



State monitoring of a population system in changing environment

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Abstract: For Lotka-Volterra population systems, a general model of *state monitoring* is presented. The model includes time-dependent environmental effects or direct human intervention (“treatment”) as control functions and, instead of the whole state vector, the densities of certain indicator species (distinguished or lumped together) are observed. *Mathematical systems theory* offers a sufficient condition for local observability in such systems. The latter means that, based on the above (dynamic) partial observation, the state of the population can be recovered, at least near equilibrium. The application of this sufficient condition is illustrated by three-species examples such as a one-predator two-prey system and a simple food chain.

1. Introduction

Conservation ecology is aimed at the maintenance of biologically valuable ecosystems by means of human intervention or treatment. The biological motivation of the present paper is a practical problem of conservation ecology: in order to propose an appropriate intervention, we have to know the time-dependent state of the system in consideration. In certain situations, it may be technically difficult or too expensive to continuously measure all state variables of the system. The question arises whether we can single out certain state variables such that, observing only these in function of time, we can recover the rest of the state variables, in other words, we can monitor the whole system. An efficient state monitoring can also facilitate a “just in time” human intervention.

In this paper, we address this *monitoring problem* in the context of a multi-species population system in a changing environment, applying tools of mathematical systems theory, such as the concept of observability and related theorems. In our case, the dynamics of the community will be described by a nonlinear system of differential equations with the vector of the densities as state variable.

We note that another basic concept of mathematical systems theory is controllability which may also be rele-

vant for conservation ecology. As a result of any abiotic effect (industrial pollution and climatic changes) the coefficients of the dynamical mathematical model of the population system may change, and these time-dependent coefficients can be considered as control functions of the considered system. At the same time, the treatment performed for conservation purposes can also be considered as control. Then the controllability of the system would imply, for example, that by an appropriate treatment the population system can be steered into a desired (equilibrium) state. In general terms, mathematical systems theory may be an instrument to set-up a theoretical background of the design of complex systems in conservation biology.

As a classical description of a simple population system, the first continuous-time deterministic model of a predator-prey interaction was proposed by Lotka (1925) and Volterra (1932). This model explained certain qualitative features of the behaviour that had been observed empirically (such as the periodic change of densities with a certain delay or the decrease and increase in time-mean density of predator and prey fish populations, respectively, due to harvesting activity.) In Volterra (1932), a detailed qualitative analysis of a generalized n -species model was given, specifying two important classes of models: in analogy with mechanical systems (the so-

called conservative systems) in case of a disturbance of a polymorphic equilibrium, the system *remains* near this equilibrium. In dissipative systems, after such a disturbance the system *returns* to the equilibrium in the long run, providing stable coexistence of the considered species. For a collection of further classical works on the subject, we refer the reader to Scudo and Ziegler (1978). For further references on the Lotka-Volterra model see, e. g., Freedman (1980) and Yodzis (1989). From the methodological point of view, it seems reasonable to start out from this classical model of population interaction, because practically any nonlinear dynamic population interaction system can be approximated by a Lotka-Volterra type system near the equilibrium.

The application of mathematical systems theory to population biology is relatively new. An early initiative was Metz (1977, see also Metz and Diekmann 1989). Controllability of Lotka-Volterra systems, using constant controls was considered in Petrosjan and Zakharov (1997). For a recent application of observers for model validation concerning a particular class of population models, see Bernard et al. (1998). In Varga (1989, 1992) general sufficient conditions for local controllability and observability of non-linear systems with invariant surface were proved in terms of mathematical systems theory and applied to Fisher's model of natural selection. These general sufficient conditions turned out to be appropriate for the analysis of other frequency dependent evolutionary models, see, e.g., Scarelli and Varga (2002) and Gámez et al. (2002). For their applications to reaction kinetics models, see Farkas (1998ab).

Regarding the approach to the analysis of the Lotka-Volterra model in terms of systems theory, a control-observation (input-output) system was considered in Szigeti et al. (2002). Applying a new system inversion method it was shown that, based on the observation of the biomass of certain species, *the time-dependent environmental effects* can be recovered.

