# OBSERVABILITY AND OBSERVERS IN A FOOD WEB

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ABSTRACT. The problem of the possibility to recover the time-dependent state of a whole population system out of the observation of certain components has been studied in earlier publications, in terms of the observability concept of mathematical systems theory. In the present note a method is proposed to effectively calculate the state process. For an illustration an observer system for a simple food web is numerically constructed.

## 1. INTRODUCTION.

In population ecology and conservation biology we often face the problem of planning an appropriate control of a population system into a desired state. However, before any human intervention we have to know the actual state of the system. In many cases, for technical or/and economical reason we observe (measure) only certain components of the state vector. Then, in a dynamical setting, from the observed components we have to recover the whole state process. The concept of observability of mathematical systems theory can guarantee at theoretical level that the state process can be determined from the observation in a unique way. However, the corresponding results don't give a constructive method to calculate the state process. In this note we propose the application of a so-called observer system (or shortly observer), which makes it possible to effectively calculate the whole state process, on the basis of the observed (indicator) species, at least asymptotically, near the equilibrium.

A general sufficient condition for the local observability of nonlinear dynamical systems with invariant manifold was developed and applied by [1]. Later, this result became a useful tool in the analysis of different frequency-dependent models of population genetics, evolutionary theory [2], [3], [4] and reaction kinetics ([5], [6]). Observability problems for particular Lotka-Volterra models were considered in [7]. In [8] sufficient conditions were obtained to guarantee local observability of a simple trophic chain.

The design of observers for nonlinear observation systems is a widely studied area of mathematical systems theory, motivated mainly by problems of control engineering. In this note we apply the recent results by [9], to design a local exponential observer for a 5-species food web. A numerical illustration is also presented.

## 2. MODEL DESCRIPTION AND OBSERVABILITY

We consider a food web with five species: one carnivore, two different herbivores and two different plants, where the interaction between the species can be described in the following way. On the one hand, species 3 (carnivore) is fed on species 2 (herbivore A) which is fed on species 1 (plant A). On the other hand, species 3 also is fed on species 4 (herbivore B) which is fed on species 5 (plant B). There

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is no other interspecific interaction. In order to reduce the calculations we also suppose that intraspecific interaction in every single species, except species 3, can be neglected. Therefore, the community matrix has the form

$$\Gamma = \begin{bmatrix} 0 & \gamma_{12} & 0 & 0 & 0 \\ \gamma_{21} & 0 & \gamma_{23} & 0 & 0 \\ 0 & \gamma_{32} & \gamma_{33} & \gamma_{34} & 0 \\ 0 & 0 & \gamma_{43} & 0 & \gamma_{45} \\ 0 & 0 & 0 & \gamma_{54} & 0 \end{bmatrix} \tag{2.1}$$

with

$$\gamma_{33} > 0, \quad \gamma_{21},\ \gamma_{32},\ \gamma_{34},\ \gamma_{45}\ < 0 \quad \text{and} \quad \gamma_{12}, \gamma_{23},\ \gamma_{43}, \gamma_{54}\ > 0. \tag{2.2}$$

We suppose that the Lotka-Volterra model describes the behaviour of these species, such that for the time-dependent density $x_i$ of the $i^{th}$-species we have the differential equation

$$\dot{x}_i = f_i(x_1, x_2, x_3, x_4, x_5) := x_i[\epsilon_i - \sum_{j=1}^{5} \gamma_{ij} x_j]; \qquad i \in \{1, 2, \ldots, 5\} \tag{2.3}$$

where $\epsilon_i$ are the Malthus parameters and $\Gamma$ is the above community matrix, $x = (x_1, \ldots, x_5)$ represents the state vector of the population; and define $f : \mathbb{R}^5_+ \to \mathbb{R}^5$ with $f = (f_1, \ldots, f_5)$. (For the basic applications of the Lotka-Volterra models in the study of food webs see e.g. [10]).

Throughout the paper we shall suppose that there exists a unique state of coexistence in the system in the sense that $\Gamma$ is invertible and the equilibrium $x^* = \Gamma^{-1}\epsilon$ is positive ($x^* \in \mathbb{R}^5_+$).

