Monitoring in a Lotka-Volterra model

I. López, M. Gámez, J. Garay, Z. Varga

Abstract

The problem of monitoring arises when in an ecosystem, in particular in a system of several populations, observing some components, we want to recover the state of the whole system in function of time. Due to the difficulty to construct exactly this state process, we look for an auxiliary system called *observer*, the solution of which reproduces this process with certain approximation. This means, that the solution of the observer tends to that of the original system.
For this work an important concept is observability which means, that from the observation it is possible to recover the state process in a unique way, however without determining a constructive method to obtain it. If observability holds for the original system, it guarantees the existence of an auxiliary matrix which makes it possible to construct an observer of the system.
The considered system of populations is described by the classical Lotka-Volterra model with one predator and two preys and the construction of its observer is illustrated with a numerical example. Finally, it is shown how the observer can be used for the estimation of the level of an abiotic effect on the population system.

Key words: population system, observability, observer system.

1 Introduction

A particular problem of monitoring arises when in an ecosystem with several populations we observe only the density of certain population(s) considered indicator(s), and we want to recover the state of the whole system in function of time. Such a partial observation may be convenient when the direct observation of state of all considered populations is technically complicated or expensive.

In solving this problem a key concept is the observability which means that from the observation of a transformed of the time-dependent state, it is possible to recover the original state process in function of time in a unique way. A simple algebraic condition can guarantee local observability near an equilibrium, however, it does not provide a method to reconstruct the original state process. Therefore we shall construct an auxiliary system called observer whose solution tends to that of the original system.

This condition also was applied to several models in genetic populations and to frequency dependent evolutionary models in López (2003), López et al. (2003, 2004). Observability was analyzed in Varga et al. (2002, 2003) in different Lotka-Volterra models, in Shamandy (2005) in simple trophic chains. Bernard et al. (1998) used observers for the validation of a phyto-planktonic growth model. We also notice, that based on a general theorem of Varga (1992), observability in different frequency-dependent population models was studied in López (2003) and López et al. (2003, 2004).

In this work we shall use a general sufficient condition for observability of nonlinear observation systems, proved by Lee and Markus (1971).

For construction of the observers, we shall apply a local observer design method for nonlinear systems presented in Sundarapandian (2002).

2 Concept of Observability

Given m, n positive integers, we suppose that the following functions

$$f : \mathbb{R}^n \to \mathbb{R}^n, \qquad h : \mathbb{R}^n \to \mathbb{R}^m$$

are continuously differentiable and for some $x^* \in \mathbb{R}^n$ we have that $f(x^*) = 0$ and $h(x^*) = 0$.

We consider the following observation system

$$\dot{x} = f(x) \tag{2.1}$$

$$y = h(x) \tag{2.2}$$

where h is the observation function.

Definition 2.1 *Observation system (2.1)-(2.2) is called locally observable near the equilibrium* x^* *over a given time interval* $[0,T]$, *if there exists* $\epsilon > 0$, *such that for any two different solutions* x *and* $\overline{x}$ *of system (2.1) with* $| x(t) - x^* | < \epsilon$ *and* $| \overline{x}(t) - x^* | < \epsilon$ $(t \in [0,T])$, *the observed functions* $h \circ x$ *and* $h \circ \overline{x}$ *are different. (*$\circ$ *denotes the composition of functions. For brevity, the reference to* $[0,T]$ *shall be omitted).*

For the formulation of a sufficient condition for local observability consider the linearization of the observation system (2.1)-(2.2), consisting in the calculation of the Jacobians

$$A := f'(x^*) \qquad \text{and} \qquad C := h'(x^*).$$

Theorem 2.2 (Lee and Markus, 1971). *Suppose that*

$$rank[C \mid CA \mid CA^2 \mid \ldots \mid CA^{n-1}]^T = n. \tag{2.3}$$

Then the observation system (2.1)-(2.2) is locally observable near the equilibrium x^*.

3 Application to a predator-prey model

We consider the biological model of 2 preys and 1 predator of the form $\dot{x} = f(x)$, determined by the following differential system

$$\begin{aligned} \dot{x}_1 = &\quad x_1(a_1 - b_{11}x_1 - b_{12}x_2) \\ \dot{x}_2 = &\quad x_2(-a_2 + b_{21}x_1 - b_{22}x_2 + b_{23}x_3) \\ \dot{x}_3 = &\quad x_3(a_3 - b_{32}x_2 - b_{33}x_3) \end{aligned} \tag{3.1}$$

with $a_i, b_{ij} > 0$ for all $i, j = 1, 2, 3$.

