time series data sets. Low power in detecting density dependence associated with small sample size is always a problem in any test and dynamic modeling method.

For longer time series data sets considered in this study, we clearly see that the study of time series data may provide important information about historical population dynamics using complex dynamic modeling. Additional nonlinear models regarding more time lags, population density, density dependent and density independent factors need to be formulated in the future, such as various nonlinear models presented in Tong (1990). Complex modeling results may provide general conclusions related to density dependent and density independent factors operating in the field. If some detailed environmental information is available, it should be included in modeling, as it may improve the fit and prediction of the data, and help test a hypothesis. However, I think that a model with moderate complexity, which includes a few environmental factors may be easier for us to improve the fit and prediction of the data than in highly complex models. A direct consequence of considering more variables in modeling is that more parameters then need to be estimated statistically. A model with more than enough parameters and factors may be less likely to be considered as the best model regarding information gains in the fit and prediction of the ecological time series.

When more environmental covariates from the field are used for statistical modeling, one may still not find the causal relationships among variables based on observations, which are not obtained from a controlled experiment. However, it may provide the motivation to design new experiments to study regulation and population dynamics under the influence from density dependent and density independent factors. Field experiments need to be carefully designed to consider any trends in density dependent and independent factors in order to isolate different types of noises or influences on the population dynamics. New procedures for detecting population regulation using within and inter-generation data and metapopulation dynamics should be developed to solve the problems associated with the length of the time series data (Taper et al., manuscript in progress).

In ecological applications, the best population dynamic model form detected can be used to form the hypothesis of the outbreak of insect pest populations, and to evaluate the performance of biological control agents of insect pests and weeds. For example, the complex dynamics should be expected for both host and specialist biological control agent under natural conditions. In conservation biology, methods regarding complex dynamic modeling and structural changes in this study can be used to develop population management models (e.g., for endangered or commercial species), generate realistic estimates of extinction time distributions in minimum viable population analysis, evaluate the influence of the human disturbance, assess efforts to improve the conservation, and monitor the population and environmental changes.

Current statistical tests used to test for regulation are relatively "simple" and provide little insight into understanding natural populations. More complex statistical tests may be developed in the future, but they may be too cumbersome to be used as a general tool for detecting various patterns of population regulation. Hence, it seems more appropriate to model the dynamics and population regulation processes based on alternative models and real data. The statistical modeling approach used in this study, which combined the best part of theoretical modeling and knowledge about population dynamics, makes an important improvement as a research tool for studying field population dynamics and regulation, because it provides great advantages in forming and testing hypotheses, and in evaluating the overall interactions between the environment and the organisms. Theoretical modeling also holds some great advantages in explaining the population dynamics and natural phenomena such as chaos. It is my belief that the theoretical models cannot be testable without the help from alternative models and model identification methods based on real data sets. I believe, that only through a combination of the theoretical modeling, statistical modeling techniques, and well-designed biological studies, will we be able to understand the dynamic patterns of field populations and communities in space and time.

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APPENDICES

Appendix A

TABLES

Table 1. Time-varying parameter structure of population dynamic models used in this study.

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§						

* Ar-First order autoregressive; Rw-Random walk; Rc-Random coefficient; Cp-Constant parameter; P-Presence of system noise; A-Absence of system noise. For growth parameter, Cp (.) P=Rc (.) A.
†Ricker or Gompertz model.
‡Exponential growth.
§Random walk.

Table 2. Parameter estimation results and model selection of AR(1) with the AR(1) slope by Monte Carlo simulations.

Given conditions*				Estimation from constant parameter model					
σ_β^2	σ^2	T	ϕ	$\hat{a}$	$\hat{\beta}$	$\hat{\sigma}^2$	MSEa†	MSEβ	MSEσ^2
0.16	0.64	25	0.5	0.571	0.489	1.510	0.067	0.085	11.248
0.36	0.64	25	0.5	0.709	0.458	19.266	0.103	0.593	5.52E4
0.16	0.64	50	0.5	0.522	0.571	1.889	0.040	0.037	15.945
0.36	0.64	50	0.5	0.728	0.580	34.755	0.067	0.606	7.88E4
0.16	0.16	25	0.5	0.507	0.563	0.740	0.063	0.041	3.113
0.36	0.16	25	0.5	0.759	0.531	19.265	0.105	1.578	2.02E4
0.16	0.16	50	0.5	0.449	0.638	2.219	0.054	0.037	221.754
0.36	0.16	50	0.5	0.734	0.603	22.911	0.054	0.425	1.19E4
0.16	0.64	25	0.8	8.354	0.583	1.08E5	0.250	6.99E3	1.97E12
0.04	-	25	0.8	0.248	0.814	0.812	0.129	0.100	69.838
0.16	-	25	0.8	2.560	0.808	3.10E4	0.212	842.280	1.84E11

* Parameter α and β are 0.5 and 0.5, respectively.

† MSE= $\sum$(estimated value-true value)^2/number of success trials.

‡ Sometimes, nonlinear optimizations may fail.

§ Significance test carried for the variance of the parameter noise (H_0: $\sigma_\beta^2 = 0$).

Table 2. (Cont.)

				Estimation from time-varying parameter model					
$\hat{a}$	$\hat{\beta}$	ϕ	$\hat{\sigma}_\beta^2$	$\hat{\sigma}^2$	MSEa	MSEβ	MSE$\hat{\sigma}_\beta^2$	MSE$\hat{\sigma}^2$	MSEϕ
0.564	0.442	0.199	0.148	0.552	0.080	0.073	0.021	0.087	0.315
0.554	0.418	0.225	0.342	0.561	0.086	0.103	0.067	0.114	0.248
0.544	0.478	0.313	0.148	0.596	0.040	0.033	0.012	0.039	0.190
0.526	0.482	0.381	0.333	0.621	0.037	0.044	0.027	0.056	0.094
0.546	0.473	0.277	0.156	0.134	0.045	0.066	0.014	0.010	0.192
0.542	0.472	0.308	0.326	0.137	0.045	0.115	0.033	0.015	0.164
0.521	0.489	0.379	0.158	0.147	0.022	0.035	0.005	0.005	0.102
0.518	0.493	0.416	0.356	0.144	0.015	0.039	0.017	0.007	0.048
0.605	0.450	0.430	0.173	0.537	0.105	0.183	0.026	0.104	0.171
0.437	0.561	0.590	0.035	-	0.023	0.057	0.000	-	0.057
0.459	0.548	0.603	0.139	-	0.020	0.142	0.002	-	0.057

Table 2. (Cont.)

Correct identification of the model (%)					Simulation times	
p=0.05	p=0.10	AIC	AICc	SIC	Total	No. of success ‡
10.20	14.03	26.28	19.39	13.78	400	392
25.94	32.49	56.93	48.61	41.81	400	397
7.54	13.07	52.01	54.52	33.42	400	398
33.50	44.25	87.00	88.50	71.50	400	400
39.47	46.40	48.00	38.67	30.67	400	375
65.42	70.78	75.07	67.83	59.79	400	373
61.62	69.44	82.07	83.08	59.60	400	396
92.93	94.95	98.23	98.23	94.19	400	396
10.05	14.43	51.80	47.16	41.75	400	388
-	-	87.25	87.00	79.75	400	400
-	-	96.22	95.97	93.20	400	397

Table 3. Parameter estimation results and model selection of AR(1) with a random coefficient slope by Monte Carlo simulations.

Given conditions					Estimation from constant parameter model			
σ_β^2	σ^2	T	$\hat{a}$	$\hat{\beta}$	$\hat{\sigma}^2$	MSEa	MSEβ	MSEσ^2
0.04	0.64	25	0.588	0.397	0.657	0.072	0.049	0.041
0.16	0.64	25	0.599	0.373	0.941	0.081	0.065	0.262
0.04	0.64	50	0.550	0.441	0.673	0.036	0.022	0.022
0.16	0.64	50	0.562	0.428	0.962	0.035	0.026	0.213
0.04	0.16	25	0.592	0.398	0.187	0.046	0.046	0.004
0.16	0.16	25	0.604	0.368	0.360	0.050	0.061	0.072
0.04	0.16	50	0.546	0.443	0.202	0.019	0.019	0.004
0.16	0.16	50	0.556	0.429	0.390	0.023	0.030	0.079
0.04	-	25	0.572	0.422	0.036	0.025	0.032	0.000
0.16	-	25	0.624	0.363	0.171	0.042	0.059	0.018

* Parameter a and β are 0.5 and 0.5, respectively.

† MSE = $\sum$ (estimated value-true value)^2/number of success trials.

Table 3. (Cont.)

Estimation from time-varying parameter model							
$\hat{a}$	$\hat{\beta}$	$\hat{\sigma}_\beta^2$	$\hat{\sigma}^2$	MSEa	MSEβ	MSE$\hat{\sigma}_\beta^2$	MSE$\hat{\sigma}^2$
0.578	0.410	0.071	0.552	0.072	0.048	0.017	0.056
0.582	0.401	0.168	0.608	0.075	0.060	0.037	0.090
0.446	0.584	0.052	0.584	0.022	0.029	0.005	0.025
0.545	0.453	0.156	0.617	0.032	0.023	0.017	0.042
0.578	0.413	0.056	0.129	0.047	0.046	0.006	0.006
0.562	0.420	0.167	0.149	0.041	0.054	0.022	0.010
0.539	0.451	0.046	0.148	0.019	0.018	0.003	0.003
0.523	0.469	0.164	0.151	0.017	0.021	0.008	0.005
0.534	0.463	0.037	-	0.015	0.000	0.000	-
0.516	0.488	0.144	-	0.011	0.020	0.018	-

Table 3. (Cont.)

Correct identification of the model (%)					Simulation times	
p=0.05	p=0.10	AIC	AICc	SIC	Total	No. of success
2.00	2.25	14.00	7.25	7.50	400	400
7.27	11.53	34.09	22.06	22.06	400	399
1.25	3.50	15.50	11.50	6.75	400	400
16.00	31.25	55.25	51.00	40.75	400	400
8.38	12.44	22.34	12.18	12.44	400	394
24.08	34.29	52.62	42.93	43.19	400	382
9.05	14.82	29.40	24.12	13.07	400	398
49.75	65.83	80.90	76.63	66.08	400	398
-	-	83.50	83.50	83.50	400	400
-	-	90.91	90.91	90.91	400	396

Table 4. Parameter estimation results and model selection of AR(1) with a random walk slope by Monte Carlo simulations.

