Distinguishing forms of statistical density dependence and independence in animal time series data using information criteria
by Mark M Hooten

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

Abstract:
This study was designed to explore whether we can use well understood and documented statistical methods to simultaneously decide which model, among statistical population models, best describes an animal population time series process. Specifically, I brought into question the utility of information criteria (IC forms) for making such decisions.

Ultimately, I wished to distinguish whether animal time series could be appropriately classified as density dependent or density independent, and whether the actual form of density-related process model may have generated a time series. These issues have deeply seated historical precedence in ecology and have a number of contemporary applications, such as population viability analysis.

In a comparative approach, 5 IC forms prevalent in the literature were used for this study. These IC forms were the Akaike IC , Hurvich and Tsai's IC, consistent IC, Bayesian IC, and Hannan and Quinn's IC. All forms estimate twice the negentropy of statistical models based on the likelihood of data. Each IC form can make simultaneous estimations of the negentropy of a multitude of statistical models and do not require that models are related.

It was my contention that the question of how well IC forms could draw distinctions between models based on their negentropy was an empirical question. Forming a basis for an empirical approach were Monte Carlo methods. Using 117 animal time series, parameters were estimated under 6 population models; 5 parametric and 1 nonparametric forms. Parameters were used to generate new time series of lengths 8, 17, 35, 50, and 100. Likelihood calculations were made for each simulated time series and negentropy calculations were made with each IC form using each likelihood calculation.

In all, 23,400 bootstrap iterations were carried out at each time series length and the estimated results of model selection, based on negentropy calculations, were compared to the known origin of the (simulated) time series on which they were based.

Results were tallied and measures were formed to evaluate the performance of each IC form. Performance measures were density dependent and independent model family selection, model family selection, rejection, and identification, a measure of how concordant model selection and rejection were, and the bias that may be shown by an IC form to overfit or underfit a model. All IC forms performed above expectation in >95% of the cases of performance measures. The validity of method application was cast into doubt for time series of lengths <17. The AIC and AICc tended to overfit models, while the CAIC, BIC, and AIChq tended to underfit models.

I conclude that the BIC was the most consistently useful IC form for studies of this nature. I then used the BIC to classify 121 time series as to model family and model and explore associations with ecological variables of taxonomic classification, trophic classification, climatic source, and migratory status. The results were greatly heuristic but show that in virtually every category roughly 70-75% of

the time series were identified as density dependent.

DISTINGUISHING FORMS OF STATISTICAL DENSITY DEPENDENCE AND INDEPENDENCE IN ANIMAL TIME SERIES DATA USING INFORMATION CRITERIA

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Mark M. Hooten Mark M. Hooten

Date 12/14/95

This work, albeit far from complete, represents the endpiece of thirteen years of university education, and I have many people to thank.

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ABSTRACT

This study was designed to explore whether we can use well understood and documented statistical methods to *simultaneously* decide which model, among statistical population models, best describes an animal population time series process. Specifically, I brought into question the utility of information criteria (IC forms) for making such decisions.

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I conclude that the BIC was the most consistently useful IC form for studies of this nature. I then used the BIC to classify 121 time series as to model family and model and explore associations with ecological variables of taxonomic classification, trophic classification, climatic source, and migratory status. The results were greatly heuristic but show that in virtually every category roughly 70-75% of the time series were identified as density dependent.

DISTINGUISHING FORMS OF STATISTICAL DENSITY DEPENDENCE AND INDEPENDENCE IN ANIMAL TIME SERIES DATA USING INFORMATION CRITERIA

Introduction

Goal And Objectives Of Study

This study was designed to answer the following question central to the discipline of population biology: Can we use well understood and documented statistical methods to simultaneously decide which model, among statistical population models, best describes an animal population time series process? The emphasis here is on whether we can achieve this goal by *simultaneously* considering population models in nested or non-nested sets. When we consider more than two models at a time for "best fit" to a time series process, we are forced outside of the realm of standard hypothesis testing.

Hypothesis testing with regard to nested models proceeds stepwise, adding parameters if their entry into a model is considered significant by the test criteria (e.g. model building by regression analysis [Neter et al. 1990]). When testing non-nested models for best-fit to a time series process, we step out of the framework of standard hypothesis tests and, more specifically, previous population studies that have attempted to select a best fit model in a hypothesis testing fashion. Consequently, we need a different but well established technique to wander into the new realm of simultaneous population model comparison.

Likelihood methods for model identification have been employed in statistics for years. With these methods maximum likelihood estimators for model parameters are obtained and one model is tested against another by direct comparison of likelihood statistics or by likelihood ratio statistics. These methods are difficult to implement when considering multiple nested models or non-nested models. Furthermore, likelihood ratio statistics require intensive calculation for determining test statistic distribution, test size and power.

Consider the simple case of multiple nested models, i.e. models in a nested set with different numbers of parameters. Each more highly parameterized model in the set is capable of a broader range of process description. For a given set of data, the more highly parameterized models will naturally have a lower residual variance and a greater likelihood than the less parameterized models. In general, we need a simple way to correct the likelihood statistics for the bias presented by parameterization in the nested set. With this, we need a way to correct bias in the calculation of the mean expected likelihood due to bias in maximum likelihood parameter estimates.

Fortunately, there exists methods that can correct the estimated bias that likelihood calculations present. Akaike presented the "AIC" (Akaike information criterion) as a technique to resolve the issue of calculating "negentropy" (Akaike 1973). A preview of this measure requires a slight digression. The entropy of a data arrangement is the logarithm of the probability (or we can substitute likelihood) of the occurrence of the arrangement with respect to a particular (true) model. If we are considering a true model, this is the log likelihood statistic. The "negentropy" is the negative of the entropy and is used as a measure of "goodness-of-fit." As it turns out, the AIC and all other information criteria (IC forms) attempt to calculate an unbiased estimate of the negentropy of data. When performing multiple comparisons of models, then, the only requirement for directly comparing their likelihood statistics via AIC is that the conditions of a single likelihood equation are met by each model under consideration.

The AIC and other IC forms give us a framework for multiple comparisons of nested and non-nested population models and for finding the best fit model for a set of data. In what follows, I will apply the technique of Akaike and other authors to find a population model from a finite set that best describes animal time series data collected from the field. My aim is to consider biologically informative models that have been traditionally used in the literature to describe either density dependent or density independent processes. Additionally, however, I will explore a less informative nonparametric form that satisfies the conditions of stationarity for time series processes (Royama 1992). It is the feature of stationarity that defines a statistical model for density dependence. This feature will be common among all density dependent models that I will employ, even though not all the models will be nested. A distribution-free approach, such as AIC, allows us to avoid the pitfalls of hypothesis testing for model identification.

For this study, I made maximum likelihood estimates for model parameters by using data that were gathered from natural animal populations. I define the region of parameter space (under each model) sampled by the estimated parameters as a "reasonably complete" sample. This was, by no means, an exhaustive sample, and one might argue thai it created a bias. However, I simply used readily available data, and did not attempt to devise a sampling plan for animal data sets at large. So any bias that may be represented in the outcome of this study was purely from the haphazard availability of data. I therefore considered the parameter space that I viewed as an adequate representation of nature with respect to population models employed.

Furthermore, I took a preliminary look at the associations of gross ecological characteristics of the animal populations used, with the model forms identified for their respective time series. This step was designed to provide motivation for taking the results of this study and giving them some interpretive biological meaning. I conclude with suggestions for application of results in the practice of population biology and management.

Having provided the aim of this study, I will first consider some of the basic background and definitions that provide it with meaning. I will define density dependence and density independence., then consider their ecological and statistical meanings. I will motivate the idea of "biologically meaningful models" and then move to a historical view of statistical tests for density dependence. Parenthetically, any discussion of the history of testing for density dependence requires a basic view of the models involved. Finally, I will (more thoroughly than above) introduce likelihood and AIC testing foundations.

Defining Density Dependence And Independence

As an outcome of observations on natural populations, naturalists have long conjectured a “balance” of nature. The basic thought was that animal and plant populations had positive connections and negative feedback built into a multidimensional system of biotic interactions that somehow governed the structure of the system. In this sense, the system was largely self-sustaining, given certain constants of the abiotic environment. From the observations of negative feedback and the imposing structure of the physical environment grew the notions that biotic populations are governed by factors intrinsic and extrinsic to each population. It was also noted (not entirely accurately, but with a flavor of intuition) that as population densities of certain organisms waxed and waned the influences of intrinsic and extrinsic feedback had different magnitudes of impact on each and every individual in the population.

Observations of naturalists have given rise to a plethora of questions. The most salient questions when considering density dependence and independence are as follows. Do populations stabilize and does this constitutes regulation? Can a population be stable or regulated and trend negatively or positively? And, what is intrinsic to biological populations about regulation and persistence?

Somehow, acceptable definitions of density dependence and independence must encompass the notions of stability, regulation and trend. Population density is an issue of resource volume and availability with respect to population numbers. Thus, in a large sense, density dependence can be thought of as the feedback on population growth or decline from limiting or enabling agents of population change arising from a limited resource volume. Conversely, density independence can be thought of as a function of limiting or enabling agents of population growth or decline arising independently of resource volume or availability. Indeed, the vehicle of density independent population effects may be direct impacts on resource volume and availability. But this latter notion grays the distinction between the above "ecological" definitions of density dependence and independence. Not diminishing the importance of what I have coined (rather ambiguously) ecological density dependence and independence, I will try to clarify these issues by moving on to more conventional definitions of biological density dependence and independence.

Change in population density with increases or decreases in the density of the population *require* mechanisms of positive and negative feedback to individuals in the population. This requires naming mechanisms and a target for feedback in order to become tenable. The mechanisms implied are competition among individuals for limiting physical and biotic resources, and competition for reproductive status or resources. These forms of competition either increase in intensity or relax with the waxing and waning of the population. The target of the feedback is individual mortality, reproductive potential, urge to emigrate, and aggression toward immigrants. Thus, the standard definition of density dependence in animal populations is simply *per capita change in the rates of birth, death, immigration and emigration with changes in population density.*

Now we can make a clear separation between density dependence and density independence. Density independent population changes are those that occur independently of the density of the population. A density independent event will impact an individual in the population with equal intensity no matter what the density of the population. How an individual experiences such events is conditional on individual living circumstances when those events occur.

In all likelihood, population density affects survival potential of individuals in non-uniform ways (although this is not necessarily true). That is to say, given the effects of density, each individual has a different probability of survival. Density independent effects, conversely, are indiscriminate.

From the above statements we can see that populations may experience a mixture of density dependent and independent effects. Both kinds of effects can play significant roles in structuring populations, both ecologically and evolutionarily. Ecological and evolutionary changes in population structure, however, are bound to change the ways that members of a population experience effects of density-related and density-unrelated processes. With this circular dynamic, one can see that density dependence is an emergent property of populations and that density independence simply acts on populations.

I will complete my view of density dependent and independent processes by considering the concomitant processes of population stability, regulation , trend, and persistence.

Population "stability without regulation" is simply a phenomenon where the population is fluctuating with some regularity around an average or other central measure for an observably meaningful period of time, but with no regulation or bounds on the fluctuation. Stability can be impacted by either biotic or abiotic phenomena and can be associated with or without regulation. Stability without regulation is fragile since no mechanism exists of negative or positive feedback to individuals in the population regarding urges to reproduce or emigrate. Also, competition does not intensify or relax with changes in population size under stability without regulation. Therefore, there is no feedback to individuals that either causes or relaxes mortality, or that either broadens or narrows acceptance of immigrants. A stable population that is unregulated is simply undergoing a relatively even random walk in the snippet of time that we may have chosen to view it.

The converse can be said about stability with regulation. The implication is that there are mechanisms that cause the population to stabilize around some average or central measure. These mechanisms may be part of the biological response of the members of the population to their environment and density, or mechanisms can be imposed as an arbitrary but restrictive physical measure. (The latter case, known as density independent regulation, has been debated hotly for years (Andrewartha and Birch (1982). I will return to the topic later).

Observable trend in biotic populations makes the detection of stability and regulation more difficult. In a population that is stable and unregulated, trend is purely disruptive and part of a random walk. This is true since trend reveals the random movement of the population. An example from the modeling world would be the stochastic exponential model (discussed under "Methods"). In a population that is stable and regulated, on the other hand, trend is a reflection of a "shifting equilibrium". Thus, with a shifting equilibrium, a population tracks equilibrium either positively or negatively through time.

Considering the arguments above and since the world is stochastic in nature, the notion that populations are stable, regulated and trending is the expectation, not the exception. As a natural outcome of these properties, we can also expect that populations will persist through time. Indeed, a population responding to a shifting equilibrium through time will likely form some non-uniform distribution of population numbers. Thus, extremes are relatively rare and the population will likely remain extant for many generations. Since most populations persist lengthy periods of time, we can readily observe the outcome of regulation (i.e. persistence). Unregulated populations are just as likely to go extinct as they are to remain extant or even explode in numbers. Since we do not observe the outcome of no regulation in populations with regularity, we typically do not expect it, unless a population is in jeopardy of extinction.

The question remains, is regulation a density dependent or density independent process? To answer this question I will argue first that natural selection is at work in a Darwinian world. In this kind of world, the effects of natural selection are felt by each member of a population differentially (an outcome measured by individual fitness). It is precisely this property that is manifest in density dependent population responses. Each member of a population experiences the impact of population density differentially. This is the only logical outcome of regulation in a Darwinian world. If, conversely, density independent regulation were the norm, then the experience of differential density of a population would be purely arbitrarily realized by each member of the population. This mechanism would be as stochastic as the system that would govern it, thus leading to inescapably short average times to population extinctions. By its very definition, density independent population regulation is fragile and does not match the robust nature of biotic populations.

Tenets For Modeling Density-Related Processes

I have established that long-term persistence of populations requires density dependent regulation and not simple or unregulated stability. Additionally, density dependence is a process realized as an emergent property by populations in a Darwinian world. Translations of this process have been historically weak. Modelers, however, must be able to translate the biotic processes observed into simple mathematical expressions. Thus, density dependence is expressed superficially in statistical form, with our underlying motivation being detection, not simply description.

So, what is needed in models to adequately represent the complex processes involved in nature? Shall density dependent processes be viewed as discretely realized or continuously realized? To answer the latter question, we must only consider the gross processes involved in density dependent population regulation. If we consider birth, death, emigration and immigration as being continuously or discretely realized in a population, then we can ascribe those properties to our model.

Most multicellular organisms are not in a continuous reproductive state, nor do they have continuous emigration. Death processes are decidedly discrete for the most part, and follow cycles of birth and/or migration. For organisms occupying subtropical, temperate, and subarctic/arctic climatic zones these coincide with distinct seasons. For tropical organisms, highest mortality usually follows cycles of birth. Immigration is a more complex process, especially in tropical organisms. However, most populations experience the impact of immigrants during periods of greatest emigration. For organisms that have discrete reproductive cycles, this often follows periods of weaning.

Certainly, there are many exceptions to the above patterns. Clearly, however, when considering the effects of density dependence on most populations of multicellular organisms we can probably best measure those effects in some discrete form. This is further reinforced by the fact that we are most often limited to measuring biotic populations at discrete intervals. Therefore, the most judicious approach is to employ discrete-time statistical models.

For discrete-time time series models, we must build-in certain properties to be descriptive of observations on natural populations. First, we must have some form of return tendency to a (stochastic) equilibrium. Second, we need the flexibility of either independence or non-independence of population change on population levels at a previous time step or steps (i.e. an autocorrelation effect). Third, models must include some measure of the strength of return, i.e., a lag time of the return. Fourth, we must include the myriad of unexplainable events and processes by having a stochastic perturbation effect that appropriately impacts model parameter(s) of interest, and thus model predictions. These properties must be appropriately scaled to population size (the fundamental unit of measurement). A statistical definition of density dependence is simply a stationary time series process with lag time of one or more. For a more rigorous description of this process, see Royama (1992), pages 16-19. To reemphasize, the models that we construct must be descriptive of the biotic population process of density dependence based on our fundamental unit and form of measurement.

Biologically Meaningful Modeling

Now we are prepared to ask what is a biologically meaningful model? Following my argument above, a biologically informative model based on population census must include the following basic features: 1) A census or population estimation; 2) A feature of serial dependence of census, i.e. a reasonable lag feature; 3) A return time or strength of return feature; and 4) A stochastic term on the per-unit-abundance growth rate. Of these features, (2) and (3) imply parameterization for an innate population growth "urge," and a fundamental response to population density. Notice that these nuts-and-bolts features are terribly simplified abstractions of the *effects* of population growth (birth plus immigration) and decline (death plus emigration) processes. Therefore, from the standpoint of how we parameterize models, we are already twice removed from the experiences of individuals in the population. Following Royama (1992) we should derive our model with maximum descriptive power in mind, yet as a relatively simple abstraction of the complex processes of nature.

The model universe that fits with the above descriptions is infinite. More highly parameterized models, however, require more observations for accuracy in parameter estimation and model identification. This result leaves modelers unsettled by the fact that most biological time series are not very long (usually less than 20 observations). So, I simply choose what appears to be a reasonable model or models and go from there. For simplicity in the inception and implementation of this study, I have chosen models that have lag 1 only. The general form of parametric model that I have chosen for this study is an exponential form of the theta-logistic model. Four nested models can be attributed to the work of Ricker (1954). The most highly parameterized form is known as the θ-*Ricker* model. This model includes a noise term (additive to the growth rate) that stochastically impacts the per-unit-abundance growth rate of the population. I will consider the model in detail in Methods. For now, let it suffice to say that all of the parametric forms that I consider are of the general form. In this vein, I have a flexible set of models that are broadly representative of many density dependent and density independent forms. They include three density dependent forms: the θ-Ricker model, Ricker (exponential form of the logistic) model, Gompertz model (a non-nested form); and two density independent forms: the exponential model and random walk model. These models are all historically widely used.

A single advantage of the parametric forms used is that they can never deliver a prediction of zero or less (since they are in exponential form). Not getting a prediction of zero might be a little troublesome to those that insist populations must be at zero to be extinct, however, an extinction threshold can be set. Besides, we are not always dealing with “count” data, but rather density data that can approach zero.

One troubling feature of parametric models is that they are inflexible compared to nonparametric models. By including a single nonparametric form we can capture the essence of the distribution of observations in every time series that we consider, without making assumptions of how that distribution may look. By using our time series as an arrangement of observations that empirically describe a probability density function from which the observations were drawn, we will reconstruct the distribution using the available information. Since the distribution will be non-uniform, random draws will produce time series that have return tendencies to a single region of high probability, and fit the definition of stationarity. However, since each observation in a single time series is considered to be drawn independently from an identical distribution, there is no autocorrelation component. I will call this function the "IIDD" model for "independent identically distributed density" model, and consider it the most general case of density dependence.

The IIDD model is completely uninformative with respect to describing form or strength of density dependence, as are the parametric models. However, the IIDD model provides us with a way to detect density dependence without making assumptions about model parameters or their derivation.

Detecting Statistical Density Dependence

After sorting through the arguments above we are now left with the task of finding what makes the chosen models detectable. Perhaps more interesting is the question of how density dependence and density independence have been tested for historically. I will fist establish the foundation of historical tests, then I will briefly describe them. Lastly, I will motivate a new approach.

Central to the issue of detection if density dependence is what the fundamental units of measurement are on population of consideration. The greatest mass of literature on the detection of density dependence deals with data that are time series population censuses or estimates. Population estimates are often indexes, that is they are not overall population estimates, but rather counts that serve as surrogate estimates for the population at large.

Although some have argued that the only way to accurately detect density dependence is to utilize life table data, the vast majority of tests that have been developed are strictly on population count data. The outcomes of operable density dependence and density independence, however, are manifest in the population census over time (as discussed above). So, I will adhere to the realm of testing census-type data.

The technique of "key factor analysis" was developed by Morris (1959) in an attempt to test for the presence of density dependence in a time series. His technique amounted to taking the natural log of the observations in a time series and regressing these "X" values as X_{t+1} on X_t. The idea was that if a value of the estimator of the regression coefficient β tested to be significantly <1, this implied negative density dependence. Although the logic appears correct, Ebelhardt (1970) demonstrated that this method was increasingly unreliable as variation in natural population time series increased. Furthermore, Eberhardt demonstrated how density dependence would often be detected with regression techniques, even if sequential observations were taken as random draws from a uniform distribution whose random variables are independent and identically distributed (IID). This makes intuitive sense, since the test amounts to a measure of return tendency to a central measure. Putting Morris's test to empirical rigourism, Slade (1977) and Vickery and Nudds (1984) showed that Morris's test over-identified density dependence with respect to test size for β.

Following Morris, Varley and Gradwell (1963) proposed a regression test where X_{t+1} was be regressed on X_t and X_t was regressed on X_{t+1}. Similar to Morris, if the estimator of the regression coefficient β tested significantly <1 in *both* cases, then negative density dependence was said to have been demonstrated. This test was shown to be too conservative with respect to test size for β (Slade 1977, Vickery and Nudds 1984).

The major axis test and standard major axis test (*cited in* Pollard 1987), both of which are special forms of regression tests, and Bulmer's (1975) autoregression test have had limited success under certain conditions. The major axis test was shown by Slade (1977) and Vickery and Nudds (1984) to be fairly robust in identifying density dependence in time series that had significant trend. However, the definition of "significant trend" was considered ambiguous by these authors and others (Gaston and Lawton 1987, Pollard et al. 1987). Several authors conclude that Bulmer's test requires that no significant trend be present in the time series in order to show appropriate power (Gaston and Lawton 1987, Pollard 1987, Slade 1977, Vickery and Nudds 1984, 1991).

