

Common Structure in Panels of Short Ecological Time Series

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Abstract

Typically, in many studies in ecology, epidemiology, bio-medicine and others, we are confronted with panels of short time series of which we are interested in obtaining a biologically meaningful grouping. Here, we propose a bootstrap approach to test whether the regression functions or the variances of the error terms in a family of stochastic regression models are the same. Our general setting includes panels of time series models as a special case. We rigorously justify the use of the test by investigating its asymptotic properties, both theoretically and through simulations. The latter confirm that for finite sample size, bootstrap provides a better approximation than classical asymptotic theory. We then apply the proposed tests to the mink-muskrat data across 81 trapping regions in Canada. Ecologically interpretable groupings are obtained, which serve as a necessary first step prior to a fuller biological and statistical analysis of the food chain interaction.

Keywords: Bootstrap; Canadian mink-muskrat data; Common structure; Cluster analysis; Non-linear time series; Predator-prey interaction; Similarity measure; Threshold modelling

1 INTRODUCTION

Following Elton's (1924) pioneering work, one of the key issues in ecology has been to understand the mechanisms underlying the periodic population fluctuations of northern regions. For terrestrial vertebrates such as microtine rodents and the Canadian snowshoe hare, attention has recently been focused on the food chain interaction (*e.g.* plant-herbivore and predator-prey interactions) as a possible explanatory mechanism (*cf.* Hanski *et al.* 1993, Krebs *et al.* 1995, Stenseth *et al.* 1996a, Stenseth *et al.* 1997, Stenseth *et al.* 1998a). Such food chain interactions are typically nonlinear (May 1981, 1986), which may reflect the so-called *phase-dependence* due to, among other things, the different hunting (or escaping) behaviour of the predator (or the prey) at different stages of the population cycle (Framstad *et al.* 1997, Stenseth *et al.* 1998b). It is therefore an important question whether the food chain interactions may be grouped according to exogenous factors such as habitat (*cf.* Stenseth *et al.* 1999). Often we have only partial information of the food chain interactions. For example, there is a general lack of data on both predator and prey from the same area and over the same time period. As a result, many statistical analyses of food chain dynamics rely on formulating models in delay coordinates based on either the predator or the prey data only (see, *e.g.* Stenseth 1999). The time series modelling of Canadian lynx data is a typical case in point (see, *e.g.* Section 7.2 of Tong 1990).

Here we study the annual numbers of muskrats and minks caught over 81 trapping regions in Canada for a period of 25 years (see Erb *et al.* 2000). The data are extracted from the records compiled by the Hudson Bay Company on fur sales at auction in the period 1925 – 1949. Such data are typically referred to as panel time series since we have parallel series in the same time period over 81 posts (see, *e.g.* Baltagi 1995). Any approach to modelling the mink-muskrat time series inevitably faces the difficulty of having only 25 points vis-a-vis a cycle length of, for example, around 10 years. In order to perform a more powerful analysis based on a larger sample size, the first important step is to pool the data from those regions which share a common or similar structure. In fact, this is a common problem within the field of ecology since population abundance data are often available only for relatively short time span. However, sometimes, several such time series of referring to more or less the same ecological process do exist. Another similar example is the Hokkaido grey-sided vole data analysed in Hjellvik and Tjøstheim (1999) (see also Stenseth *et al.* 1996b, Bjørnstad *et al.* 1996, Bjørnstad *et al.* 1998, Lindström *et al.* 1998). In order to perform a more powerful analysis based on a larger sample size it is essential to pool the time series data from those regions which share a similar dynamic structure.

The mink and muskrat data constitute an exceptional set of field data, in that we have

information on *both* prey (the muskrat) and its key predator (the mink) (*cf.* Errington 1961, 1963). These data sets therefore offer a unique opportunity to carry out systematic statistical analyses aiming at a deeper understanding of the ecological interaction from a quantitative point of view. Figure 1(a) shows the locations of the 81 posts. Most posts are located in the so-called boreal forest. Figure 1(b) depicts the time series plots of the mink and muskrat data from 8 randomly selected posts. Most series exhibit cycles with a period of around 10 years (*e.g.* Erb *et al.* 2000). There exists a clear synchrony between the fluctuations of the two species with a delay of about one or two years. The ecological interaction between the two species may differ from one region to another, not the least in opportunities for the muskrat to hide and thereby avoid the chance of being preyed upon by the mink. Hence, the mink-muskrat data provides us with both the motive and a testing ground for developing tests for common structure. Whereas asymptotic results for large data sets are available, the problem of testing for common structure in *small* data sets has received little attention. In this paper, we develop a new statistical test based on a bootstrap approach that serves exactly this purpose. The bootstrap is known to be a particularly powerful tool for data analysis. Its good performance in many important statistical problems such as estimation and model fitting has been established by theoretical analyses, by simulation studies and by applications to real data (see, *e.g.* Efron and Tibshirani 1993, Shao and Tu 1995.)