	Given Conditions*		Estimation from constant parameter model			
σ_β^2	σ^2	T	$\hat{\sigma}_\beta^2$	$\hat{\sigma}^2$	MSE$\hat{\sigma}_\beta^2$†	MSE$\hat{\sigma}^2$
0.04	0.64	25	0.048	0.643	0.005	0.122
0.16	0.64	25	0.146	0.656	0.011	0.267
0.04	0.16	25	0.042	0.164	0.002	0.010
0.16	0.16	25	0.152	0.168	0.007	0.035
0.04	0.64	50	0.035	0.651	0.000	0.060
0.16	0.64	50	0.147	0.700	0.003	0.163
0.04	0.16	50	0.036	0.170	0.000	0.007
0.16	0.16	50	0.154	0.171	0.003	0.018

Table 4. (Cont.)

Correct identification of the model (%)					Simulation times	
p=0.05	p=0.10	AIC	AICc	SIC	Total	No. of success
21.19	28.94	29.20	28.94	28.94	400	387
57.54	67.77	65.47	64.71	64.71	251	391
32.23	37.08	31.97	32.23	32.48	400	391
60.71	71.28	69.27	68.26	68.26	400	397
55.38	62.05	66.15	65.90	64.87	393	390
88.25	92.06	90.79	90.79	89.52	315	315
60.10	67.10	68.13	68.13	67.36	389	386
89.10	92.95	90.38	91.67	90.06	313	312

* Initial parameter a_1 and β_1 are 0.5 and 0.5, respectively.
† MSE= $\sum$ (estimated value-true value)^2/number of success trials.

Table 5. Results of parameter estimation and fit of population time series data.

Species	Model	Estimated Parameters $\hat{a}$	$\hat{b}(\hat{b}_1)$	$\hat{b}_2$	$\hat{\sigma}^2$ $(\hat{\sigma}^2_a, \hat{\sigma}^2_b)$	Information Criterion Ln(L)	AIC	AICc	SIC		$\hat{p}$†
1. *Operophtera*	RW				1.150	-26.802	55.603	56.403	56.494		
brumata,	*G(1)	1.607(0.881)	-0.427(0.209)		0.919	-24.782	55.564	58.641	58.235		
larvae	R(2)	0.938(0.344)	-0.00348(0.0024)	-0.00761(0.00248)	0.634	-20.250	51.352	57.128	54.881	B	0.076
2.	RW				0.783	-23.338	48.676	49.476	49.567		
adults	R(1)	0.665(0.318)	-0.0674(0.025)		0.556	-20.253	46.506	49.582	49.177		
	CpRcA-G	1.049(0.0484)	-0.542(0.104)		0.154(0.0514)	-18.810	43.619	46.696	46.291	B	0.040
3. *Bupalus*	RW				1.310	-21.757	45.514	46.605	46.153		
piniarius,	R(1)	1.080(0.397)	-0.0919(0.0271)		0.719	-17.551	41.102	45.546	43.019		
larvae(Aug).	CpRcA-R	1.029(0.105)	-0.084(0.0269)		0.0052(0.00196)	-13.260	32.519	36.964	34.436	B	<0.001
4. larvae	RW				1.800	-23.981	49.962	51.053	50.601		
(Sept.).	R(1)	1.139(0.448)	-0.112(0.0338)		1.0064	-19.910	45.820	50.264	47.737		
	CpRcA-R	1.148(0.085)	-0.108(0.0363)		0.0114(0.00431)	-15.796	37.592	42.037	39.51	B	0.002
5. pupae	RW				1.290	-20.101	42.201	43.401	42.766		
	G(1)	0.391(0.299)	-0.669(0.258)		0.85	-17.390	40.779	45.779	42.474	B	0.268
	G(2)	0.423(0.327)	-0.672(0.291)	-0.112(0.289)	0.899	-16.386	44.169	55.002	46.270		
6. adults	RW				1.720	-21.973	45.945	47.145	46.510		
	*G(1)	-0.271(0.265)	-0.914(0.260)		0.876	-17.583	41.166	46.166	42.861	B	0.063
	G(2)	-0.389(0.274)	0.933(0.266)	-0.343(0.250)	0.802	-15.705	42.695	53.529	44.796		
7. *Bupalus*	RW				1.430	-19.174	40.347	41.682	40.834		
piniarius,	R(1)	0.616(0.368)	-0.0317(0.0115)		0.873	-16.210	38.419	44.133	39.873		
pupae (Varley)	R(2)	0.741(0.401)	-0.0279(0.0101)	-0.0146(0.0102)	0.662	-13.337	37.827	50.918	39.563	B	0.187
8. *Phyllopertha*	RW				0.747	-35.637	73.274	73.754	74.606	BN	
horticula	G(1)	0.876(0.515)	-0.231(0.135)		0.675	-34.226	74.451	76.190	78.448		
3rd instar	*R(2)	0.293(0.210)	0.00178(0.00256)	-0.00557(0.0028)	0.648	-34.452	75.605	78.568	80.980		
9. 3rd instar,	RW				0.610	-19.929	41.858	42.716	42.692		
Hawes End	G(1)	0.891(0.481)	-0.365(0.153)		0.429	-16.937	39.873	43.206	42.373		
Farm	G(2)	0.985(0.518)	-0.746(0.211)	0.295(0.218)	0.312	-13.373	36.918	43.293	40.201	B	0.084
10. *Zeiraphera*	*RW				6.667	-44.983	91.965	92.715	92.910		
diniana	*G(1)	0.919(0.672)	-0.299(0.152)		5.520	-43.190	92.379	95.236	95.212		
	G(2)	1.898(0.364)	0.387(0.113)	-0.983(0.121)	1.248	-27.532	66.568	71.845	70.326	B	<0.001

Table 5. (Cont.)

11. *Choristoneura*	RW				2.031	-24.825	51.649	52.740	52.288	BN	
fumiferana	G(1)	0.611(0.420)	-0.285(0.148)		1.591	-21.222	52.234	56.679	54.152		
3rd instar larvae	G(2)	0.881(0.490)	-0.191(0.305)	-0.213(0.254)	1.463	-20.920	53.674	53.674	56.108		
12.	RW				2.230	-23.660	49.321	50.521	49.886	BN	
3rd instar	G(1)	0.484(0.370)	-0.427(0.179)		1.533	-13.105	48.444	53.444	50.139		
larvae	G(2)	0.856(0.390)	-0.536(0.281)	-0.143(0.225)	1.225	-18.243	48.192	59.025	50.294		
13. *Aleurotrachelus*	RW				1.217	-16.690	35.379	36.879	35.777		
jelinekii, 4th instar	R(1)	0.0667(0.301)	6.653E-6(2.778E-6)		0.634	-12.578	32.210	38.876	33.403		
larvae, in pop. 1	R(2)	0.360(0.215)	3.35E+6(1.035E-5)	3.504E-6(1.99E-5)	0.207	-6.305	22.671	39.171	24.003	BI	0.008
14. 4th instar	RW				0.643	-13.181	28.362	29.862	28.760		
larvae in pop. 2	R(1)	0.322(0.285)	-4.1E-5(6.034E-5)		0.576	-12.578	31.156	37.822	32.349		
	R(2)	0.582(0.215)	-4.7E5(6.447E-5)	-3E-05(6.762E-5)	0.288	-7.970	26.335	42.835	27.666	B	0.22
15. 4th instar	RW				1.370	-17.340	36.68	38.18	37.078		
larvae	G(1)	2.464(1.004)	-0.615(0.224)		0.793	-14.335	34.670	41.336	35.863		
in pop. 3	CpRcA-G	2.397(0.743)	-0.598(0.198)		0.0407(0.0173)	-13.621	33.242	39.909	34.436	B	0.109
16. *Nebria*	RW				0.350	-8.941	19.882	21.596	20.185	BN	
brevicollis,	G(1)	3.445(1.558)	-0.526(0.0590)		0.234	-6.925	19.851	27.851	20.759		
Adults	G(2)	3.006(1.825)	-0.808(0.306)	0.363(0.289)	0.212	-5.695	21.767	43.989	22.643		
17. *Acleris*	*RW				2.206	-19.960	41.920	43.420	42.318		
variana	*L(1)	0.838(0.536)	-0.00436(0.0025)		1.690	-18.863	42.994	49.661	44.188		
	G(2)	2.538(0.556)	0.208(0.148)	-0.874(0.154)	0.432	-9.995	30.789	47.289	32.120	B	0.014
18. *Panolis*	RW				1.502	-95.725	193.45	193.664	195.527		
flammea	G(1)	0.297(0.158)	-0.441(0.112)		1.191	-97.061	183.726	184.467	189.959		
	CpRcP-G	0.264(0.115)	-0.327(0.147)	$\hat{\sigma}^2_b$=0.44(0.178)	0.472(0.134)	-81.938	171.876	173.007	180.185	B	<0.001
19. *Dendrolimus*	*RW				1.80	-101.059	204.119	204.333	206.196		
pini	G(1)	0.207(0.188)	-0.233(0.0804)		1.572	-116.446	200.121	200.861	206.353		
	CpRcP-G	0.201(0.140)	-0.266(0.115)	$\hat{\sigma}^2_b$=0.212(0.105)	0.738(0.198)	-90.766	189.531	190.664	197.842	B	0.001
20. *Bupalus*	RW				3.591	-121.431	244.862	245.077	246.940		
piniarius	G(1)	0.773(0.327)	-0.311(0.0943)		3.0327	-116.446	238.892	239.633	245.125		
	G(2)	1.0689(0.319)	-0.0519(0.122)	-0.369(0.121)	2.642	-110.469	232.885	234.058	241.269	B	0.007
21. *Ursus*	*RW				0.0166	10.076	-18.151	-17.228	-17.379		
arctos	*G(1)	0.419(0.615)	-0.101(0.166)		0.0146	11.133	-16.266	-12.630	-13.948		
horribilis	CpArA-G	-0.377(0.30)	0.113(0.0811)	$\hat{\phi}_b$=-0.712(0.158)	5.03E-4(1.78E-4)	16.760	-25.519	-19.519	-22.429	B	<0.001

Table 5. (Cont.)