The technique common to both Slade's (1977) and Vickery and Nudds's (1984) assessment of the various regression tests was the employment of Monte Carlo simulations. The basis of Monte Carlo techniques is to have a known model generate data that has, in this case, a known density independent or density dependent form. One then tests the data for density dependence with the above techniques and compares results to what is known about the origin of the data. This delivers an empirical estimate of the true size and power characteristics of the test.

Pollard et al. (1987) broke free of the long-practiced tests discussed above by developing their "randomization test." The randomization test employed Monte Carlo techniques and had the utility of detecting density dependence irrespective of trend in time series data (see Pollard et al. for details). The shortcoming of this test is that it has low statistical power (den Boer and Reddingius 1989b, Holyoak 1993 a & b, Vickery and Nudds 1992). At nearly the same time, Reddingius and den Boer (1989) developed a similar test that they coined the "permutation test" for density dependence. The randomization and permutation tests have been shown by Crowley (1992) and Holyoak (1993) to be subject to significant losses of power when time series length drops below 20 observations. These tests also lose power with increasingly chaotic fluctuations in time series, and Reddingius and den Boer's test is adversely affected by increasing positive or negative trend in time series (Holyoak 1993).

In an innovative approach, the "attraction test" was developed by Crowley (1992) as an alternative to the standard regression, randomization, and permutation tests. One feature of the standard regression, randomization, and permutation tests is that the density dependent models that they were based on could be ascribed single point or stochastic equilibria. Crowley treats density dependence more as an emergent property of repulsive and attractive ecological forces to which a population may be responding, rather than a trait of the population (see Crowley [1992] for details). However, in tests of Crowley's random walk attraction test, especially for single species and short time series (<20), the test often fails to reject the null hypothesis (Crowley 1992, Holyoak 1993).

The disappointment of the tests mentioned above is how each suffers more or less from a lack of statistical power and having constraints on trend of observations in the time series, magnitude of variation therein, and length of the time series that are being scrutinized for the presence or absence of density dependence. Most of these tests are constructed with regard to the estimate of the slope parameter β in a regression of X_{t+1} on X_t. In order to break free of the constraints that these tests possess, recent authors have taken advantage of modern computing power and developed significant new tests that are served by the rigours of bootstrapping.

Dennis and Taper (1994) developed the parametric bootstrap likelihood ratio test with the intent of resolving the above issues. Their test was based on likelihood ratio statistics that would "represent the practical limits of power that could be attained for the stochastic logistic growth model." Wolda and Dennis (1993) stated that the test is the "best kind of test that one can hope for" based on its well understood statistical properties. Indeed, the test does remarkably well at appropriately rejecting the null hypothesis when testing for density dependence based on data generated by a logistic growth model. Test size is also preserved when considering data generated by a random walk model. However, Wolda and Dennis (1993) caution that the test does as well at detecting density dependence from rainfall data and data that are increasingly "sloppy" or noisy, as it does from biological time series (Wolda and Dennis 1993). Their cautionary note summons the notion that a conclusion of "density dependence at work" should not be invoked if the potential causes are unlikely or, as with rainfall, clearly absurd to apply.

Holyoak (1993) questions the implications of some of Dennis and Taper's (1994) work. He expressed skepticism of a method that has a greater likelihood of detection of density dependence in time series that contain high degrees of noise than those that do not. Holyoak also rightfully questioned the appropriateness of density dependence tests on time series that were not the result of appropriate sampling periodicity (that is, not at a time when the population was at a discrete reproductive generation), or when the animals sampled have overlapping generations, are iteroparous, and/or have significantly delayed density responses.

Dennis and Taper (1994), clearly illustrate how their test is viable with models that include higher order delays. Thus, one could follow procedures of classical time series analysis (e.g. Wei 1990) to determine an appropriate lag time to incorporate into a population model (Royama 1992) and then proceed with Dennis and Taper's test.

That which characterizes Dennis and Tapers test as "the best available test for density dependence" is it employs the well understood properties of likelihood ratio statistics with the power of parametric bootstrapping. Their test, however, is still limited to testing the null (density independence) against a single alternative (density dependence) hypothesis (Dennis et al. 1995), and is quite calculation-intensive.

Ideally, we need a relatively simple procedure that represents a test with known properties that delivers a readily accessible result for model selection from multiple models *simultaneously*. Although it is certainly possible to pursue population model identification from multiple population models in a hypothesis testing framework, such procedures are done stepwise and are notoriously poor at identifying the correct model (Flack and Chang 1987).

Classical time series analysis has long employed techniques to detect the most likely model from a set that are descriptive of data. Borrowing somewhat from this, information criterion techniques can be used in Monte Carlo simulation to gain a relatively precise idea of how well we can identify models that generate time series from a set of >2 models. We can tally results to get an empirical idea of how well the techniques do. Thus, we do not need to rely on statistical theory in order to evaluate the goodness of our test. Yet, in order to understand information criteria and model identification, we must proceed with a solid introduction to what is at the bottom of these techniques.

Likelihood Foundations

In order to make the connection between data and a model we need to specify a likelihood function. The likelihood statistic, $L(\vec{y}|M^*,\vec{\omega}^*)$, describes the probability that a data vector $\vec{y}$ could arise from a model M^*, given a parameter vector $\vec{\omega}^*$. One expects that if a large number of data vectors were generated from a "true" model and parameter vector, that the mean likelihood of data sets $\{\vec{y}\}$ will be greatest calculated under the true model and parameter vector (i.e. $\{M^*,\vec{\omega}^*\}$) than any others (i.e. $\{M,\vec{\omega}\}$). We can express this concept as follows: $E(L(\vec{y}|M^*,\vec{\omega}^*)) > E(L(\vec{y}|M,\vec{\omega}))$ given

$\{M,\vec{\omega}\} \neq \{M^*,\vec{\omega}^*\}$ and $\{M^*,\vec{\omega}^*\}$ gives rise to all $\{\vec{y}\}$. In general, one does not know $\{M^*,\vec{\omega}^*\}$, the true model and parameter vector, and they must be estimated with a model of our own design.

The function $L\left(\vec{y}\middle|\hat{M},\hat{\vec{\omega}}\right)$ requires that an estimated parameter vector $\hat{\vec{\omega}}$, is a vector of maximum likelihood parameter estimates for $\hat{M}$. Maximum likelihood parameter estimates are defined as those that jointly maximize $L\left(\vec{y}\middle|M,\vec{\omega}\right)$ (Bain and Engelhardt 1987). Also, maximum likelihood parameter estimates have the desirable properties of being asymptotically efficient, consistent, asymptotically unbiased, and have distributions that approach normal distributions for large samples. For all of the parametric models used in this study, parameter estimates will be maximum likelihood estimates.

The appropriate likelihood function for the models that I use in this study is developed fully by Dennis and Taper (1994). In brief, if $\ln\left(\vec{N}\right) = \{X_0, X_1, \ldots, X_t\}$ are the natural logarithms of time series observations on a biotic population, then $\vec{y} = \{X_1 - X_0, X_2 - X_1, \ldots, X_t - X_{t-1}\}$ are normally distributed random variables with mean $\mu = 0$ and variance σ^2. The function specified by this relationship is the joint conditional likelihood, i.e. it is the joint pdf of $X_0, X_1, \ldots, X_{t-1}$ conditional on $X_0 = x_0$. The function, specified under "Methods," is the joint conditional likelihood of the transitions $X_1 - X_0, X_2 - X_1, \ldots, X_t - X_{t-1}$.

The issue of specifying a likelihood function for the IIDD model is more simple than it is for parametric models. Since there are no parameter estimates for this model, the likelihood function is simply the product of the empirical probabilities of the observations (or equivalently, the sum of the natural log of the empirical probabilities of the observations). The IIDD model is specified under "Methods."

Likelihood Functions To Negentropy

It turns out that $L_{\max}\left(\vec{y}\middle|\hat{M},\hat{\vec{\omega}}\right)$ is a biased estimate of $E\left(L\left(\vec{y}\middle|M,\vec{\omega}\right)\right)$, even if our model is precisely correct and the estimated parameters for M are maximum likelihood estimates (Bozdogan 1987, Hurvich and Tsai 1989). We are motivated to seek a way to reduce bias intrinsic to likelihood statistics. Information criteria correct for the bias, in various ways, that is inherent to these methods (Tong 1975, 1990). To understand how IC forms correct for bias, and especially how this can be accomplished under conditions where the true model is unknown, I shall next consider the information-theoretic basis of model selection.

Information theory is based on the notion of entropy. The entropy of a system is defined as the logarithm of the probability of the occurrence of its particular arrangement. Translated into the language of statistics, this means that the mean log-likelihood statistic for data generated from a fully known model *is* the entropy of the system. This is very convenient when considering the discussion of likelihoods, above. The joint conditional log-likelihood, as above for Dennis and Taper (1994), characterizes the total entropy of data in the form of time series data, given that our model is truth. Stated differently, if we have a model that generated a particular arrangement of data, the log-likelihood of that data set is the entropy of the arrangement. Conversely, the negative of the entropy is the *negentropy,* and is commonly the preferred form of information criterion statistics, as will be expanded upon below. Still, how can we calculate the negentropy of a data set when we do not know the model that generated it?

Consider the possibility that we have two models with identical numbers parameters. One model is our data-generating model, i.e. it is truth, and the other model is our estimation of truth from a finite set of data. We can calculate the log-likelihood for the data set (arrangement) under truth and our estimated model. These log-likelihoods will differ, since in practice, data will not yield a perfect estimate of truth and maximum likelihood parameter estimates yield biased estimates of the mean expected log-likelihood (Anderson et al. 1994, Bozdogan 1987, Tong 1990). Somehow, we must find a way to adjust the estimated log-likelihood such that the more data we have, the closer our estimated entropy will be to the true entropy of the data arrangement.

Adopting the information-theoretic approach, Akaike (1973) argued that $\ln(L) - k$ is an asymptotic estimate of the mean expected log-likelihood (which is an unbiased estimate of the entropy), where k is the number of free parameters (the dimension) in our estimated model. I will sketch the underpinnings to Akaike's approach, but for rigorous expositions of Akaike's argument, see Bozdogan (1987) and Tong (1990). For reasons of historical consistency (Anderson et al. 1994), the AIC (Akaike information criterion) is calculated as a measure of twice the negentropy of the data arrangement: $\mathrm{AIC}(k) = -2\ln(L) + 2k$. If a set of models *actually contains the true model*, then the model that minimizes the AIC [= AIC(k)] will be considered the best fit. If, however, a set of models *does not* contain the true model, then the AIC can be considered a measure of badness of fit (Tong 1990) and its minimization is practical. No matter how a person wishes to view it, the AIC is a measure of parsimony; given available data, a minimum AIC estimate implies that the information yielded by one model from a set of models is the most that can be derived (Tong 1990).

The foundation for Akaike's basic tenet is the Kullback-Leibler information quantity (K-L quantity). The K-L quantity is a direct but theoretical measure of negentropy. Specifically, let us assume that we have two probability density functions $f(\mathbf{x},\theta^*)$ and $f(\mathbf{x},\theta)$, with two parameter vectors: θ^*, a true parameter vector, and θ, an estimated parameter vector, each K-dimensional and members of a limited K-dimensional space. Observations $\mathbf{x}$ are sampled from $\mathbf{X}$~iid, $f(\mathbf{X},\theta_K^*)$. The "closeness" or goodness-of-fit of $f(\mathbf{x},\theta)$ to $f(\mathbf{x},\theta^*)$ is measured by the generalized entropy (Bozdogan 1987). Conversely, the K-L quantity is the negative of this measure. Following Bozdogan (1987) this is defined as

$$-I(\theta^*,\theta) = \int f(\mathbf{x}|\theta^*)\ln f(\mathbf{x}|\theta)\,dx - \int f(\mathbf{x}|\theta^*)\ln f(\mathbf{x}|\theta^*)\,dx, \qquad (1)$$

where the first term on the right is the expected log-likelihood or "cross-entropy" and the second term is a constant (the negative Shannon entropy). It is the cross-entropy that determines the goodness-of-fit of $f(\mathbf{x},\theta^*)$ to $f(\mathbf{x},\theta)$. For all practical purposes, the second term on the right can be dropped. It can be seen that the negentropy is zero if the model $f(\mathbf{x},\theta)$ is essentially true, i.e. it is equal to $f(\mathbf{x},\theta^*)$, almost everywhere. Thus, any discrepancy represents a negative amount of information about $f(\mathbf{x},\theta)$ with respect to $f(\mathbf{x},\theta^*)$, in other words, a badness-of-fit.

Equation 1 can be seen to be an expected log odds ratio of $f(\mathbf{x},\theta)$ over $f(\mathbf{x},\theta^*)$. Also, if k is a subset of K-dimensional space, it turns out that the mean log-likelihood is a consistent estimate of $I(\theta^*,\hat{\theta}_k)$. Bozdogan (1987) shows that Akaike cleverly estimated -2n(log odds ratio) with

$$2nE\left(I\left(\theta^*,\hat{\theta}_k\right)\right) \cong -\left[2\ln L\left(\hat{\theta}_k\right)+2k\right]+\left[2\ln L\left(\hat{\theta}_K\right)-K\right], \qquad (2)$$

where n is a "sufficiently large" number of observations, L are the likelihood functions for k- and K-dimensional models $f\left(\mathbf{x},\hat{\theta}_k\right)$ and $f\left(\mathbf{x},\ \theta_K^*\right)$, respectively. What "sufficiently large n" is, is left to the ambiguities of the research and appears to be an empirical question. The second half of equation 2 is common to every model considered part of K-dimensional space and is thusly dropped as a constant term. This leaves us with the AIC(k) as an unbiased estimator of minus twice the negentropy or mean expected log-likelihood. This means that $\exp\left(-\frac{1}{2}\mathrm{AIC}(k)\right)$, where $(k=1,2,\ldots,K)$, is an asymptotically unbiased estimator of the mean expected log-likelihood (Bozdogan 1987).

There are at least two major problems associated with the AIC. First, the true model may not in many instances be even vaguely realized and the approximation of equation 2 may not be good. Second, parameterization of candidate models is often limited by sample size. Practicality suggests that ecological processes are likely to be complex beyond our dreams, let alone our ability to model. So, models must form a basis for understanding process, and not necessarily causation. To this end, we can construct models that are informative and minimize the need of parameterizing every potential cause of a single effect. Thus, we have practical limits of model parameterization that extend well beyond the limits of sample size. Certainly, the fewer data we have, the less complex our models should be.

Traditionally, the AIC is employed when time series are considered stationary processes and residuals are independent and identically distributed. The latter of these assumptions is often violated with Markov processes and the former is violated with particular processes like exponential growth. So, for this study, we can expect that our employment of the AIC and other IC forms is not optimal, yet our techniques should address, albeit indirectly, just how robust IC forms are to these violations.

Still, we are left with the philosophically unsettling issue that our models may be miles away from the "model" (process) that generated our data. At the bottom, however, if our true model is of extraordinary order, i.e. K is very large, and the models that we propose can mimic the process that created the data, then our parameters are a *practical* realization of K-space. In this vein, models do not have to be nested, but may be drawn from distinctly different "regions" of K-space (Takane 1987). This liberal interpretation comes with the warning that overinterpretation of our models will only be misleading and our view of our models' outcome must be as narrow as the parameter space considered. To the end of AIC, we can view the inferences into model choice as attempts to balance the risks of over- and underfitting models that are only crude approximations of an ecologically complex process.

One last question belies proceeding with this study. It is simply, why are there so many different information criteria (IC forms) and which do I use? To this question, I can find no satisfying theoretical or practical answer. Two authors have derived estimations of negentropy independently of Akaike. Schwarz (1978) developed a "Bayesian" derivative of AIC, while Hurvich and Tsai (1989) developed a small sample derivative. Each of these authors has their significant theoretical reasons for motivating different approaches, consistency (asymptotically correct choice of k as $n \rightarrow \infty$) of the IC form being at the center of their arguments. Two additional authors, Bozdogan (1987) and Hannan and Quinn (1979), have developed IC forms that are both consistent and contain *ad-hoc* parameter penalty properties. Bozdogan added 1 to the parameter penalty portion of Schwarz's IC form for the explicit purpose of conservative model selection (Bozdogan 1987). Hannan and Quinn modified Schwarz's form with the intention that an investigator could adjust the parameter penalty to be appropriate for the length of the time series under consideration (Tong 1990).

I will give the equations of the IC forms mentioned above under "Methods." For now, let it suffice to say that there appear to be numerous reasons to be inclined to choose one IC form or another, but ultimately, the best reason for any research is the set of goals maintained by the researcher. For this study, I consider the question empirical, and will set out to test which IC form is best according to criteria of measurement that are important to this study. I will develop these measures fully under "Methods."

Levels Of Inference

We can now proceed with the fundamental task of model selection using IC forms, with what I term "biologically meaningful" models. I will apply the results of the

Monte Carlo simulations to the time series that were utilized for the study. By this I mean that I will identify the model that best fits the time series in question. What will result will be density dependent and density independent model assignments to 115 of the 117 time series that I used for the Monte Carlo simulations, plus 6 additional time series collected after the simulations. As a footnote, the reason that 2 of the 117 time series will not be given model assignments is that their origin is unknown. This is immaterial for the simulations but critical for making inferences about the population described by the time series.

My aim is to describe density independent and dependent process *as modeled*, and not to suggest cause, so any ecological inferences made regarding the "form" of density dependence or independence must be left only to description. To reemphasize, it is important that we do not fool ourselves into assigning cause to these models. Any correlates of models with ecological process will simply be made to guide us toward better description of density dependence and independence and not imply cause of the emergence of density dependence and independence from living populations.

Some natural choices of properties to consider are the phylogenetic associations of the organisms, whether they undergo large scale migrations, what climatic zone is preferred for reproduction and/or primary residency, and whether they are herbivore or carnivore. Again, these assignments will be heuristic, serving only to guide and stretch our thinking toward the goal of *seeking* causation; and not intended to be rigorous or to serve as nails in a coffin.

Application

I will consider and conclude with what the most direct application is for this study. This will be for conservation biology and the use of biological models in population viability analysis. A population viability analysis (PVA) uses population models to yield probability statements on time to extinction or lower thresholds of concern for a given population. These estimates are strongly dependent on the model used to make population projections. Unfortunately, the choice of a population model has often been left to the best guess of the investigators or, by historical default, to a version of the logistic equation. Model misidentification may lead to gross under or over estimates of the expected time to extinction. For example, Stacey and Taper (1992), Dennis et al. (1991), Ginzburg et al. (1990), and Soule′ (1986) have shown that if density independent models are used to forecast population persistence, these led to significantly more pessimistic forecasts than density dependent population models. So, by basing model selection on an objective criterion such as AIC, one can make more rigorous statements on both the projected times to extinction, *and* the probability of the outcome. Model identification with IC methods takes a large portion of the guess work out of the PVA process.

Methods

Simulations

To study the performance of IC forms in identifying population models, I utilized Monte Carlo methodology. I will describe the big view of this approach before detailing the population models, parameter estimation, or IC forms used. I simply wish to provide a birds-eye-view of the machinery of simulation before dismantling the machine.

This study depended on time series observations from natural populations. Without belaboring the effort of finding time series, I began with 117 available time series of different lengths and spanning 4 taxonomic classes.

For this study, each time series represented a single observation or trajectory. The reason for this is that each time series yielded only a single set of parameter estimates for parametric models and a single empirical probability distribution for the nonparametric IIDD model. So I began with 117 sets of parameter estimates and 117 empirical probability distributions to run simulations with.

Let us first consider in brief the general parametric model, parameters to estimate, and the IIDD model, then we can move on to the operation of the Monte Carlo loop.

The general population model that I used will be fully developed in this section under "Models." However, I will present this model here so that a basic understanding of the simulation process can be made. Below, equation 3 represents the general model

$$X_{t+1} - X_t = a + b\left[f\left(N_t\right)\right]^{\theta} + \varepsilon_t, \tag{3}$$

where $X = \ln(N)$ and $\overline{X_{t+1} - X_t} = \vec{y}$, a vector of the per-capita-abundance growth rate. The parameter $\varepsilon_t = \sigma Z$ is a stochastic noise term that I shall explain below. For the Gompertz model, $f\left(N_t\right) = X_t$ and for all other parametric models, $f\left(N_t\right) = N_t$. Each set of parameter estimates included "σ^2" the population variance on the per capita abundance growth rate, the intrinsic rate of increase *"a,"* the density dependence parameter *"b,"* and "θ", the parameter for the curvature of density dependence. Coefficient *"a"* was estimated for the exponential model by taking $mean(\bar{y})$. Coefficients *"a"* and *"b"* were estimated for both the Ricker and the Gompertz models using standard regression methods. It was only necessary to estimate "θ" for the θ-Ricker model. This was done by minimizing the sum of squared error $\sum\left(\bar{y}_{observed} - \hat{\bar{y}}\right)^2$ for all possible values of *"a"* and *"b"* over a set range of values of "θ".

The IIDD model will be detailed later. For now, it is sufficient to say that an empirical distribution for $\vec{X}$ was calculated over a range of minus and plus 4 standard deviations from the mean value of $\vec{X}$ in each original time series. The "shape" of the distribution was based on a kernel density estimator that essentially calculated the probability density in 500 "yields," or equally spaced regions of the X axis, based on the relative density of the original observations along the X axis. So, for all 117 time series, I calculated a set of 500 probability densities that represented particular X values over a range of 8 standard deviations. These were my 117 IIDD model distributions.

