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Sammendrag:

A bivariate bilinear time series model is introduced as a stochastic discrete time version of the deterministic Lotka-Volterra prey-predator model. It allows a discussion of how stochastic environmental variables effect the populations. Moreover, with time series methods the parameters of the model can be estimated directly from the population time series data.

Det introduseres en bivariat bilineær tidsrekkemodell som er en stokastisk versjon av bytte-jeger-modellen til Lotka og Volterra. Den tillater en drøfting av hvorledes stokastiske miljøvariabler påvirker populasjonene. Med tidsrekkemetoder kan man dessuten estimere modellens parametre direkte fra tidsrekkedata for populasjonene.

Emneord - norsk:
1. Bilineær tidsrekkemodell
2. Bytte-jeger-modellen
3. Miljøvariabler

Emneord - engelsk:
1. Bivariate bilinear time series model
2. Prey-predator model
3. Environmental variables

Boonchai K. Stensholt
Prosjektleder

Seksjonsleder

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Multivariate bilinear time series; alternative models in population dynamics?

by

Boonchai K. Stensholt

Abstract

The general form of the class multivariate bilinear time series model is given by

$$X(t) = \sum A_i \cdot X(t-i) + \sum M_j \cdot e(t-j) + \sum\sum\sum B_{dij} \cdot X(t-i) \cdot e_d(t-j) + e(t).$$

Here the state *X(T)* and noise *e(t)* are n-vectors and the coefficients *Ai, Mj,* and *Bdij* are n by n matrices. If all *Bdij = 0*, we have the class of well-known vector ARMA-models. The bilinear models include additional product terms $B_{dij} \cdot X(t-i) \cdot e_d(t-j)$; as the name indicates these models are linear in state *X(t)* and in noise *e(t)* separately, but not jointly. From a theoretical point of view, it is therefore natural to consider bilinear models in the process of extending the existing linear theory to non-linear cases.

But there are at least equally good practical reasons. Continuous-time bilinear models were studied in control theory in the 1960s (*e(t)* is the control); the name bilinear was introduced by R.R.Mohler. A large number of applications, also on ecology, made it natural to consider stochastic analogues of these deterministic models. The discrete time series versions were introduced by Granger and Anderson, 1976, but they considered only univariate models (i.e. n=1)
Multivariate versions were formulated and studied in Stensholt and Tjøstheim 1985, Stensholt and Subba Rao 1987, Stensholt 1989, and Liu 1990. The main results give conditions for stationarity, ergodicity, invertibility, and consistency of least square estimates. Computer programs have been written to find the estimates of the coefficient matrices. These have been used for simulation studies of the distribution and robustness of the estimates.

A particular reason for introducing bilinear time series in population dynamics, is that they are suitable for modelling environmental noise. One may start with a deterministic system with (constant) parameters that describe conditions which actually depend on a fluctuating environment. The idea is to replace them by stochastic parameters. As an example we consider the familiar prey-predator system

$$\frac{dN_1}{dt} = r_1 \cdot N_1 \cdot (1 - a \cdot N_1 - b \cdot N_2)\,, \quad \frac{dN_2}{dt} = r_2 \cdot N_2 \cdot (-1 + c \cdot N_1 - d \cdot N_2)$$

Linearizing about the equilibrium, replacing derivatives by differences, and adding noise terms in the coefficients lead to a single lag bilinear bivariate (i.e. n=2) model. Similar models for two competing species may be treated the same way.

1. THE BILINEAR "PARADIGM"

Consider a population growing exponentially, $N(t) = (1+r)^t \cdot N(0)$, i.e. satisfying the difference equation

$$N(t) - N(t-1) = r \cdot N(t-1) \qquad (1.1)$$

Assume the non-linear limitations to growth are not yet essential. Another important practical objection however can be that a deterministic approach is inadequate. So modify the model to be

$$N(t) - N(t-1) = r \cdot N(t-1) + e(t) \qquad (1.2)$$

where *e(t)* is the "environmental noise" which covers various relevant factors that fluctuate from season to season. Assuming the *e(t)* for different values of t are identically and independently distributed, this is a standard first order univariate autoregressive time series model. This is a linear model in the sense that the solutions N are linear in the noise *e*: if *e* is repaced by 2*e*, *2N* becomes a solution.