22. *Cervus*	EG	0.111			0.0205	5.753	-7.506	-4.077	-6.710		
elaphus	R(1)	0.468(0.0637)	-4.1E-5(7E-6)		0.00489	13.655	-21.309	-14.642	-20.115	B	0.003
	CpRcA-G	2.492(0.475)	-0.265(0.0531)		7.84E-5(3.3E-5)	13.654	-18.493	-11.827	-17.300		
23. *Cervus*	RW				0.0671	-1.439	4.878	5.545	5.922		
elaphus	R(1)	0.731(0.231)	-0.00049(1.56E-4)		0.0443	2.934	0.132	2.632	3.266	B	0.056
	CpRcA-G	4.349(1.440)	-0.598(0.198)		8.73E-4(2.69E-4)	2.931	0.920	3.420	4.054		
24. *Cervus*	*RW				0.0149	16.410	-30.821	-30.249	-29.643		
elaphus	G(1)	7.298(1.511)	-0.808(0.167)		0.00765	24.417	-42.834	-40.729	-39.30		
	CpRcA-G	7.317(1.514)	-0.810(0.168)		9.4E-5(2.69E-5)	24.454	-42.908	-40.803	-39.37	B	0.002
25. *Anas*	RW				0.044	4.252	-6.503	-6.059	-5.102	BN	
strepera	R(1)	0.403(0.154)	-2.64E-4(1.0012E-4)		0.0357	18.326	-8.801	-7.201	-4.597		
	ArCpA-R	-1.129(0.249)	-7.6E-4(1.568E-4)	$\hat{\phi}_a$=0.701(0.154)	0.0319(0.0083)	7.400	-9.553	-7.053	-3.949		
26. *Anas*	RW				0.0193	16.638	-31.275	-30.831	-29.874	BN	
platyrhynchos	G(1)	1.858(1.121)	-0.208(0.124)		0.0173	18.326	-30.651	-29.051	-26.447		
	CpRcA-G	1.885(1.133)	-0.211(0.126)		0.00021(5.48E-5)	18.326	-30.647	-29.047	-26.444		
27. *Vulpes*	RW				0.245	-30.788	63.576	63.876	65.337		
spp.	*R(1)	0.0605(0.11)	-1.6E-5(1.187E-5)		0.232	-29.619	65.238	66.290	70.521		
	ArCpA-G	2.541(1.378)	-0.306(0.163)	$\hat{\phi}_b$=0.620(0.173)	0.173(0.0372)	-23.483	54.966	56.587	62.011	B	0.015
28. *Canis*	RW				0.325	-36.839	75.678	75.978	77.439		
latrans	G(1)	1.210(0.861)	-0.132(0.0915)		0.309	-35.793	77.585	78.637	82.868		
	R(2)	0.106(0.162)	-3.7E-6(1.23E-5)	-1.4E-5(1.236E-5)	0.242	-29.761	69.130	70.836	76.246	B	0.033
29. *Mustela*	RW				0.124	-16.141	34.281	34.581	36.043	BN	
vison	G(1)	1.490(1.060)	-0.160(0.116)		0.118	-15.086	36.172	37.225	41.456		
	CpRcA-G	1.691(1.0625)	-0.182(0.116)		0.00137(2.95E-4)	-14.409	34.818	35.871	40.102		
30. *Ondatra*	*RW				3.489	-87.880	177.761	178.061	179.522		
zibethica	*G(1)	5.526(1.614)	-0.437(0.126)		2.726	-82.578	171.156	172.209	176.440		
	G(2)	7.404(1.731)	-0.252(0.145)	-0.335(0.145)	2.467	-78.561	169.055	170.761	176.171	B	0.002
31. *Lynx*	*RW				0.681	-138.669	279.338	279.446	282.065		
canadensis	*G(1)	1.396(0.391)	-0.206(0.0575)		0.612	-132.567	271.133	271.503	279.315		
	*G(2)	2.435(0.277)	0.384(0.063)	-0.748(0.063)	0.274	-86.359	182.332	182.903	193.303	B	<0.001

Data sets 1-16 were from Den Boer and Reddingius (1989). Data sets 21-23 were from Dennis and Taper (1994). Data sets 24-26 were from Hooten (1995). Results listed includes the best model between random walk and exponential growth models, the best model between the Ricker and Gompertz model, and the best model among time-varying parameter models (except the model which failed in optimization) and second order models.

Model type. RW-Random walk, EG-Exponential growth, G-Gompertz model; R-Ricker model; 1- the first order model, 2-the second order model; B-Best model, I-Inverse density dependence, N-No density dependence was detected.

* Non independent, identically distributed residuals were detected by a Ljung and Box (1978) modified Q test at 5% probability level. In model CpRcA, the residual is: $\varepsilon_t = (X_t - X_{t-1} - a - bf(N_{t-1}))/f(N_{t-1})$ and in model CpArA, $\varepsilon_t = b_t - (\phi_b(b_{t-1} - b) + b)$.

† Estimated probability value based on 1000 parametric bootstrap time series data.

Table 6. Time-varying parameter modeling results for *Panolis flammea*.

	$\hat{a}$	$\hat{b}$	ϕ_b	σ_b^2	$\hat{\sigma}^2$	Ln(L)	AIC	AICc	SIC
Year 1881-1913									
Random walk					1.681	-53.716	109.431	109.845	110.897
Gompertz	0.311	-0.496			1.298	-49.574	105.148	106.630	109.545
SE	0.220	0.162							
ArRcA-G	0.593	-0.566	0.820	0.179	0.795	-43.042	96.083	99.443	103.412
SE	0.416	0.235		0.128	0.089	0.300			
year (1914-1940)									
Random walk					0.626	-30.797	63.594	64.116	64.852
Year 1881-1918									
Random walk					1.990	-65.231	132.462	132.815	134.073
Gompertz	0.236	-0.601			1.376	-58.406	122.811	124.061	127.644
SE	0.206	0.148							
ArRcA-G	0.354	-0.555	0.783	0.188	0.778	-50.240	110.481	113.281	118.535
SE	0.320	0.218	0.144	0.092	0.278				
Year (1919-1940)									
Random walk					0.575	-23.996	49.992	50.659	51.036

Table 7. The parameter estimates of second order Gompertz model with one random coefficient for the *D. pini* population using the Kalman filter.

a	b_1	b_2	$\hat{\sigma}_{b1}^2$	$\hat{\sigma}^2$
0.213	-0.233	0.219	-0.0427	0.744
0.146*	0.159	0.117	0.128	0.206

Ln(L)=-89.057, AIC=191.357, AICc=193.033, SIC=201.837.
$\varepsilon_{t,2}$ are set to zero
* Standard error.

Table 8. The parameter estimates of second order Gompertz model with random coefficients for the *Lynx* population.

b_1	$\hat{\sigma}_{b1}^{2}$	b_2	$\hat{\sigma}_{b2}^{2}$	$\hat{c}(\omega_{t,1},\omega_{t,2})$	$\hat{\sigma}^2$	Ln(L)	AIC	AICc	SIC	Method
Second order Gompertz random coefficient model (The correlation of the parameter noises is considered)										
0.3844	0.0821	-0.7479	0.0770	-0.0694	0.1930					Least squares
0.0636*		0.0636								
0.4274	0.0839	-0.8073	0.0663	-0.0489	0.1593	-84.561	181.123	182.199	197.434	ML
0.0716	0.0544	0.0722	0.0605	0.0460	0.0646					
Second order Gompertz model (constant parameters)										
0.3844		-0.748			0.2737	-86.363	178.727	179.100	186.882	Kalman filter
0.0630		0.0631			0.0366					
Second order Gompertz random coefficient model (The correlation of the parameter noises is set to zero)										
0.4094	0.04577	-0.7972	0.01354		0.1857	-85.383	180.767	181.566	194.359	ML
0.0676	0.0403	0.0681	0.0309		0.06777					
0.4094	0.04577	-0.7972	0.01354		0.1857	-85.383	180.767	181.566	194.359	Kalman filter
0.0676	0.0403	0.0681	0.0309		0.06777					

* Standard error.

Appendix B

FIGURES

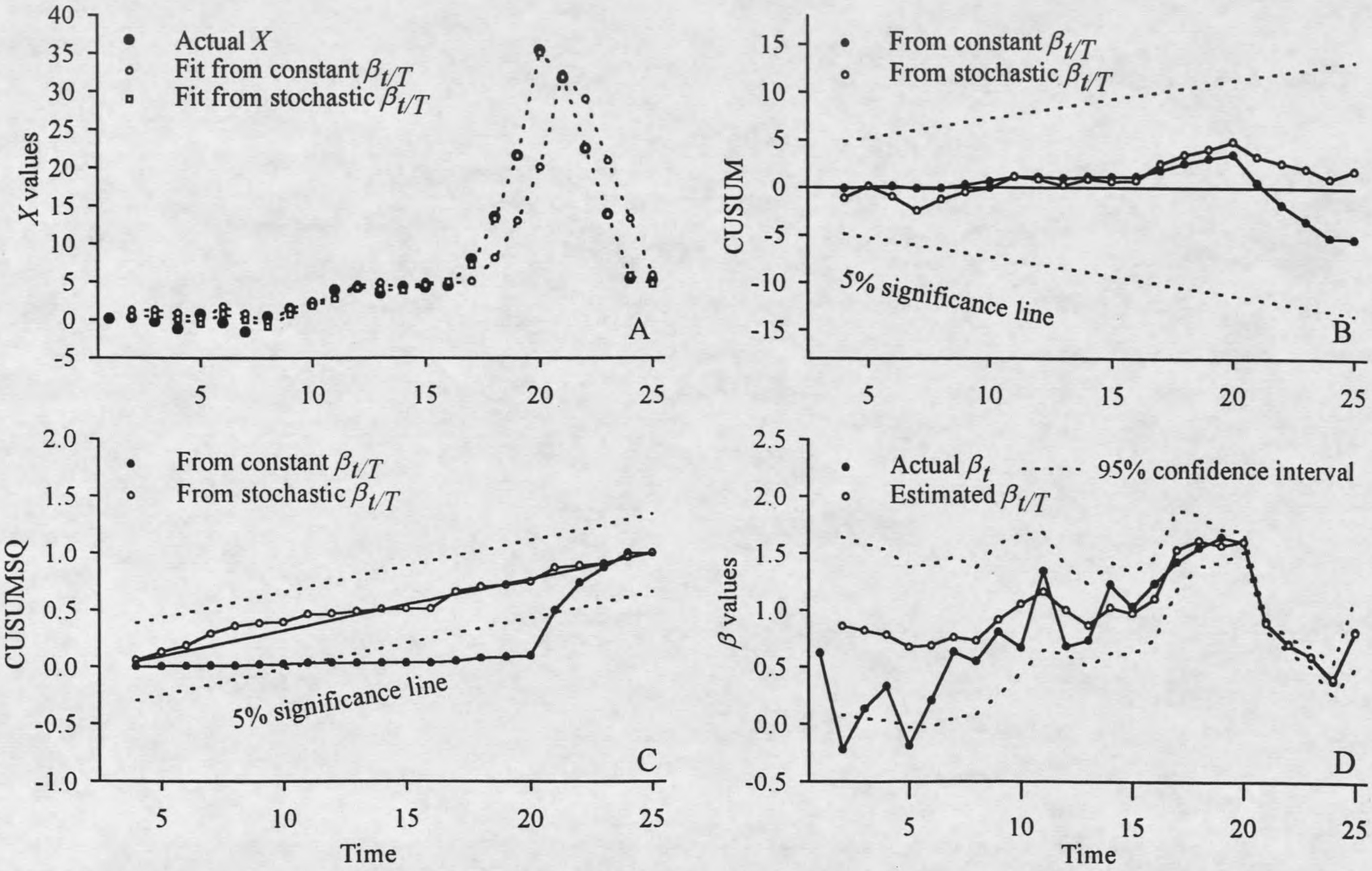

Figure 1. Performance of the parameter estimates for the first autoregressive model with a first autoregressive coefficient β_t.
Given conditions: $a = 0.5$, $\beta = 0.5$, $\phi = 0.8$, $\omega_t \sim N(0, 0.16)$, $\varepsilon_t \sim N(0, 0.64)$.