Within a general setting of regression models, we will perform tests of homogeneity in the regression functions and the variances. We justify the applicability of the bootstrap methods by showing that the asymptotic bootstrap distributions are indeed the asymptotic distributions of the test statistics under the null hypotheses. We conduct simulations for a set of linear models, which show that for *finite* sample sizes the bootstrap provides better approximation to the distributions of the test statistics than classical asymptotic theory.

The paper is organized as follows. In Section 2 we introduce the statistical hypotheses of common structure and the bootstrap tests. The application to the Canadian mink-muskrat data is presented in Section 3, where we also touch on the identification of regions in which the mink and the muskrat interact with each other in a similar manner, although this is not the main focus of this paper. The asymptotic results which rigorously justify the use of the test are given in two appendices. Numerical examples using simulated models are reported in Appendix 3.

2 TESTS FOR COMMON STRUCTURE

2.1 Test statistics

Consider p regression models

$$Y_{ik} = m(X_{ik}, \theta_k) + \varepsilon_{ik}, \quad i = 1, \dots, n_k, \quad k = 1, \dots, p, \quad (2.1)$$

where Y_{ik} is a random variable, X_{ik} is a $q \times 1$ random vector, the functional form of m is known from biological theory, θ_k is an unknown $d \times 1$ parameter vector (θ_k stands for the autoregressive parameter in the mink-muskrat dynamic model in Section 3 below), $\{\{\varepsilon_{ik}\}, k = 1, \dots, p\}$ are p independent stochastic sequences with mean zero and variance

$$\text{Var}(\varepsilon_{ik}) = \sigma_k^2. \quad (2.2)$$

Note that for an autoregressive time series model the set of covariates consists of lagged values of the response variable, *i.e.* $X_{ik} = (Y_{i-1,k}, \dots, Y_{i-q,k})^\tau$.

A common structure implies that the parameters in the regression functions and the error variances are the same. Thus, we formulate two null hypotheses

$$H_0 : \theta_1 = \dots = \theta_p, \quad (2.3)$$

$$J_0 : \sigma_1^2 = \dots = \sigma_p^2. \quad (2.4)$$

Under the assumption of normality of ε_{ik} , classical statistical theory provides us with the log-likelihood ratio statistics for testing H_0 and J_0 . These are, respectively, given by

$$T_H = \sum_{k=1}^p n_k \{\log S_k(\hat{\theta}) - \log S_k(\hat{\theta}_k)\}, \quad (2.5)$$

$$T_J = n \log\{n^{-1} \sum_{k=1}^p S_k(\hat{\theta}_k)\} - \sum_{k=1}^p n_k \log\{n_k^{-1} S_k(\hat{\theta}_k)\}, \quad (2.6)$$

where $n = n_1 + \dots + n_p$. S_k stands for the sums of squares of error

$$S_k(\theta) = \sum_{i=1}^{n_k} \{Y_{ik} - m(X_{ik}, \theta)\}^2, \quad (2.7)$$

$$\hat{\theta}_k = \arg \min_{\theta} S_k(\theta), \quad \hat{\theta} = \arg \min_{\theta} \sum_{k=1}^p n_k \log\{S_k(\theta)\}, \quad (2.8)$$

where $\hat{\theta}_k$ is the least squares estimator of the parameters of the k 'th individual model and $\hat{\theta}$ is the weighted least squares estimator based on an overall model.

The standard theory of likelihood ratio tests entails that T_H and T_J are both asymptotically χ^2 -distributed under H_0 and J_0 respectively. In fact, this asymptotic property still holds under a more general condition (Theorem 1 in Appendix B). In most cases, the least squares estimation in (2.8) involves solving a nonlinear optimisation problem. We adopt the Downhill Simplex Method (Chapter 10.4 in Press *et al.* 1992) for the simulations and applications reported in this paper.

We now develop the bootstrap testing approach for both testing problems where we make use of the likelihood ratio test statistics evolving from classical normal theory.

2.2 Bootstrapping

Bootstrapping for testing H_0 . Let

$$Y_{ik}^* = m(X_{ik}, \hat{\theta}) + \varepsilon_{ik}^*, \quad i = 1, \dots, n_k; \quad k = 1, \dots, p, \quad (2.9)$$

where $\hat{\theta}$ is the estimate given in (2.8) from the pooled data from all p models. The $\{\varepsilon_{ik}^*\}$ are independent samples from the empirical distribution of the centered residuals $\{\hat{\varepsilon}_{ik} - \bar{\varepsilon}_k, i = 1, \dots, n_k\}$, where

$$\hat{\varepsilon}_{ik} = Y_{ik} - m(X_{ik}, \hat{\theta}_k), \quad \bar{\varepsilon}_k = \frac{1}{n_k} \sum_{i=1}^{n_k} \hat{\varepsilon}_{ik}, \quad (2.10)$$

and $\hat{\theta}_k$ is the least squares estimator in (2.8). It can be seen that $E(\varepsilon_{1k}^* | \{X_{ij}, Y_{ij}\}) = 0$.