For a convenient description of the observation situation when certain coordinates (or their sum) are observed, fix $m \in \{1, 2, 3, 4\}$ and the indices of the observed components of the system $1 \leq j_1 < \ldots < j_m \leq 5$.

Now, in terms of the corresponding basic unit vectors $e_{j_1}, \ldots, e_{j_m}$ of $\mathbb{R}^5$ we define the observation matrix $C = [e_{j_1} \mid \ldots \mid e_{j_m}]^T$.

Then, for any state vector $x \in \mathbb{R}^5$, the components of the vector $Cx$ are the observed coordinates. For technical reason, instead of the observation of the actual densities, we shall consider their deviation from their equilibrium values:

$$h : \mathbb{R}^5_+ \to \mathbb{R}^m, \qquad h(x) := C(x - x^*). \tag{2.4}$$

To keep the amount of calculations at a reasonable level, and to obtain still biologically interpretable algebraic conditions, in this paper we will only consider the observation of one or two coordinates of the state vector.

It may also be convenient or necessary to observe certain species without distinction. If these are species with indices $1 \leq k_1 < k_2 < \ldots < k_r \leq 5$ with some $r \in \{1, \ldots, 5\}$, then in the observation function of (2.4) we put a row matrix $C$ with 1 in the positions $k_1, \ldots, k_r$, and zero elsewhere.

In the Appendix we recall the linearization method of [11] which gives a general sufficient condition for local observability of nonlinear systems. Now, we shall use this method in order to obtain conditions for local observability of the considered observation system.

*i) Observation of the carnivore species*

Let us observe the time varying density of species 3 (carnivores), i.e., the coordinate $x_3$ of the state of system (2.3), defining the observation matrix as $C := [0\ 0\ 1\ 0\ 0]$. For the application of the Theorem A1 of the Appendix, calculate the matrix $A := f'(x^*)$. Fix $i, k \in \{1, \dots, 5\}$. Then, for all $x \in \mathbb{R}^5_+$, for the partial derivative functions we have

$$D_k f_i(x) = \begin{cases} -\gamma_{ik} x_i & \text{if} \quad i \neq k, \\ \epsilon_k - \sum_{j=1}^{5} \gamma_{kj} x_j - \gamma_{kk} x_k & \text{if} \quad i = k \end{cases}$$

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

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

Hence the Jacobian of $f$ at $x^*$ is

$$A := -Diag\, x^*\, \Gamma = - \begin{bmatrix} 0 & \gamma_{12} x_1^* & 0 & 0 & 0 \\ \gamma_{21} x_2^* & 0 & \gamma_{23} x_2^* & 0 & 0 \\ 0 & \gamma_{32} x_3^* & \gamma_{33} x_3^* & \gamma_{34} x_3^* & 0 \\ 0 & 0 & \gamma_{43} x_4^* & 0 & \gamma_{45} x_4^* \\ 0 & 0 & 0 & \gamma_{54} x_5^* & 0 \end{bmatrix}. \tag{2.5}$$

Hence we obtain that

$$det[C \mid CA \mid CA^2 \mid CA^3 \mid CA^4] = -\gamma_{21}\gamma_{32}^2\gamma_{34}^2\gamma_{45} x_2^* (x_3^*)^4 x_4^* (\gamma_{12}\gamma_{21} x_1^* x_2^* - \gamma_{45}\gamma_{54} x_4^* x_5^*)^2,$$

and by Theorem A1 of Appendix, we have the following

**Theorem 2.1.** *Suppose that for the food chain described in Section 2 with community matrix (2.1), the interspecific interaction coefficients satisfy (2.2) and*

$$\gamma_{12}\gamma_{21} x_1^* x_2^* \neq \gamma_{45}\gamma_{54} x_4^* x_5^*. \tag{2.6}$$

*Then system (2.3) with the observation of the carnivore species is locally observable near equilibrium $x^*$.*

Thus, whenever an abiotic effect (change in the environment or a human intervention causing a deviation from the equilibrium) is small enough, the whole system state can be monitored only observing the carnivore population.

In the following we shall see some parallel statements for different observation situations.

*ii) Undistinguished observation of herbivore species*

Let us suppose we observe the two herbivore populations, i.e., species 2 and 4, without distinction. Then the observation matrix is $C := [0, 1, 0, 1, 0]$.