For an additive noise component, ε in equation 3, the Box-Mueller transformation was used to convert from uniform random numbers to standard normal random numbers:

$$\varepsilon_t = \sigma Z = \sigma\sqrt{-2 \cdot \ln(rnd(1))} \cdot \cos(2 \cdot \pi \cdot rnd(1)). \qquad (4)$$

The parameter, σ, is the standard deviation of the per-capita-abundance growth rates of the original time series, and $rnd(1)$ is a uniform random number generator in Mathcad PLUS 5.0 (1994) that generates values between 0 and 1.

The time series lengths that I used for simulations were 8, 17, 35, 50, and 100. These lengths were chosen since the shortest of the 117 time series was 8 observations, more than 50 percent were 17 observations, the longest were 39 and 40 observations, so I bracketed those lengths, and length 100 was just a stab at "sufficiently large *n*" after Akaike (mentioned under "Introduction," above). Moreover, most available time series of population data are between 10 and 20 observations, with some that are longer and very few reaching 50 to 100 observations.

Using the estimated parameters, Monte Carlo simulations began with calculating new time series under each population model using the first observation from the original time series as a starting point. This means that for all 117 sets of parameter estimates and empirical IIDD distributions, a new time series of the same length as the original would be generated under the six models employed in the study. The model that generated each new time series was treated as an unknown until after model selection.

For every new time series, a new set of parameters was estimated under each parametric model and a new empirical probability density function was calculated under the IIDD model. Necessary data were then passed to the appropriate likelihood function resulting in a set of 6 likelihood statistics for *each* of the 6 new time series. Before the next step could be taken, the number of parameters needed to be specified for each model. For the random walk model there was 1 parameter (σ^2), 2 for the exponential model (a, σ^2), 3 for the Ricker and Gompertz models (a, b, σ^2), and 4 for the θ-Ricker model (a, b, θ, σ^2). For the IIDD model, the number of "parameters" were specified as the degrees of freedom lost in the calculation of the empirical pdf. I will detail this calculation under

"Population Models" in this section. So for each set of likelihood statistics there was a corresponding set of the number of parameters.

Likelihood statistics and k = *[# of parameters]* were passed, set by set, through each of the five IC forms employed. From each resulting set of six IC statistics, the lowest (equaling the lowest negentropy) was chosen as representative of the model closest to the model that generated the time series. This was then checked against the model *known to have generated the time series.* The results for each IC form were tallied in a matrix that summed results with each loop of the program. This "tally matrix" kept track of the true models that generated the time series and the estimated models that were *identified* as having generated the time series. Each IC form had its own tally matrix.

What resulted from each pass of the Monte Carlo loop was 117 time series generated under each of 6 models evaluated for the model that originated it by five different IC forms. For the five time series lengths above, I ran the Monte Carlo loop 200 times. This means that there were 200 repetitions of the process for all 117 time series, or a total of (200 X 117) = 23,400 repetitions at each time series length. This completed the simulations.

For greater understanding of the details in the above simulations, I will move on to deliberations of the time series involved, the population models, parameter estimations, degrees of freedom for the IIDD model, likelihood models, and IC forms. Following these expositions, I will return to a full description of the tally matrix and the measures that were made to evaluate how well IC forms "performed." Next, I will present the methods used to apply model identification to the original time series. I will reserve the argument used for the employment of these methods until the “Results” section of this paper. With the anticipation of results of these methods in mind, however, I will present methods used to see if there are any associations of population model form and ecological category or process (as introduced under “Introduction - Levels Of Inference”).

Time Series

One hundred seventeen biological time series were used for the simulation portion of this study. Six additional time series were used when I considered ecological processes in association with time series and their respective model identifications. Time series were annual census, index, or densities measured for a number of taxa and by a variety of workers. I have listed all time series below by taxonomic class. Two are of unknown origin: “Sugar1” and “Sugar2,” 8 observations apiece.

Birds. One time series, 13 observations, was used from Scott et al. (1984) on the Hawaiian bird “palila” (*Loxioides balleui*). One time series, 10 observations, was used from Stacey and Taper (1992) on an acorn woodpecker (*Melanerpes formicivorus*) population in Arizona. Thirteen time series, each 9 observations, on North American species of ducks were used from Vickery and Nudds (1984). Two time series used from the breeding bird survey (U.S. Fish and Wildlife Service) were communicated from Brian Dennis; one on Mallards, one on Gadwalls, each 31 observations.

Fish. Two time series, one of spring-run Chinook salmon, another of summer-run Chinook on the Columbia river were communicated from Brian Dennis. Each time series contained 27 observations.

Insects. Sixty-nine time series were used from Wolda and Dennis (1993). These were of cicadellid homopteran species collected over 17 years from light traps on Barro Colorado Island. The list of species was unavailable. One additional time series communicated to me by Brian Dennis is cited in Wolda and Dennis (1993) as a moth (probably *Autographa gamma* [Lepidoptera: Noctuidae]) time series taken from the Czech Republic. All sixteen time series from den Boer and Reddingius (1989) were used. These include winter moth (Lepidoptera: Noctuidae) larvae and adults, pine looper (Lepidoptera: Geometridae) larvae, pupae and adults, garden chafer (Coleoptera: Scarabaeidae) larvae, grey larch bud moth (Lepidoptera) larvae, Spruce budworm (Lepidoptera) larvae, viburnum whitefly (Homoptera: Aleyrodidae) immatures, and *Nevia brevicollis* (Coleoptera: Carabidae) adults. These time series varied in length from 11 to 29 years. One of their time series requires correction. This is the 9th time series in their table 1. The second-to-last observation in the time series is redundant to the observation before it. (In other words, there are two 2's in a row in the series, and there should only be one). Four time series on grasshoppers in Montana (Orthoptera: Acrididae), three with 39 and one with 40 observations, were acquired from Kemp and Dennis (1993, and Kemp, *personal communication*).

Mammals. Two time series on grizzly bear (*Ursus arctos horribilis*) of Yellowstone National Park were used; one, 17 observations, from Dennis and Taper (1994) and the other, 31 observations, from Eberhardt et al. (1986). Three time series on elk (*Cervus elephus*) were used; one, 12 observations, on the northern Yellowstone elk population from Dennis and Taper (1994), and two, 25 and 22 observations on elk in Jackson Hole and Teton National Park, Wyoming, respectively, from Boyce (1989). Peter Goodman communicated seven time series taken from the Mkuzi Game Reserve, Natal. These were one time series, 16 observations, on hippopotamus, and five time series, 10 observations, on impala, wildebeest, zebra, warthog, nyala, and duiker.

Model Dimension And Parameter Space

In order to speak the language of models we should take note of two basic concepts of parametric modeling. These concepts, dimension and parameter space, are inseparable, but parameter space can be thought of as the limit of dimension. That is, a single dimension can be visualized as a point or a line. If a point, then the parameter value that is that point describes the dimension. But if a dimension is characterized by a range, then that range is the parameter space of the dimension and there are many, if not infinite, parameter values associated with the dimension. Dimensions can be independent or they can interact. The interaction of two dimensions creates a plane, and the interaction of three or more dimensions creates a volume. Both planes and volumes are hyperparametric spaces, since interaction of any unique combination of the involved parameters results in a single outcome in space.

With statistical population models, the dimension of the model is often referred to as the order of the model. This is easily seen upon inspection of the model by counting the number of parameters. Nested models and models of similar form often overlap in parameter space, even though their axes may be distinct.

Indeed, in the region(s) of overlap, one model might describe an outcome as well as another. Nested models are a good case-in-point. If, for example, we have an observation in 3-space that falls close to a plane (that is a subset of that space) created by two of the parameters, a model of lower order that "nests" the two parameters that form the plane might provide a good approximation of the observation. So, low-dimension models may do quite well at describing high-dimension phenomena, depending on the intersection of parameter spaces. Furthermore, if non-nested models have overlapping parameter spaces, then one model may be as descriptive as the other for outcomes in intersecting space.

So, as I inspect the population models that I used, below, I will refer to the order of the model and the nature of overlap that one model has with others. Ultimately, we will use the IC forms to determine what order a model is and the goodness-of-fit approximation of a particular model.

The above discussion will lend us some perspective on some potential limitations and strengths of model identification by IC forms. This should also temper our view with respect to certain performance measures of IC forms. We should expect that IC forms will err in model identification, but the question becomes, can we do consistently better than expected? I will discuss these issues further after consideration of population models, parameter estimates, time series simulation, and likelihood forms.

Population Models

All parametric models follow the form of the general model, below.

$$N_{t+1} = N_t \cdot \exp\left(a \cdot \left(1 - \left(\frac{N_t}{K} \right)^{\theta} \right) + \varepsilon_t \right) \tag{5}$$

If we multiply through by a, and take the natural logarithm of both sides, then equation 5 takes on the form of equation 3. The difference that we readily observe is that the term $-a/K = b$. What this implies is that K, the carrying capacity, interacts with the intrinsic rate of increase to produce a density dependent term or effect. If b is negative, then we realize the classic case of negative density dependence. This is where the population experiences negative feedback with respect to changes in population size or density away from K. The strength of this action is realized in the exponent θ. This parameter is the curvature of density dependence. This is linear for $\theta = 1$. For $\theta > 1$, the result is a proportionally greater density dependent effect (convex curvilinear relationship of density dependence with population size), and the opposite for $0 < \theta < 1$. The curvature parameter can also be <1. Under this circumstance, density dependence is considered weak.

I refer readers to equation 4 for the detail of the noise term ε_t. The variance, σ^2, is specific to each model and will be detailed under "Parameter Estimation."

Next, let us consider the nested population models and how one can reduce to another. Following this we can have a look at the Gompertz model and then the IIDD model.

Of the four nested models, the θ-Ricker model is the most flexible. I will present this model first and demonstrate how the other three nested forms are simplifications. The θ-Ricker model is identical to equation 5, but I will present it with the parameter *b* included, below:

$$N_{t+1} = N_t \cdot \exp\left(a + bN_t{}^{\theta} + \sigma Z_t\right) \qquad (6)$$

Each parameter can assume a range of values. If, however, $\theta = 1$, then the θ-Ricker model reduces to the Ricker model, equation 7 below, which is an exponential form of the logistic model.

$$N_{t+1} = N_t \cdot \exp\left(a + bN_t + \sigma Z_t\right) \qquad (7)$$

The Ricker model is the simplest form of density dependent model in the nested set. If, however, there is no density dependent effect, i.e. $b = 0$, then equations 6 and 7, reduce to an exponential growth model with noise.

$$N_{t+1} = N_t \cdot \exp\left(a + \sigma Z_t\right) \qquad (8)$$

The parameter *a* is often referred to as the “drift” factor of the exponential model. The implication is that individuals in a population have no mechanism of response to population density. So for the population there is a property of positive growth response, no matter what its density is. This amounts to little more than a random walk with individuals in the population maintaining a constant average rate of reproduction - an implausible biological scenario. If *a* is presumed zero, then equation 8 reduces to a random walk with no drift factor, equation 9, below.

$$N_{t+1} = N_t \cdot \exp(\sigma Z_t) \qquad (9)$$

This concludes the exposition of nested forms.

The Gompertz model is superficially a strange case of the θ-Ricker model. It is not a nested form, however, since parameters do not span the same dimension. Expressed in a form similar to the θ-Ricker model, the Gompertz model takes on the form of equation 10, below.

$$N_{t+1} = N_t \cdot \exp\left(a + bN_t^{\left[\frac{\ln(X_t)}{\ln(N_t)}\right]} + \sigma Z_t \right) \qquad (10)$$

It is easy to see that if $X = \ln(N)$, then equation 10 reduces to

$$N_{t+1} = N_t \cdot \exp(a + bX_t + \sigma Z_t), \qquad (11)$$

which is how the Gompertz model is normally expressed in exponential form. Equation 10 makes clear why the Gompertz model is not a nested form of the θ-Ricker. For the Gompertz model, the "parameter" θ is a function of a ratio dependent on population size and not an independently derived quantity, as it is for the θ-Ricker model.

The IIDD distribution required a vastly different approach than parametric models. Recall, the idea was to calculate the probability of observations falling into one of 500 equally spaced points along an axis that represented all possible observations. Given that such an axis is theoretically infinite, I restricted the span of this axis to plus and minus 4 standard deviations from the mean of *X*. So, all of what is presented herein are the peculiarities of calculating an empirical probability distribution from data, where $X = \ln(N)$.

To begin, I needed to specify a yield width. This I did following the methods of Silverman (1986), presented in equation 12 , below.

$$h = 0.9 \cdot A \cdot n^{-\frac{1}{5}} \tag{12}$$

The scalar 0.9 and the exponent are arbitrary (Silverman 1986), and "*A*" is the minimum of either the interquartile distance of the time series (*iqd*) divided by 1.34, i.e. $\left({}^{iqd}\!/_{1.34}\right)$, or the standard deviation of $\vec{X}$, and *n* is the number of observations in the time series.

Next, I used Silverman's (1986) Gaussian kernel density estimator, equation 13 below, to estimate the empirical probability density. Silverman's equation is

$$f(x, X, h) = \sum_{t=0}^{n-1} \frac{k\left(\frac{x_i - X_t}{h}\right)}{t \cdot h}, \tag{13}$$

where x_i are the middles of all 500 yields for which one is calculating the probability density, *h* is the window width, and *k* is the Gaussian kernel, equation 14, as given by Silverman (1986):

$$k(v) = \frac{e^{-\left(\frac{v^2}{2}\right)}}{\sqrt{2 \cdot \pi}}: \tag{14}$$

Thus, the probabilities were calculated as the average estimated probabilities of each of 500 yield middles covering 4 standard deviations (or *iqd* if smaller) on either side of the mean of *X*.

Parameter Estimation

The clearest approach to detailing parameter estimation for each model will be to start with the one commonality, i.e. the form of the variance, then move to a description of the simplest nested form, the random walk model, and sequentially through these to the most complicated, the θ-Ricker. I will follow these descriptions with parameter estimates for the Gompertz model, and end with a "degrees of freedom" estimate for the IIDD model.

The estimated variance for all the parametric models is given by

$$\hat{\sigma}^2 = \frac{1}{q} \cdot \sum_{t=1}^{q} \left(y_t - E(y_t)\right)^2. \qquad (15)$$

where q are the number of transitions in the time series, $y = X_{t+1} - X_t$, and the expression for the expectation of y is unique to the form of the model. For descriptions of the variances of parametric forms, I will only give the expectation of y.

The random walk model has only the estimation of the variance as its sole parameter. The expected growth rate for the random walk model, at any population size, is zero. So, $E(y_t) = 0$ and the variance reduces to a simple variance calculation on y.

For the exponential model, the estimated parameter a is $\hat{\bar{y}}$, the average of the observed per-unit-abundance growth rates. So the variance for the time series is on the observed per-unit-abundance growth rates where $E(y_t) = \bar{y} \cong \hat{\bar{y}}$.

For the Ricker model, the parameters were estimated using regression techniques. The relationship of parameters and time series was simply $y_t = a + bN_t$. The intrinsic rate of increase and density dependence parameters were estimated by $\hat{a} = \text{intercept}(\vec{y}, \vec{N})$, and by $\hat{b} = \text{slope}(\vec{y}, \vec{N})$, respectively. The variance was estimated using equation 15 where $E(y_t) = \hat{\vec{y}}$, where $\hat{\vec{y}}$ are the fitted values of y.

Parameter estimations for the Gompertz model were the same as those for the Ricker model but where $\hat{a} = \text{intercept}(\vec{y}, \vec{X})$, and by $\hat{b} = slope(\vec{y}, \vec{X})$.

The θ-Ricker model presented some unique challenges to model fitting. Since the curvature parameter is not directly estimable with regression techniques, I had to improvise with numerical methods. I first selected a range of "reasonable" values for θ. Stacey and Taper (1992) observed a value of $\theta = 11$, so I considered values of θ that spanned $\theta = \{-12, -11.8, -11.6, \ldots, 12\}$. For each value of θ, I exponentiated all observations in the time series. If we let $N' = N^{\theta}$ for all values of θ, I then calculated a fitted y vector, i.e. $\hat{\vec{y}}'$, for each N'. From there, the task was simply to perform the regression $y' = a + bN'$, and estimate the parameters a, b, and σ the same way that I did for the Ricker model. Next, I would explore all sum of squared deviations of observed y from $\hat{\vec{y}}'$, and choose as my vector of fitted values of y, the vector from $\hat{\vec{y}}'$ that minimized the sum of squares. The θ value that corresponded with this vector of fitted values of y would be my chosen θ value.

The IIDD model, as we have seen, has no parameters to estimate. We can, however, derive an approximation of the "degrees of freedom" lost for estimating this model. This approximation can substitute for the parameter penalty (k = # of free parameters) that is found in the various IC forms. The degrees of freedom were calculated following Hastie and Tibshirani (1990) as

$$p = \sum_{t} \frac{\frac{1}{\sqrt{2 \cdot \pi}}}{\sum_{n} k\left(\frac{\ln(N)_n - \ln(N)_t}{h}\right)}, \tag{16}$$

where h is that of equation 12 and k is equation 14. As the number of observations and/or variance in the time series increased, the estimated degrees of freedom also increased.

Variance for the IIDD distribution was given by the sample variance

$$\hat{\sigma}^{2} = \frac{1}{n-1} \cdot \sum_{t=0}^{n-1} \left(X_t - \overline{X}\right)^2. \tag{17}$$

Time Series Simulation

Models and parameter estimates from the original time series were used to generate new time series for Monte Carlo simulations. This simply involved using the first observation from each original time series as a starting point for each Monte Carlo simulation. I then generated 117 new time series under each model. For parametric models, this was a matter of building the model sequentially with the effect of lag time equal to 1. For the IIDD model, however, new time series were generated by taking random draws from any of the 500 points of the empirical distribution weighted by the probability density at each point, with the exception that the first observation was the first of the original time series. (As mentioned under "Simulations," these time series were then pushed through the entire Monte Carlo loop as if they were complete unknowns).

Likelihood Calculations

For all of the parametric models, the joint likelihood calculations were for the transitions $\vec{y} = X_{t+1} - X_t$. Equation 3 indicates that $\vec{y}$ are considered normally distributed with mean $X_{t+1} - X_t + a + bf\left(N_t\right)^{\theta}$ and variance σ^2. The likelihood equation for each parametric model is therefore the product of normal pdf's in the form

$$L(y,\sigma) = \prod_{t=1}^{q} p\left(y_t | E(y_t)\right) = \left(\sigma^2 2\pi\right)^{-q/2} \exp\left(-\frac{1}{2\sigma^2} \sum_{t=1}^{q} \left(y_t - E(y_t)\right)^2 \right), \tag{18}$$

where q is the number of transitions in the time series. Upon taking the natural log of equation 18, the likelihood reduces to a more manageable form, found in equation 19, below.

$$lnL(y,\sigma) = -\frac{q}{2} \cdot \ln(2\pi\sigma^2) - \frac{1}{2\sigma} \sum_{t=1}^{q} \left(y_t - E(y_t)\right)^2 \tag{19}$$

The IIDD model's likelihood is simply a product of the likelihoods (estimated probabilities) for each of the observations X found in the time series. When expressed as a log likelihood, the product naturally becomes the sum

$$lnL(X,h) = \sum_{t=1}^{n} \ln\left[f\left(X_t, \vec{X}, h\right)\right], \tag{20}$$

where *f* is equation 13.

Information Criteria

Five information criteria (IC forms) were selected for study due only to their prevalence in recent literature. At the foundation of all information criteria is the Akaike information criterion (AIC), as discussed above. After presenting the AIC, I will review the other IC forms chronologically. These will be the Bayesian AIC (BIC; Schwarz 1978), Hannan and Quinn's AIC (AIChq; Hannan and Quinn 1978), the consistent AIC (CAIC; Bozdogan 1987), and Hurvich and Tsai's AIC (AICc; Hurvich and Tsai 1989). Since the underlying theory of the IC forms was outlined in the "Introduction," I shall only remark on the nuts-and-bolts of each form.

For each IC form, $\ln\left(L\left(y,\sigma\right)\right)$, is the natural-log-likelihood as given in equations 19 and 20. The variable *p* is the number of parameters for each of the parametric models or the estimated degrees of freedom (equation 16) for the IIDD model, and *obs* is the number of observations in the time series.

The IC forms are calculated as follows:

$$AIC = -2\ln\left(L\left(y,\sigma\right)\right) + 2p \tag{21}$$

$$BIC = -2\ln\left(L\left(y,\sigma\right)\right) + \ln\left(obs\right)p \tag{22}$$

$$AIChq = -2\ln\left(L\left(y,\sigma\right)\right) + \left(2c\ln\left(\ln\left(obs\right)\right)\right)p \tag{23}$$

$$CAIC = -2\ln(L(y,\sigma)) + (\ln(obs)+1)p \qquad (24)$$

$$AICc = -2\ln(L(y,\sigma)) + 2p + \left(\frac{2(p+1)(p+2)}{obs-p-2}\right). \qquad (25)$$

Note that all of the forms are estimations of twice the negentropy. Also, the second term of each IC form includes a constant multiplied by a variable number of parameters. The difference between the IC forms is in the constant. The most unusual of the forms is the AICc of Hurvich and Tsai. Note, however, that the first two terms are simply the AIC. The third term is a second order correction for bias in the calculation of twice the negentropy, made for small samples (i.e. < 50 observations).