We define a bootstrap statistic T_H^* in the same way as T_H in (2.5) with $\{X_{ik}, Y_{ik}\}$ replaced by $\{X_{ik}, Y_{ik}^*\}$. We reject H_0 if T_H is greater than the upper α -point of the conditional distribution of T_H^* given $\{X_{ik}, Y_{ik}\}$. The latter can be evaluated via repeated samplings from (2.9). In fact, the p -value of the test is the relative frequency of the event $\{T_H^* \geq T_H\}$ in the bootstrap replications.

Bootstrapping for testing J_0 . We generate bootstrap samples from the equation

$$Y_{ik}^* = m(X_{ik}, \hat{\theta}_k) + \varepsilon_{ik}^\dagger, \quad i = 1, \dots, n_k; \quad k = 1, \dots, p, \quad (2.11)$$

where $\hat{\theta}_k$ is given as in (2.8), and $\{\varepsilon_{ik}^\dagger\}$ are independent samples from the empirical distribution of $\{\bar{\varepsilon}_{ik}, i = 1, \dots, n_k\}$, and

$$\bar{\varepsilon}_{ik} = \hat{\sigma}_k^{-1} \left\{ \sum_{l=1}^p \hat{\sigma}_l^2 / p \right\}^{\frac{1}{2}} (\hat{\varepsilon}_{ik} - \bar{\varepsilon}_k), \quad \hat{\sigma}_k^2 = \frac{1}{n_k} \sum_{i=1}^{n_k} (\hat{\varepsilon}_{ik} - \bar{\varepsilon}_k)^2, \quad (2.12)$$

where $\hat{\varepsilon}_{ik}$ and $\bar{\varepsilon}_k$ are given as in (2.10). We define $\{\tilde{\varepsilon}_{ik}\}$ in such a way that the null hypothesis J_0 holds under model (2.11). It can be seen that

$$E(\varepsilon_{1k}^\dagger | \{X_{ij}, Y_{ij}\}) = 0, \quad \text{Var}(\varepsilon_{1k}^\dagger | \{X_{ij}, Y_{ij}\}) = \sigma_*^2 \equiv \frac{1}{p} \sum_{l=1}^p \hat{\sigma}_l^2. \quad (2.13)$$

We define a bootstrap statistic T_J^* in the same way as T_J in (2.6) with $\{X_{ik}, Y_{ik}\}$ replaced by $\{X_{ik}^*, Y_{ik}^*\}$. We reject J_0 if T_J is greater than the upper α -point of the conditional distribution of T_J^* given $\{X_{ik}, Y_{ik}\}$.

The use of the bootstrap tests is justified rigorously by Theorems 1 and 2 (Appendix B) which state that the asymptotic conditional distribution of T_H^* (or T_J^*) is almost surely equal to the asymptotic distribution of T_H (or T_J) under hypothesis H_0 (or J_0).

3 CANADIAN MINK-MUSKRAT DATA

3.1 CLASSIFICATION

In this section, we aim at classifying the time series from the 81 trapping posts shown in figure 1(a) into a smaller number of groups, such that within each group the mink and the muskrat interact in a similar manner. Before applying techniques of cluster analysis, we need to formulate an ecological model to describe the mink-muskrat interaction. Based on the food chain interaction model developed by May (1981), Stenseth *et al.* (1997) proposed a deterministic model to describe the predator-prey interaction, namely

$$\begin{cases} X_{t+1} - X_t &= a_0(\theta_t) - a_1(\theta_t)X_t - a_2(\theta_t)Y_t, \\ Y_{t+1} - Y_t &= b_0(\theta_t) - b_1(\theta_t)Y_t + b_2(\theta_t)X_t, \end{cases} \quad (3.1)$$

where X_t and Y_t denote the population abundances, on a natural logarithmic scale, of a prey and the predator at time t , $a_i(\cdot)$ and $b_i(\cdot)$ are non-negative functions, and θ_t is an indicator representing *the regime effect* at time t , which is determined by X_t and/or Y_t . Biologically speaking, $a_1(\theta_t)$ and $b_1(\theta_t)$ reflect the within species regulation whereas $a_2(\theta_t)$ and $b_2(\theta_t)$ reflect, among others, the food chain interaction between the two species (see *e.g.* Stenseth 1997, 1998a), and $a_0(\theta_t)$ and $b_0(\theta_t)$ are the intrinsic rates of changes. The implementation of the above food chain models for the purpose of data analysis has been facilitated by using a threshold to reflect the regime effect (see *e.g.* Stenseth 1999). Successful applications of this strategy include Framstad *et al.* (1997), Stenseth *et al.* (1998a,b) and Chan *et al.* (2000). Accordingly, we model the population abundance of mink at year $(t + 1)$, *i.e.* Y_{t+1} , as a threshold regression on its lagged value Y_t and the population abundance of muskrat at year t , *i.e.* X_t , with a threshold on X_t . The implied model in which Y_t is moved from the LHS of the equation to the RHS, with added random noise,

has the form

$$Y_{t+1} = \begin{cases} b_{10} + b_{11}Y_t + b_{12}X_t + \epsilon_t & \text{if } X_t \leq r, \\ b_{20} + b_{21}Y_t + b_{22}X_t + \epsilon_t & \text{if } X_t > r, \end{cases} \quad (3.2)$$

where r is the threshold which divides the state space into two regimes called the lower and the upper regime, respectively. It is easy to see from the second equation in (3.1) that in the above model, both b_{12} and b_{22} should be non-negative. The following analysis is based on model (3.2), where we model the mink as a function of the immediate lagged values of both mink and muskrat.