In the present paper, the problem of state monitoring is modelled in the following way. Abiotic environmental effects are described in terms of time-dependent Malthus parameters and/or interaction coefficients as control functions (input), and the densities of certain indicator species are observed as output. A linearization method of Lee and Marcus (1971) recalled in the Appendix will be applied to find conditions for local observability. The latter means that based on the above (dynamic) observation, the state of the population can be recovered, at least near equilibrium. The application of this sufficient condition is illustrated by three-species examples such as a one-predator two-prey system and a simple food chain.

2. A general model of state monitoring of Lotka-Volterra systems

We start out from the classical n -species Lotka-Volterra system with Malthus parameters ε_i and community matrix $\Gamma=[\gamma_{ij}]_{n \times n}$. For the dynamics of density x_i of the i -th species we have

$$\dot{x}_i = x_i \left[\varepsilon_i - \sum_{j=1}^n \gamma_{ij} x_j \right] \quad (i \in \overline{1, n})$$

or, with $\varepsilon := (\varepsilon_1, \varepsilon_2, \dots, \varepsilon_n)$,

$$\dot{\mathbf{x}} = \text{Diag} \mathbf{x} [\varepsilon - \Gamma \mathbf{x}] \quad (1)$$

where $\text{Diag} \mathbf{x}$ stands for the diagonal matrix formed from vector \mathbf{x} . Let us suppose now that the system parameters may change in the function of time, as a result of abiotic effects such as pollution, any other human intervention or changing environment. For example, in a nearly natural lake the immission of juvenile and/or harvesting of mature individuals of a fish population will appear in the model as a change in the Malthus parameter (see, e. g., Nagy et al. 2002). It is also known that a variable toxic effect can result in time-dependent interaction parameters in Lotka-Volterra models (see Gragnani 2002). This time-dependence will be described by an additive term in the Malthus parameters and in the interaction coefficients, respectively: $\varepsilon_i + v_i(t)$ and $\gamma_{ij} + w_{ij}(t)$. For a technically convenient, structured model we assume first that certain (not necessarily all) Malthus parameters are affected. Define a matrix $\mathbf{P} := [p_{ij}]_{n \times n}$ such that

$$p_{ij} = \begin{cases} 1, & \text{if } i = j \text{ and } \varepsilon_i \text{ is affected} \\ 0 & \text{otherwise} \end{cases}$$

Then, the corresponding changed vector of Malthus parameters is $\varepsilon + \mathbf{P}\mathbf{v}$, where \mathbf{v} is an n -dimensional control vector.

Similarly, for the structured description of the human or environmental effect on the interaction coefficients, for each $i, j \in \overline{1, n}$, define an $n \times n$ matrix \mathbf{R}_{ij} with all items equal to zero except that with indices ij , which is 1, if γ_{ij} is affected and zero otherwise. In terms of the mapping

$$\Psi: \mathfrak{R}^{n \times n} \rightarrow \mathfrak{R}^{n \times n}, \quad \Psi(\mathbf{w}) := \sum_{i, j=1}^n w_{ij} \mathbf{R}_{ij}.$$

the effect on the community matrix can be described in the form

$$\Gamma + \Psi(\mathbf{w}).$$

Now, with the identification

$$\mathfrak{R}^n \times \mathfrak{R}^{n \times n} = \mathfrak{R}^{n+n^2},$$

considering $\mathbf{u} = (\mathbf{v}, \mathbf{w})$ as control variable, our control system takes the form

$$\dot{\mathbf{x}} = \text{Diagx}[\boldsymbol{\varepsilon} + \mathbf{P}\mathbf{v} - (\boldsymbol{\Gamma}\mathbf{x} + \boldsymbol{\Psi}(\mathbf{w}))\mathbf{x}],$$

or

$$\dot{\mathbf{x}} = \text{Diagx}(\boldsymbol{\varepsilon} - \boldsymbol{\Gamma}\mathbf{x}) + \text{Diagx}[\mathbf{P}\mathbf{v} - \boldsymbol{\Psi}(\mathbf{w})\mathbf{x}]. \quad (2)$$

Since we wish to consider the monitoring of a population system near equilibrium, let us suppose that $\boldsymbol{\Gamma}$ is invertible and $\mathbf{x}^* := \boldsymbol{\Gamma}^{-1}\boldsymbol{\varepsilon} > \mathbf{0}$. Then \mathbf{x}^* is an equilibrium state of co-existence where all species are present.