The idea of bilinearity can now be introduced through the growth parameter *r*. We then also assume that the environmental noise *e(t)* in season t also affects the growth rate *r* by an amount proportional to *e(t),* to become $r + b \cdot e(t)$ for some constant *b*. So the increase *N(t)-N(t-1)* is proportional both to the population and the growth rate in season *t-1*, and we now have the model

$$N(t) - N(t-1) = (r + b \cdot e(t-1)) \cdot N(t-1) + e(t) \qquad (1.3)$$

In standard notation, we have

$$N(t) = (1+r) \cdot N(t-1) + b \cdot e(t-1) \cdot N(t-1) + e(t) \qquad (1.4)$$

i.e. *N(t)* is expressed by one autoregressive, one bilinear, and one noise term. If the noise *e(t)* is considered as given, this would usually be classified as a linear difference equation in *N(t)*. However, equations of this kind has come from control engineering where *e(t)* denotes the control and *N(t)* the state variable. Since the state variable is not linear in the control

Just solve by back substitution, starting with

$$N(t) = \left[(1+r) + b \cdot e(t-1)\right] \cdot \left[(1+r) + b \cdot e(t-2)\right] N(t-2) + \left[(1+r) + b \cdot e(t-1)\right] \cdot e(t-1) + e(t)$$

and express *N(t)* by $N(t_0)$ and $e(t_0)$, $e(t_0+1)$, ... *e(t)*.

It is classified as non-linear. The term bilinear indicates that the expression for *N(t)* is linear in state and noise/control separately, but not jointly.

Wiener (1958) studied a model which in the discrete parameter takes the form

$$N(t) = \sum g_u \cdot e(t-u) + \sum \sum g_{uv} \cdot e(t-u) \cdot e(t-v) + \sum \sum \sum g_{uvw} \cdot e(t-u) \cdot e(t-v) \cdot e(t-w) + \ldots$$

Here $e(t)$ is "input) and $N(t)$ "output". Such a representation is known as the Volterra series expansion. Volterra (1930) showed that general non-linear systems can be expressed as the limit of series expansion of this type. Nisio (1960. 1961) shows that an arbitrary strictly stationary stochastic process can be approximated (in law) by a process of this form when $\{e(t)\}$ is a Gaussian white noise.

Tong (1983) discusses and gives reasons why linear models are inadequate to approximate nonlinear models. Bilinear models were originally developed by control engineers to approximate the general Volterra series expansion to a reasonable degree of accuracy (d'Allesandro, Isidori and Ruberti 1974, Brockett 1976, Sussmann 1976). This property of the bilinear models may be illustrated by back substitution of the noise term $e(t-1)$ in (1.4)

$$N(t) = (1+r)\cdot N(t-1) + b\cdot e(t-1)\cdot N(t-1) + e(t)$$
$$= (1+r)\cdot N(t-1) + b\cdot\{N(t-1) - (1+r)\cdot N(t-2) + b\cdot e(t-2)\cdot N(t-2)\}\cdot N(t-1) + e(t)$$
$$= (1+r)\cdot N(t-1) + b\cdot N(t-1)^2 - b\cdot(1+r)\cdot N(t-1)\cdot N(t-2) + b^2\cdot e(t-2)\cdot N(t-1)\cdot N(t-2)$$
$$=\ldots.etc.$$

2. A GENERAL PREY PREDATOR-DYNAMIC SYSTEM

A two species system $(N_1(t),N_2(t))$ may be modelled by

$$\frac{dN_1}{dt} = N_1\cdot G_1(N_1,N_2)\,,\ \frac{dN_2}{dt} = N_2\cdot G_2(N_1,N_2) \qquad (2.1)$$

In case $N_1(t)$ and $N_2(t)$ denote prey and predator respectively, it is assumed that:

$$\frac{\partial G_2}{\partial N_1} > 0\,,\ \frac{\partial G_1}{\partial N_2} < 0$$

Let A and B be critical prey levels for prey and predator respectively:

$G_1(N_1,N_2) < 0$ for $0< A < N_1$, $G_2(N_1,N_2) < 0$ for $0< \; < N_1 <B$.

A general phase plane analysis of this system can be done if $G_1(0,0) > 0$ and the curve $G_1 = 0$ and $G_2 = 0$ has a finite number of intersections; these are supposed to be transverse (i.e. not tangential).

If there are points (N_1,N_2) such that $G_1(N_1,N_2) >0$ and $G_2(N_1,N_2) > 0$, there exists a stable equilibrium or limit cycle. (Hirsch and Smale 1974, Ch. 12, problem4).