Assuming a model of the form (3.2) for each of the 81 posts, we apply the bootstrap tests for H_0 and J_0 to each possible pair chosen from the 81 posts. For each test, we search for the threshold r among the 60% inner sample range of X_t , and we replicate bootstrap sampling 400 times. Since the p -values across different tests are not always directly comparable in the sense that smaller p -values do not necessarily imply stronger statistical evidence against null-hypotheses across different tests (see Gibbons and Pratt 1975), we introduce the following similarity measure for each pair

$$D(T, T^*) = \frac{1}{1 + \{(T - \mu(T^*))_+\}^2 / \sigma^2(T^*)}, \quad (3.3)$$

where T is the test statistic defined as in (2.5), T^* denotes its bootstrap counterpart, $\mu(T^*)$ and $\sigma^2(T^*)$ are the conditional mean and the conditional variance of T^* given the original observations. In the above expression, $(\cdot)_+$ denotes the truncation at 0, *i.e.* $(x)_+$ equals x if $x > 0$ and 0 otherwise. Without this truncation, $D(T, T^*)$ is the data depth defined by Mahalanobis (1936), which measures the depth (or the centrality) of a given point T with respect to the (conditional) distribution of T^* (see also Liu and Singh 1997). We truncate $(T - \mu_*)$ since our tests are one-sided.

Testing H_0 involves solving a nonlinear optimisation problem for each replication of the bootstrap which is time consuming, especially if we also conduct a genuine search for the threshold parameter r . To speed up the calculation, we assume in the test for H_0 that the threshold parameters are given in the bootstrap replications and are equal to their estimated values from the original data.

The next step is to perform the classification. There are several alternatives and we describe below one feasible method. A full development of optimal classification lies outside the scope of this paper. Since the data are the numbers of furs sold in the market, it is conceivable that different posts have different sampling weights. Therefore, we first standardised the mink series and the muskrat series separately for each post; *i.e.* we subtract the mean from original data and then divide them by the standard deviation for each series with length 25. We apply the following grouping strategy:

- apply a test for common structure for each pair among the 81 posts based on the threshold regression model (3.2)
- form a similarity measure for each pair based on the above test using the modified Mahalanobis' data-depth (3.3)
- group the posts by the complete linkage method (Cluster Analysis, see, for example, chapter 7.5 in Sharma 1996).

We use the complete linkage method in order that all the posts in each cluster have the similar structure in the sense the similarity measure between each pair within each cluster is as large as possible. The discrepancy in the regression functions across different posts is larger than the one in the variances. Further, the posts may be divided into three to seven clusters according to the similarity in the regression functions. Figure 2 presents the geographical map (using the longitude-latitude convention) of the classification with six clusters in Figure 2(a) and three clusters in Figure 2(b). In Figure 2(b), the majorities of Clusters 1, 2 and 3 are located in the western, middle and eastern area, respectively. This grouping has a clear geographic component and is therefore interesting from an ecological point of view (see Stenseth *et al.* 1999).

On the other hand, we may also divide the posts into three to five clusters according to the discrepancy in the variances. Figure 3 presents the two maps for such classifications with five and three clusters respectively. It seems that geographical location plays a less active role in determining the discrepancy of the variances.

3.2 Fitting the pooled data

As an illustration, we report the results on modelling the pooled data for three selected groups which consist of posts in Clusters 1, 2 and 3 in Figure 2(b). Specifically, Group 1 consists of the western posts in Cluster 1, Group 2 consists of the middle posts in Cluster 2, and Group 3 consists of all the eastern posts which belong to Cluster 3. The locations of the posts in the three groups are shown in Figure 2(c). Model (3.2) is fitted to each group where the data is pooled from the posts within these groups. The parameters are estimated by least squares and the threshold r is searched within the 60% inner sample range. The estimated variance of noise $\hat{\sigma}^2$ is defined as the sum of squares of residuals divided by the sample size N minus 7 (corresponding to 7 free parameters in the model). The results are summarised in Table 1. The standard errors of the estimated coefficients are reported in parentheses, which are calculated under the assumption that the threshold r is given (see Tong, 1990, for an asymptotic justification).

The estimated coefficients of X_t are almost always positive. This reflects the fact that a large muskrat population will facilitate growth of the mink population, although the intensity of the increase is stronger in the middle core boreal forest (Group 2) than in the western and eastern groups (Groups 1 and 3). In fact, the food chain interaction of muskrat on mink is at its weakest in the eastern area where there may be a larger array of prey-species for the mink to feed on. It should first be observed that the values of the estimated parameters are consistent with the predator-prey interaction specified in (5.1). Our parameter estimates do specifically support earlier suggestion (e.g., Errington 1961, 1963) that the mink and the muskrat relate to each other in a specialized food chain manner.