Now we consider two observation systems.

2.1 Observation of certain indicator species

Let us give now the pattern of monitoring. Suppose that for technical or economical reason we wish to observe only the densities of certain species. If the observation of this set of species turns out to be sufficient to recover the densities of the rest of the species, or in other words, the system is *observable* then in the given context these observed species can be considered as *indicators* for the whole population system, which is a methodological answer to the monitoring problem. For a convenient description of the situation when the densities of certain species are observed, fix $m \in \overline{1, n}$ and consider the indices of the observed species

$$1 \leq j_1 < j_2 < \dots < j_m \leq n.$$

Define the observation matrix

$$\mathbf{C} = [\mathbf{e}_{j_1} | \mathbf{e}_{j_2} | \dots | \mathbf{e}_{j_m}]^T.$$

Then the components of the vector $\mathbf{C}\mathbf{x}$ are the observed densities. For technical reason, instead of the observation of the actual densities, we shall consider its deviation from its equilibrium value:

$$g : \mathfrak{R}^n \rightarrow \mathfrak{R}^m, g(\mathbf{x}) := \mathbf{C}(\mathbf{x} - \mathbf{x}^*). \quad (3)$$

2.2 Observation of certain species without distinction

Assume now that we lump together species j_1, j_2, \dots, j_m , observing their ‘total density’. Define the row matrix $\mathbf{D} = [d_i]_{1 \times n}$ with

$$d_i = \begin{cases} 1, & \text{if } i = j_l \text{ with some } l \in \overline{1, m} \\ 0 & \text{otherwise} \end{cases}$$

Then the observed quantity is the deviation of the ‘total density’ from its equilibrium value:

$$h : \mathfrak{R}^n \rightarrow \mathfrak{R}, \quad h(\mathbf{x}) := \mathbf{D}(\mathbf{x} - \mathbf{x}^*). \quad (4)$$

3. Linearization of the control-observation system

In the following sections we shall present illustrative examples of monitoring systems in order to see whether we can uniquely recover the state of the whole population system, observing only certain indicator species. A key concept is local observability. Intuitively, a control-observation system (in particular, system (2), together with observation (3) or (4)) is said to be locally controllable near a given equilibrium, if to different solutions of the system there correspond different observations, at least in the neighbourhood of the equilibrium, provided the controls (environmental effects or human intervention) are small enough. A formal definition of local controllability is given in the Appendix.

For the application of the general *Theorem* of the Appendix we shall need the linearization of the considered control system *dynamics* (2) completed with *observation* equations (3) and (4), respectively. For the linearization of the dynamics we have to calculate only the Jacobian of the right-hand side of system (2) at the equilibrium, corresponding to the zero control. The linearization of observations (3) and (4) is obvious. The application of the above mentioned *Theorem* will provide local observability, no matter what the applied small controls are.

3.1 Linearization of the dynamics

For the right-hand side of dynamics (2) put

$$f(\mathbf{x}, \mathbf{u}) := f(\mathbf{x}, \mathbf{v}, \mathbf{w}) := \text{Diagx}(\boldsymbol{\varepsilon} - \boldsymbol{\Gamma}\mathbf{x}) + \text{Diagx}[\mathbf{P}\mathbf{v} - \boldsymbol{\Psi}(\mathbf{w})\mathbf{x}].$$

for $(\mathbf{x}, \mathbf{u}) \in \mathfrak{R}_+^n \times \mathfrak{R}^{n+n^2}$.

Fix $i, k \in \overline{1, n}$. Then for all $\mathbf{x} \in \mathfrak{R}_+^n$, for the corresponding partial derivative functions we have

$$D_k f_i(\mathbf{x}, \mathbf{0}) = \begin{cases} -\gamma_{ik} x_i, & \text{if } i \neq k, \\ \boldsymbol{\varepsilon}_k - \sum_{j=1}^n \gamma_{kj} x_j - \gamma_{kk} x_k, & \text{if } i = k \end{cases}$$