The design, according to each of the authors, is for each form to provide an asymptotically unbiased measure of twice the negentropy. Akaike addressed this feature by providing a large sample measure. Schwartz, in a Bayesian approach, was more concerned with providing such a measure over a wider range of sample sizes, so he scaled the constant to the number of observations. Neither Hannan and Quinn nor Bozdogan were satisfied with the outcomes that the derivations of Akaike or Schwartz provided and chose to take ad-hoc measures that addressed the issue of conservatism in model selection. This issue is simply that it is better to err on the side of lower order than higher order models when constructing a model for predictive power. So, as is obvious, Bozdogan (CAIC) simply added 1 to the constant of Schwarz's BIC. Hannan and Quinn (AIChq) reduced the magnitude of the sample size contribution to the BIC's constant by twice taking the logarithm of the observations, but they multiplied it by 2 and an arbitrary scalar "*c*," where $1 \le c \le 4$.

These observations provide some fodder for a few intuitive remarks. The constant in Schwarz's estimation of the parameter penalty provides a compelling reason for not testing time series with fewer observations that 8: simply, $\ln(8) \approx 2$, i.e. Akaike's large sample estimation for this term. This means, right-off-the-bat, that the constant associated with the parameter penalty for estimation of the order of a model exceeds the information content of the time series with fewer than 8 observations.

These last remarks are an intuitive leap of faith in Schwartz and Akaike. Pressing the point, however, I suggest that this gives us some insight into how we can expect the IC forms to behave. To repeat, the claim that all of the authors of IC forms make is that their form is asymptotically unbiased (biases approach zero as $q \to \infty$). However, all of the IC forms are based on large samples, when considering biological time series. Even the AICc is built for far bigger time series than are generally available for biological populations. Nevertheless, when time series have few observations, we can see that the parameter penalty term fails to do its job and the IC form should be expected to do no better than make a random selection of model order (let alone correct model). Thus, for samples of an unknown small size, we should expect each of the IC forms to behave aberrantly.

This discussion begs the question of how well we can expect the IC form to do at model order selection at the lengths of time series chosen for study (recall, 8, 17, 35, 50, 100). Based on the above arguments, I would suggest that we could not expect the IC forms to do well at model order selection, or other rigorous criteria, with time series of 35 or less. But now we need a variety of rigorous performance measurements to see if this prediction bears out.

IC Performance Measures And The Tally Matrix

Using the Monte Carlo simulation technique, the final output was a matrix for each IC form that tallied the identifications of population models and sorted these by the models known to have generated time series. The least confusing way to present this is with a generic "tally matrix." Figure 1 is one example of a tally matrix. Each row in the matrix sums to 23,400, which is the number of repetitions in the Monte Carlo simulations. The rows are also representative of the origin of the models that initially created the time series. These are the "true" models. Columns represent the way that an IC form identified models. Thus, as described under "Simulations" every row and column has one cell that matches the true model with the identified model.

The cells that match the true model with the identified model are deemed "correct selections" and are on the diagonal of Figure 1. If an IC form were simply "selecting" models at random, then the proportionalized expected value of correct selections would be 3,900/23,000 = 0.167.

One might argue that correct selections are all that there is to correct model identification. Yet, IC forms are blind to what is being "fed" to them, and so there is a rejection structure to the tally matrix. The "correct rejections" are calculated column by column using the cells that are not on the diagonal of the tally matrix. So, each column has five off-diagonal cells that are incorrect selections. Correct rejections are calculated

Figure 1. An example of a tally matrix. (Numerical values are from the tally matrix of AICc for time series length 50 [also see Appendix 2]). For a complete description of the tally matrix and measures made on it, see text in "Methods."

Identified Model						***True Model***
Random Walk	**Exponential**	**Ricker**	**Gompertz**	**IIDD dist. Model**	**θ-Ricker**	
11,745	1,272	3,895	4,491	2	1,995	**RW**
9,293	3,115	4,696	4,185	8	2,103	**Exp**
426	172	15,802	4,759	655	1,586	**Rick**
466	11	4,656	15,137	1,508	1,622	**Gomp**
0	0	215	7,962	14,806	417	**IIDD**
489	108	5,761	7,027	832	9,183	**θ-Rick**

as the average $\left[23{,}400-\dfrac{\sum \text{off- diagonal cells}}{5}\right]\Big/23{,}400$. The expected value for correct rejections was 0.833.

These measures, correct selections and rejections, can be more or less concordant in magnitude. This is to say that the discrepancy of the two measures may be small, in which case they would be very concordant measures, or they could be large and discordant. The value of such a measure is to see if an IC form is blanketly selecting or rejecting population models of one kind or another. Put on the level of proportion, the measure that I developed for "concordance" was

$1-\left|\text{correct selections} - \text{correct rejections}\right|/23{,}000$. The expected value for concordance was 0.333.

Despite the concordance of the correct selection and rejection measures, the two were averaged to give the "correct model identifications" that an IC form makes. Naturally, the expected value for this measure is 0.50.

Clearly, there is another concern with correct identifications. This is whether the model identified is even in the right model *family*. The two model families that I refer to are the density independent and density dependent model families. So, if a time series was generated from a density independent model, it is best identified as a density independent process, even if the correct model was not identified. The same goes for time series generated by density dependent models. Correct model family identification is a measure of the proportion of selections that were made in the right model family over the entire tally matrix. The expected value of correct model family identifications is 0.50.

The final measure of performance that I calculated on the tally matrix was "average order bias," or simply for convenience, "order bias." Order bias was used to calculate if an IC form identified, on average, models that were of higher or lower order than the one that generated a time series. In other words, how well did an IC form correctly select the order of the model that generated it? The IIDD model required that I do this on-the-fly during simulation, so I omitted it. However, the tally matrix contains all of the information necessary to make this measurement for all of the parametric models.

For the given set of population models, the lowest order was 1 (random walk) and the highest was 4 (θ-Ricker). Thus, the potential for overfitting and underfitting ranged as integer values from -3 to 3, depending on the model that generated the time series and the model that was subsequently identified. For example, an order bias of -3 was observed when a time series generated by a θ-Ricker model was identified as a random walk, and the opposite for a value of 3. Note that the order bias is zero for selection of a Gompertz model when a Ricker model generated the time series, or vice-versa. Since the order bias measure is an average over all simulations, it could be any non-integer or integer value in the range. Zero is the expected value for order bias, given no tendency for an IC form to underfit or overfit the order of all models.

Animals, Ecological Associations, And Population Model Form

Organisms on which the original time series observations were made were classified into four broadly descriptive but ecologically relevant categories. These were the taxonomic class level taxa, the climatic zone in which organisms spend the preponderance of their time, their trophic status, and their migratory status. These categorical variables were used to view the relationships of ecology and population model selected as best-fit for the original time series.

The taxonomic categories were, as listed above, birds, fish, insects, and mammals. I made four very large categories for climatic associations; these were tropical-subtropical, temperate, subarctic, and arctic. However, I only employed time series from the former two climatic categories. Trophic status was limited simply to those categories of herbivore and carnivore. All animals were considered either migratory or non-migratory. The latter category included organisms like winter moth that are far-reaching dispersers but have no return trip.

The categorization of organisms is intended to be heuristic and therefore no statistical rigor followed the categorization. A much larger study is required for valid analyses, for instance ANOVA, to be employed. However, the probability of assigning the most likely population model to have generated the original time series, *i.e. if they had been generated by these models*, was assigned to each time series from the results of the simulations

For reasons that will be developed fully under "Results: Tallied Results And Summary Statistics," I used the BIC to make final selections of population model for all of the various time series. The probability of correctly assigning the best fit population model was available for the BIC (and each IC form) at time series lengths 8, 17, 35, 50, and 100. Probabilities for intermediate time series lengths were estimated utilizing Mathcad PLUS 5.0 (1994) linear spline interpolation procedure. For estimates of the errors associated with these probabilities, one should be conservative and choose the error associated with the closest known value for a shorter time series.

Results

Parameter Space

The coverage of parameter space was a tricky issue since I was only considering those spaces defined by the parameters estimated from the original time series. This was done to lend an air of realism to the simulations, but it could be seen as an unnecessary limitation on the broader validity of the study. Thus, I must digress and consider limitations.

We must consider a catch-22. One might begin a study like this one by arbitrarily defining parameter space for every model. This might be an educated guess that restricts the range of parameters in each model and considers every possible combination of parameters in space. The outcome of this approach may be closer to thorough than the way the present study was initiated. The intensity of the search that one conducts, however, is arbitrary since there is an infinitum of combinations, and ultimately there is no guarantee of realism. So, one may argue that the current approach and a more thorough approach be melded so that time series be used to estimate a "reasonable" parameter space which can then be thoroughly explored. This would be a plausible approach, except that not all parameter estimates yielded for each model are reasonable, thus the catch-22. I will illustrate with what follows.

Consider table 12, Appendix 1, parameters for the θ-Ricker model. Some of the estimates for the θ-Ricker model parameter *"b"* are clearly extraordinary, showing unbelievable positive density dependence. A concomitant inspection of Ricker model parameter "b," table 13, Appendix 1, makes the consideration of a θ-Ricker model an obvious error for time series with extraordinarily positive *"b"*. Also, the reader should take note in table 12 of the time series that had the θ-Ricker model as the "best-fit" model. Most values for *"b"* were near zero and negative while associated values of *"a"* and "θ" were negative. In the cases where *"b"* was positive, both *"a"* and "θ" were negative. So, we are back to where we left off: ultimately one must judge what is "reasonable" parameter space. In the end, and without attempting a huge and exhaustive study, I decided to let the time series speak for themselves and rely on the parameter combinations that were estimated as the basis for all simulations. These combinations for each population model over all time series are presented in tables 12 through 15, Appendix 1.

I have plotted parameters *"a"* versus *"b"* for the θ-Ricker, Ricker, and Gompertz models in Figures 2 through 4, Appendix 1. Figure 1 for the θ-Ricker model has excluded 40 parameter combinations where the value of *"b"* exceeded 12. I deem these values for *"b"* completely unreasonable by my own inspection. In reality, values of *"b"* greater than 1 are probably outrageous given that *"b"* is almost never less than -1 in situations of negative density dependence.

Figure 4, Appendix 1, simply depicts the estimated parameter *"a"* for all time series under the exponential model. Note that few of the values approach $|0.3|$. This is one demonstration of my claims (that I made in the "Introduction") that populations generally do not exhibit exponential growth as an emergent property of population growth and decline, and that any calculation of an exponential model approximates a random walk when stochastic effects are included. Additionally, note that no IC form chose the exponential model as "best-fit" for any time series.

Table 16, Appendix 1, presents the calculated degrees of freedom or effective number of parameters for estimating the IIDD model for each time series. This table is presented only to show that the effective parameter penalties, necessary for IC calculation, were generally in the same range as the number of parameters found in the parametric models.

A final remark is that many simulations were done from parameter combinations that may have been "unreasonable." So, what we have, ultimately, is a view of how well IC forms do in a much broader range of parameter space than may be truly applicable. I wish to emphasize that this is likely to have yielded conservative results when considering IC performance measures.

Tallied Results And Summary Statistics

By far the most informative results are the tally matrices. These are presented in Appendix 2. The reader should refer to Figure 1 for direct interpretation of the tally matrices. Also in Appendix 2 are a number of summary results that are derived for each IC form and simulated time series lengths 8, 17, 35, 50, and 100. These latter statistics are specific to each population model for each IC form. Below, I summarize the average performance for each IC form.

Density Independent And Dependent Model Family Identifications. Model family identifications, recall, represent the average of correctly selected models with respect to whether they are density independent or density dependent. The expected value for this measure under conditions of random selection is 50 percent. Table 1 shows that for all time series lengths, every IC form does better than expectation, within twice the standard error.

The AIC delivered the lowest percent correct model family identifications in every case, except for time series (TS) of length 8. The AIChq and CAIC consistently delivered the highest values for model family identifications. The AICc and BIC performed with intermediate results. The AICc started out on the high end and ended on the low end with correct model family identifications for the various TS lengths. The BIC, however, did consistently well.

Table 1. Average percent correct model family identification and percent standard errors (s.d.) over all IC forms and simulated time series lengths. See text for comments.

IC Form	Time Series Length (TSL)				
	TSL = 8	**TSL = 17**	**TSL = 35**	**TSL = 50**	**TSL = 100**
AICc	63.600	71.691	73.495	72.886	77.717
(s.d.)	5.773	6.016	5.655	5.242	4.929
CAIC	67.779	79.330	88.715	91.853	93.878
(s.d.)	5.563	5.137	4.224	3.839	3.658
AIC	68.723	78.029	78.046	76.270	72.483
(s.d.)	4.282	5.629	5.495	5.156	4.911
BIC	63.590	77.290	86.656	89.674	92.002
(s.d.)	5.847	5.696	4.770	4.302	4.134
AIChq	64.979	78.873	88.354	91.165	92.900
(s.d.)	5.783	5.359	4.442	4.054	3.906

Take note that some of the IC forms performed worse with time series of greater length. This might be expected for the AICc since it was derived for time series analysis with limited data (fewer than 50 observations), and for the AIC since the parameter penalty does not increase with sample size. Please note that the difference in the AIC's correct model family identifications for TS lengths 50 and 100 is not significant.

The CAIC, BIC, and AIChq all improved in correct model family identifications from TS length 8 through TS length 100. The improvement tended to level out between TS lengths 50 and 100.

Model Order Identification. The correct average order identification over all models provides us with a clear view of how well IC forms are living up to what they are designed to do; i.e. select the order of an autoregressive model. Results are presented in Table 2, below. The expected value of this measure, if IC forms were selecting population models at random, is 23.333 percent.

Since this measure requires a weighting of the measurements of model selection, I have not calculated a standard error for it. As a ballpark estimate, refer to the respective standard errors for correct model selection, given in the next section below.

Table 2. Average percent correct model order selection for each IC form over all models. See text for comments.

IC Form	Time Series Length (TSL)				
	TSL = 8	**TSL = 17**	**TSL = 35**	**TSL = 50**	**TSL = 100**
AICc	27.489	46.761	54.961	56.491	57.086
CAIC	34.868	43.869	55.986	60.275	64.601
AIC	36.216	45.704	52.544	54.485	55.900
BIC	36.089	46.413	57.170	60.954	65.026
AIChq	36.080	45.246	56.789	60.854	64.976

Most notably, all IC forms improved for this measure *and* did better than expectation for all TS lengths. This was especially surprising for shorter time series lengths. In this vein it was odd that the AICc did not do well except for TS length 17, where it did best of all, since it was designed for short time series. The IC form that delivered the most consistent good results was the BIC.

Parenthetically, we will note in measures presented herein that the BIC is a very consistently impressive form for how well it stands up to all performance measures, even if it does not always deliver the best results (as with correct model family identification, above).

Model Selection. Under conditions of random selection of models, the expected value for average correct model selection was 16.667 percent. Table 3 shows the observed values for this measure. All IC forms performed significantly better than expectation beyond two standard errors from the average. Even at TS length 8, all IC forms performed remarkably well. As TS length increased all IC forms improved with respect to this measure, but the BIC and AIChq appeared to do the best, with no significant difference between them.

Table 3. Average percent correct model selection and percent standard errors (s.d.) over all IC forms and simulated time series lengths. See text for comments.

IC Form	Time Series Length (TSL)				
	TSL = 8	**TSL = 17**	**TSL = 35**	**TSL = 50**	**TSL = 100**
AICc	25.534	37.195	46.346	49.707	54.350
(s.d.)	0.953	1.484	1.505	1.451	1.415
CAIC	26.382	36.964	48.951	54.087	54.672
(s.d.)	1.332	1.347	1.205	1.113	1.047
AIC	24.668	34.979	44.104	47.936	53.860
(s.d.)	1.373	1.540	1.538	1.483	1.423
BIC	25.136	36.954	49.034	54.195	56.294
(s.d.)	1.471	1.480	1.330	1.217	1.149
AIChq	25.849	37.177	49.224	54.364	55.722
(s.d.)	1.394	1.394	1.241	1.164	1.088

Model Rejection. Under conditions of random selection of models, the expected value for average correct model rejection was 83.333 percent. Table 4 shows the observed values for this measure. As with correct model selection, all IC forms did better than expected, but not significantly so at TS length 8. Improvement in correct model rejection was small as TS length grew, none-the-less it was enough to be significant. The

BIC and AIChq, again appeared to do best. Based on current results, it would be best to avoid rejecting a population model if observations are few.

Table 4. Average percent correct model rejection and percent standard errors (s.d.) over all IC forms and simulated time series lengths. See text for comments.

IC Form	Time Series Length (TSL)				
	TSL = 8	**TSL = 17**	**TSL = 35**	**TSL = 50**	**TSL = 100**
AICc	85.107	87.439	89.269	89.941	90.870
(s.d.)	0.915	1.027	0.978	0.924	0.903
CAIC	85.276	87.393	89.790	90.817	90.934
(s.d.)	1.140	0.957	0.767	0.659	0.630
AIC	84.938	86.996	88.821	89.587	90.772
(s.d.)	1.213	1.132	1.035	0.965	0.917
BIC	85.027	87.391	89.807	90.839	91.259
(s.d.)	1.222	1.050	0.841	0.730	0.710
AIChq	85.170	87.435	89.845	90.873	91.144
(s.d.)	1.211	0.987	0.793	0.686	0.678

Model Identification. Recall, correct model identification is an average of the previous two measures of correct model selection and rejection. Therefore, the expected value of this measure is 50 percent. Significance of the results, table 5, should be tempered by the results for the individual measures that contribute to correct model identification. For example, even though correct model identification is significantly greater than expectation for all TS lengths (i.e., averages minus two standard errors exceeds expectation), the results of the measure of correct model rejection casts into doubt the significance for the current measure at TS length 8.

Naturally, the BIC and AIChq can be identified as having done the best (since they did so with correct model selections and rejections).

One can see that the results of correct model selection and rejection can differ

Table 5. Average percent correct model identification and percent standard errors (s.d.) over all IC forms and simulated time series lengths. See text for comments.

IC Form	Time Series Length (TSL)				
	TSL = 8	**TSL = 17**	**TSL = 35**	**TSL = 50**	**TSL = 100**
AICc	55.321	62.317	67.808	69.824	72.610
(s.d.)	0.934	1.276	1.269	1.216	1.187
CAIC	55.829	62.179	69.371	72.452	72.803
(s.d.)	1.239	1.168	1.010	0.914	0.864
AIC	54.813	60.987	66.426	68.762	72.316
(s.d.)	1.295	1.351	1.311	1.251	1.197
BIC	55.082	62.172	69.421	72.517	73.776
(s.d.)	1.323	1.283	1.113	1.003	0.955
AIChq	55.509	62.306	69.535	72.618	73.433
(s.d.)	1.306	1.208	1.042	0.956	0.907

widely within an IC form (refer to tables 3 and 4). How greatly these measures differ is a good indicator of how well IC forms are doing at model selection relative to rejection, even if rejection is no better than expectation. We can consider this relationship in the next section on "concordance."

Concordance. Recall, concordance is the measure of how close or even correct model selection and rejection are. Overall, correct model rejection rose more slowly than correct model selection. so rises in concordance with time series length were largely due to improvements in model selection.

Concordance may range from 0 to 100 percent with the expected value being 33.333 percent. Anything less than expectation implies that an IC form is not selecting as well as it should be with respect to how it is rejecting, or vice-versa. A low concordance is a good sign that the model identifications at a particular time series length are not to be trusted.

The values for average (over all population models) percent concordance for each IC form and TS length are presented in table 6, below.

Table 6. Average percent concordance over all IC forms and simulated time series lengths. See text for comments.

IC Form	Time Series Length (TSL)				
	TSL = 8	**TSL = 17**	**TSL = 35**	**TSL = 50**	**TSL = 100**
AICc	28.898	49.756	57.077	59.765	63.480
CAIC	41.105	44.171	53.352	57.634	57.647
AIC	39.750	47.983	55.283	58.349	63.088
BIC	40.109	49.563	59.195	61.920	61.554
AIChq	40.679	48.263	55.607	59.468	59.870

Concordance rose for all IC forms with TS length, except for an insignificant dip at TS length 100 for the BIC. Only the AICc showed a remarkably low concordance at TS length 8. However, it is my intuition that all IC forms show suspiciously low concordance at that TS length. The message is simple: steer clear of very short time series.

Order Bias. This final measure of IC performance turns out to be very illuminating. As was mentioned in the "Methods," order bias gives us a measure of how much, on average, an IC form underestimated or overestimated the order of a model. Since our lowest order form is considered 1 and our highest 4, the order bias can range from -3 to 3, and will not necessarily be an integer. This measure provides us with the vital information of whether IC forms are living up to their built-in conservative nature, asymptotic nature, or other expected features discussed in "Methods."

In table 7, below, negative values of the order bias imply that the IC form was on average underfitting models by that many parameters; this is considered conservative. Positive values in table 7 imply the opposite of the previous statement.

Table 7. Average order bias over all IC forms and simulated time series lengths. See text for comments.