The coefficients of Y_t in model (5.2) correspond to the degree of self-regulation. The smaller are b_{11} and b_{21} , the stronger is the self-regulation. Hence, we may conclude that the weakest self-regulation in the mink is found in Group 3. The strongest self-regulation within the mink population is found in Group 2, where also the dependency on the muskrat in general is the largest. This suggests that Group 2 corresponds to the region where there exists the closest predator-prey interaction between the mink and the muskrat. It seems plausible that this group corresponds to the core habitat of the muskrat in the boreal forest of Canada.

To reinforce the above analysis, we repeat the fitting for the pooled data from all posts in each of western and central areas (without deleting the ‘outliers’). The sample size is now 667 for the western area and 989 for the central area. The results are reported in Table 2. Comparing it with Table 1, the fitted models are not adversely different from the models based on the selected groups. The basic pattern described before is unchanged.

The threshold r defines the phases: the lower regime corresponds to the low and early increase phase whereas the upper regime corresponds to the peak and decrease phase. Table 2 shows a clear phase-dependency (see Framstad *et al.* 1997, Stenseth *et al.* 1998b) where the coefficients of the two regimes are significantly different for each of Y_t and X_t . The only exception is Group 3 where the coefficients of X_t are very close to zero. The results for Group 3 are different from those of the other two groups. In the light of what is known about this region, this should not be surprising: not only is there a larger array of prey-species for the mink to feed on (making it less dependent on the muskrat) but also it is observed that foxes have a much more pronounced influence on the entire system of this region (e.g., Elton 1942).

4 Conclusion

By combining the information in panels of short time series, we have been able to deduce the structure of the ecological process which in our example is the predator-prey interaction between muskrat and mink over most part of Canada. We have also deduced the existence of three ecological zones, each of which being characterised by different parameters in the ecological model. In the follow-up papers we will explore the ecological implications of the observed common ecological structure within the three regions. Over and beyond the ecological insight deduced from the model-fitting (briefly summarised in Section 3.2), we believe that our approach is of general interest and of wide applicability to the analysing ecological and epidemiological of time series (both focusing on population biological processes) and to other fields wherever we face with panels of short time series which share common or similar underlying structure.

There has been a huge amount of literature on analysing panel data in econometrics (see, e.g., Baltagi, 1995 and references within). In this paper we have focused specifically on the issue of population dynamics (as exemplified by the muskrat-mink interaction in Canada). It is our hope that the approach developed in this paper will be of general applicability beyond the field of population biology. Indeed, we believe that the interplay between statistics and the areas posing difficult scientific problems may be greatly and mutually beneficial. Through the example used in this paper, we have shown the great merits of such work within the field of population ecology.

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APPENDIX A: REGULARITY CONDITIONS

We always assume that $n_k = t_k n$ for some fixed $t_k \in (0, 1)$ when $n \rightarrow \infty$, $k = 1, \dots, p$.

(C1) $\{\{\varepsilon_{ik}\}, k = 1, \dots, p\}$ are p independent sequences. For each fixed k , $\{X_{ik}, Y_{ik}\}$ is jointly strictly stationary, and $\{\varepsilon_{ik}\}$ is a sequence of independent and identically distributed random variables with $E(\varepsilon_{ik}) = 0$ and $\text{Var}(\varepsilon_{ik}) = \sigma_k^2$.

Furthermore, ε_{ik} is independent of $\{X_{jk}, j \leq i\}$ for each i and k .

(C2) All the second order partial derivatives of $m(z, \theta)$ with respect to θ exist, and

$$E_{\theta_k} |\dot{m}_{j_1}(X_{s_1,k}, \theta_k) \dot{m}_{j_2}(X_{s_2,k}, \theta_k) \dot{m}_{j_3}(X_{s_3,k}, \theta_k) \dot{m}_{j_4}(X_{s_4,k}, \theta_k)| < \infty,$$

$$\text{for } 1 \leq j_i \leq d, \quad 1 \leq s_i \leq n_k \text{ and } 1 \leq k \leq p,$$

where $\dot{m}_i(x, \theta)$ denotes the partial derivative of m w.r.t. the i -th component of θ .

(C3) $L_k(\theta) = E_{\theta_k} \{Y_{1k} - m(X_{1k}, \theta)\}^2$. Then $\frac{\partial L_k(\theta)}{\partial \theta} = 0$ if and only if $\theta = \theta_k$, and

$$\left. \frac{\partial^2 L_k(\theta)}{\partial \theta \partial \theta^\tau} \right|_{\theta=\theta_k} > 0, \quad k = 1, \dots, p.$$

Further, for $L(\theta) \equiv \sum_{k=1}^p t_k \log\{L_k(\theta)\}$, there exists a unique θ_0 under hypothesis H_0 for which

$$\left. \frac{\partial L(\theta)}{\partial \theta} \right|_{\theta=\theta_0} = 0, \quad \left. \frac{\partial^2 L(\theta)}{\partial \theta \partial \theta^\tau} \right|_{\theta=\theta_0} > 0.$$

(C4) For $k = 1, \dots, p$, $E_{\theta_k}(|\varepsilon_{1k}|^{4+\eta}) < \infty$, where $\eta > 0$ is a constant.