Since \mathbf{x}^* is an equilibrium, at \mathbf{x}^* for both $i \neq k$ and $i = k$ we obtain

$$D_k f_i(\mathbf{x}^*, \mathbf{0}) = -\gamma_{ik} x_i^*.$$

Hence the Jacobian of f with respect to the vector variable \mathbf{x} at $(\mathbf{x}^*, \mathbf{0})$ is

$$\mathbf{A} := -\text{Diagx}^* \boldsymbol{\Gamma} \quad (5)$$

3.2 Linearization of the observation

In both cases 2.1 and 2.2, the observation is actually an affine (that is, linear plus a constant) function of the state, so we have

$$g'(\mathbf{x}^*) = \mathbf{C},$$

$$h'(\mathbf{x}^*) = \mathbf{D}.$$

Remark 1. Observe that, although matrix \mathbf{A} does not depend explicitly on the Malthus parameters, the equilibrium densities actually do.

4. One-predator/two-prey system

Let us consider a three-species system where species 1 and 3 are predated by species 2, and there is no interaction between species 1 and 3. Then the community matrix is of the form

$$\begin{bmatrix} \gamma_{11} & \gamma_{12} & 0 \\ \gamma_{21} & \gamma_{22} & \gamma_{23} \\ 0 & \gamma_{32} & \gamma_{33} \end{bmatrix},$$

where

$$\gamma_{12}, \gamma_{32} > 0; \gamma_{21}, \gamma_{23} < 0. \quad (6)$$

Remark 2. Notice that the existence of intra-specific competition in all species, together with conditions (6) imply that

$$\det \Gamma = \gamma_{11}(\gamma_{22}\gamma_{33} - \gamma_{23}\gamma_{32}) - \gamma_{12}\gamma_{21}\gamma_{32} > 0.$$

Therefore, there exists an equilibrium in mathematical sense. However, for a biological equilibrium its positiveness or non-negativeness depends on the Malthus parameters, too. (Recall that $\gamma_{11}, \gamma_{22}, \gamma_{33} > 0$, $\det \Gamma \neq 0$ are necessary conditions for the dissipativeness of the considered Lotka-Volterra system, see Volterra 1931.)

4.1 Observation of a prey species

Suppose first that the density of one of the preys, say, species 3 is observed:

$$\mathbf{C} := [0 \ 0 \ 1].$$

Then, easy calculation shows that

$$\det [\mathbf{C} \mid \mathbf{CA} \mid \mathbf{CA}^2]^T = x_2^* x_3^{*2} \gamma_{32}^2 \gamma_{21} < 0,$$

implying local observability near the equilibrium \mathbf{x}^* for an arbitrary choice of intra-specific interaction parameters $\gamma_{11}, \gamma_{22}, \gamma_{33}$ and any interspecific interaction coefficients satisfying conditions (6). Thus, if this system is not far from the equilibrium, it is enough to observe the density of one prey over a time interval, and the densities of the other two species can be uniquely recovered.

4.2 Observation of the predator

Let us assume now that the density of the predator is observed:

$$\mathbf{C} := [0 \ 1 \ 0].$$

We easily obtain that

$$\begin{aligned} \Delta &:= \det [\mathbf{C} \mid \mathbf{CA} \mid \mathbf{CA}^2]^T = \\ &x_2^{*2} \{ \gamma_{21}(x_2^* \gamma_{22} \gamma_{23} + x_3^* \gamma_{23} \gamma_{33}) - \gamma_{23}(x_1^* \gamma_{21} \gamma_{11} + x_2^* \gamma_{22} \gamma_{21}) \} \\ &= x_2^{*2} \gamma_{21} \gamma_{23} (x_3^* \gamma_{33} - x_1^* \gamma_{11}). \end{aligned}$$

For the local observability it is enough to guarantee that $\Delta \neq 0$. This inequality determines a set in the parameter space with the following biological interpretation. By the equations

$$\begin{aligned} \dot{x}_1 &= \varepsilon_1 - \gamma_{11}x_1 - \gamma_{12}x_2 \\ \dot{x}_3 &= \varepsilon_3 - \gamma_{32}x_2 - \gamma_{33}x_3 \end{aligned}$$

and $\gamma_{11}x_1^*$ can be considered as loss in relative rate of increase due to the intra-specific competition in the respective prey populations at the equilibrium state. Thus, if these quantities are different for the two prey populations then $\Delta \neq 0$ and local observability near the equilibrium is guaranteed. Therefore, near equilibrium the whole population system can be monitored by observing only the predator species.