IC Form	Time Series Length (TSL)				
	TSL = 8	**TSL = 17**	**TSL = 35**	**TSL = 50**	**TSL = 100**
AICc	-1.7398	-0.7049	0.0894	0.2942	0.6065
CAIC	-0.7891	-1.1810	-1.0746	-1.0129	-0.8784
AIC	0.0055	0.1289	0.4031	0.4960	0.6984
BIC	0.0342	-0.5805	-0.6659	-0.6986	-0.6641
AIChq	-0.1920	-0.9500	-0.9291	-0.8899	-0.7593

The BIC and AICc order bias changed sign as TS length increased. An aberrant calculation of the order bias for TS length 8 is not unexpected given the behavior of the above performance measures. Indeed, what appears to be happening is that the IC forms are nearly randomly assigning to the various population models at TS length 8. This is substantiated by the way that the order bias tends to level off for all of the IC forms, except the AICc, from TS length 17 through 100. In fact, at TS length 100, order bias for the CAIC, BIC, and AIChq move back toward zero from that of TS length 50. The order bias for the AIC and the AICc, on the other hand, tend to worsen from TS length 50 to 100. The AIC overfits the order of a model and this tendency increases with TS length. The AICcunderfits at low TS length and overfits at high TS length, making it unattractive as an IC of choice.

Of the CAIC, BIC, and AIChq, the BIC has the least order bias and is conservative, with some indication of asymptotic behavior as TS length increases. It is greatly for this reason and the reasons that the other performance measures for the BIC are relatively strong that I employed this IC form in the next phase of this study, below.

Animals, Ecological Associations, And Population Model Form

For reasons outlined in the previous section, I used the BIC to identify population models that best fit the original time series. These results are presented in table 8, below. Presented with these results are the estimated probabilities of correct model and model family identifications, given that the time series arose from processes that could be described by the set of population models employed. P-values other than those associated with time series lengths 8, 17, 35, 50, and 100 were estimated with the linear spline interpolation method of Mathcad PLUS 5.0 (see Methods for details). Latin binomials are provided where necessary and available from sources cited in Methods, otherwise, common names are provided.

Table 8. Population model selection by the BIC for all original time series. Organisms are listed by taxonomic order, then by species, with a number assigned to each for reference. Tables 10-13 are cross-indexed with the reference numbers. Population models are assigned the following numbers: 0) random walk, 1) exponential, 2) Ricker, 3) Gompertz, 4) stationary distribution, 5) θ-Ricker. The "Est. P-val., Models" is the probability of correct model assignment, given the choice of models. "Est. P-val., Model Family" is the same for the model family. See text for further explanation.

Ref. No.	Organism Name	Observations in TS	Population Model	Est. P-val., Models	Est. P-val., Model Family
	Birds				
0	Acorn Woodpecker	10	4	0.5677	0.6696
24	Palila	13	0	0.5923	0.7178
32	Mallard	9	2	0.5593	0.6528

Table 8, continued.

	Birds				
33	American Widgeon	9	4	0.5593	0.6528
34	Gadwall	9	4	0.5593	0.6528
35	European Teal	9	4	0.5593	0.6528
36	Blue-winged Teal	9	5	0.5593	0.6528
37	Pintail	9	4	0.5593	0.6528
38	Northern Shoveler	9	5	0.5593	0.6528
39	Lesser Scaup	9	2	0.5593	0.6528
40	Redhead	9	3	0.5593	0.6528
41	Canvas-back	9	4	0.5593	0.6528
42	Bufflehead	9	4	0.5593	0.6528
43	Ruddy Duck	9	4	0.5593	0.6528
44	Ring-necked Duck	9	5	0.5593	0.6528
17	Gadwall, bbs	31	0	0.6836	0.8580
22	Mallard, bbs	31	0	0.6836	0.8580
	Fish				
29	Spring Chinook Salmon	27	2	0.6709	0.8459
31	Summer Chinook Salmon	27	0	0.6709	0.8459
	Insects				
1	Winter moth, larvae	19	0	0.6342	0.7944
2	Winter moth, adults	19	2	0.6342	0.7944
3	Pine looper, larvae, August	15	4	0.6077	0.7471
4	Pine looper, larvae, September	15	4	0.6077	0.7471
5	Pine looper, pupae	14	4	0.6001	0.7329
6	Pine looper, adults	14	4	0.6001	0.7329
7	Pine looper, pupae, Staffordshire, UK	13	2	0.5923	0.7178
8	Garden chafer, Ambleside, UK	29	0	0.6776	0.8527
9	Garden chafer, Keswick, UK	18	3	0.6282	0.7842
10	Grey larch bud moth, larvae, Switzerland	20	0	0.6399	0.8037
11	Spruce budworm, larvae, Plot G4	15	0	0.6077	0.7471
12	Spruce budworm, larvae, Plot G5	14	0	0.6001	0.7329
13	Viburnum whitefly,	12	2	0.5843	0.7022

	Population 1				
14	Viburnum whitefly, Population 2	12	0	0.5843	0.7022
15	Viburnum whitefly, Population 3	12	3	0.5843	0.7022
16	*Nebria brevicollis* (Coleoptera: Carabidae)	11	0	0.5761	0.6861
46 - 114	69 populations of Homoptera: Cicindellidae	17	Model & Count 0 = 18 1 = 0 2 = 13 3 = 20 4 = 13 5 = 5	0.6217	0.7729
25	Grasshoppers	38	3	0.7015	0.8728
26	Grasshoppers	39	3	0.7038	0.8749
27	Grasshoppers	39	3	0.7038	0.8749
28	Grasshoppers	40	2	0.7061	0.8770
	Mammals				
18	Grizzly bear, Yellowstone Park	17	0	0.6217	0.7729
19	Grizzly bear, Yellowstone Park	31	0	0.6836	0.8580
45	Roosevelt elk, Yellowstone	12	5	0.5843	0.7022
20	Roosevelt elk, Jackson Hole	25	3	0.6634	0.8372
21	Roosevelt elk, Teton Park	22	4	0.6502	0.8194
116	Hippopotamus	16	0	0.6149	0.7605
117	Impala	10	4	0.5677	0.6696
118	Wildebeest	10	0	0.5677	0.6696
119	Zebra	10	0	0.5677	0.6696
120	Warthog	10	4	0.5677	0.6696
121	Nyala	10	4	0.5677	0.6696
122	Duiker	10	0	0.5677	0.6696

Two time series of length 8 that were used in the simulations were not evaluated for the above since their origin was not known.

From table 8, we can see how many time series were identified as density independent and density dependent and evaluate this with time series length. This provides us with a view of how TS length may influence the identification of density dependence. Previous authors indicate that this may be an important consideration when evaluating the power of tests for density dependence (Holyoak 1993, Slade 1977, Vickery and Nudds 1984). These results are presented in table 9, below.

Table 9. Ecological status of organisms studied. Columns are length of animal time series used in this analysis, the number of each length analyzed, and the respective numbers identified as either density dependent or density independent.

Time Series Length	Number Analyzed	Number Density Dependent	Number Density Independent.
9	13	13	0
10	7	4	3
11	1	0	1
12	4	3	1
13	2	1	1
14	3	2	1
15	3	2	1
16	1	0	1
17	70	51	19
18	1	1	0
19	2	1	1
20	1	0	1
22	1	1	0
25	1	1	0
27	2	1	1
29	1	0	1
31	3	0	3
38	1	1	0
39	2	2	0
40	1	1	0

Inspection of table 9 shows that there is no noticeable trend of identification of density dependence among time series of increasing length. A bit counter-intuitively, this is somewhat reassuring since it implies that identification of density dependence using the methods developed is not strongly dependent on time series length. This is not to say that the reliability (P-value) is not influenced by time series length, as is obvious from table 8.

Since the emergence of density dependence is what is expected from healthy animal populations, past authors have often been concerned with the percent density dependence identified from a set of time series. These percentages have often been less than 50 percent (Bulmer 1975, Slade 1977, Vickery and Nudds 1984, Pollard 1987). In this study, 70.83 percent of the original time series were identified as density dependent. What is more, we can assign a P-value to *both* the recognition of density dependence and the selection of a population model from a given set.

The above results can be taken many directions, however for this study, I considered the association of model form and gross scale ecological variables. For clarity, the ecological "status" of the organisms considered are given in table 10, below.

Table 10. Taxon is the taxonomic class that the organism belongs to; 1 is bird, 2 is fish, 3 is insect, and 4 is mammal. Climatic Zone is the zone that the organism spends most of their life in; 1 is tropical-subtropical, 2 is temperate (There were no subarctic or arctic animals). Trophic levels are 1 for herbivores, 2 for carnivores. All animals are classified as either non-migrants (1) or migrants (2).

Ref. No.	Organism Name	Taxon	Climatic Zone	Trophic Level	Migratory Status
	Birds				
0	Acorn Woodpecker	1	2	2	1
24	Palila	1	2	1	1

Table 10, continued.

Ref. No.	Organism Name	Taxon	Climatic Zone	Trophic Level	Migratory Status
32	Mallard	1	2	2	2
33	American Widgeon	1	2	2	2
34	Gadwall	1	2	2	2
35	European Teal	1	2	2	2
36	Blue-winged Teal	1	2	2	2
37	Pintail	1	2	2	2
38	Northern Shoveler	1	2	2	2
39	Lesser Scaup	1	2	2	2
40	Redhead	1	2	2	2
41	Canvas-back	1	2	2	2
42	Bufflehead	1	2	2	2
43	Ruddy Duck	1	2	2	2
44	Ring-necked Duck	1	2	2	2
17	Gadwall, bbs	1	2	2	2
22	Mallard, bbs	1	2	2	2
	Fish				
29	Spring Chinook Salmon	2	2	2	2
31	Summer Chinook Salmon	2	2	2	2
	Insects				
1	Winter moth, larvae	3	2	1	1
2	Winter moth, adults	3	2	1	1
3	Pine looper, larvae, August	3	2	1	1
4	Pine looper, larvae, September	3	2	1	1
5	Pine looper, pupae	3	2	1	1
6	Pine looper, adults	3	2	1	1
7	Pine looper, pupae, Staffordshire, UK	3	2	1	1
8	Garden chafer, Ambleside, UK	3	2	1	1
9	Garden chafer, Keswick, UK	3	2	1	1
10	Grey larch bud moth, larvae, Switzerland	3	2	1	1
11	Spruce budworm, larvae, Plot G4	3	2	1	1
12	Spruce budworm, larvae, Plot G5	3	2	1	1
13	Viburnum whitefly, Population 1	3	2	1	1
14	Viburnum whitefly,	3	2	1	1

	Population 2				
15	Viburnum whitefly, Population 3	3	2	1	1
16	Nebria brevicollis (Coleoptera: Carabidae)	3	2	2	1
46 - 114	69 populations of Homoptera: Cicindellidae	3	1	1	1
25	Grasshoppers	3	2	1	1
26	Grasshoppers	3	2	1	1
27	Grasshoppers	3	2	1	1
28	Grasshoppers	3	2	1	1
	Mammals				
18	Grizzly bear, Yellowstone Park	4	2	2	1
19	Grizzly bear, Yellowstone Park	4	2	2	1
45	Roosevelt elk, Yellowstone	4	2	1	2
20	Roosevelt elk, Jackson Hole	4	2	1	2
21	Roosevelt elk, Teton Park	4	2	1	2
116	Hippopotamus	4	1	1	1
117	Impala	4	1	1	2
118	Wildebeest	4	1	1	2
119	Zebra	4	1	1	2
120	Warthog	4	1	1	1
121	Nyala	4	1	1	2
122	Duiker	4	1		2

Now, considering each of the ecological variables and their respective subcategories, the percentages of time series that were associated with each population model are presented in table 11, below.

Across all taxa, the percentages of time series associated with each population model were 28.69% random walk, 0% exponential, 16.39% Ricker, 21.31% Gompertz, 8.20% θ-Ricker and 25.41% IIDD model.

Table 11. Percentages of population models selected in each ecological subcategory. Each ecological category comprises 100 percent of the time series.

Ecological Category	Ecological Subcategory	Population Model					
		Random Walk	Expo-nential	Ricker	Gompertz	IIDD	θ-Ricker
Taxon	Birds	17.65	0	11.77	5.88	52.94	11.77
	Fish	50.00	0	50.00	0	0	0
	Mammals	27.78	0	18.89	26.67	20.00	6.67
	Insects	50.00	0	0	8.33	33.33	8.33
Trophic Status	Herbivore	29.00	0	17.00	25.00	22.00	7.00
	Carnivore	28.57	0	14.29	4.76	42.86	9.52
Climatic Zone	Trop.-Subtrop.	28.95	0	17.11	25.00	21.05	7.90
	Temperate	28.89	0	15.56	15.56	33.33	6.67
Migratory Status	Migratory	30.21	0	17.71	25.00	20.83	6.25
	Non-mig.	24.00	0	12.00	8.00	44.00	12.00

One final comparison of interest is how many of the Vickery and Nudds (1984) time series on ducks (reference numbers 32-44, table 8) were identified as showing density dependence, and the same for the insect time series from den Boer and Reddingius (1989, [reference numbers 1-16, table 8]). Both sets of time series have been repeatedly tested for density dependence utilizing a variety of tests (den Boer and Reddingius 1989 for the latter, Pollard et al. 1987, and Vickery and Nudds 1991 for the former). Vickery and Nudds found that the time series from Louisiana, all length 9, were too short to be reliably tested with all tests preceding their own test and study. With their own test, den Boer and Reddingius found only one of their 16 time series to show any sign of having been produced by a density dependent process.

My study paints a different picture with *all* of Vickery and Nudds's time series being identified as having come from a density dependent process, and 9 of 16 of den Boer and Reddingius's time series as the same (including the one that they identified [reference number 4, table 8]). The advantage is not only a relative form of density dependence but also a probability of that form and a probability of correct model family association.

Discussion

I wish to lead the reader through a brief conclusion of results as they may be consequential to the validity of the methods employed in this study. Following these comments, I will revisit the issue of parameter space. I will make some recommendations for the use of information criteria in studies of population model selection and studies on density dependence. Following this, I will review the outcome of ecological associations made with the animal time series using Schwarz's BIC. Lastly, I will make some recommendations for how conservation biology may benefit from these techniques, and take the liberty of making comments on the ramifications of this study with respect to ecology and evolution.

Validity Of Method

This study provides a clear answer to the question of whether we can employ well understood and documented statistical methods to decide which model, from a set of population models, best describes an animal time series process. We are also provided a clear view of some of the limitations of using IC forms as a tool for selecting a population model from a reasonable set. I found the AIC and other IC forms performed significantly better than expectation under virtually every condition tested, even with short time series.

Furthermore, they appeared to be robust to violations of assumptions that the Markov property of population time series may create.

We have stepped out of the realm of hypothesis testing regarding the parameter *"b,"* as so many previous studies have endeavored. The validity of the techniques employed comes from a direct measurement of the probability of model family and model identification and the associated errors of those measurements. These measures are tempered by the other judicial measures of average order bias (order bias) and concordance.

The strength of the Monte Carlo test is demonstrated by the clear purveyance of information provided by the order bias statistic. For example, the AIC tends to overestimate the order of a model, as expected, while the CAIC, BIC, and AIChq all tend to underestimate the order of a model, also as expected (Bozdogan 1987, Tong 1991). The Monte Carlo methods gave empirical validation to the expectations of theory. Moreover, the generality of the theory was substantiated with models that were not of the traditional genre of time series analysis.

Of the generalities that I must highlight, the issue of time series length and the employment of these techniques must be in the forefront. Clearly from the results regarding every IC form, the outcomes of model family and model identification are not reliable for time series length 8. And, if left to conservatism, I must remark the same about time series length (TS length) 17, although the property of order bias appeared to show relatively regular behavior at TS length 17 when compared to other TS lengths.

From my results, it would be imprudent to expect IC forms to do their job at TS lengths <17.

I believe also, it is important to reemphasize that a set of "candidate" models may be wholly inadequate as descriptors of a time series. However, if subjected to the analysis above, a model from the set *will* be deemed "best-fit" by an IC form, no matter its inadequacy. Thus, it is important for an investigator to know up-front just how limited or appropriate his or her models are for describing time series processes. As I discussed in "Methods, Model Dimension And Parameter Space," recognition of model limitations should not daunt an investigator, unless the models must be deemed clearly inappropriate.

The exponential model is a clear case-in-point as a model that is inappropriate for investigation of density dependence and independence. Although Pollard et al. (1987) recommend the use of the exponential model as the null hypothesis for standard tests for density dependence, it is clear from results of this study that the stochastic exponential model amounts to little more than an overparameterized random walk. The poor performance of IC forms with identification of the exponential model is attributable to the fact that almost all of the error associated with its identification was its misidentification as a random walk. Additionally, the exponential model parameter *"a"* for virtually every time series was near zero, which implies a random walk. Therefore, I strongly recommend the exclusion of the exponential model in future studies of density dependence and recommend the random walk as an appropriate density independent form.

Among remarkable outcomes is the seamless quality with which IC forms treat non-nested models. There appears to be no particular preference in selecting or rejecting the Gompertz or IIDD models when considered along with the θ-Ricker nested model forms, or vice-versa. The use of the nonparametric IIDD model provides the most innovative step in consideration of density dependent forms. We can now recognize the presence of density dependence in a time series without attempting to apply restrictions of parametric form. This may prove to free the minds of researchers who wish to make the simple inference of whether a population is displaying patterns of density dependence or density independence.

Parameter Space, Revisited

A number of comments ancillary to the issue of parameter space have been commented on above. It is clear that the coverage of parameter space was adequate for this study and generalizable for similar studies. However, more sophisticated models might be appropriate for population studies. Specifically, models that incorporate higher order lags will address the issue of iteroparity that is often a concern of workers in this area of ecology. These models will have more parameters and be more complicated to interpret with respect to their parameter space.

With higher order lags comes a loss of degrees of freedom, i.e. the number of transitions in the time series drops to $n - lag$. So, the minimum length of time series that can be considered for rational population model choice will necessarily increase. Thus, there may be practical limitations as to the number of lags built into models and how highly parameterized one may wish to make them. The insight here, however, is that an investigator must decide up-front what the useful limitations are of the degree and lag of models in a chosen set.

Recommendations

From a combination of performance measures associated with a particular time series length (or particular set of time series of varying lengths) we can decide which of the IC forms we might wish to employ for any given circumstance. The circumstance may be governed by statistical practicality or by a policy issue that is concerned with how conservatively the order of a model is chosen. Certainly, one must consider the various performance measures of each IC form and the set of models that are being considered before selection of an IC form.

For this study, as remarked in "Results," the BIC proved most useful for model identification for the given set of time series. For animal population time series this may be generally applicable, unless one is after greater conservativism in which case the CAIC or AIChq would prove useful. The AIChq might be the most useful form overall *if a researcher adjusts the constant* "c" *to optimize the outcome* for his or her time series. This is clearly an empirical question and, to be answered, would require a similar study to the present varying *"c"* over each likelihood statistic used to calculate the AIChq.

The AIC and AICc are the least conservative IC forms. For this reason, it is unlikely that either would be desirable in studies of population biology. Additionally, the relatively low model family identifications of the AIC and AICc for long time series makes these forms undesirable. The cause of their relatively poor performances cannot be assigned, but clearly noted.

There may be some motivation to use more than one IC form when making multiple levels of inference. For example, at time series length 35 there may be significant motivation to employ the AIChq for model family identification but use the BIC for model identifications. This is because the AIChq has high and almost identical model family measures (for density independence and density dependence) while the BIC has equally high or higher model identification but also better concordance of selection and rejection measures than the AIChq. Every such case must be carefully evaluated, but the notion of employing multiple IC forms for different measures or time series lengths is a matter of practicality.

Ecological Associations

A large number of time series from the taxa birds and mammals were identified as showing density dependent patterns. This is initially surprising because of the expected presence of higher order lags in iteroparous organisms, which tend to mask the influence of density dependence when trying to assess it with lag-1 models. It may be that if we considered models with higher time lags that identification would be even higher than observed above. Yet, it may be that the greater part of density dependent effects in populations are experienced with lag 1. The individual organism considered should be the focus of concern for more specific research.

Insects can often have rather ephemeral or unpredictable associations with particular localities or even regions. Factors that influence their abundance are not well understood for the vast majority of species. The clarity of issues involving semelparity of insect populations is not great. For example, many insects are multivoltine, or semivoltine, or iteroparous. Thus, the result that 50 percent of the insect species came up density independent is not too surprising. We need to be as cautious of our selection of appropriate models for insects as we are for birds and mammals.

There were simply not enough fish time series to draw any conclusions. We should, however, be mindful of the same issues regarding fish as we are regarding birds, mammals, and insects.

Other life history characteristics may be well worth the concern of a researcher. For example, Vickery and Nudds (1984) were concerned with the expectation that diving ducks show more density dependence than dabbling ducks, due to the influence on duck populations of the permanence of respective habitats. In such a case, not only is the presence or absence of density dependence important, but also the form. Whereas all duck populations may display density dependence, those with less permanence may display a weaker form. In sum, the myriad of life history characteristics and their model associations may lead us to a greater understanding of why density dependence and independence emerges from populations.

By convention, more highly migratory organisms are more likely to have their time series identified as density independent. However, most of the time series of migratory organisms in this study were identified as density dependent (76%). This was about the same as the outcome for migratory organisms. This has the flavor that migration may not be the right consideration when it comes to density dependence and its emergence in animal populations.

The high degree of correlation between my categorization of climatic zone of preference and migratory status made the expectation of the prevalence of density dependence roughly the same for the former category as with the latter. This expectation proved to be true, therefore making it difficult to remark on the prevalence of density dependence due to climatic zone association. We may expect with more exact studies that the more sedentary and localized a population may be, the more likely the effects of density dependence are to be *detected.*

There are no compelling reasons to expect higher incidences of density dependence among herbivores than carnivores, or vice-versa, with the exception that it may be more difficult to measure population numbers of carnivores. If carnivore populations are displaying density dependence, then a consistent measurement error in both directions of "actual" would likely increase the likelihood of detecting density dependence since it may increase the magnitude of the parameter *"b."* Aside from this sampling anomaly, we can expect herbivores and carnivores to show the same incidence of density dependence; indeed they did in the time series of this study.