Suppose now that, contrary to the hypothesis (2.6) of the previous subsection, the following equality holds:

$$\gamma_{12}\gamma_{21} x_1^* x_2^* = \gamma_{45}\gamma_{54} x_4^* x_5^*. \tag{2.7}$$

Then we obtain that $det[C \mid CA \mid CA^2 \mid CA^3 \mid CA^4]$ is

$$\gamma_{12}\gamma_{21}^2\gamma_{33}\gamma_{45}(\gamma_{32} - \gamma_{34})^2(\gamma_{23} x_2^* + \gamma_{43} x_4^*)^3 x_1^* (x_2^*)^2 (x_3^*)^3 x_4^*.$$

Assume in addition that for the predator the "net conversion rate", i.e. the increase in relative growth rate due to its predation on species 2 and 4 is different ($\gamma_{32} \neq \gamma_{34}$). Then by condition (2.2) and the positivity of the equilibrium, applying Theorem A1 of Appendix, we obtain that the observation of both herbivore species lumped together results in local observability near the equilibrium.

*Remark.* The basic conditions (2.6) and (2.7) for local observability in the above cases i) and ii), respectively, are complementary. This means that, near the equilibrium, for the monitoring of the whole population system in case i) the observation of the density of the predator population is reasonable. In case ii) the undistinguised observation of the two herbivore populations is enough, provided that for predator the net conversion rates $\gamma_{32}$ and $\gamma_{34}$ are different.

*iii) Observation of a plant species*

Let us observe now the time-dependent density of species 1 (plant of type A), i.e., the coordinate $x_1$ of the state of system (2.3), defining the observation matrix as $C := [1\ 0\ 0\ 0\ 0]$.

Then it is easy to see that the columns of partitioned matrix $[C \mid CA \mid CA^2 \mid CA^3 \mid CA^4]$ are linearly independent. Therefore, $rank[C \mid CA \mid CA^2 \mid CA^3 \mid CA^4]^T = 5$ and by Theorem A1 of Appendix we obtain that observing only the plant species 1 the whole system state can be monitored.

## 3. Construction of local observer

Now we shall construct a local observer system for the model (2.3) with observation of the carnivore species, applying a theorem of [9] recalled in the Appendix.

With matrices $A$ in (2.5) and $C := [0\ 0\ 1\ 0\ 0]$ we shall suppose that the hypotheses of Theorem 2.1 are satisfied. Then the considered system is locally observable at $x^*$. Now, we are going to define a matrix $K$ such that $A - KC$ is stable. Thus, by Theorem A2 of Appendix we shall obtain the required local exponential observer system.

Let us define

$$K := col[k_1 \quad k_2 \quad k_3 \quad k_4 \quad k_5] \tag{3.1}$$

where $k_1 = k_2 = k_4 = k_5 = 0$ and $k_3 > 0$.

Then by the Routh-Hurwitz criterion (see e.g. [12]), matrix $A - KC$ is stable and therefore, by Theorem A1 of the Appendix we obtain the required local exponencial observer for system (2.3) with $\Gamma$ given in (2.1) and with the observation of the carnivore species.

Summing up the above reasoning, we have the following

**Theorem 3.1.** *Let us suppose that for the food chain described in Section 2 the conditions of Theorem 2.1 are fulfilled, $x^*$ is Lyapunov stable and dynamical system*

$$\dot{z} = f(z) + K[y - h(z)] \tag{3.2}$$

*with matrix $K$ defined in (3.1), is a local exponencial observer for system (2.3) with the observation of the carnivore species.*

*Illustrative example*

We consider the food chain described in Section 2 with the following parameters and the observation of the carnivore species

$$\begin{aligned}
\dot{x}_1 &= x_1(0.9 - 4x_2)\\
\dot{x}_2 &= x_2(2 + 6x_1 - 4.5x_3)\\
\dot{x}_3 &= x_3(0.8 + 4x_2 - 2.6x_3 + 5.8x_4)\\
\dot{x}_4 &= x_4(3 - 4x_3 + 2.8x_5)\\
\dot{x}_5 &= x_5(0.25 - 3x_4)\\
y &= x_3 - x_3^*,
\end{aligned}$$

where the positive equilibrium is $x^* = (0.296474, 0.225, 0.839744, 0.0833333, 0.128205)$.