4.3 Undistinguished observation of preys

Suppose that we observe the two prey populations without distinction. This is a particular case of the model in section 2.2. Now $j_1=1, j_2=3$,

$$\mathbf{D} := [1 \ 0 \ 1]$$

and a little tedious calculation provides

$$\begin{aligned} \Delta &:= \det [\mathbf{D} \mid \mathbf{DA} \mid \mathbf{DA}^2]^T = - \{ (\gamma_{11}x_1^* - \gamma_{33}x_3^*) \\ &(\gamma_{11}\gamma_{12}x_1^{*2} + \gamma_{12}\gamma_{22}x_1^*x_2^* + \gamma_{32}\gamma_{22}x_3^*x_2^* + \gamma_{33}\gamma_{32}x_3^{*2}) \\ &+ (\gamma_{12}x_1^* + \gamma_{32}x_3^*) [\gamma_{33}^2x_3^{*2} - \gamma_{11}^2x_1^{*2} + x_2^* (\gamma_{23} - \gamma_{21}) \\ &(\gamma_{12}x_1^* + \gamma_{32}x_3^*)] \} \end{aligned}$$

Suppose now that, contrary to the hypothesis of the previous section, at the equilibrium state the loss in relative rate of increase due to the intra-specific competition is the same for both prey populations: $\gamma_{11}x_1^* = \gamma_{33}x_3^*$. In particu-

lar this is the case when there is no intra-specific competition in either of the prey populations. Then, we have

$$\Delta = -(\gamma_{12}x_1^* + \gamma_{32}x_3^*)^2 x_2^* (\gamma_{23} - \gamma_{21}).$$

Assume in addition that for the predator the increase in relative growth rate due to its predation on species 1 and 3 is different ($\gamma_{21} \neq \gamma_{23}$). Then, the observation of both prey species lumped together results in local observability near the equilibrium. Thus, whenever small change in the environment and the human intervention is “soft enough”, the whole system state can be monitored observing only the prey populations without distinction.

Remark 3. The basic conditions for local observability in sections 4.2 and 4.3 are complementary: $\gamma_{11}x_1^* \neq \gamma_{33}x_3^*$ and $\gamma_{11}x_1^* = \gamma_{33}x_3^*$ respectively. This means that, near the equilibrium, for the monitoring of the whole population system in case a) the observation of the density of the predator population is reasonable. In case b) the undistinguished observation of the two prey populations is enough, provided that for the predator the “net conversion rates” γ_{21} and γ_{23} are different.

5. Food chain

Let us consider now a simple food chain of three species. Species 1 is a plant consumed by the herbivorous species 2 that is in turn predated by the carnivorous species 3. Then, the community matrix has the same structure as in the one-predator/two-prey system except for the sign conditions of (6), which are substituted by conditions corresponding to the chain structure:

$$\gamma_{12}, \gamma_{23} > 0; \quad \gamma_{21}, \gamma_{32} > 0; \quad (7)$$

5.1 Observation of the plant population

With $C := [1 \ 0 \ 0]$ we easily get

$$\det [C \mid CA \mid CA^2]^T = -x_1^* x_2^* x_3^* \gamma_{12}^2 \gamma_{23} < 0,$$

implying again local observability without any further condition.

5.2 Observation of the predator

Now we have $C := [0 \ 0 \ 1]$ and

$$\det [C \mid CA \mid CA^2]^T = -x_2^* x_3^* \gamma_{32} \gamma_{21} > 0,$$

implying local observability again without any further requirements on the interaction parameters.

Remark 4. Let us emphasize that in the above cases of observation of the food chain the presence or absence of intra-specific competition turned out to be indifferent.

6. Discussion

For the dynamic monitoring of the state of a population system, a control-observation model of mathematical systems theory has been suggested, where the inputs (control functions) are the time-dependent coefficients of a Lotka-Volterra model undergoing environmental effects or direct human intervention. A sufficient condition for local observability of non-linear systems can guarantee that observing only certain indicator species, the densities of the rest of the species can be, in principle, uniquely recovered, at least near equilibrium. The local character of this observability result is not very restrictive, if the underlying Lotka-Volterra system is either conservative or dissipative, since in such cases the system has the tendency to be near the equilibrium state of coexistence. In the illustrative three-species examples, by checking ranks of matrices calculated from the parameters of the reference system, the following results have been obtained.