3. A WELL-KNOWN SPECIAL CASE

Being this general, the result is almost an a-priori insight. For specific modelling however, e.g. with stock estimation and management in mind, we must commit ourselves to more specific classes of functions. The first choice may be linear G_1 and G_2. Then (1) specializes to

$$\frac{dN_1}{dt} = r_1\cdot N_1\cdot(1-a\cdot N_1 - b\cdot N_2)\,,\ \frac{dN_2}{dt} = r_2\cdot N_2\cdot(-1+c\cdot N_1 - d\cdot N_2) \quad (3.1)$$

with *a, b, c, d* positive constants. In absence of predators *(N_2=0)* prey grows logistically between *0* and carrying capacity a^{-1}. With insufficient prey *($N_1 < c^{-1}$)*, predators cannot exist. Similarly *'b'* and *'d'* express certain living conditions, i.e. the effect on either species of the number of mutual encounters $\left(\alpha N_1 \cdot N_2\right)$. If *c>a*, there is one interesting equilibrium,

$$(N_1^*, N_2^*) = \left(\frac{b+d}{ad+bc}, \frac{c-a}{ad+bc}\right) \qquad (3.2)$$

Introducing *(X_1,X_2) = (N_1,N_2)* - (N_1^*, N_2^*) and linearizing about (N_1^*, N_2^*), one gets

$$\frac{dX_1}{dt} = r_1 \cdot N_1^* \cdot (-a \cdot X_1 - b \cdot X_2), \quad \frac{dX_2}{dt} = r_2 \cdot N_2^* \cdot (c \cdot X_1 - d \cdot X_2) \quad (3.3)$$

From *-(a+d) < 0* and *ad+bc > 0* we see that the eigenvalues have negative real parts. Hence the equilibrium (N_1^*, N_2^*) of (2) is (locally) asymptotically stable. As remarked by Hirsch and Smale, it is not easy to determine its basin of attraction, and whether there are limit cycles. (Recall that the Lotka-Volterra specialization *a=d=0* is structurally unstable with all nontrivial solutions being cyclical.)

4. A TIME SERIES VERSION

In discrete time, the analogue of (4) is:

$$X_1(t) - X_1(t-1) = r_1 \cdot N_1^* \cdot \left[-a \cdot X_1(t-1) - b \cdot X_2(t-1)\right] \qquad \text{and}$$
$$X_2(t) - X_2(t-1) = r_2 \cdot N_2^* \cdot \left[c \cdot X_1(t-1) - d \cdot X_2(t-1)\right]. \qquad (4.1)$$

Under constant conditions, the change from season *t-1* to season *t* is determined by the populations in season *t-1*. The assumption of constant conditions, both in (3.1) and (4.1) may be unrealistic. This may be improved with a *stochastic* extension.

Such an extension of a modified (3.1) has been studied (Morton and Corrsin 1969; May 1974). To keep the non-linear dynamics of (3.1) and include stochasticity as well is clearly quite difficult. So it is naturalize to linearize first. Clearly, except for small deviations from the equilibrium (3.2), much of the realism of (3.1) as a model of the dynamic mechanism may well be lost through the linearizations of (3.3) and (4.1)

However a stochastic version of (4.1) leads to a class of time series models which can offer other advantages: They are relatively simple, results exist on stationarity, invertibility, etc., and the model parameters can be estimated from observations.

First we introduce additional "noise terms" *$e_1(t)$* and *$e_2(t)$* in order to model how the changes deviate from (4.1) because of chance fluctuations in relevant living conditions (temperature, precipitation, alternative food supplies, etc.) which make season *t* good or bad. These added forms of *$e_1(t)$* and *$e_2(t)$* express the composite influence of such causes on the survival in season *t* from prey and predator, respectively.

Next we assume that this noise also influence some of the parameters of the model. For example, we may add terms $\alpha e_1(t-1)$ and $\alpha e_2(t-1)$ to the birth rate r_1 and r_2 in (5). Thus we arrive at a model

$$\begin{bmatrix} X_1(t) \\ X_2(t) \end{bmatrix} = \begin{bmatrix} e_1(t) \\ e_2(t) \end{bmatrix} + \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \cdot \begin{bmatrix} X_1(t-1) \\ X_2(t-2) \end{bmatrix} + \begin{bmatrix} b_{111} & b_{112} \\ b_{121} & b_{122} \end{bmatrix} \cdot e_1(t-1) \cdot \begin{bmatrix} X_1(t-1) \\ X_2(t-1) \end{bmatrix}$$
$$+ \begin{bmatrix} b_{111} & b_{112} \\ b_{121} & b_{122} \end{bmatrix} \cdot e_2(t-1) \cdot \begin{bmatrix} X_1(t-1) \\ X_2(t-1) \end{bmatrix}.$$