It is easy to provide a simple algebraic condition for the existence of an equilibrium in mathematical sense, however its positivity depends on the model parameters. Throughout the paper we shall suppose that there exists an equilibrium $x^* > 0$ for the considered model.

Observation of preys without distinction

We suppose that we observe the total quantity of population preys without distinction between them, i.e., the observation equation is

$$y = h(x) = x_1 + x_3 - x_1^* - x_3^*.$$

Then

$$C = \frac{\partial h}{\partial x}(x^*) = [1 \quad 0 \quad 1]$$

and linearizing the Lotka-Volterra system (3.1) we obtain

$$A = \frac{\partial f}{\partial x}(x^*) = \begin{bmatrix} -b_{11}x_1^* & -b_{12}x_1^* & 0 \\ b_{21}x_2^* & -b_{22}x_2^* & b_{23}x_2^* \\ 0 & -b_{32}x_3^* & -b_{33}x_3^* \end{bmatrix}.$$

We suppose that at equilibrium state the loss in relative rate of increase due to the intra-specific competition is the same for the two prey species (see Varga et al. 2003):

$$b_{11}x_1^* = b_{33}x_3^*.$$

(In particular, this is the case when there is no intra-specific competition in either of the prey populations).

Then

$$det[C \mid CA \mid CA^2]^T = -(b_{12}x_1^* + b_{32}x_3^*)^2 x_2^*(b_{21} - b_{23}).$$

Assume in addition that for the predator the increase in relative growth rate due to its predation on species 1 and 3 is different

$$b_{21} \neq b_{23}.$$

Then by Theorem 2.2 the system is locally observable near the equilibrium: the whole system state can be monitored observing only the prey populations without distinction.

4 Construction of an observer system

Now we prove that system (3.1) is asymptotically stable for an equilibrium $x^* = (x_1^*, x_2^*, x_3^*)$.

In the positive octant $\mathbb{R}^3_+$, we define $V : \mathbb{R}^3_+ \to \mathbb{R}$ as

$$V(x) := \alpha F(\frac{x_1}{x_1^*}) + \beta F(\frac{x_2}{x_2^*}) + \gamma F(\frac{x_3}{x_3^*}) - (\alpha + \beta + \gamma)$$

where

$$\alpha = \frac{b_{21}}{x_2^* x_3^* b_{12}}, \quad \beta = \frac{1}{x_1^* x_3^*}, \quad \gamma = \frac{b_{23}}{x_1^* x_2^* b_{23}}$$

and $F : (0, \infty) \to \mathbb{R}$ is defined by $F(z) := z - \ln z$. It is easy to prove that for all $x \in \mathbb{R}^3_+ \setminus \{x^*\}$ we have $V(x) > 0$ and for the derivative of V with respect to system (3.1), $DV(x) := V'(x)f(x) < 0$ holds. Therefore V is a Lyapunov function for the system at equilibrium x^* and hence x^* is globally asymptotically stable in the positive octant of $\mathbb{R}^3$.

Now, by the asymptotic stability, any solution of system (3.1) would be an asymptotic estimation of the solution we want to recover from the observation. Our purpose will be to find the solution of the observer system that tends more quickly than the solution of the original system, with the same initial value. To this end below we recall some concepts and results on stable matrices and on the construction of an observer system.

Definition 4.1 *A matrix $A \in \mathbb{R}^{n \times n}$ is said to be "stable", if all its eigenvalues have negative real parts.*

In case of a 3×3 matrix the general Routh-Hurwitz criterion reduces to the following simple conditions, given in terms of the coefficients characteristic polynomial.

The Routh-Hurwitz criterion for $n = 3$: Let $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$ be the characteristic polynomial of $A \in \mathbb{R}^{3\times3}$. Then A is stable if and only if $a_1, a_2, a_3 > 0$ and $a_1 a_2 > a_3$.

We remind then how it is possible to construct the observer of a system.

Now, the construction of an observer system will be based on Sundarapandian (2002).