(C5) For each $1 \leq k \leq p$, $\{X_{ik}\}$ is ergodic, *i.e.* for any measurable f ,

$$\frac{1}{n_k} \sum_{i=1}^{n_k} f(X_{ik}) \xrightarrow{a.s.} E_{\theta_k} \{f(X_{1k})\} \quad \text{as } n_k \rightarrow \infty,$$

provided $E_{\theta_k} |f(X_{1k})| < \infty$.

Remark 1. It is easy to see that $\frac{\partial L_k(\theta)}{\partial \theta} = 0$ if $\theta = \theta_k$. The assumption that θ_k is its unique root (as well as the uniqueness of θ_0) in (C3) is imposed in order to simplify the proof and is not essential.

APPENDIX B: ASYMPTOTIC PROPERTIES

We now present some theoretical properties of our tests. Theorem 1 states the asymptotic distributions of the test statistics under their null hypotheses. Theorem 2 presents the results for their bootstrap counterparts. The proofs of the theorems are available upon request. We always assume in this section that the regularity conditions (C1) and (C2) — (C5) listed in Appendix A hold.

Theorem 1. As the sample size n tends to ∞ ,

(i) T_H converges in distribution to a χ^2 -distribution with $(dp - d)$ degrees of freedom under hypothesis H_0 .

(ii) T_J converges in probability to the quadratic form $U^\tau \Phi U$ under hypothesis J_0 , where U is a $d \times 1$ standard normal vector, and $\Phi \equiv (\varphi_{ij})$ is a $p \times p$ symmetric matrix with

$$\varphi_{ii} = \frac{1 - t_i}{2} \{E_{\theta_i} \{(\varepsilon_{1i}/\sigma_i)^4\} - 1\},$$

$$\varphi_{ij} = -\frac{1}{2} (t_i t_j)^{1/2} [E_{\theta_i} \{(\varepsilon_{1i}/\sigma_i)^4\} - 1]^{1/2} [E_{\theta_j} \{(\varepsilon_{1j}/\sigma_j)^4\} - 1]^{1/2}, \quad i \neq j.$$

Further, if $E_{\theta_k} \{(\varepsilon_{1k}/\sigma_k)^4\} \equiv 3$ for all $1 \leq k \leq p$, the asymptotic distribution of T_J is χ^2 with $(p - 1)$ degrees of freedom.

Theorem 2. Conditionally on $\{X_{ik}, Y_{ik}\}$, it holds almost surely as n tends to ∞ that

- (i) T_H^* converges in distribution to a χ^2 -distribution with $(dp - d)$ degrees of freedom,
and
(ii) T_J^* converges in probability to the quadratic form $U^\tau \Phi U$,

where U and Φ are the same as in Theorem 1.

APPENDIX C: NUMERICAL PROPERTIES

We illustrate the methods via a set of linear models. The basic model is set as

$$Y_t = a + 2.5X_t + 1.8Z_t + \epsilon_t,$$

where X_t , Z_t and ϵ_t are independent. We allow the intercept a as well as the distributions of X_t , Z_t and ϵ_t to vary as follows:

	a	X_t	Z_t	ϵ_t
Model 1	1	$N(0, 1)$	$N(0, 0.25)$	$N(0, 1)$
Model 2	1	$U[0, 1]$	$U[-1, 1]$	$U[-\sqrt{3}, \sqrt{3}]$
Model 3	1	$N(0, 1)$	$N(0, 4)$	$N(0, 0.25)$
Model 4	0	$U(0, 1)$	$N(0, 1)$	$N(0, 1)$

Note that Model 4 has a different mean function from the others while the variance of the noise in Model 3 differs from the other three models. We test H_0 and J_0 for five different combinations of the models: the first three models, Models 1, 2 and 4, Models 1 and 2, Models 1 and 3, and Models 1 and 4. We set the sample size $n_k \equiv 24$, the bootstrap replications are 200 times. We repeat the simulation 200 times.

Figures 5(a) and 5(b) display the boxplots of the p -values. We cannot reject H_0 when the first three models are considered together, although there is overwhelming evidence to reject J_0 then. The hypothesis H_0 would be rejected but not J_0 when Models 1, 2 and 4 are considered. We could not reject both H_0 and J_0 when we narrow our attention to Models 1 and 2. The hypothesis J_0 would be rejected but not H_0 when we compare Models 1 and 3, and the hypothesis H_0 would be rejected but not J_0 when we compare Models 1 and 4. Note that the differences in the distributions of X_t , Z_t and ϵ_t are irrelevant to the hypotheses concerned. The reliable performance of the tests is further supported by Table 3, which reports the simulated powers of the tests at the three different nominal levels (*i.e.* $\alpha = 0.01, 0.05$ and 0.10) in the above simulation.