This is an example of *bivariate bilinear time series model.* One advantage of this type of model is that only the observed X-values are needed. The coefficients, and the distribution of the noise e, may then be *estimated* from the observations. No separate assessment of the parameters is required. On the other hand, it may then often be necessary with longer series than is available. A famous series is the Canadian for (furs of) mink (X_1) and muskrat (X_2). A least squares estimate of the matrices based on 62 years has led to

$$\begin{bmatrix} 0.58 & 0.29 \\ -0.52 & 0.79 \end{bmatrix} \cdot \begin{bmatrix} X_1(t-1) \\ X_2(t-2) \end{bmatrix} + \begin{bmatrix} 0.03 & 0.09 \\ -0.3 & 0.17 \end{bmatrix} \cdot e_1(t-1) \cdot \begin{bmatrix} X_1(t-1) \\ X_2(t-1) \end{bmatrix}$$
$$+ \begin{bmatrix} 0.30 & -0.28 \\ 0.59 & -0.44 \end{bmatrix} \cdot e_2(t-1) \cdot \begin{bmatrix} X_1(t-1) \\ X_2(t-1) \end{bmatrix}.$$

Here the negative sign of b_{222} indicated that the muskrat (X_2) population gets high enough for the growth to be slowed down as in logistic growth. The negative sign of b_{212} indicates a "diminishing return to scales" of muskrat supply in the mink's utility; notice that a_{12}, b_{212} and b_{122} are all positive. The negative a_{21} and b_{121} are obvious: more mink is bad for the muskrat.

5. MULTIVARIATE BILINEAR TIME SERIES MODELS

A general bilinear time series model with vector variable $X(t)$ may be written:

$$X(t) =$$
$$\alpha + \sum A_i \cdot X(t-i) + \sum M_j \cdot e(t-j) + \sum\sum\sum B_{dij} \cdot X(t-i) \cdot e_d(t-j) + e(t).$$

(α is a constant and its inclusion does not make the theory of (5.1) different of the model in the abstract.) In case all matrices $B_{dij} \equiv 0$, (5.1) is an ARMA model. If $B_{dij} \equiv 0$ for all $i<j$ $(i>j)$, the model is sub-diagonal (super-diagonal). The model (4.2) is both, i.e. diagonal. Bilinear time series models are comparatively recent, but systems like (4.2) and similar continuous time dynamic systems had already been studied in system theory. In system theory $X(t)$ is the state and $e(t)$ the control.

From the theoretical point of view, the bilinear models may be considered as the first choice for extension of the established linear models, as they are linear both in state and in control (noise) separately. The similarity between the control systems and the time series is obvious, but the problems to be faced are quite different. It makes an essential difference whether the "control" actually is under control or is an imposed random disturbance.

6. THEORETICAL RESULTS AND SIMULATIONS

Results about the models (5.1) concern sufficiency conditions for the existence of stationary and ergodic solutions, for (various kinds of) invertibility and consistency of the least squares estimators. An important theme has been to extend the methods of Pham and Tran (1981) from the univariate to the multivariate models.

Sufficiency criteria for stationarity and invertibility are given; they are stated as inequalities for the norms of certain matrices that contain model coefficients and expectations of stochastic terms. As an example the subdiagonal model is stationary if

$$\|A_1\| + \sum_j \sum_d \|B_{dij}\| \cdot \sigma_d < R^{-2} \cdot 2^{1-R} \text{ for all } 1 \le i \le R, \qquad (6.1)$$

where *X(t-R)* is the largest lag in the state variable *X* in any autoregressive or bilinear term, and $\sigma_d = Ee_d(t)$. To state more general results, it is convenient first to introduce a number of alternative ways of writing the model (7).

Notice how the unknown coefficient matrix entries, denoted by a vector θ, are estimated by the θ*-value* which minimizes the residual sum of squares

$$\sum_{t=1}^{n} \left[X(t) - E_\theta(X(t))\right]^T \cdot \left[X(t) - E_\theta(X(t))\right]$$

where

$$E_\theta(X(t)) =$$
$$\alpha + \sum A_i \cdot X(t-i) + \sum M_j \cdot e(t-j) + \sum\sum\sum B_{dij} \cdot X(t-i) \cdot e_d(t-j).$$

Here the *e(t-j), j>0,* actually denote values which are recursively calculated from the observations *X(t)* and from some initially chosen values by means of (5.1). Hence the *X(t-j)* in (6.2) depend on θ.

In this way models have been fitted to some existing data sets, including the well-known mink/muskrat data (1848-1911) of the Hudson Bay company. Due to a three years lag between muskrat peaks and mink peaks, the coefficient matrices A_1, A_2, A_3 were estimated. Deeming from the residual sum of squares the B_{d23} are the most relevant bilinear terms.

Moreover, the distribution of the estimated parameters have been studied by means of simulation experiments. Tables of simulation results, the FORTRAN listing for estimation of parameters, for testing stationarity and invertibility are included in Stensholt (1989).

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