Applications In Conservation Biology

The area of primary interest for the application of these techniques is population viability analysis. As remarked in the introduction, the outcomes of a population viability analysis (PVA) are the estimated time to extinction of a biotic population, an associated probability of time to extinction, and a lower threshold of population viability. Density dependent population models deliver far more liberal estimates for a PVA than density independent population models. All outcomes of a PVA are contingent on the population model employed in the analysis.

Until now in a PVA, there were no ways to make statements of the probability of models employed with some measure of correctness, e.g. correct model identification from a given model set. From this study, we now have a reliable machine to work with as a foundation to first saying a population is displaying density dependence or independence and second implying the correctness of the model ultimately employed. This greatly advances the rigor of PVA studies.

Finally, I wish to reemphasize the utility of rigorously demonstrating the presence or absence of density dependence in a biotic population. This is simply that we have a reliable foundation for stating that a population may or may not be showing signs that it is in imminent danger of extinction. The demonstration of density independence is certainly not a causal explanation for a population's decline but it is the red flag of concern for that decline.

Ecological And Evolutionary Ramifications

I believe it is important to remark on the limitations and meanings of this study when considering either ecological interactions between organisms or evolution. Clearly, this study, in a gross sense, is about the appropriate application of certain statistical techniques in ecology. The only direct meaning that can be found is just how reliable the techniques are. Yet, the phenomena of density dependence and independence in ecology and evolutionary biology beg the application of reliable statistical techniques in order to establish causation for such phenomena arising in biological populations. This is what set me on the path that is almost parenthetical to my central work; i.e. the ecological associations and forms of density dependence and independence.

As was remarked in the introduction, density dependence should logically emerge from biotic populations due to the differential experiences of individuals with impacts on fitness from density-related phenomena. Looking for density dependence is a concern of pure science and conservation. Density independence and dependence are also the most basic ecological properties of populations. All other properties that concern the whole population as the unit of measurement, must be viewed in light of density dependence and independence. Following identification of density dependence and after thoroughly considering its strength and form, only then are we poised to begin the search for cause; prior to identification, cause is not a tractable realm. It is my hope that this study has sufficiently served as the middle ground of this progression.

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APPENDICES

APPENDIX 1

PARAMETER ESTIMATES FROM ORIGINAL TIME SERIES USED FOR SIMULATION (WITH GRAPHICAL ILLUSTRATION)

Table 12: Parameter values calculated for each time series under the θ-Ricker model. If the θ-Ricker model was chosen as the “best fit” for the original time series, then a “YES” appears in the row. Reference numbers are to the species list found in table 8. See text for details.

Parameter “a”	**Parameter “b”**	**Parameter “θ“**	**Was θ-Ricker model chosen as best fit for time series?**	**Reference Number**
0.292	-3.01e-10	5.4		0
2.133	-0.9741	0.2		1
0.2341	-7.13e-6	3.8		2
1.182	-0.1602	0.8		3
1.203	-0.1824	0.8		4
-0.8711	1.637	-0.6		5
-0.9979	1.596	-0.8		6
0.237	-2.27e-7	2.6		7
-8.787e-2	277.2	-3		8
-1.774	2.818	-0.2		9
0.7675	-0.1076	0.4		10
0.5318	-4.823e-2	0.8		11
0.2124	-2.70e-21	12		12
0.2499	1.52e-13	2.4		13
4.711e-2	4.23e+25	-12		14
-122.6	125.1	-0.005		15
-7.068e-2	4.37e+28	-12		16
0.1679	-2.14e-12	3.4		17
5.423e-2	-2.15e-16	8.2		18
-7.36e-3	2.58e+17	-12		19
-0.4581	8.58e+5	-1.6		20
0.3609	-8.38e-9	2.4		21
-7,166e-2	2.19e+17	-4.8		22
-0.8718	16.45	-0.8		23
0.2163	-2.16e-8	2		24
0.8352	-0.2859	0.6		25
-0.9473	1.86	-0.4		26
-0.762	2.949	-0.8		27
0.4325	-3.919e-2	1.2		28
0.4318	-3.62e-10	1.8		29
1.196e-2	-2.89e-42	12		30
0.01196	-2.886e-42	12		31
-0.2731	4.363e+21	-7.2		32

Table 12, continued.

Parameter "a"	Parameter "b"	Parameter "θ"	Was θ-Ricker model chosen as best fit for time series?	Reference Number
0.2652	-1.646e-17	4		33
0.8749	-1.886e-4	2		34
-255.7	260.3	-0.005		35
138.1	-135.6	0.005	YES	36
-0.1081	8.95e+11	-12		37
0.2715	-1.48e-13	6.6	YES	38
-0.4235	79.96	-2		39
0.3517	-4.13e-6	3.8		40
0.3957	-1.004e-4	1.8		41
-1.249	4.246	-0.4		42
-0.5561	125.1	-2.4		43
0.6423	-2.079e-2	1.8	YES	44
2.64	-0.7994	0.6	YES	45
0.8654	-0.1811	1.2		46
-2.335	7.115	-0.2		47
-4.169	9.605	-0.2		48
-2.087	5.61	-0.2		49
0.4827	-5.182e-3	1		50
3.66	-1.653	0.2		51
-1.085	12.02	-0.6		52
0.5901	-1.1e-4	1.2		53
0.2605	-4.82e-04	1.6		54
0.2506	-1.762e-4	1.2		55
-0.384	2.516	-0.6		56
3.169	-1.116	0.2		57
-0.1785	2.65e+14	-12		58
-0.5725	13.79	-0.8		59
0.5784	-8.399e-4	1		60
1.44	-0.1969	0.4		61
125.1	-122.5	0.005		62
4.673	-1.411	0.2		63
0.2798	-5.55e-9	2.8		64
-0.4835	301.4	-1.4		65
-1.151	18.13	-0.6		66
-0.6531	2676	-2		67
3.485	-1.429	0.2		68

Table 12, continued.

Parameter "a"	**Parameter "b"**	**Parameter "θ"**	**Was θ-Ricker model chosen as best fit for time series?**	**Reference Number**
5.497	-2.403	0.2		69
0.8924	-2.66e-2	0.8		70
6.138e-2	1.38e+7	-9		71
0.8963	-8.96e-3	1		72
-0.4988	5.24e+04	-1.6		73
0.4726	-1.271e-4	1.4		74
-0.8086	12.19	-0.8		75
2.409	-0.3247	0.4		76
1.441	-9.947e-2	0.6		77
0.6036	-5.464e-2	0.6		78
-0.9811	10.11	-0.6		79
-1.102	9.422	-0.4		80
8.75e-2	-2.26e-22	9.6		81
-2.714	6.034	-0.2		82
-0.7167	41.87	-0.8		83
0.6425	-2.751e-2	0.6		84
-0.6493	1.868	-1		85
-0.5643	3.154	-1.2	YES	86
-0.5229	5203	-2.2		87
2.579e-2	1.13e+11	-12		88
-0.7284	1057	-1.4		89
0.4164	-9.96e-6	2		90
-0.776	119.8	-1		91
-2.542	21.65	-0.4		92
-0.1984	29.46	-1		93
-6.3e-2	1.84e+6	-3		94
0.1045	-1.40e-38	12		95
-1.536	14.2	-0.4		96
-0.4418	27.33	-1		97
-0.5864	135.4	-1.2		98
0.606	-2.163e-3	1		99
0.8654	-1.094e-2	1		100
1.059	-2.208e-2	0.8		101
1.285	-1.43e-2	0.8		102
4.743	-1.998	0.2		103
0.5035	-2.42e-4	1.8		104

Table 12, continued.

Parameter “a”	Parameter “b”	Parameter “θ“	Was θ-Ricker model chosen as best fit for time series?	Reference Number
2.536	-1.03	0.2		105
1.8	-0.2766	0.4	YES	106
-6.292e-2	6.53e+8	-12		107
-195.2	199.9	-0.005	YES	108
-0.4719	1.32e+4	-2.4		109
-222.6	229.6	-0.005		110
0.317	-6.304e-4	1.4	YES	111
-0.5957	399.1	-1.8		112
3.589	-0.6526	0.4		113
0.6682	-1.127e-4	1.8		114
-0.3465	204.7	-1.4	YES	115
5.888e-2	8.67e+8	-8.2		116

Table 13: Parameter values calculated for each time series under the Ricker model. If the Ricker model was chosen as the “best fit” for the original time series, then a “YES” appears in the row. Reference numbers are to the species list found in table 8. See text for details.

Parameter “a”	Parameter “b”	Was Ricker model chosen as best fit for time series?	Reference Number
1.22711	-0.027791		0
0.38771	-0.005408		1
0.639983	-0.058662	YES	2
0.978031	-0.076828		3
0.996704	-0.089493		4
0.540116	-0.156155		5
0.726557	-0.363122		6
0.62142	-0.030016	YES	7
0.167298	-0.001790		8
-0.000351	-0.004925		9
0.440259	-0.000990		10
0.462217	-0.020515		11
0.411481	-0.045798		12
0.066625	6.65336e-6	YES	13
0.32181	-4.1459e-5		14
0.327903	-0.003536		15

Table 13, continued.

Parameter "a"	**Parameter "b"**	**Was Ricker model chosen as best fit for time series?**	**Reference Number**
0.569292	-0.000669		16
0.402742	-0.000263		17
0.140024	-0.002341		18
0.13482	-0.002845		19
0.850162	-0.000100		20
0.739812	-0.000501		21
0.173622	-2.3166e-5		22
0.78368	-0.013439		23
0.497326	-0.000167		24
0.471542	-0.07474		25
0.321518	-0.052119		26
0.493434	-0.079175		27
0.536153	-0.075084	YES	28
0.775811	-7.32718e-6	YES	29
0.128988	-6.44011e-5		30
0.154367	-2.56357e-6		31
1.60698	-0.024817	YES	32
1.35641	-0.036585		33
0.607696	-0.015859		34
0.950377	-0.044492		35
0.425883	-0.005640		36
1.27055	-0.081450		37
0.8205	-0.052504		38
0.598216	-0.005998	YES	39
1.12535	-0.048742		40
0.796555	-0.069200		41
1.13883	-0.175205		42
1.82159	-0.235043		43
1.01151	-0.280786		44
0.468349	-4.13463e-5		45
0.443706	-0.001355		46
1.21761	-0.010172		47
0.518571	-0.002905		48
0.482687	-0.005182		49
0.680816	-0.009796		50
0.553529	-0.008457		51
0.69437	-0.000550	YES	52

Table 13, continued.

Parameter "a"	Parameter "b"	Was Ricker model chosen as best fit for time series?	Reference Number
0.376736	-0.001936		53
0.299181	-0.000737		54
0.15063	-0.000877		55
0.614867	-0.002651		56
0.523952	-0.004408		57
0.558597	-0.006815		58
0.578437	-0.000839	YES	59
0.387765	-0.001613		60
0.753926	-0.008888		61
0.825299	-0.001862		62
0.401668	-0.001461		63
0.608582	-0.003649		64
1.21529	-0.008862		65
0.768003	-0.007273		66
0.614886	-0.005719		67
0.992311	-0.014508		68
0.75262	-0.009062	YES	69
0.522482	-0.005465		70
0.896261	-0.008960	YES	71
0.718014	-0.000440		72
0.66185	-0.001955	YES	73
0.400659	-0.006821		74
0.99001	-0.006040		75
0.798144	-0.008113	YES	76
0.356449	-0.005995		77
0.550613	-0.007828		78
0.455216	-0.001851		79
0.453546	-0.005343		80
0.504656	-0.007837		81
0.134864	-0.000734		82
0.37086	-0.001810		83
-0.007614	-0.001529		84
-0.041830	-0.000662		85
0.735291	-0.007750		86
0.37962	-0.003721		87
1.07307	-0.005614		88
0.675648	-0.003455	YES	89

Table 13, continued.

Parameter "a"	**Parameter "b"**	**Was Ricker model chosen as best fit for time series?**	**Reference Number**
0.752914	-0.003403		90
0.959129	-0.004117		91
0.273157	-0.001027		92
0.462043	-0.000878		93
0.361331	-0.000644		94
0.567346	-0.001713		95
0.775069	-0.009834		96
0.692268	-0.005289		97
0.605992	-0.002162	YES	98
0.865446	-0.010935	YES	99
0.905763	-0.006946	YES	100
1.10805	-0.003905	YES	101
1.07952	-0.011451		102
0.775549	-0.012141	YES	103
0.587931	-0.005879		104
0.76386	-0.005728		105
0.474267	-0.004768		106
0.646588	-0.004180		107
0.51885	-0.003826		108
0.430617	-0.000653		109
0.47926	-0.005987	YES	110
0.653546	-0.008536		111
1.50352	-0.019561		112
1.09415	-0.009019		113
0.691326	-0.005917		114
-0.188754	-7.46728e-6		115
0.189255	-0.002900		116

Table 14: Parameter values calculated for each time series under the Gompertz model. If the Gompertz model was chosen as the "best fit" for the original time series, then a "YES" appears in the row. Reference numbers are to the species list found in table 8. See text for details.

Parameter "a"	**Parameter "b"**	**Was Gompertz model chosen as best fit for time series?**	**Reference Number**
4.36901	-1.15749		0
1.64016	-0.430887		1
1.13212	-0.525202		2

Table 14, continued.

Parameter "a"	Parameter "b"	Was Gompertz model chosen as best fit for time series?	Reference Number
1.80762	-0.791888		3
1.65557	-0.789747		4
0.613404	-0.543208		5
0.499065	-0.782337		6
1.37219	-0.540344		7
0.852804	-0.221787		8
0.721778	-0.305003	YES	9
0.896973	-0.260459		10
0.686771	-0.295472		11
0.773468	-0.507236		12
-1.52604	0.198121		13
0.58177	-0.055248		14
2.47017	-0.612116	YES	15
3.44508	-0.525621		16
2.25551	-0.308837		17
0.418354	-0.10122		18
0.517884	-0.134733		19
7.29774	-0.807696	YES	20
4.57304	-0.628643		21
1.85839	-0.20842		22
2.72296	-0.706787		23
4.19602	-0.530578		24
0.85573	-0.502327	YES	25
0.642847	-0.37242	YES	26
1.02135	-0.582665	YES	27
0.970741	-0.539691		28
8.56551	-0.743932		29
0.970606	-0.127671		30
1.7231	-0.157557		31
5.8273	-1.41795		32
4.56832	-1.27882		33
2.44511	-0.690649		34
2.49814	-0.829699		35
0.974169	-0.218762		36
3.05674	-1.12663		37
1.59074	-0.596777		38
2.08452	-0.451778		39
2.0699	-0.6715	YES	40

Table 14, continued.

Parameter "a"	Parameter "b"	Was Gompertz model chosen as best fit for time series?	Reference Number
2.27902	-0.96184		41
2.07384	-1.13464		42
2.01513	-1.08241	YES	43
0.93788	-0.80638		44
2.5702	-0.27373		45
2.6138	-0.465547		46
4.08976	-0.954191	YES	47
2.22553	-0.446964	YES	48
2.16127	-0.492662		49
2.74229	-0.701531		50
2.55959	-0.628877	YES	51
4.35377	-0.616934		52
1.02653	-0.210236		53
1.42375	-0.24619		54
1.24322	-0.283112	YES	55
3.31918	-0.642729	YES	56
2.54477	-0.564828		57
2.38495	-0.571936	YES	58
2.4646	-0.392704		59
3.36256	-0.714274		60
2.65934	-0.624793	YES	61
5.56864	-0.933818	YES	62
0.614839	-0.106991		63
3.81129	-0.775613		64
4.25907	-0.897439	YES	65
4.2548	-0.955227		66
2.95126	-0.668874	YES	67
4.56227	-1.10865		68
2.19409	-0.513363		69
1.26128	-0.281949		70
3.83841	-0.872235		71
6.02572	-0.821492	YES	72
3.65549	-0.640364		73
2.07341	-0.554096	YES	74
4.40427	-0.88987	YES	75
3.82759	-0.88942		76
1.38432	-0.357533		77
2.58224	-0.641184	YES	78

Table 14, continued.

Parameter "a"	Parameter "b"	Was Gompertz model chosen as best fit for time series?	Reference Number
2.46584	-0.45606		79
1.94997	-0.454786		80
2.16559	-0.538131	YES	81
1.89136	-0.3647		82
2.08779	-0.40656		83
0.479364	-0.22307		84
0.579108	-0.228915		85
3.9435	-0.888335		86
0.92309	-0.220457		87
5.66635	-1.08298		88
2.6622	-0.509493		89
4.7907	-0.919381		90
5.50425	-1.02268		91
1.51543	-0.288231		92
2.71907	-0.445542		93
1.86618	-0.302403		94
3.67212	-0.652592		95
2.70645	-0.635226		96
3.46749	-0.735047	YES	97
2.17621	-0.393448		98
2.64958	-0.655154		99
2.74551	-0.584321		100
2.65396	-0.474371		101
3.19153	-0.744151	YES	102
2.36432	-0.590741		103
2.1746	-0.485594	YES	104
3.11414	-0.687611	YES	105
2.13801	-0.509514		106
4.64736	-0.97539		107
3.53939	-0.75343		108
6.87135	-1.10955		109
2.4333	-0.57537		110
3.8262	-0.94644		111
5.80274	-1.38043	YES	112
4.458	-0.936961		113
3.03393	-0.646723		114
0.294084	-0.064125		115
0.478801	-0.113187		116

Table 15. Parameter values calculated for each time series under the exponential model. If the exponential model was chosen as the "best fit" for the original time series, then a "YES" appears in the row. Reference numbers are to the species list found in table 8. See text for details.

Parameter "a"	Was Exponential model chosen as best fit for time series?	Reference Number
-0.0265811		0
-0.129514		1
-0.0409417		2
-0.0240337		3
-0.0439829		4
-0.0102716		5
-0.0541551		6
-0.0607998		7
0.0380883		8
-0.173848		9
0.0417933		10
0.0165316		11
0.0172831		12
0.502106		13
0.204953		14
-0.187532		15
0.0876088		16
0.00808817		17
0.0405017		18
0.0122575		19
0.00756899		20
0.00491468		21
-0.0212075		22
0.0626381		23
-0.0744158		24
-0.00427939		25
-0.0176107		26
-0.00566965		27
0.00836929		28
-0.0304965		29
0.0011515		30
-0.0360489		31
-0.0278929		32
-0.0521117		33
0.0327955		34
0.00490259		35

Table 15, continued.

Parameter "a"	**Was Exponential model chosen as best fit for time series?**	**Reference Number**
0.135418		36
0.00806732		37
0.124816		38
0.0890707		39
0.156595		40
0.069952		41
0		42
0		43
0.0638532		44
0.11109		45
-0.0870121		46
0.27604		47
0.115232		48
-0.0808701		49
0.0752483		50
0.0048726		51
0.0684153		52
-0.0794039		53
0.02883		54
-0.0489225		55
0.0399627		56
-0.0505879		57
0.0712952		58
0.12338		59
-0.0322635		60
0.0812052		61
0.0464812		62
0.165938		63
0.0118464		64
0.101892		65
-0.0170808		66
0.0854298		67
-0.0269239		68
0.0978522		69
0.146762		70
0.0400023		71
-0.0149025		72
0.0336221		73
-0.0985572		74

Table 15, continued.

Parameter "a"	**Was Exponential model chosen as best fit for time series?**	**Reference Number**
0.0590857		75
0.161708		76
-0.0160268		77
0.0104409		78
0.00389014		79
-0.0367367		80
-0.0214124		81
-0.115593		82
-0.0654158		83
-0.188471		84
-0.151637		85
-0.0698261		86
0.168414		87
-0.00530622		88
0.0506831		89
0.0751028		90
0.0222002		91
0.0779395		92
0.0781074		93
0.0494142		94
0.0480993		95
0.0755852		96
0.0360264		97
0.089805		98
0.0958706		99
0.149051		100
0.204731		101
0.215624		102
0		103
0.0686633		104
0.0409629		105
0.104145		106
0.0561213		107
-0.0400601		108
-0.182295		109
-0.0715708		110
-0.0272074		111
0.0217692		112
0.021434		113

Table 15, continued.

Parameter "a"	Was Exponential model chosen as best fit for time series?	Reference Number
0.00345938		114
-0.212014		115
0.0962302		116

Table 16: The calculated degrees of freedom or "parameter penalty" for the IIDD model. If the IIDD model was chosen as the "best fit" for the original time series, then a "YES" appears in the row. Reference numbers are to the species list found in table 8. See text for details.

Estimated degrees of freedom (parameterr penalty)	Was IIDD model chosen as best fit for time series?	Reference Number
2.62431	YES	0
3.08348		1
3.26827		2
3.08094	YES	3
3.04215	YES	4
3.1484	YES	5
3.25456	YES	6
3.12098		7
3.58388		8
5.1186		9
2.92625		10
2.82902		11
3.4659		12
4.40379		13
2.65124		14
3.14481		15
2.88325		16
4.3128		17
3.0002		18
4.36918		19
3.87803		20
3.52375	YES	21
4.55545		22
3.07404	YES	23
3.62578		24
6.04693		25
4.86973		26

Table 16, continued.