We also compare the bootstrap approximations with the asymptotic approximations provided by Theorem 1. Figure 5 presents the (approximated) distribution functions under the null hypotheses in two different settings: (a) the distribution of T_H in testing H_0 for the first three models, and (b) the distribution of T_J in testing J_0 for Models 1 and 4. We plot the empirical distribution of a test statistic in a simulation with 200 replications, together with its asymptotic approximation which is $\chi^2(6)$ in case (a) and $\chi^2(1)$ in case (b), and three typical examples of its bootstrap approximations. A typical bootstrap approximation is selected in such a way that the corresponding p -value is equal to its 25th percentile (dotted curve), or the median (dot-dashed curve), or the 75th percentile (dashed curve). For the given sample size, bootstrap provides a better approximation than the asymptotic method even for linear models.

References

- Baltagi, B.H. (1995). *Econometric Analysis of Panel Data*. John Wiley, New York.
- Bjørnstad, O.N., Champely, S., Stenseth, N.C., and Saitoh, T. (1996). Cyclicity and Stability of grey-sided voles, *Clethrionomys rufocanus*, of Hokkaido: evidence from spectral and principal component analysis. *Phil. Trans. Roy. Soc. B*, **351**, 867-873.
- Bjørnstad, O.N., Stenseth, N.C., Saitoh, T., and Lingjaerde, O.C. (1998). Mapping the regional transition to cyclicity in *Clethrionomys rufocanus*: spectral densities and functional data analysis. *Res. Popul. Ecol.* **40**(1), 77-84.
- Chan, K.S., Tong, H. and Stenseth, N.C. (2000). Analysing short time series data from periodically fluctuating rodent populations by threshold model: a nearest block bootstrap approach. (A preprint.)
- Erb, J., Stenseth, N.C. and Boyce, M.S. (2000). Geographic variation in population cycles of Canadian muskrats (*Ondatra zibethicus*). *Canadian J. Zoology*, **78**, 1009-1016.
- Efron, B. and Tibshirani, R.J. (1993). *An Introduction to the Bootstrap*. New York: Chapman and Hall.

- Elton, C.S. (1924). Periodic fluctuations in the numbers of animals: their causes and effects. *British J. of Experimental Biology*, **2**, 119-163.
- Elton, C.S. (1942). *Voles, Mice and Lemmings*. Oxford: Clarendon Press.
- Errington, P.L. (1961). *Muskrats and Marsh Management*. Lincoln: University of Nebraska Press.
- Errington, P.L. (1963). *Muskrat Populations*. Ames: Iowa State University Press.
- Framstad, E., Stenseth, N.C., Bjørnstad, O.N., and Falck, W. (1997). Limit cycles in Norwegian lemmings: tensions between phase-dependence and density-dependence. *Proc. Roy. Soc. B*, **264**, 31-38.
- Gibbons, R.D. and Pratt J. (1975). *P*-values: interpretation and methodology. *American Statisticians* **29**, 20-25.
- Hanski, I., Turchin, P., Korpimäki, E. and Henttonen, H. (1993). Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature*, **364**, 232-235.
- Hjellvik, V. and Tjøstheim, D. (1999). Modeling panels of intercorrelated autoregressive time series. *Biometrika*, **86**, 573-590.
- Krebs, C.J., Boutin, S., Boonstra, R., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K., Turkington, R. (1995). Impact of food and predation on the snowshoe hare cycle. *Science*, **269**, 1112-1115.
- Lindström, J., Kokko, H., Ranta, E., and Linden, H. (1998). Predicting population fluctuations with artificial neural networks. *Wildlife Biology*, **4**, 47-53.
- Liu, Y. and Singh, K. (1997). Notions of limiting *p* values based on data depth and bootstrap. *J. Amer. Statist. Assoc.* **92**, 266-277.
- May, R.M. (1981). Models for two interacting populations. In *Theoretical Ecology* ed by R.M. May, 78-104, Oxford: Blackwell.
- May, R.M. (1986). When two and two do not make four: nonlinear phenomenon in ecology. *Proc Roy Soc.*, **B**, **228**, 241-266.
- Mahalanobis, P.C. (1936). On the generalized distance in statistics. *Proceedings of the National Academy of Indian*, **12** 49-55.
- Press, W.H., Teukolsky, S.A., Vetterling, W.T. and Flannery, B.P. (1992). *Numerical Recipes in C*. Cambridge University Press, Cambridge.
- Shao, J. and Tu, D. (1995). *The Jackknife and Bootstrap*. New York: Springer-Verlag.
- Sharma, S. (1996). *Applied Multivariate Techniques*. New York: John Wiley & Sons.
- Stenseth, N.C. (1999). Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos*, **87**, 427-461.
- Stenseth, N.C., Bjørnstad, O.N., and Falck, W. (1996a). Is spacing behaviour coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern-oriented studies. *Proc. Roy. Soc. B*, **263**, 1423-1435.