If we observe the density of a prey in a one-predator two-prey system, or the density of the plant in a plant-herbivorous-predator food chain, then local observability is obtained without any further conditions either on the Malthus parameters or on the coefficients of the intra-specific competition.

For the state monitoring of a one-predator/two-prey system near the equilibrium the following sufficient conditions for local observability have been proved: If the loss in relative rate of increase due to the intra-specific competition within the two prey populations is different in the equilibrium state then the observation of the predator is sufficient. If the above loss in the relative rate of increase is the same for both prey populations but the predator converts the two preys at different rates, then for state monitoring it is enough to observe the prey populations lumped together.

If we observe both prey populations lumped together, then to guarantee local observability we need that for the predator the increase in relative growth rate due to predation on the single prey species is different.

According to the concept of local observability, a general conclusion is that for small environmental effects observability does not depend on the presence of these effects. This result makes our approach applicable to population systems in *slightly changing environments and with “soft” human treatment* as well. For an effective application of the proposed methodology of mathematical systems theory, a further development of efficient numerical methods will be necessary.

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Appendix

Here, in technical terms we recall the concept of local observability near equilibrium of a non-linear system and a sufficient condition to guarantee this property. With certain technical simplifications, our treatment is based on Lee and Markus (1971).

Given positive integers m, n, r , suppose that the functions

$$f: \mathfrak{R}_+^n \times \mathfrak{R}^r \rightarrow \mathfrak{R}^n, \quad g: \mathfrak{R}^n \rightarrow \mathfrak{R}^m$$

are continuously differentiable and for some $\mathbf{x}^* \in \mathfrak{R}^n$ we have $f(\mathbf{x}^*, \mathbf{0}) = \mathbf{0}$ and $g(\mathbf{x}^*) = \mathbf{0}$. Then the differential equation

$$\dot{\mathbf{x}} = f(\mathbf{x}, \mathbf{u}) \tag{A1}$$

is considered as a *control system* with a time-dependent, piece-wise continuous control parameter (control function) \mathbf{u} , \mathbf{x}^* is an equilibrium of the ('uncontrolled' or 'zero input') reference system. Given a positive T , there exists a neighbourhood of \mathbf{x}^* such that any solution of (A1) starting from this neighbourhood is defined on the interval $[0, T]$. Together with dynamics (A1), consider that

$$\mathbf{y}(t) := g(\mathbf{x}(t)) \quad (t \in [0, T]) \tag{A2}$$

is the *observed function*.

Definition. The control-observation system (A1)-(A2) is called *locally observable near the equilibrium \mathbf{x}^** over the interval $[0, T]$, if there exists $\varepsilon > 0$, such that for any control function \mathbf{u} with $|\mathbf{u}(t)| < \varepsilon$ ($t \in [0, T]$) and any two different solutions \mathbf{x} and $\bar{\mathbf{x}}$ of system (A1) with $|\mathbf{x}(t) - \bar{\mathbf{x}}(t)| < \varepsilon$ and $|\bar{\mathbf{x}}(t) - \mathbf{x}^*| < \varepsilon$ ($t \in [0, T]$), the observed functions $g(\mathbf{x}(t))$ and $g(\bar{\mathbf{x}}(t))$ ($t \in [0, T]$) are different.

For the formulation of a sufficient condition for local observability consider the linearization of the control-observation system (A1)-(A2), consisting in the calculation of the Jacobians

$$\mathbf{A} := D_1 f(\mathbf{x}^*, \mathbf{0}) \quad \text{and} \quad \mathbf{C} := g'(\mathbf{x}^*).$$

We have the following

Theorem. Suppose that

$$\text{rank}[\mathbf{C} | \mathbf{C}\mathbf{A} | \mathbf{C}\mathbf{A}^2 | \dots | \mathbf{C}\mathbf{A}^{n-1}]^T = n.$$

Then, the control-observation system (A1)-(A2) is locally observable near the equilibrium \mathbf{x}^* .

Throughout the main body of the paper, for the sake of simplicity, the term 'local observability near the equilibrium' is always used without reference to the fixed time interval $[0, T]$.