The estimates: $a = 0.947$ (0.224), $\beta = 0.320$ (0.353), $\phi = 0.67$ (0.206), $\sigma_\beta^2 = 0.0896$ (0.0426), $\sigma^2 = 1.08$ (0.482).

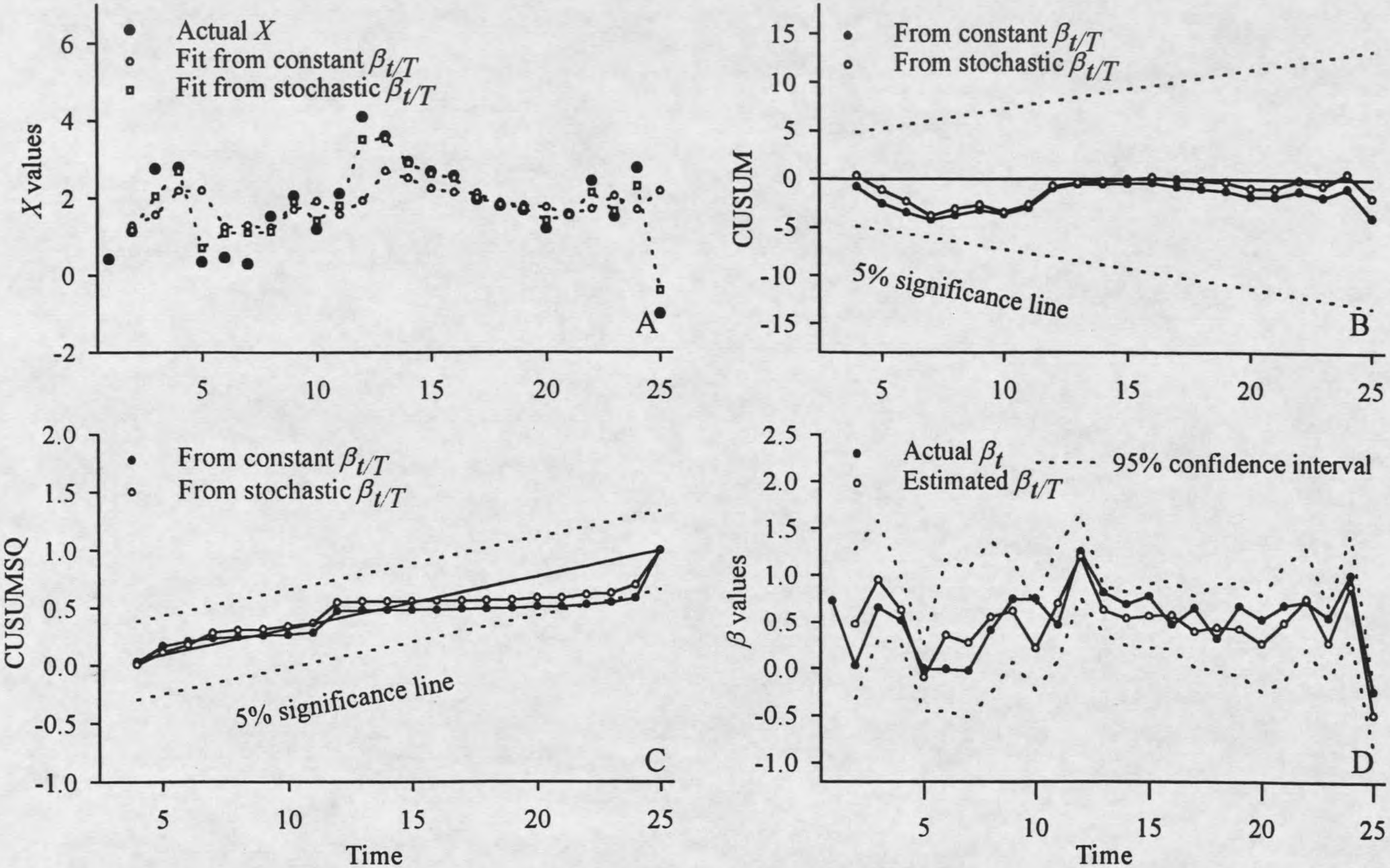

Figure 2. Performance of the parameter estimates for the first autoregressive model with a random coefficient β_t.

Given conditions: $a = 0.5$, $\beta = 0.5$, $\omega_t \sim N(0, 0.16)$, $\varepsilon_t \sim N(0, 0.64)$.

The estimates: $a = 0.974$ (0.352), $\beta = 0.485$ (0.222), $\sigma_\beta^2 = 0.183$ (0.104), $\sigma^2 = 0.317$ (0.0245).

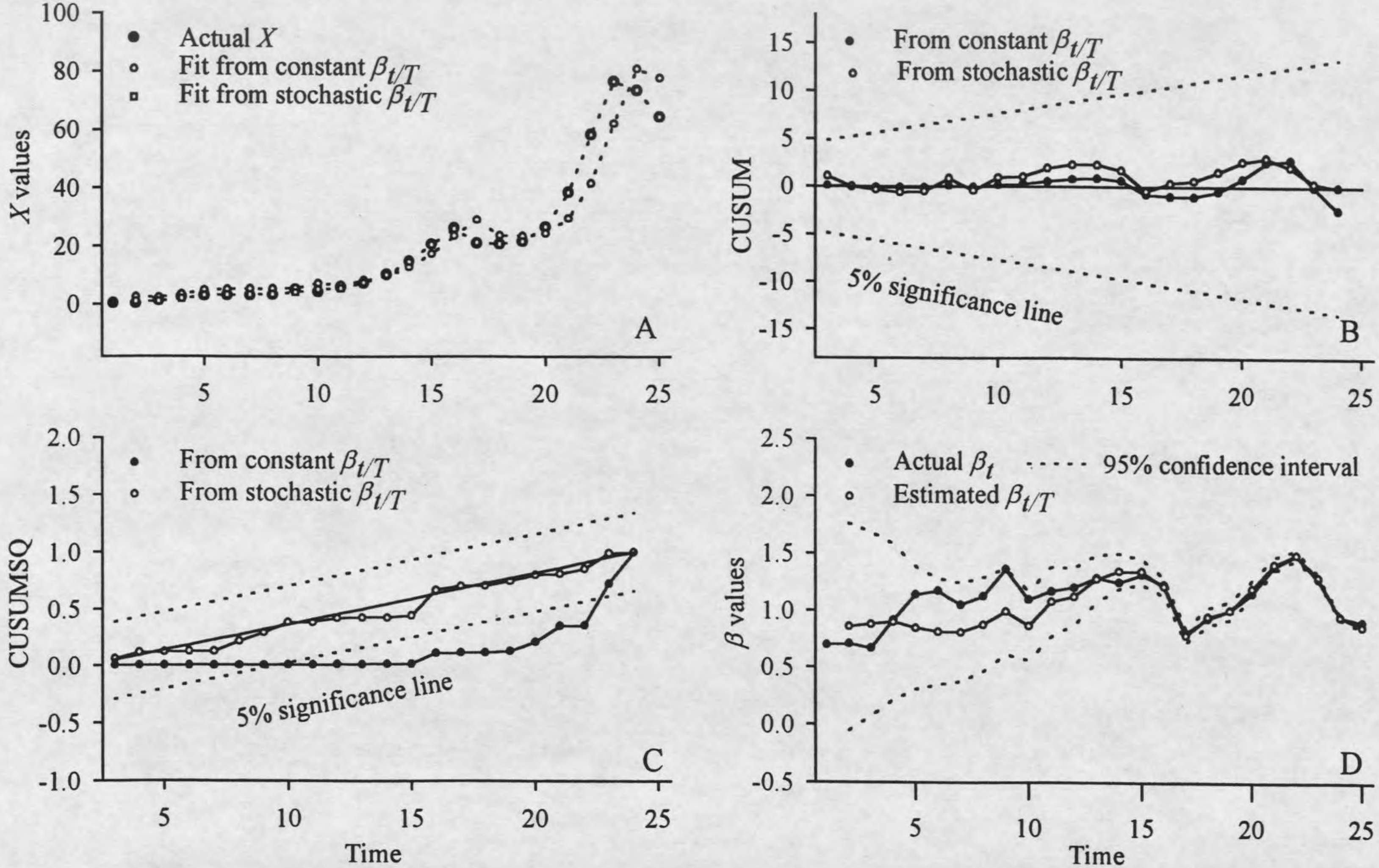

Figure 3. Performance of the parameter estimates for the first autoregressive model with a random walk coefficient β_t.

Given conditions: $a = 0.5$, $\beta = 0.5$, $\omega_t \sim N(0, 0.04)$, $\varepsilon_t \sim N(0, 0.64)$.

The estimates: $\sigma_\beta^2 = 0.03999$ (0.0151), $\sigma^2 = 0.481$ (0.28).