- Stenseth, N. C., Bjørnstad, O.N., and Saitoh, T. (1996b). A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. *Proc. Roy. Soc. B*, **263**, 1117-1126.
- Stenseth, N.C., Falck, W., Bjørnstad, O.N., and Krebs, C.J. (1997). Population regulation in snowshoe hare and Canadian lynx; Asymmetric food web configurations between hare and lynx. *Proc. Natl. Acad. Sci. USA* **94**, 5147-5152.
- Stenseth, N.C., Falck, W., Chan, K.S., Bjørnstad, O.N., Tong, H., O'Donoghue, M. Boonstra, R., Boutin, S., Krebs, C.J., and Yoccoz, N.G. (1998a). From patterns to processes: Phase and density dependencies in the Canadian lynx cycle. *Proc. Natl. Acad. Sci. USA* **95**, 15430-15435.
- Stenseth, N.C., Chan, K.S., Framstad, E., and Tong, H. (1998b). Phase- and density-dependent population dynamics in Norwegian lemmings: interaction between deterministic and stochastic processes. *Proc. Roy. Soc. B*, **265**, 1957-1968.
- Stenseth, N.C., Chan, K.S., Tong, H., Boonstra, R., Boutin, S., Krebs, C.J., Post, E., O'Donoghue, M., Yoccoz, N.G., Forchhammer, M.C., and Hurrell, J.M. (1999). Common Dynamic Structure of Canada Lynx Populations Within Three Climatic Regions. *Science*, **285**, 1071-1073.
- Tong, H. (1990). *Non-Linear Time Series: A Dynamical System Approach*. Oxford: Oxford University Press.

Table 1: Fitting mink-model (3.2) to the data in the selected groups

Group	N	Regime	Intercept	Coefficient of Y_t	Coefficient of X_t	r	$\hat{\sigma}^2$
1	432	lower	-0.14 (0.11)	0.48 (0.05)	0.36 (0.08)	-0.35	0.41
		upper	-0.12 (0.06)	0.63 (0.04)	0.18 (0.08)		
2	720	lower	-0.28 (0.12)	0.11 (0.05)	0.35 (0.09)	-0.58	0.46
		upper	-0.07 (0.04)	0.43 (0.04)	0.53 (0.05)		
3	216	lower	-0.46 (0.18)	0.64 (0.10)	-0.03 (0.15)	-0.26	0.65
		upper	0.15 (0.11)	0.45 (0.10)	0.06 (0.14)		

Table 2: Fitting mink-model (3.2) to the data in the western and central areas

Area	N	Regime	Intercept	Coefficient of Y_t	Coefficient of X_t	r	$\hat{\sigma}^2$
Western	667	lower	-0.31 (0.09)	0.39 (0.05)	0.25 (0.08)	-0.35	0.44
		upper	0.09 (0.05)	0.61 (0.04)	0.20 (0.06)		
Central	989	lower	-0.19 (0.11)	0.27 (0.05)	0.29 (0.08)	-0.57	0.46
		upper	-0.09 (0.03)	0.45 (0.03)	0.53 (0.04)		

Table 3: Simulated powers of the bootstrap tests for H_0 J_0 for the four linear models.

Models tested	Hypothesis tested	Average p -value	Power ($\alpha = 0.01$)	Power ($\alpha = 0.05$)	Power ($\alpha = 0.10$)
1-2-3	H_0	0.510	0.01	0.04	0.09
	J_0	0.011	0.84	0.95	0.98
1-2-4	H_0	0.063	0.47	0.70	0.79
	J_0	0.493	0.01	0.05	0.10
1-2	H_0	0.569	0.01	0.03	0.06
	J_0	0.515	0.02	0.04	0.14
1-3	H_0	0.482	0.02	0.06	0.11
	J_0	0.029	0.70	0.82	0.92
1-4	H_0	0.058	0.54	0.72	0.84
	J_0	0.470	0.05	0.11	0.16

Figure caption

- Figure 1: (a) A map of 81 trapping posts for the mink and the muskrat in Canada in 1925 – 1949. The boreal forest is marked with a darker shading. The lighter shading refers to more open forests. (b) Time series plots of mink and muskrat data (on the natural logarithmic scale) from 8 randomly selected posts. Solid lines — mink; dashed lines — muskrats.
- Figure 2: Classification of mink-muskrat posts based on tests for hypothesis H_0 . Locations of the posts labelled according to the classification with (a) 6 clusters, and (b) 3 clusters. (c) The locations of the posts in the three selected groups from (b). Posts not in the groups are plotted without labels.
- Figure 3: Classification of mink-muskrat posts based on tests for hypothesis J_0 . Locations of the posts labelled according to the classification with (a) 5 clusters, and (b) 3 clusters.
- Figure 4: The simulation results for four linear models : (from left to right) boxplots of p -values for testing Models 1, 2 and 3, Models 1, 2 and 4, Models 1 and 2, Models 1 and 3, and Models 1 and 4. (a) Bootstrap test for H_0 . (b) Bootstrap test for J_0 .
- Figure 5: Comparison of bootstrap approximations and asymptotic approximations for distribution functions of test statistics (a) T_H in testing H_0 for the first three models, and (b) T_J in testing J_0 for Models 1 and 4. The thick solid curve is the empirical distribution of the test statistic in a simulation with 200 replications; the thin solid curve is its asymptotic distribution; three others are typical examples of bootstrap approximations.