Estimated degrees of freedom (parameterr penalty)	Was IIDD model chosen as best fit for time series?	Reference Number
4.32371		27
6.25237		28
3.65213		29
2.33753		30
3.73953		31
2.86441		32
3.01694	YES	33
3.48381	YES	34
2.75004	YES	35
2.36693		36
3.04378	YES	37
2.6596		38
2.81975		39
2.84353		40
3.56274	YES	41
2.57295	YES	42
2.21638		43
3.07693		44
2.90197		45
3.15952		46
4.30208		47
4.50492		48
3.53229		49
4.5241	YES	50
3.52778		51
3.16663		52
4.04736		53
3.46851		54
3.54004		55
3.12502		56
4.55132		57
3.65555		58
4.78167		59
4.3272	YES	60
3.09162		61
3.97326		62
3.06948		63
4.96717	YES	64

Table 16, continued.

Estimated degrees of freedom (parameterr penalty)	**Was IIDD model chosen as best fit for time series?**	**Reference Number**
3.53092		65
3.4762	YES	66
4.91469		67
3.64131	YES	68
3.63468		69
3.41277		70
3.22759		71
4.33292		72
3.31506		73
2.98931		74
3.74345		75
5.8747		76
3.11779		77
5.30687		78
5.44468		79
3.42772		80
3.17183		81
3.21676		82
3.04314		83
3.04209		84
3.20434		85
3.18857		86
2.50463		87
3.59256	YES	88
2.89034		89
3.73455		90
3.97715	YES	91
3.38753		92
3.54191		93
3.36971		94
4.14743	YES	95
3.32461	YES	96
3.52308		97
5.02845		98
3.01294		99
3.41041		100
4.89041		101
6.01707		102

Table 16, continued.

Estimated degrees of freedom (parameterr penalty)	**Was IIDD model chosen as best fit for time series?**	**Reference Number**
2.82368		103
3.06046		104
3.13872		105
4.51031		106
5.04023	YES	107
3.27169		108
3.72662	YES	109
3.21966		110
4.49714		111
3.07816		112
3.29181	YES	113
3.73218	YES	114
2.33847		115
3.18571		116

Figure 2. Scatter plot of parameters "a" versus "b" for the θ-Ricker model. Note that many (40) of the combinations do not appear since they exceed, indeed often far exceed, "reasonable" limits. See text for details.

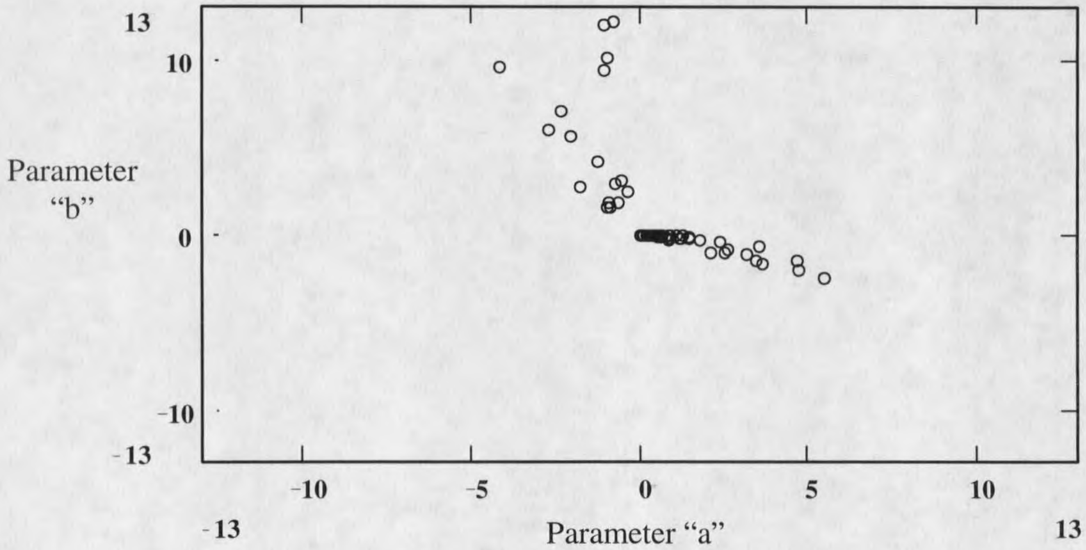


Figure 3. Scatter plot of parameters "a" versus "b" for the Ricker model. See text for details.

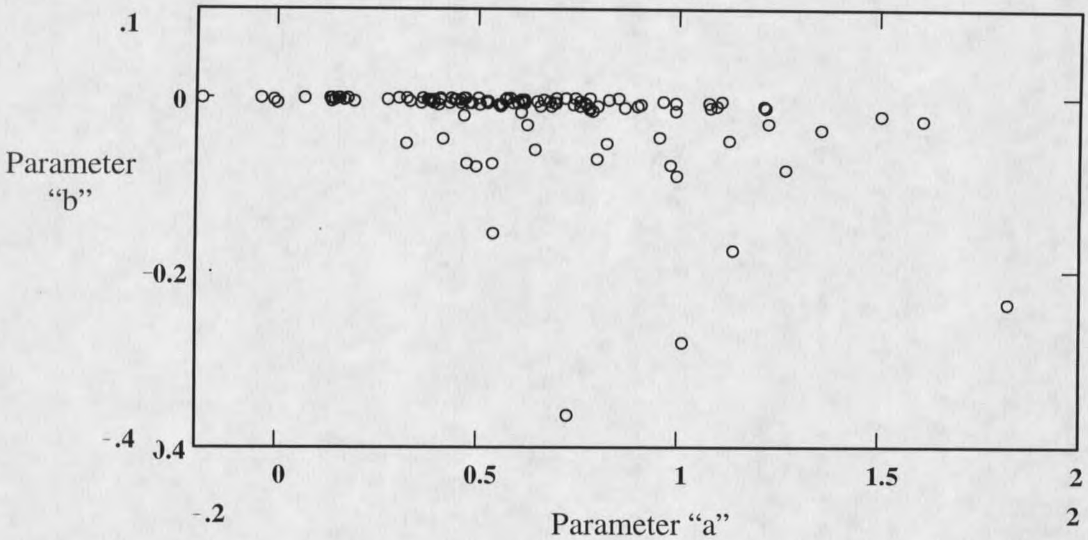


Figure 4. Scatter plot of parameters "a" versus "b" for the Gompertz model. See text for details.

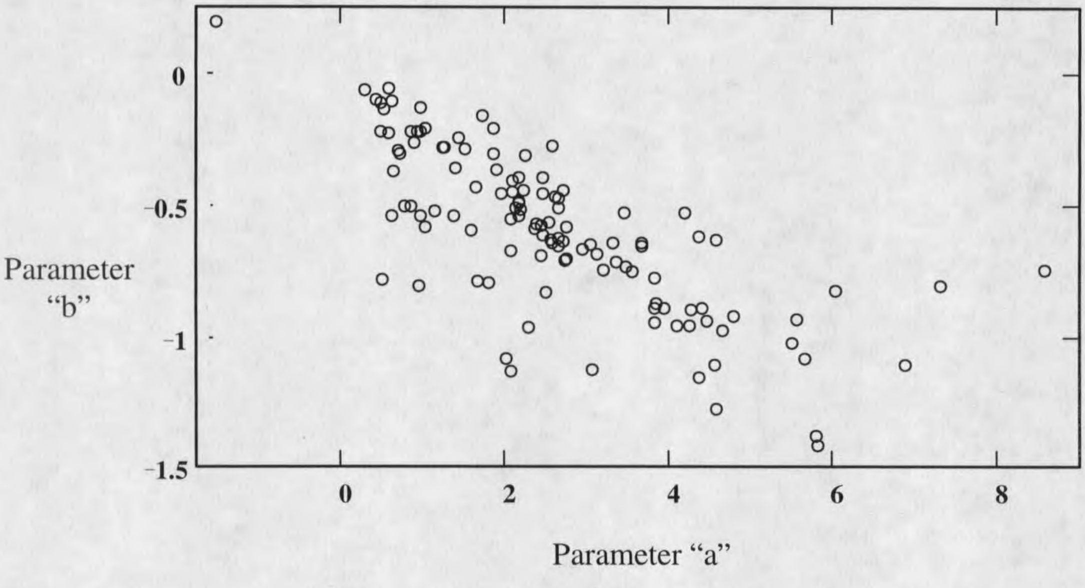


Figure 5. Scatter plot of parameter “a” for the exponential model. See text for details.

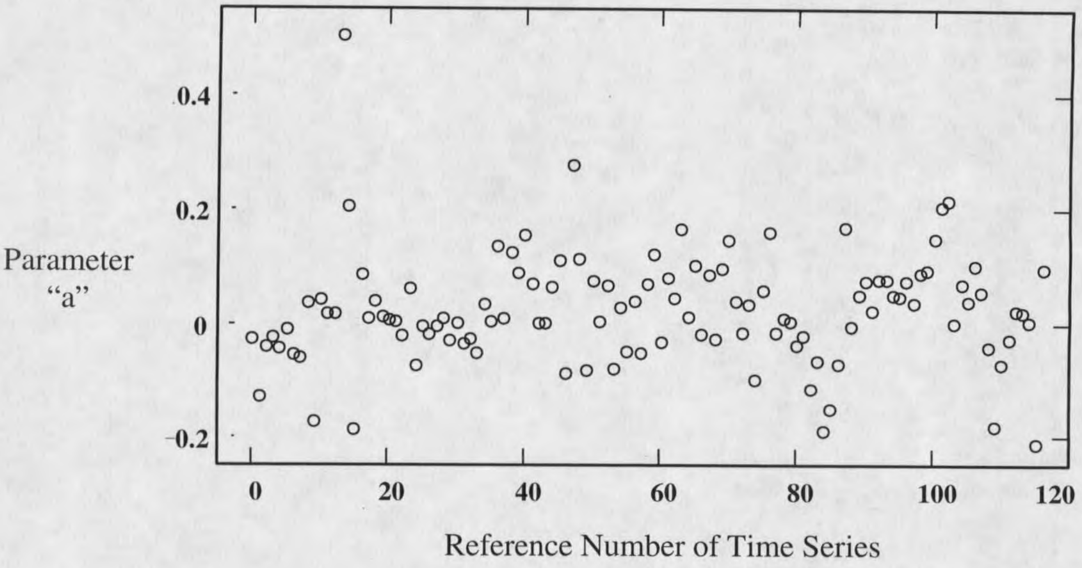
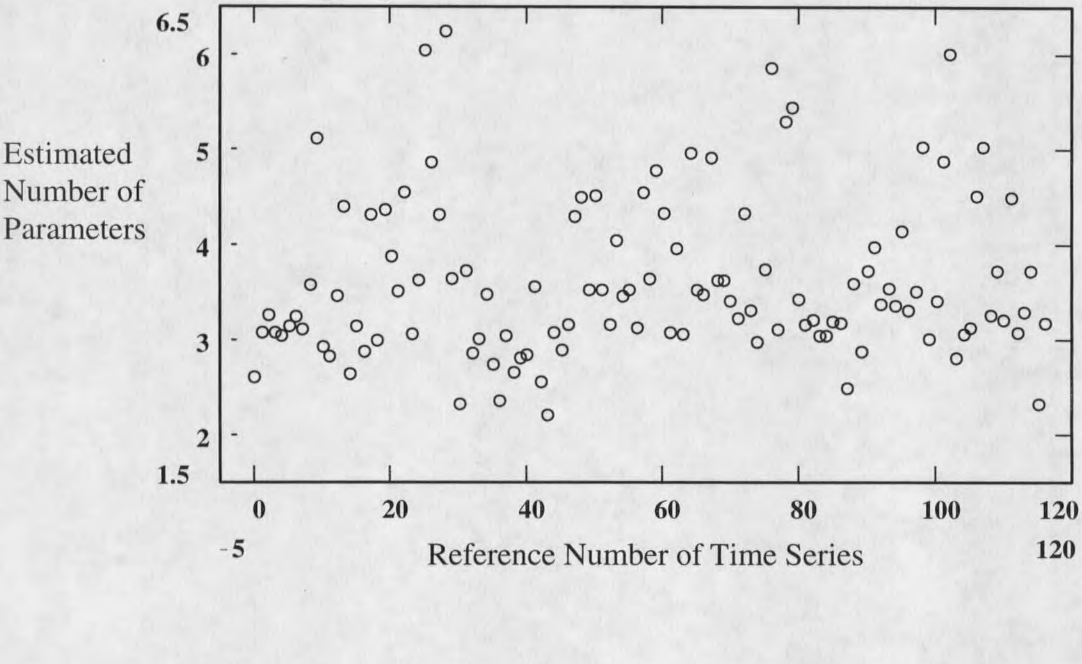


Figure 6. Scatter plot of degrees of freedom for the IIDD model. See text for details.



APPENDIX 2

TALLY MATRICES AND RESULTS OF SIMULATIONS FOR ALL INFORMATION CRITERIA OVER ALL MODELS

Tally Matrices

Matrix 1. Tally matrices for the AICc. Matrices follow Figure 1 (see text for details). Matrices follow the ascending order of time series lengths (TSL) as indicated.

TSL 8	18947	1474	461	385	2120	13
	18274	2305	456	372	1982	11
	14933	834	2084	776	4746	27
	14714	834	1322	1247	5260	23
	37	0	909	11489	10946	19
	14776	823	1805	1013	4662	321
TSL 17	15148	2054	2126	2648	699	725
	13774	3441	2453	2406	607	719
	5358	368	9582	3835	3260	997
	5375	319	4654	7683	4554	815
	0	0	514	10745	11797	344
	4719	224	5416	5194	3276	4571
TSL 35	12576	1522	3481	4131	18	1672
	10423	3430	4018	3903	10	1616
	1016	195	14247	5251	1129	1562
	1090	30	5285	13412	2088	1495
	0	0	262	8939	13732	467
	957	112	6024	7458	1176	7673
TSL 50	11745	1272	3895	4491	2	1995
	9293	3115	4696	4185	8	2103
	426	172	15802	4759	655	1586
	466	11	4656	15137	1508	1622
	0	0	215	7962	14806	417
	489	108	5761	7027	832	9183
TSL 100	10272	1145	4772	4540	0	2671
	7263	2617	5795	4564	1	3160
	85	168	17516	3128	277	2226
	85	0	2908	17269	961	2177
	0	0	517	5289	16563	1031
	135	33	4778	5854	529	12071

Matrix 2. Tally matrices for the CAIC. Matrices follow Figure 1 (see text for details). Matrices follow the ascending order of time series lengths (TSL) as indicated.

TSL 8	12269	2026	1736	1742	3899	1728
	11732	2865	1892	1701	3547	1663
	7581	914	4251	2189	6149	2316
	7332	833	3120	3272	6784	2059
	0	0	916	11012	10651	821
	7082	759	3372	2743	5712	3732
TSL 17	18829	1180	1115	1350	487	439
	17492	2471	1372	1264	398	403
	8371	288	8275	2942	2702	822
	8624	275	3819	6304	3729	649
	0	0	518	10831	11738	313
	7325	155	4648	4264	2727	4281
TSL 35	21114	441	725	935	5	180
	19043	2192	1066	968	4	127
	4279	206	13520	4470	464	461
	4730	59	4591	12799	787	434
	0	0	290	9649	13302	159
	3765	66	5884	7328	557	5800
TSL 50	21846	257	575	646	0	76
	19332	1982	1195	795	5	91
	2814	194	15668	4205	234	285
	3124	14	4140	15507	286	329
	0	0	230	8834	14247	89
	2281	58	6093	7999	281	6688
TSL 100	22291	204	494	387	0	24
	19105	1509	1896	693	1	196
	1380	207	18522	2882	167	242
	1388	1	2697	18863	175	276
	0	0	1123	14875	7130	272
	1068	34	5786	7830	238	8444

Matrix 3. Tally matrices for the AIC. Matrices follow Figure 1 (see text for details). Matrices follow the ascending order of time series lengths (TSL) as indicated.

TSL 8	6786	2674	2521	2520	5590	3309
	6494	3407	2656	2381	5222	3240
	3604	1058	4665	2633	7623	3817
	3350	936	3596	3769	8304	3445
	0	0	893	10481	10731	1295
	3344	970	3682	3118	6982	5304
TSL 17	9822	2232	3481	4096	962	2807
	8754	3459	3800	3776	833	2778
	2501	323	9537	4357	3972	2710
	2411	251	4998	7804	5648	2288
	0	0	453	9955	11979	1013
	2208	234	5380	5196	3873	6509
TSL 35	10008	1624	4146	4819	22	2781
	8216	3272	4621	4531	13	2747
	624	185	13708	5075	1512	2296
	669	30	5191	12526	2888	2096
	0	0	254	8638	13862	646
	642	107	5722	6823	1560	8546
TSL 50	9952	1321	4339	5000	2	2786
	7785	2994	5064	4587	9	2961
	286	157	15326	4611	867	2153
	338	9	4586	14359	2036	2072
	0	0	210	7765	14906	519
	369	102	5566	6558	1040	9765
TSL 100	9357	1136	5024	4740	0	3143
	6571	2541	5941	4705	1	3641
	70	165	17225	3074	313	2553
	61	0	2880	16769	1217	2473
	0	0	466	4504	17365	1065
	105	27	4659	5642	604	12363

Matrix 4. Tally matrices for the BIC. Matrices follow Figure 1 (see text for details). Matrices follow the ascending order of time series lengths (TSL) as indicated.

TSL 8	6774	2713	2683	2715	4991	3524
	6519	3453	2800	2527	4676	3425
	3668	1075	4912	2807	6895	4043
	3435	933	3775	4005	7571	3681
	0	0	895	10539	10626	1340
	3390	977	3904	3326	6282	5521
TSL 17	14776	1801	2212	2677	722	1212
	13496	3097	2551	2480	613	1163
	5047	320	9325	3826	3285	1597
	5040	269	4679	7516	4544	1352
	0	0	489	10467	11834	610
	4386	191	5249	5015	3224	5335
TSL 35	18591	790	1538	1969	11	501
	16315	2700	1992	1904	6	483
	2613	198	14092	4966	708	823
	2871	45	4971	13405	1288	820
	0	0	278	9365	13491	266
	2359	86	6031	7575	784	6565
TSL 50	19918	486	1264	1455	2	275
	17132	2406	2010	1534	5	313
	1816	199	16017	4516	311	541
	1976	13	4398	15829	582	602
	0	0	226	8522	14482	170
	1526	84	6063	7886	403	7438
TSL 100	21146	351	968	831	0	104
	17402	1831	2559	1248	1	359
	937	213	18625	3024	168	433
	855	0	2816	19030	202	497
	0	0	991	12792	9202	415
	774	54	5640	7476	253	9203

Matrix 5. Tally matrices for the AIChq. Matrices follow Figure 1 (see text for details). Matrices follow the ascending order of time series lengths (TSL) as indicated.