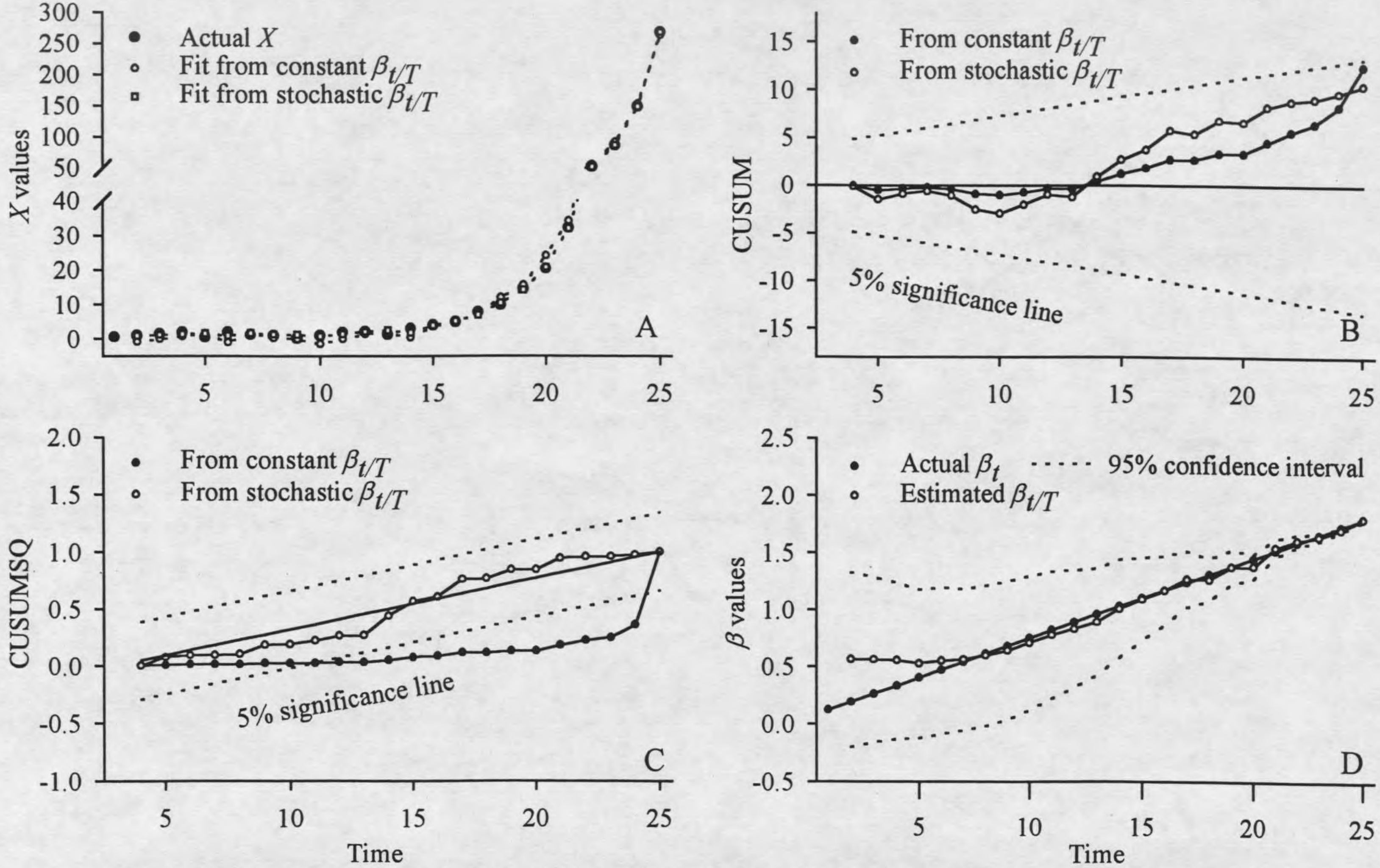

Figure 4. Performance of the parameter estimates for the first autoregressive model with a random walk coefficient β_t.

Given conditions: $a = 0.5$, $\beta_t = 0.05 + 0.07t$, $\varepsilon_t \sim N(0, 0.64)$.

The estimates: $\sigma_\beta^2 = 0.0150$ (0.0151), σ^2=0.0499 (0.190).

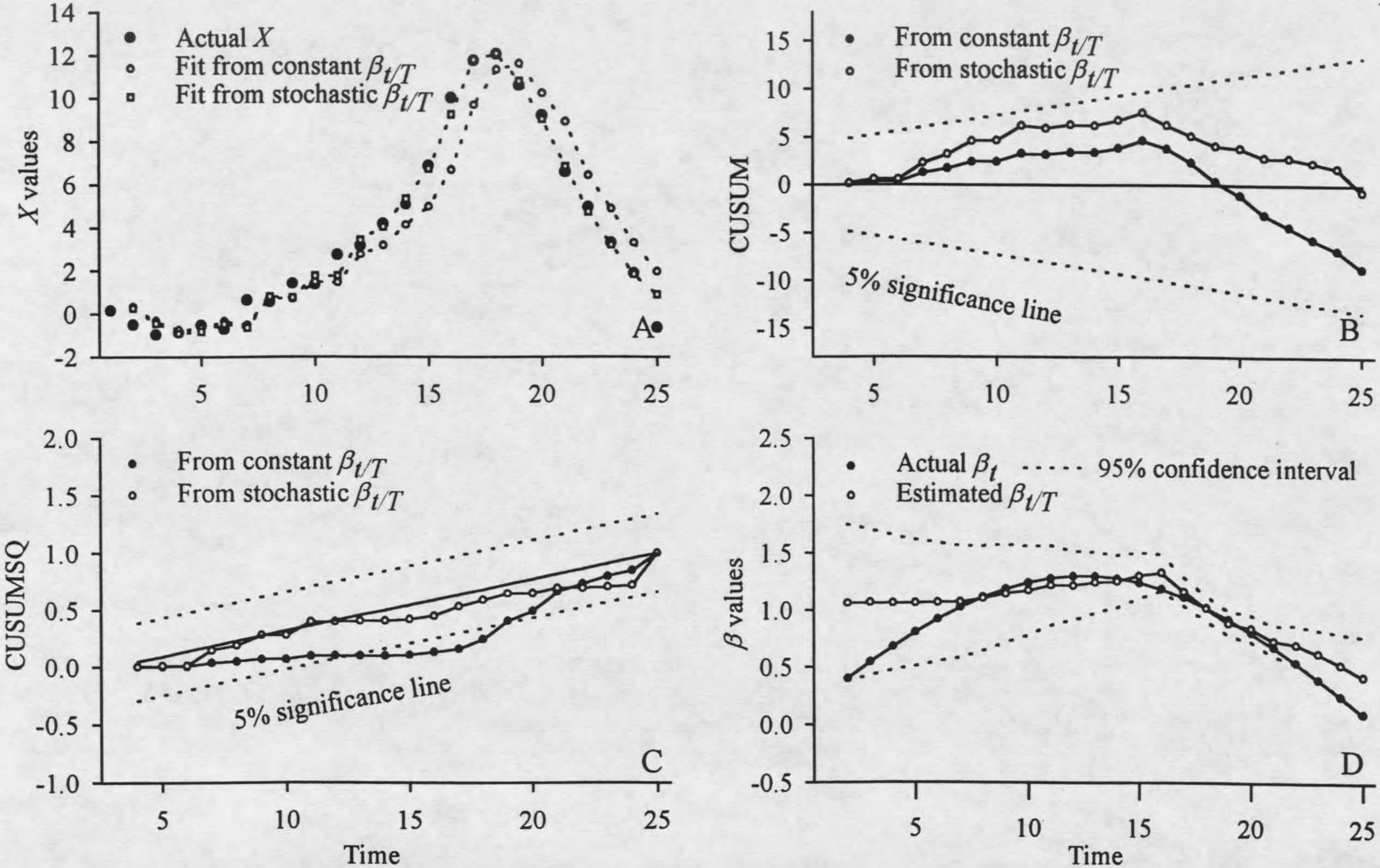

Figure 5. Performance of the parameter estimates for the first autoregressive model with a random walk coefficient β_t.
Given conditions: $a = 0.5$, $\beta_t = 0.1 + 1.2sin(2\pi t/25)$, $\varepsilon_t \sim N(0, 0.64)$.
The estimates: $\sigma_{\beta}^{2} = 0.0175\ (0.0108)$, $\sigma^2 = 0.0499\ (0.190)$

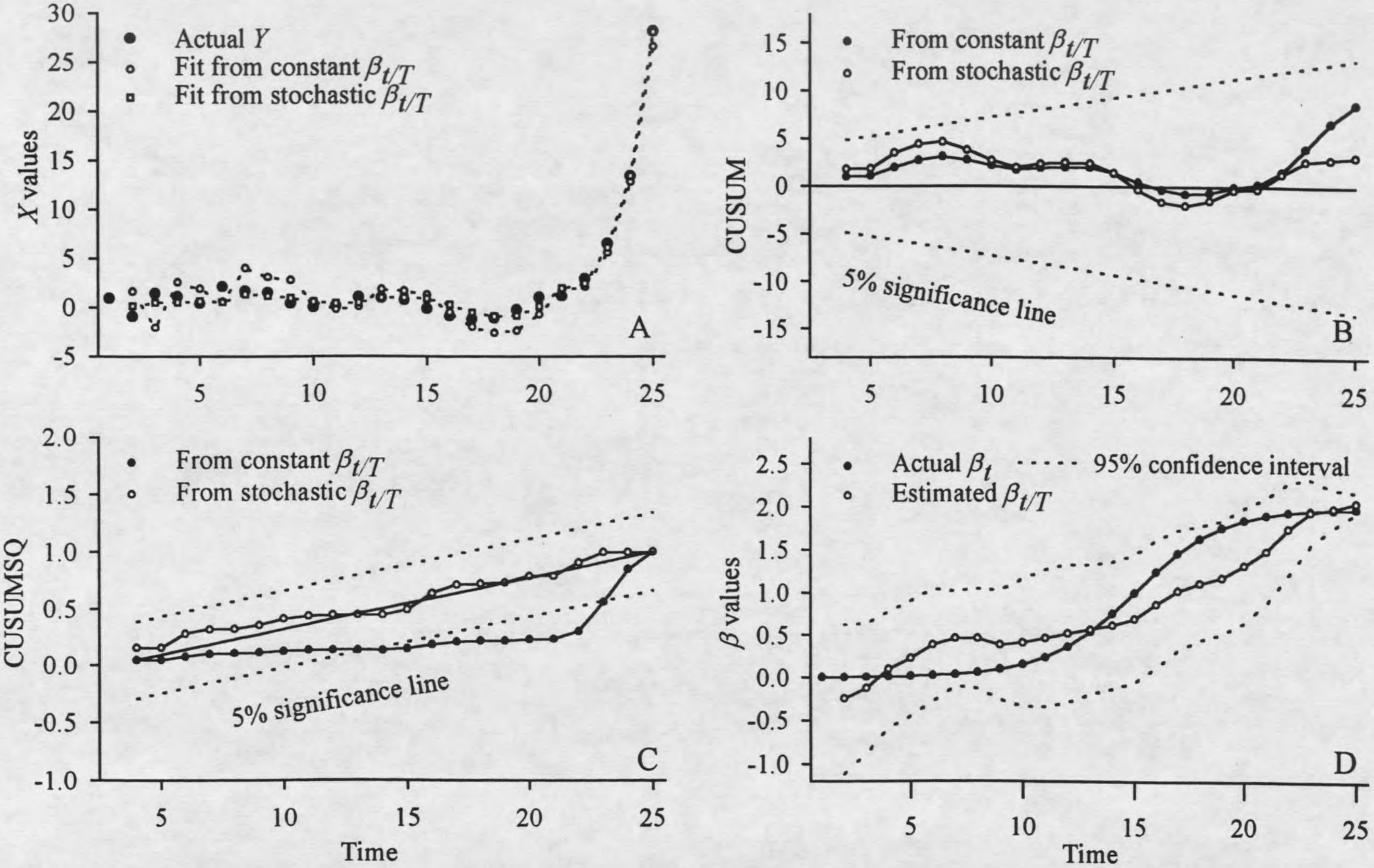

Figure 6. Performance of the parameter estimates for the first autoregressive model with a random walk coefficient β_t.
Given conditions: $a = 0.5$, $\beta_t = 2 / (1\text{-}exp(-0.5t+7.5))$, $\varepsilon_t \sim N(0, 0.64)$.
The estimates: $\sigma_\beta^2 = 0.0780\ (0.0607)$, $\sigma^2 = 0.0649\ (0.232)$