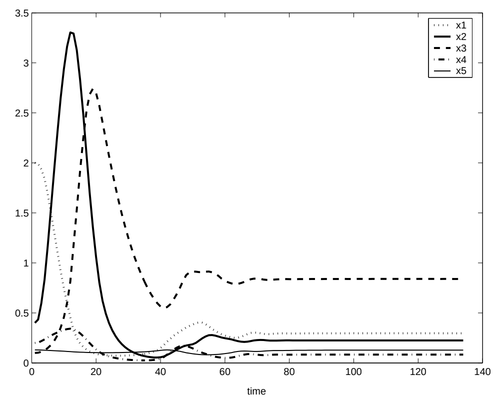


FIGURE 1. State process of the food chain

Linearizing the system we obtain the following matrices

$$A = \begin{bmatrix} 0 & -0.9 & 0 & 0 & 0 \\ 1.35 & 0 & -1.0125 & 0 & 0 \\ 0 & 3.35898 & 0 & 4.87052 & 0 \\ 0 & 0 & -0.333333 & 0 & 0.233333 \\ 0 & 0 & 0 & -0.384615 & 0 \end{bmatrix} \quad \text{and} \quad C = \begin{bmatrix} 0 & 0 & 1 & 0 & 0 \end{bmatrix}.$$

It is easy to check that conditions (2.6) of Theorem 2.1 are verified, and matrix $A$ is stable (see also Figure 1). Therefore, we can guarantee that considered system is locally observable. In order to construct the corresponding local observer system we define matrix $K$ as $K = col\,[0\ 0\ 1\ 0\ 0]$.

Then with this choice, if we calculate the eigenvalues of matrix $A-KC$ we obtain that it is stable. Then, Theorem 3.1 also provides a local exponencial observer system,

$$\begin{aligned} \dot{z}_1 &= z_1(0.9 - 4z_2) \\ \dot{z}_2 &= z_2(2 + 6z_1 - 4.5z_3) \\ \dot{z}_3 &= z_3(0.8 + 4z_2 - 2.6z_3 + 5.8z_4) + x_3 - z_3 \\ \dot{z}_4 &= z_4(3 - 4z_3 + 2.8z_5) \\ \dot{z}_5 &= z_5(0.25 - 3z_4). \end{aligned}$$

The error vector $e = z - x$ satisfies the dynamics

$$\begin{aligned} \dot{e}_1 &= 0.9e_1 - 4(e_1 + x_1)(e_2 + x_2) + 4x_1x_2 \\ \dot{e}_2 &= 2e_2 + 6(e_1 + x_1)(e_2 + x_2) - 6x_1x_2 - 4.5(e_2 + x_2)(e_3 + x_3) + 4.5x_2x_3 \\ \dot{e}_3 &= 0.8e_3 + 4(e_2 + x_2)(e_3 + x_3) - 4x_2x_3 - 2.6(e_3 + x_3)^2 + 2.6x_3^2 \\ &\quad +5.8(e_3 + x_3)(e_4 + x_4) - 5.8x_3x_4 - e_3 \\ \dot{e}_4 &= 3e_4 - 4(e_3 + x_3)(e_4 + x_4) + 4x_3x_4 + 2.8(e_4 + x_4)(e_5 + x_5) - 2.8x_4x_5 \\ \dot{e}_5 &= 0.25e_5 - 3(e_4 + x_4)(e_5 + x_5) + 3x_4x_5. \end{aligned}$$

In Figure 2 we present a simulation to show how the error vector trajectories tend to zero. We have considered the following initial conditions

$$x(0) = (2.00, 0.40, 0.10, 0.20, 0.13) \quad ; \quad z(0) = (2.03, 0.90, 0.35, 0.28, 0.16)$$