TSL 8	8319	2611	2508	2489	4433	3040
	7967	3334	2646	2393	4140	2920
	4697	1039	4947	2760	6353	3604
	4470	927	3729	3995	7029	3250
	0	0	904	10714	10579	1203
	4368	921	3899	3300	5794	5118
TSL 17	17254	1425	1554	1904	591	672
	15955	2743	1819	1733	494	656
	6909	307	8811	3318	2945	1110
	7036	270	4214	6913	4046	921
	0	0	508	10693	11771	428
	6019	162	4929	4653	2933	4704
TSL 35	20307	553	981	1275	6	278
	18114	2385	1375	1290	5	231
	3537	202	13825	4702	547	587
	3909	53	4774	13117	974	573
	0	0	284	9538	13377	201
	3145	73	5979	7464	639	6100
TSL 50	21170	335	823	931	1	140
	18416	2174	1542	1091	5	172
	2355	194	15856	4363	262	370
	2563	13	4264	15739	400	421
	0	0	226	8695	14362	117
	1936	68	6086	7955	329	7026
TSL 100	21692	281	749	618	0	60
	18132	1700	2278	1010	1	279
	1117	208	18585	2974	168	348
	1052	0	2775	19001	184	388
	0	0	1042	13647	8351	360
	881	44	5694	7629	247	8905

Results For All Models, AICc

Time Series Length 8, AICc

Table 17. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	63.68	3.68
Exponential	53.23	2.03
Ricker	52.33	2.07
Gompertz	46.67	1.82
IIDD	65.37	2.38
θ-Ricker	50.65	0.74

Table 18. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	80.97	3.78
Exponential	9.85	2.49
Ricker	8.91	2.42
Gompertz	5.33	1.97
IIDD	46.78	1.22
θ-Ricker	1.37	1.02

Table 19. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	46.38	3.56
Exponential	96.61	1.43
Ricker	95.77	1.65
Gompertz	88.00	1.65
IIDD	83.96	3.13
θ-Ricker	99.92	0.26

Table 20. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	65.41	-1.7398	27.49
Exponential	13.24		
Ricker	13.14		
Gompertz	17.33		
IIDD	62.82		
θ-Ricker	1.45		

Time Series Length 17, AICc

Table 21. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	69.88	3.95
Exponential	56.09	2.33
Ricker	63.99	3.64
Gompertz	55.81	3.75
IIDD	69.91	2.17
θ-Ricker	58.23	2.36

Table 22. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	64.74	4.52
Exponential	14.71	2.94
Ricker	40.95	4.36
Gompertz	32.83	4.42
IIDD	50.42	1.78
θ-Ricker	19.53	2.92

Table 23. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	75.02	3.28
Exponential	97.47	1.49
Ricker	87.04	2.75
Gompertz	78.78	2.93
IIDD	89.40	2.49
θ-Ricker	96.92	1.61

Table 24. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	89.72	-0.70490	46.76
Exponential	17.24		
Ricker	53.91		
Gompertz	54.05		
IIDD	61.01		
θ-Ricker	22.61		

Time Series Length 35, AICc

Table 25. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	71.11	3.64
Exponential	56.54	2.23
Ricker	72.29	3.72
Gompertz	65.97	3.85
IIDD	77.45	1.64
θ-Ricker	63.48	2.89

Table 26. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	53.74	4.56
Exponential	14.66	2.90
Ricker	60.88	4.21
Gompertz	57.32	4.42
IIDD	58.68	1.71
θ-Ricker	32.79	3.48

Table 27. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	88.47	2.39
Exponential	98.41	1.24
Ricker	83.70	3.16
Gompertz	74.63	3.18
IIDD	96.22	1.58
θ-Ricker	94.18	2.15

Table 28. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	65.27	0.08944	54.96
Exponential	16.25		
Ricker	77.18		
Gompertz	82.69		
IIDD	62.46		
θ-Ricker	38.61		

Time Series Length 50, AICc

Table 29. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	70.35	3.67
Exponential	55.99	2.19
Ricker	75.55	3.39
Gompertz	70.20	3.74
IIDD	80.35	1.41
θ-Ricker	66.32	2.76

Table 30. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	50.19	4.76
Exponential	13.31	2.93
Ricker	67.53	3.80
Gompertz	64.69	4.22
IIDD	63.27	1.53
θ-Ricker	39.24	3.15

Table 31. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	90.88	2.06
Exponential	98.66	1.01
Ricker	83.57	2.92
Gompertz	75.71	3.18
IIDD	97.43	1.27
θ-Ricker	93.40	2.30

Table 32. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	59.32	0.29423	56.49
Exponential	14.65		
Ricker	83.96		
Gompertz	88.98		
IIDD	65.84		
θ-Ricker	45.84		

Time Series Length 100, AICc

Table 33. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	68.72	3.07
Exponential	55.02	1.77
Ricker	79.41	3.35
Gompertz	76.91	3.43
IIDD	84.64	2.53
θ-Ricker	70.98	2.98

Table 34. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	43.90	3.95
Exponential	11.18	2.37
Ricker	74.86	3.82
Gompertz	73.80	3.62
IIDD	70.78	3.47
θ-Ricker	51.59	3.35

Table 35. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	93.53	1.78
Exponential	98.85	0.83
Ricker	83.96	2.79
Gompertz	80.02	3.22
IIDD	98.49	0.90
θ-Ricker	90.37	2.56

Table 36. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	50.37	0.60646	57.09
Exponential	12.33		
Ricker	90.90		
Gompertz	93.78		
IIDD	72.29		
θ-Ricker	61.21		

Results For All Models, CAIC

Time Series Length 8, CAIC

Table 37. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	61.80	4.41
Exponential	54.18	2.37
Ricker	54.37	2.81
Gompertz	48.71	2.76
IIDD	61.61	2.66
θ-Ricker	54.31	2.77

Table 38. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	54.23	5.06
Exponential	12.24	2.96
Ricker	18.17	3.02
Gompertz	13.98	2.95
IIDD	45.52	1.34
θ-Ricker	15.95	3.14

Table 39. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	71.17	3.64
Exponential	96.13	1.56
Ricker	90.57	2.59
Gompertz	83.43	2.55
IIDD	77.70	3.52
θ-Ricker	92.66	2.34

Table 40. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	81.52	-0.78911	34.87
Exponential	16.12		
Ricker	27.60		
Gompertz	30.55		
IIDD	67.82		
θ-Ricker	23.29		

Time Series Length 17, CAIC

Table 41. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	72.37	3.72
Exponential	54.47	1.96
Ricker	62.78	3.33
Gompertz	54.65	3.30
IIDD	70.79	2.06
θ-Ricker	58.03	2.28

Table 42. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	80.47	3.99
Exponential	10.56	2.48
Ricker	35.36	4.02
Gompertz	26.94	3.93
IIDD	50.16	1.77
θ-Ricker	18.30	2.91

Table 43. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	64.26	3.43
Exponential	98.38	1.23
Ricker	90.20	2.45
Gompertz	82.35	2.53
IIDD	91.42	2.32
θ-Ricker	97.76	1.38

Table 44. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	83.80	-1.18099	43.87
Exponential	12.18		
Ricker	45.17		
Gompertz	44.59		
IIDD	58.75		
θ-Ricker	20.54		

Time Series Length 35, CAIC

Table 45. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	81.52	2.57
Exponential	54.35	1.63
Ricker	73.52	3.05
Gompertz	67.37	3.41
IIDD	77.65	1.36
θ-Ricker	61.81	2.18

Table 46. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	90.23	2.51
Exponential	9.37	2.19
Ricker	57.78	3.64
Gompertz	54.70	4.10
IIDD	56.85	1.63
θ-Ricker	24.79	4.92

Table 47. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	72.81	2.63
Exponential	99.34	0.71
Ricker	89.27	2.31
Gompertz	80.04	2.53
IIDD	98.45	1.03
θ-Ricker	98.84	0.99

Table 48. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	82.58	-1.07464	55.99
Exponential	10.03		
Ricker	68.51		
Gompertz	74.65		
IIDD	58.40		
θ-Ricker	25.95		

Time Series Length 50, CAIC

Table 49. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	84.91	2.22
Exponential	54.01	1.52
Ricker	78.25	2.85
Gompertz	73.53	3.08
IIDD	80.10	1.14
θ-Ricker	63.92	1.99

Table 50. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	93.36	2.38
Exponential	8.47	2.08
Ricker	66.96	3.44
Gompertz	66.27	3.66
IIDD	60.89	1.47
θ-Ricker	28.58	2.69

Table 51. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	76.45	2.05
Exponential	99.55	0.54
Ricker	89.54	2.10
Gompertz	80.79	2.37
IIDD	99.31	0.68
θ-Ricker	99.26	0.82

Table 52. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	83.09	-1.01291	60.26
Exponential	8.92		
Ricker	77.41		
Gompertz	85.48		
IIDD	61.57		
θ-Ricker	29.33		

Time Series Length 100, CAIC

Table 53. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	87.83	1.73
Exponential	53.03	1.14
Ricker	84.45	2.59
Gompertz	78.91	2.52
IIDD	64.99	2.19
θ-Ricker	67.61	2.18

Table 54. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	95.26	1.81
Exponential	6.45	1.56
Ricker	79.15	3.01
Gompertz	80.61	2.53
IIDD	30.47	3.07
θ-Ricker	36.09	2.98

Table 55. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	80.39	1.65
Exponential	99.62	3.82
Ricker	89.75	2.10
Gompertz	77.21	2.51
IIDD	99.50	0.32
θ-Ricker	99.14	0.81

Table 56. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	85.13	-0.87841	64.60
Exponential	6.83		
Ricker	89.41		
Gompertz	96.58		
IIDD	30.97		
θ-Ricker	36.95		

Results For All Models, AIC

Time Series Length 8, AIC

Table 57. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	57.32	3.70
Exponential	54.87	2.65
Ricker	54.26	3.19
Gompertz	49.02	3.05
IIDD	58.52	2.85
θ-Ricker	54.88	3.48

Table 58. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	29.00	4.16
Exponential	14.56	3.29
Ricker	19.94	3.55
Gompertz	16.11	3.25
IIDD	45.56	1.37
θ-Ricker	22.67	3.83

Table 59. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	85.65	3.17
Exponential	95.18	1.81
Ricker	88.59	2.79
Gompertz	88.94	2.84
IIDD	71.18	3.78
θ-Ricker	87.09	3.09

Table 60. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	43.35	0.00553	36.22
Exponential	19.38		
Ricker	31.34		
Gompertz	34.17		
IIDD	74.68		
θ-Ricker	35.58		

Time Series Length 17, AIC

Table 61. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	64.20	3.98
Exponential	56.09	2.54
Ricker	62.64	3.76
Gompertz	54.97	3.74
IIDD	69.06	2.31
θ-Ricker	58.95	3.16

Table 62. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	41.97	4.81
Exponential	14.78	3.30
Ricker	40.76	4.32
Gompertz	33.35	4.11
IIDD	51.19	1.89
θ-Ricker	27.82	3.49

Table 63. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	86.43	2.90
Exponential	97.40	1.44
Ricker	84.52	3.10
Gompertz	76.60	3.33
IIDD	86.93	2.67
θ-Ricker	90.09	2.79

Table 64. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	55.54	0.12887	45.70
Exponential	17.38		
Ricker	56.24		
Gompertz	56.75		
IIDD	64.26		
θ-Ricker	37.73		

<u>Time Series Length 35, AIC</u>

Table 65. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	67.05	3.71
Exponential	56.16	2.25
Ricker	70.77	3.81
Gompertz	63.99	3.92
IIDD	77.06	1.79
θ-Ricker	63.75	3.16

Table 66. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	42.77	4.76
Exponential	13.98	2.91
Ricker	58.58	4.23
Gompertz	53.53	4.47
IIDD	59.24	1.76
θ-Ricker	36.52	3.61

Table 67. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	91.32	2.22
Exponential	98.34	1.27
Ricker	82.96	3.33
Gompertz	74.46	3.27
IIDD	94.88	1.82
θ-Ricker	90.97	2.63

Table 68. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	51.45	0.40306	52.54
Exponential	15.65		
Ricker	75.62		
Gompertz	79.07		
IIDD	64.36		
θ-Ricker	45.55		

Time Series Length 50, AIC

Table 69. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	67.51	3.63
Exponential	55.72	2.13
Ricker	74.30	3.54
Gompertz	68.49	3.83
IIDD	80.16	1.51
θ-Ricker	66.38	3.02

Table 70. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	42.53	4.75
Exponential	12.80	2.82
Ricker	65.50	4.02
Gompertz	61.36	4.34
IIDD	63.70	1.59
θ-Ricker	41.73	3.33

Table 71. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	92.50	1.95
Exponential	98.64	1.05
Ricker	83.11	2.97
Gompertz	75.62	3.25
IIDD	96.62	1.43
θ-Ricker	91.03	2.68

Table 72. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	50.30	0.49601	54.49
Exponential	14.15		
Ricker	82.39		
Gompertz	85.74		
IIDD	67.08		
θ-Ricker	50.70		

Time Series Length 100, AIC

Table 73. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	67.09	3.07
Exponential	54.86	1.69
Ricker	78.70	3.36
Gompertz	76.15	3.51
IIDD	86.19	2.53
θ-Ricker	70.92	3.07

Table 74. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	39.99	3.97
Exponential	10.86	2.24
Ricker	73.61	3.84
Gompertz	71.66	3.79
IIDD	74.21	3.43
θ-Ricker	52.83	3.36

Table 75. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	94.18	1.75
Exponential	98.87	0.82
Ricker	83.79	2.78
Gompertz	80.63	3.20
IIDD	98.18	1.02
θ-Ricker	89.00	2.74

Table 76. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	45.81	0.69842	55.90
Exponential	11.99		
Ricker	89.83		
Gompertz	91.03		
IIDD	76.03		
θ-Ricker	63.84		

Results For All Models, BIC

Time Series Length 8, BIC

Table 77. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	57.20	3.77
Exponential	54.94	2.67
Ricker	54.49	3.31
Gompertz	49.19	3.21
IIDD	59.71	2.77
θ-Ricker	54.95	3.58

Table 78. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	28.95	4.28
Exponential	14.76	3.31
Ricker	20.99	3.40
Gompertz	17.12	3.47
IIDD	45.41	1.30
θ-Ricker	23.59	3.95

Table 79. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	85.46	3.17
Exponential	95.13	1.81
Ricker	87.99	2.86
Gompertz	81.27	2.93
IIDD	74.00	3.69
θ-Ricker	86.31	3.17

Table 80. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	43.49	0.03424	36.09
Exponential	19.63		
Ricker	33.01		
Gompertz	35.85		
IIDD	71.41		
θ-Ricker	37.28		

Time Series Length 17, BIC

Table 81. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	69.62	4.12
Exponential	55.52	2.19
Ricker	63.44	3.50
Gompertz	55.61	3.71
IIDD	69.99	2.15
θ-Ricker	58.86	2.63

Table 82. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	63.15	4.81
Exponential	13.24	2.73
Ricker	39.85	4.09
Gompertz	32.12	4.32
IIDD	50.57	1.78
θ-Ricker	22.80	3.11

Table 83. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	76.10	3.28
Exponential	97.79	1.45
Ricker	87.03	2.77
Gompertz	79.09	2.98
IIDD	89.41	2.47
θ-Ricker	94.93	2.04

Table 84. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	87.05	-0.58051	46.41
Exponential	15.44		
Ricker	52.83		
Gompertz	53.03		
IIDD	61.16		
θ-Ricker	27.87		

Time Series Length 35, BIC

Table 85. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	79.40	3.08
Exponential	55.29	1.90
Ricker	73.78	3.29
Gompertz	67.63	3.58
IIDD	77.63	1.46
θ-Ricker	62.79	2.40

Table 86. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	79.45	3.58
Exponential	11.54	2.54
Ricker	60.22	3.87
Gompertz	57.29	4.18
IIDD	57.65	1.61
θ-Ricker	28.06	3.06

Table 87. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	79.35	2.47
Exponential	99.04	0.89
Ricker	87.34	2.58
Gompertz	77.97	2.85
IIDD	97.61	1.29
θ-Ricker	97.53	1.46

Table 88. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	99.90	-0.66586	57.17
Exponential	12.50		
Ricker	72.88		
Gompertz	79.32		
IIDD	60.04		
θ-Ricker	30.53		

Time Series Length 50, BIC

Table 89. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	83.00	2.57
Exponential	54.81	1.88
Ricker	78.26	2.97
Gompertz	73.60	3.39
IIDD	80.39	1.22
θ-Ricker	65.08	2.08

Table 90. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	85.12	2.95
Exponential	10.28	2.58
Ricker	68.45	3.49
Gompertz	67.65	4.04
IIDD	61.89	1.50
θ-Ricker	31.79	2.69

Table 91. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	80.81	2.11
Exponential	99.33	0.67
Ricker	88.07	2.34
Gompertz	79.56	2.57
IIDD	98.89	0.86
θ-Ricker	98.38	1.20

Table 92. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	95.69	-0.69864	60.95
Exponential	10.95		
Ricker	80.38		
Gompertz	88.08		
IIDD	63.00		
θ-Ricker	33.41		

Time Series Length 100, BIC

Table 93. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	86.65	2.26
Exponential	53.65	1.34
Ricker	84.25	2.78
Gompertz	79.82	2.81
IIDD	69.40	2.26
θ-Ricker	68.89	2.29

Table 94. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	90.37	2.60
Exponential	7.83	1.82
Ricker	79.59	3.18
Gompertz	81.33	2.83
IIDD	39.33	3.18
θ-Ricker	39.33	3.04

Table 95. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	82.93	1.86
Exponential	99.47	0.52
Ricker	88.91	2.32
Gompertz	78.32	2.79
IIDD	99.47	0.36
θ-Ricker	98.46	1.08

Table 96. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	92.57	-0.66409	65.03
Exponential	8.35		
Ricker	90.68		
Gompertz	96.99		
IIDD	39.86		
θ-Ricker	40.87		

Results For All Models, AIChq

Time Series Length 8, AIChq

Table 97. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	58.59	3.95
Exponential	54.77	2.55
Ricker	54.72	3.23
Gompertz	49.28	3.13
IIDD	60.75	2.69
θ-Ricker	54.95	3.44

Table 98. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	35.55	4.46
Exponential	14.25	3.13
Ricker	21.14	3.59
Gompertz	17.07	3.37
IIDD	45.21	1.29
θ-Ricker	21.87	3.79

Table 99. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	81.62	3.36
Exponential	95.30	1.77
Ricker	88.30	2.83
Gompertz	81.49	2.88
IIDD	76.28	3.59
θ-Ricker	88.02	3.04

Table 100. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	53.93	-0.19201	36.08
Exponential	18.95		
Ricker	32.84		
Gompertz	35.58		
IIDD	68.93		
θ-Ricker	33.85		

Time Series Length 17, AIChq

Table 101. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	71.52	3.82
Exponential	54.94	2.12
Ricker	63.26	3.31
Gompertz	55.24	3.54
IIDD	70.45	2.07
θ-Ricker	58.43	2.38

Table 102. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	73.74	4.27
Exponential	11.72	2.68
Ricker	37.65	3.88
Gompertz	29.54	4.22
IIDD	50.30	1.77
θ-Ricker	20.10	2.94

Table 103. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	69.30	3.31
Exponential	98.15	1.34
Ricker	88.87	2.62
Gompertz	80.94	2.71
IIDD	90.59	2.33
θ-Ricker	96.76	1.65

Table 104. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	95.57	-0.95001	45.25
Exponential	13.57		
Ricker	48.79		
Gompertz	48.60		
IIDD	59.71		
θ-Ricker	23.34		

Time Series Length 35, AIChq

Table 105. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	81.12	2.69
Exponential	54.72	1.78
Ricker	73.82	3.11
Gompertz	67.66	3.48
IIDD	77.66	1.39
θ-Ricker	62.24	2.21

Table 106. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	86.78	2.84
Exponential	10.19	2.38
Ricker	59.08	3.68
Gompertz	56.06	4.17
IIDD	57.17	1.60
θ-Ricker	26.07	2.88

Table 107. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	75.47	2.54
Exponential	99.25	0.79
Ricker	88.55	2.43
Gompertz	79.26	2.63
IIDD	98.14	1.15
θ-Ricker	98.40	1.20

Table 108. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	88.68	-0.92906	56.79
Exponential	10.95		
Ricker	70.53		
Gompertz	76.80		
IIDD	59.02		
θ-Ricker	27.67		

Time Series Length 50, AIChq

Table 109. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	84.44	2.42
Exponential	54.39	1.68
Ricker	78.35	2.87
Gompertz	73.79	3.23
IIDD	80.26	1.16
θ-Ricker	64.49	2.04

Table 110. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	90.47	2.74
Exponential	9.29	2.30
Ricker	67.76	3.39
Gompertz	67.26	3.86
IIDD	61.38	1.46
θ-Ricker	30.03	2.73

Table 111. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	78.40	2.04
Exponential	99.48	0.58
Ricker	88.94	1.22
Gompertz	80.31	2.45
IIDD	99.15	0.76
θ-Ricker	98.96	0.96

Table 112. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	87.93	-0.88994	60.85
Exponential	9.81		
Ricker	78.82		
Gompertz	86.95		
IIDD	62.23		
θ-Ricker	31.07		

Time Series Length 100, AIChq

Table 113. Correct model identification, and percent standard error (S.E.).

Population Model	Identification	S.E.
Random Walk	87.30	2.00
Exponential	53.41	1.27
Ricker	84.35	2.73
Gompertz	79.54	2.65
IIDD	67.59	2.10
θ-Ricker	68.42	2.27

Table 114. Correct model selection, and percent standard error (S.E.).

Population Model	Selection	S.E.
Random Walk	92.70	2.17
Exponential	7.27	1.73
Ricker	79.42	3.12
Gompertz	81.20	2.66
IIDD	35.69	2.95
θ-Ricker	38.06	3.07

Table 115. Correct model rejection, and percent standard error (S.E.).

Population Model	Rejection	S.E.
Random Walk	81.90	1.81
Exponential	99.54	0.46
Ricker	89.28	2.26
Gompertz	77.88	2.63
IIDD	99.49	0.33
θ-Ricker	98.77	0.96

Table 116. Concordance, average order bias, and average correct selection of model order. The latter two measures have just a single value over all models.

Population Model	Concordance	Order bias	Order Identification
Random Walk	89.20	-0.75930	64.98
Exponential	7.72		
Ricker	90.14		
Gompertz	96.68		
IIDD	36.20		
θ-Ricker	39.28		

Table 117. Percent correct model family identifications and associated standard errors (s.e.) for each IC form and over all time series lengths (TSL). "DI" denotes density independent family and "DD" denotes density dependent family.

IC Form	Model Family	TSL 8	TSL 17	TSL 35	TSL 50	TSL 100
AICc	DI	87.61	73.54	59.72	54.33	45.51
	(s.e.)	4.42	5.38	5.30	5.14	4.42
	DD	49.84	82.52	96.37	98.21	99.46
	(s.e.)	4.14	5.87	5.69	5.17	5.36
CAIC	DI	61.74	85.41	91.43	92.77	92.11
	(s.e.)	5.46	4.82	3.40	3.08	2.60
	DD	73.82	73.25	86.00	90.94	95.64
	(s.e.)	5.67	5.44	4.91	4.47	4.47
AIC	DI	41.37	51.85	49.40	47.12	41.89
	(s.e.)	5.21	5.68	5.35	5.07	4.38
	DD	85.83	91.53	97.59	98.65	99.54
	(s.e.)	6.29	6.33	5.94	5.41	5.42
BIC	DI	41.58	70.88	82.04	85.35	87.03
	(s.e.)	5.25	5.50	4.26	3.85	3.42
	DD	85.60	83.70	91.27	94.00	96.97
	(s.e.)	6.39	5.89	5.23	4.71	4.75
AIChq	DI	47.50	79.87	88.37	89.95	89.33
	(s.e.)	5.30	5.09	3.78	3.44	3.09
	DD	82.46	77.88	88.33	92.38	96.47
	(s.e.)	6.23	5.62	5.02	4.59	4.58