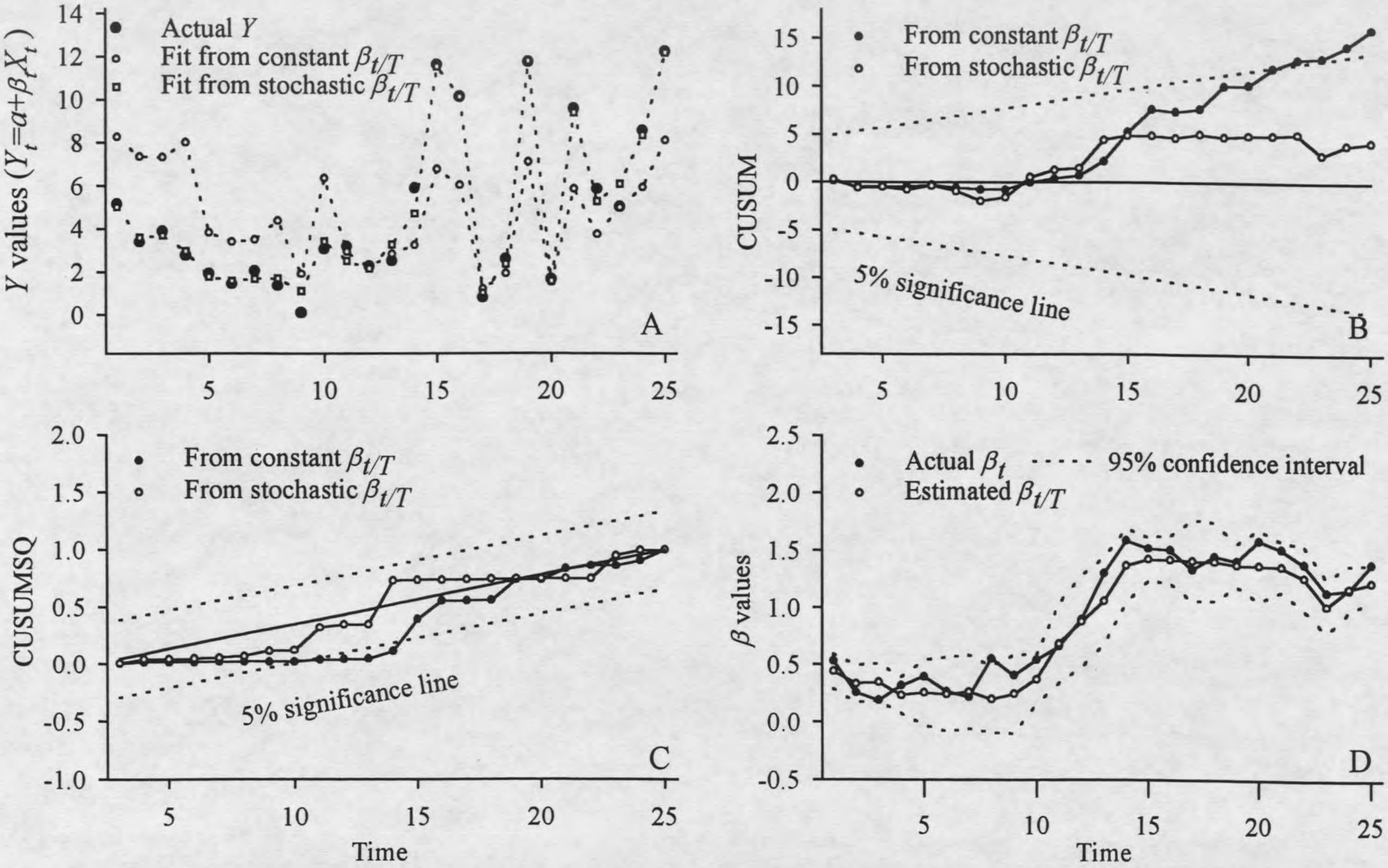

Figure 7. Performance of the parameter estimates for the simple regression model with a random walk coefficient β_t.

Given conditions: $a = 0.5$, $\beta = 0.5$, $\omega_t \sim N(0, 0.04)$, $\varepsilon_t \sim N(0, 0.64)$.

The estimates: $\sigma_\beta^2 = 0.03369$ (0.0186), $\sigma^2 = 0.488$ (0.241).

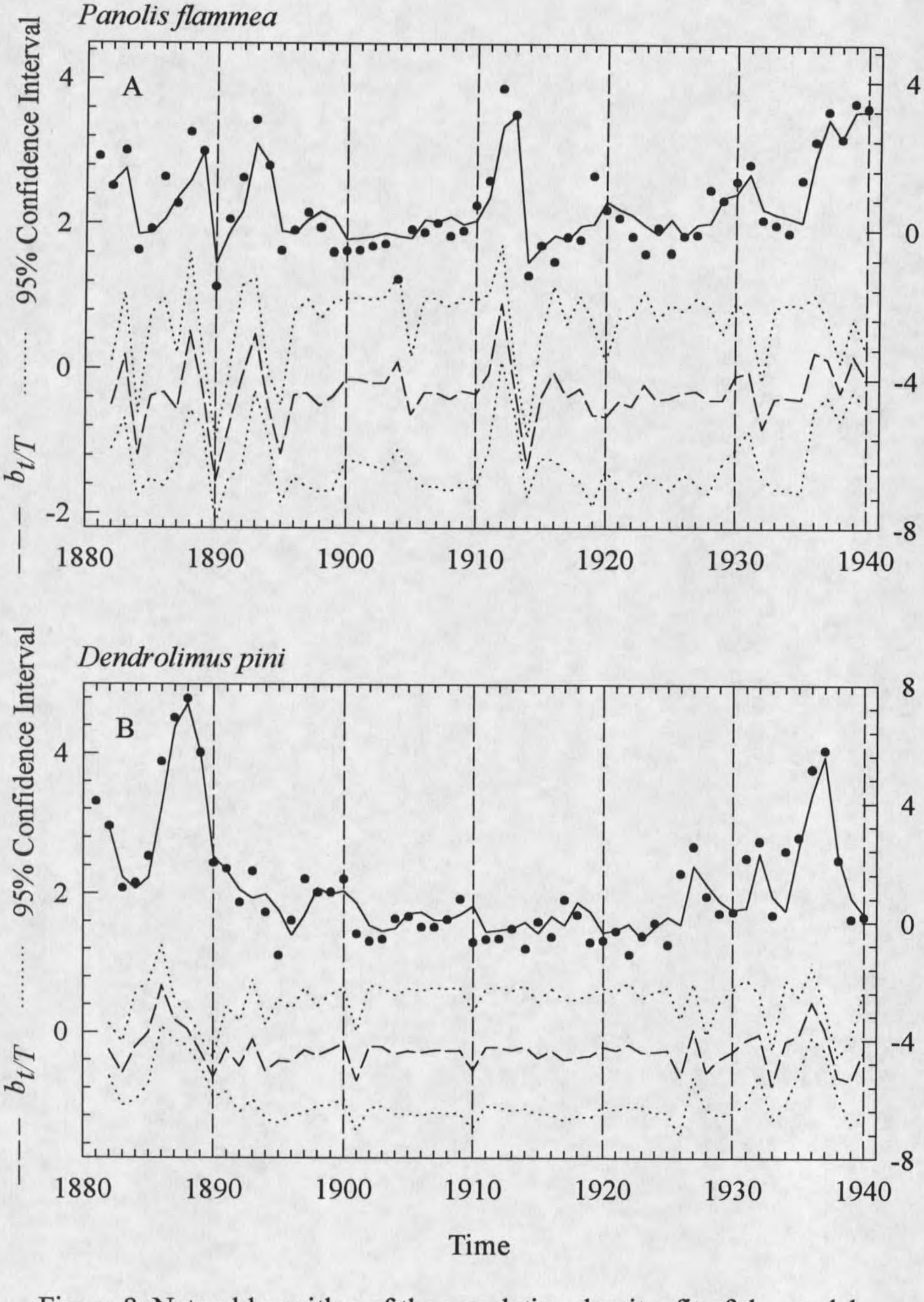

Figure 8. Natural logarithm of the population density, fit of the model and estimated time-varying density dependence parameters