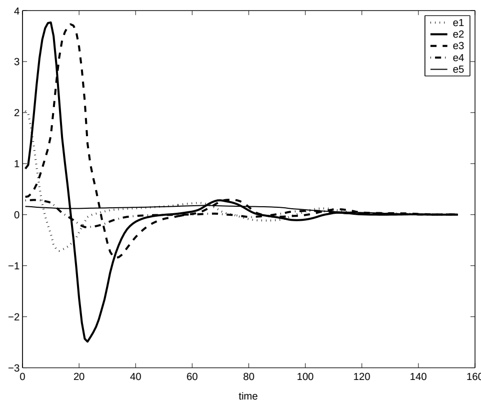


FIGURE 2. Error vector trajectories

## 4. Conclusion

For many actual problems of ecology and conservation biology an efficient monitoring methodology is a key issue. Mathematical systems theory offers tools to recover the whole state process of a population system, from the observation of certain indicator species. Under the condition of stable coexistence of all species, near this equilibrium an observer system can be constructed such that the solution of the latter asymptotically provides the state process, with an exponential velocity of convergence. From the construction of the observer system it can be seen that, with the appropriate choice of an auxiliary matrix, the transient period of the approximation can be shortened, speeding up the convergence to the required state process.

The same methodology in principle also applies to food webs with higher number of species involved, however, the biological interpretation of the algebraic conditions on the model parameters may be more difficult.

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## Appendix

First we recall in technical terms the concept of local observability near the equilibrium of a nonlinear system and a sufficient condition which guarantees this property. With certain technical simplifications, our treatment is based in [11].

For a continuously differentiable function $f : \mathbb{R}^n \to \mathbb{R}^n$ $(n \in \mathbb{N})$, we consider the system

$$\dot{x} = f(x). \tag{4.1}$$

Let $x^* \in \mathbb{R}^n$ be such that $f(x^*) = 0$, that is, an equilibrium for (4.1). Given $T > 0$, there exists a neighbourhood of $x^*$ such that any solution of (4.1) starting at a point of this neighbourhood, can be continued in the interval $[0, T]$.

For given $m \in \mathbb{N}$ let $h : \mathbb{R}^n \to \mathbb{R}^m$ be a continuously differentiable function such that $h(x^*) = 0$, and consider the observation system

$$\begin{cases} \dot{x} &= f(x) \\ y(t) : &= h(x(t)), \quad t \in [0, T] \end{cases} \tag{4.2}$$

where $y$ is interpreted as an observed function for system (4.1).

**Definition 4.1.** Observation system (4.2) is called locally observable near the equilibrium $x^*$ over the interval $[0, T]$, if there exists $\epsilon > 0$, such that for any two different solutions $x$ and $\overline{x}$ of system (4.1) with $\mid x(t) - x^* \mid < \epsilon$ and $\mid \overline{x}(t) - x^* \mid < \epsilon \quad (t \in [0, T])$, the observed functions $h(x(t))$ and $h(\overline{x}(t)) \quad (t \in [0, T])$ are different.

For the formulation of a sufficient condition for local observability, let us consider the linearization of the observation system (4.2), consisting in the calculation of the Jacobians $A := f'(x^*)$ and $C := h'(x^*)$.

From [11] we have the following

**Theorem A1:** *Suppose that*

$$rank[C \mid CA \mid CA^2 \mid \ldots \mid CA^{n-1}]^T = n. \tag{4.3}$$

*Then observation system (4.2) is locally observable near the equilibrium $x^*$.*

Throughout the main body of the paper, for the sake of simplicity, the term "local observability near the equilibrium" is always used without reference on the fixed time interval $[0, T]$.

Now, keeping the above notation let us consider observation system (4.2) over the interval $[0, +\infty[$. We recall the result of [9] we apply for the observer design.

**Theorem A2:** *Suppose that $x^*$ is a Lyapunov stable equilibrium of system (4.1), rank condition (4.3) holds, and there exists an $n \times m$ matrix $K$ such that $A - KC$ is a stable matrix (i.e. all its eigenvalues have negative real parts). Then system*

$$\dot{z} = f(z) + K[y - h(z)] \tag{4.4}$$

*is a local exponential observer for observation system (4.2). (The latter means that substituting a concrete observed function* $y$ *of system (4.2), near equilibrium* $x^*$*, we can approximate the state* $x$ *by a solution of (4.4), at an exponential rate).*

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