



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
Montana State University
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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.

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ANIMAL POPULATION DYNAMICS, COMPLEX
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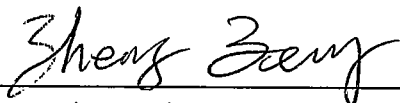
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ABSTRACT

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.

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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 et 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-semelparous 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 semelparous 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 al., 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 assess 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 addition 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 , $t = 2, \dots, T$; 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:

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

Where, $g(\cdot)$ 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:

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

Where the function $y(\cdot)$ 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):

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

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 $(1-f(N_{t-1})/K)$ can be used to measure the availability of the resource and to produce a density dependent growth process by modifying r as below ($f(N)$ is some transformation of N , K is the environmental carrying capacity, $K = f(N^*)$, where N^* is the equilibrium density):

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

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:

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

letting $X_t = \ln(N_t)$,

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

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

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