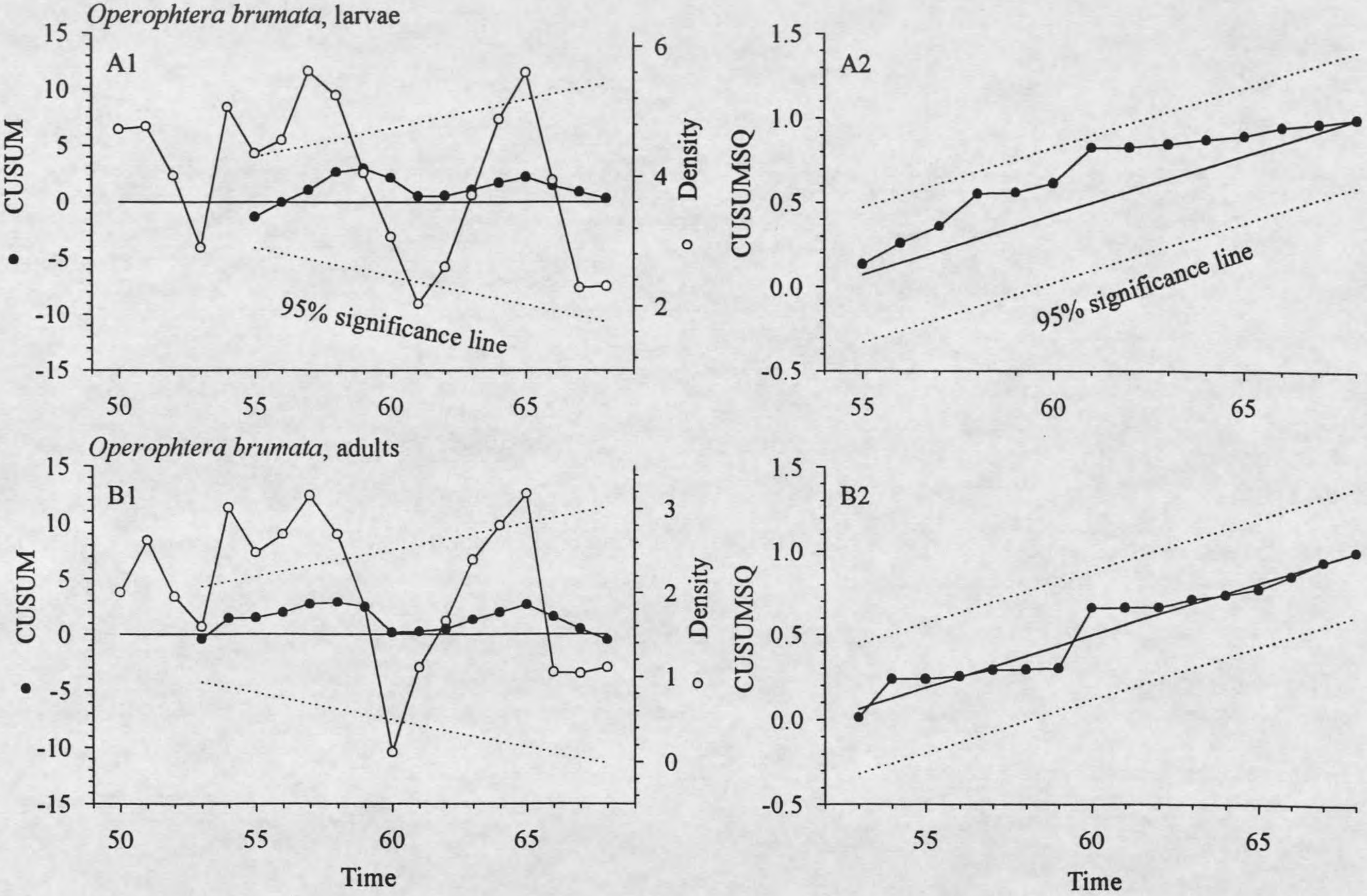

Figure 9. Population density, CUSUM and CUSUMSQ test (*Operophtera brumata*)

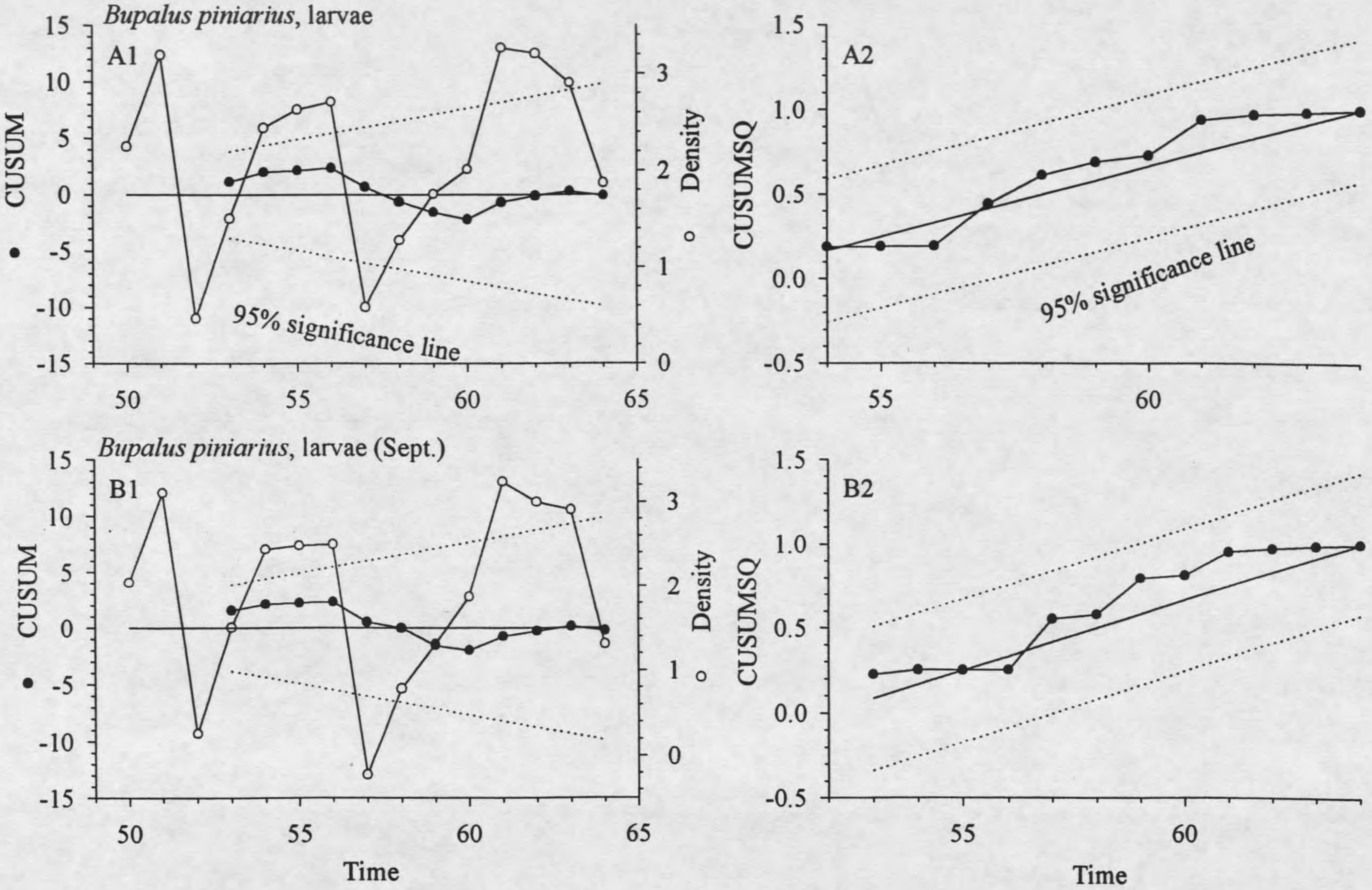

Figure 10. Population density, CUSUM and CUSUMSQ test (*Bupalus piniarius*)

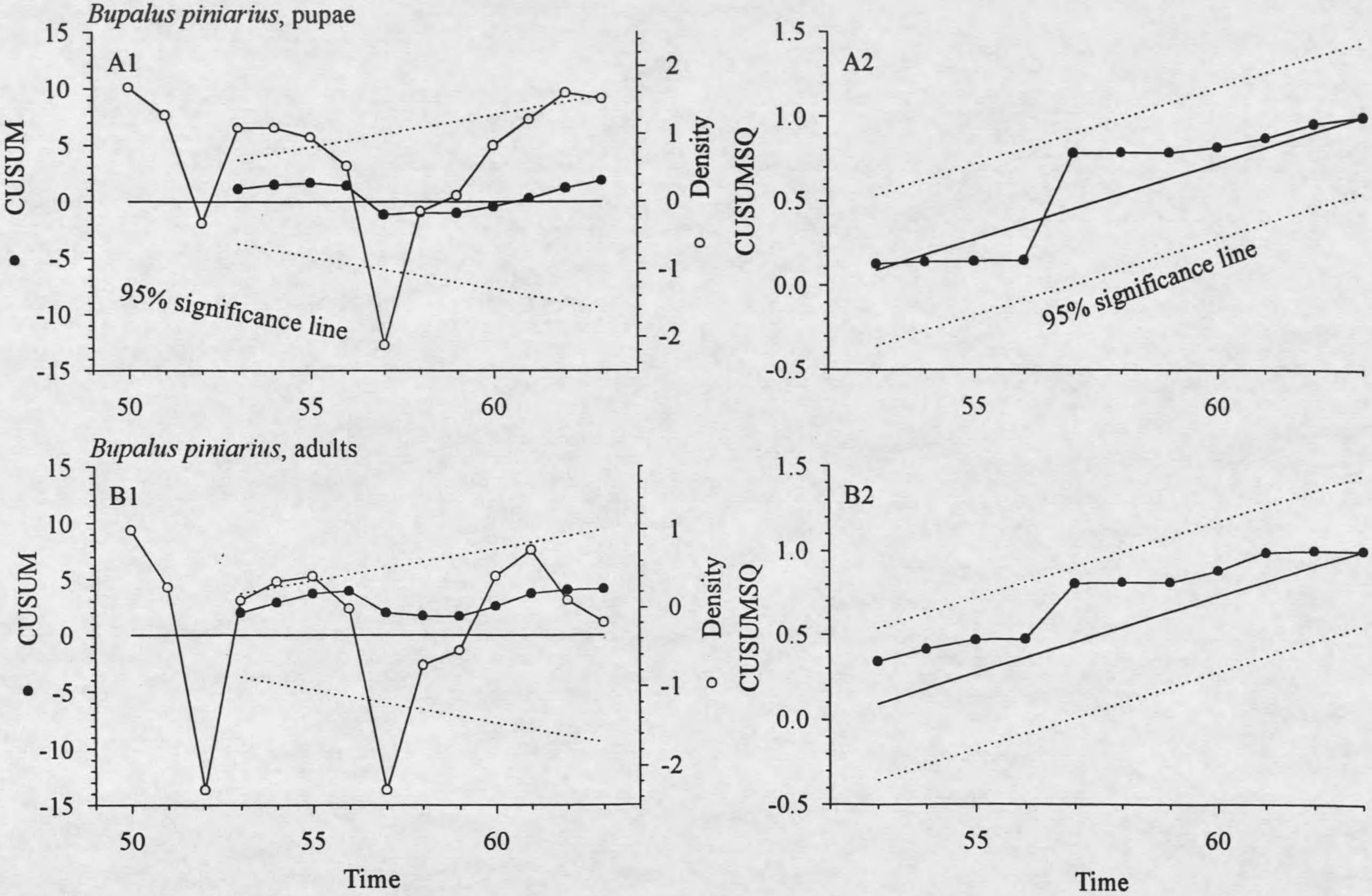

Figure 11. Population density, CUSUM and CUSUMSQ test (*Bupalus piniarius*)

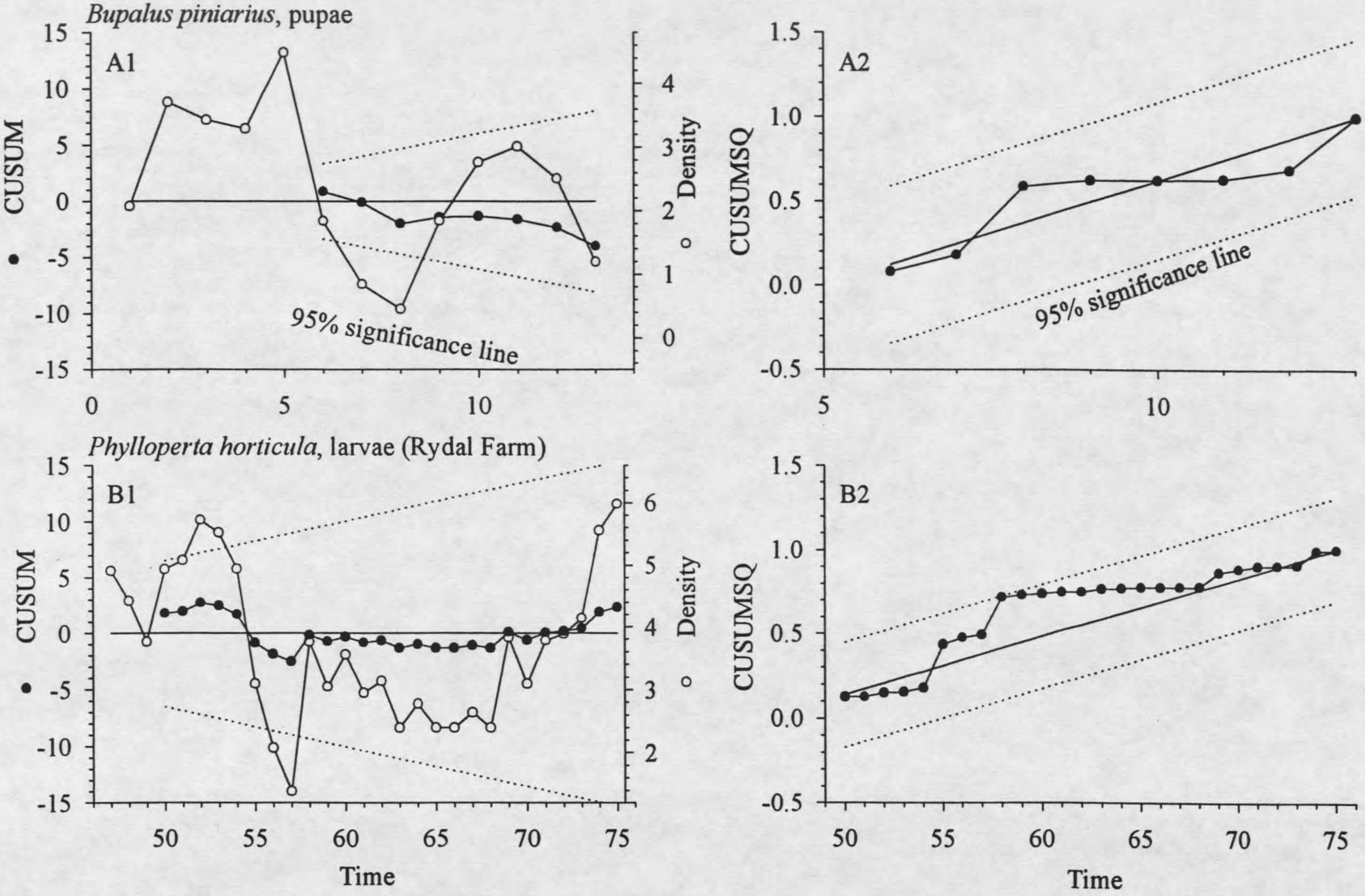

Figure 12. Population density, CUSUM and CUSUMSQ test (*Bupalus piniarius* and *Phylloperta horticula*)

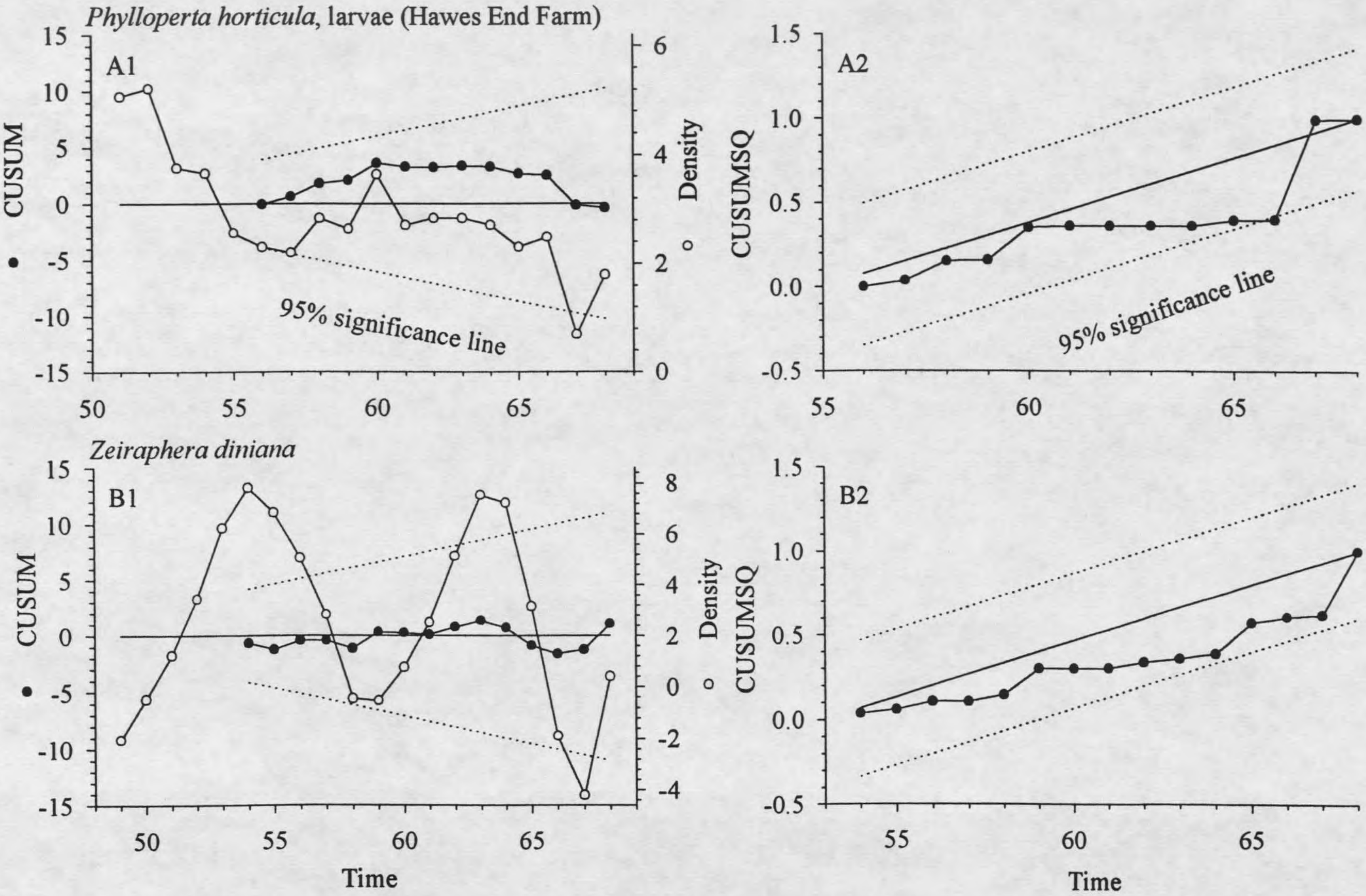

Figure 13. Population density, CUSUM and CUSUMSQ test (*Phylloperta horticula* and *Zeiraphera diniana*)

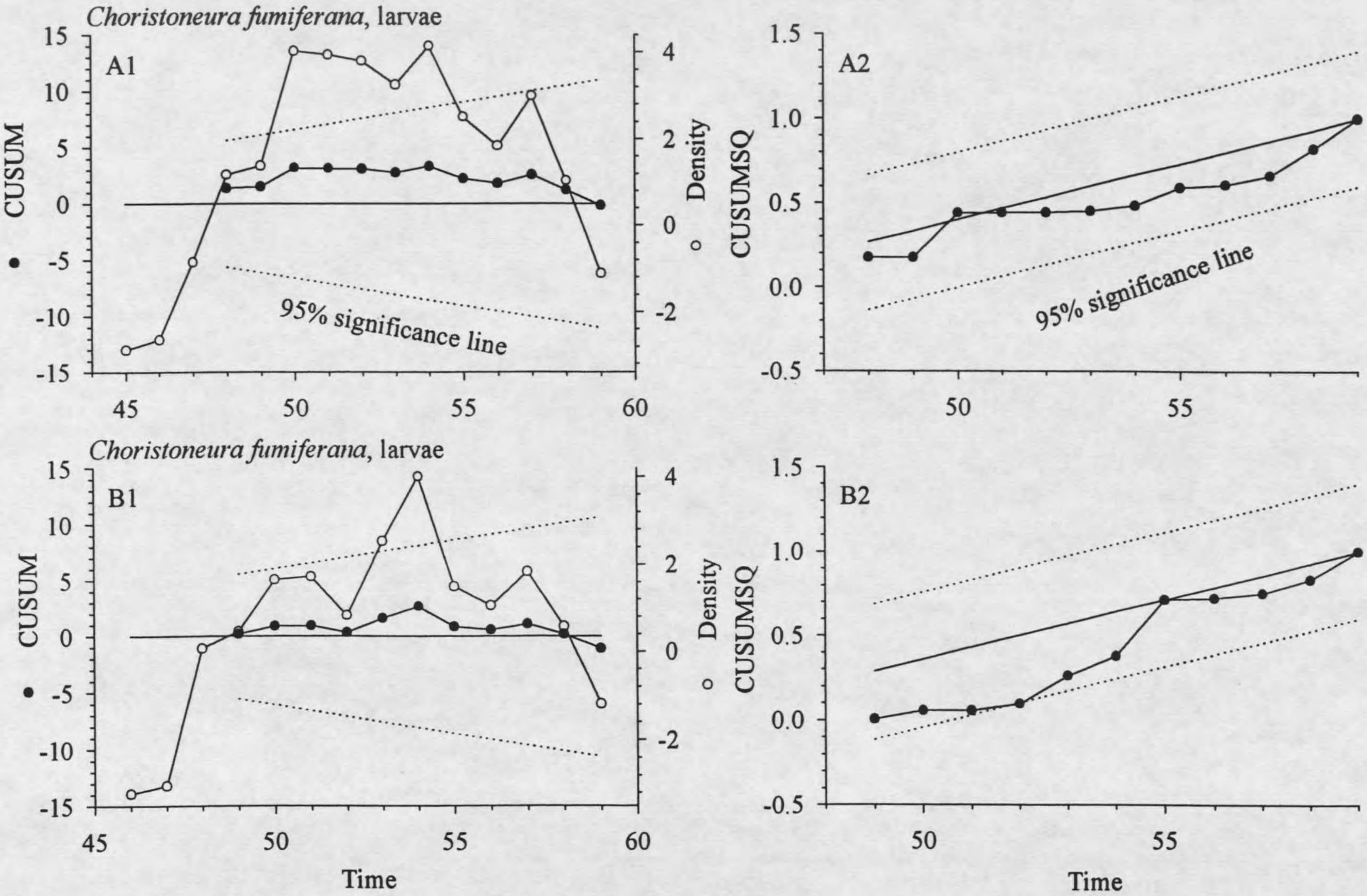

Figure 14. Population density, CUSUM and CUSUMSQ test (*Choristoneura fumiferana*)