Definition 4.2 *A $\mathcal{C}^1$ dynamical system described by*

$$\dot{z} = G(z, y), \qquad (z \in \mathbb{R}^n) \tag{4.2}$$

is called a local asymptotic (respectively, exponential) observer for observation system (2.1)-(2.2) if the composite system (2.1)-(2.2),(4.2) satisfies the following two requirements.

i) If x(0) = z(0), then x(t) = z(t), for all $t \geq 0$.

ii) There exists a neighborhood V *of the equilibrium* x^* *of* $\mathbb{R}^n$ *such that for all* $x(0),\ z(0) \in V$, *the estimation error* $z(t) - x(t)$ *decays asymptotically (respectively, exponentially) to zero.*

Theorem 4.3 (Sundarapandian, 2002). *Suppose that the observation system (2.1)-(2.2) is Lyapunov stable at equilibrium, and that there exists a matrix* K *such that matrix* $A - KC$ *is stable, where* $A = f'(x^*)$ *and* $C = h'(x^*)$. *Then dynamic system defined by*

$$\dot{z} = f(z) + K[y - h(z)] \tag{4.3}$$

is a local exponential observer for observation system (2.1)-(2.2).

Remark 4.4 *It is known (Sundarapandian, 2002) that under the sufficient conditions of section 3 for local observability, the existence of such an observer is guaranteed. The above theorem provides an efficient method to construct this observer.*

Example 4.5

We consider the one-predator and two-prey model determined by the following differential system

$$\begin{array}{rl} \dot{x}_1 = & x_1(2 - 1.1x_1 - 0.1x_2) \\ \dot{x}_2 = & x_2(-1 + x_1 - 0.2x_2 + 0.5x_3) \\ \dot{x}_3 = & x_3(3.6 - 0.8x_2 - 0.7x_3) \\ y = & h(x) = x_1 + x_3 - x_1^* - x_3^* \end{array} \tag{4.4}$$

in which we observe the total number of prey individuals. This system has a positive equilibrium: $x^* = (1.4608,\ 3.9307,\ 0.6506)$, and if we linearize it at equilibrium, we obtain the following matrices

$$A = \frac{\partial f}{\partial x}(x^*) = \begin{bmatrix} -1.6069 & -0.1461 & 0 \\ 3.9307 & -0.7861 & 1.9654 \\ 0 & -0.5205 & -0.4554 \end{bmatrix}, \qquad C = \frac{\partial h}{\partial x}(x^*) = [1\ 0\ 1].$$

As we have seen in the previous section, x^* is asymptotically stable. For the initial condition $x_0 = (1.3,\ 3.1,\ 0.4)$, the solution of system (4.4) is represented in Figure 1. It can be checked numerically, that matrix A is stable. Therefore, in Theorem 4.3 we can take $k := 0$ to obtain the original system (4.4) as local observer for itself. In particular, as we will illustrate later, near the equilibrium any solution can be asymptotically approximated by any other one.

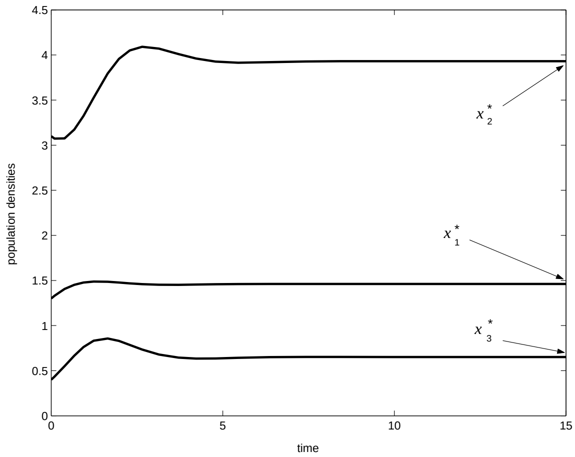

Figure 1: Solution of Lotka-Volterra system

Our purpose now is to improve this "trivial" estimation of the solution, searching a matrix K such that the solution of the corresponding observer system with a given initial value, approximates the required state process more quickly than the solution of the original system, with the same initial value. This can be achieved by an appropriate choice of matrix K. To this end it is sufficient to find a matrix K such that $A-KC$ has eigenvalues with negative real part larger in module than the negative real part of eigenvalues of matrix A. In this way we can guarantee a higher speed of (exponential) convergence to the required solution.

For $K \in \mathbb{R}^{3\times 1}$ with entries $k_1 = 0,\ k_2 = 0,\ k_3 = 2$ we obtain that matrix $A-KC$ verifies the Routh-Hurwitz conditions and therefore, is stable, moreover, the real parts of its eigenvalues dominate in module those of matrix A.

By Theorem 4.3 we obtain the observer system

$$\begin{aligned} \dot{z}_1 = &\ z_1(2 - 1.1z_1 - 0.1z_2) \\ \dot{z}_2 = &\ z_2(-1 + z_1 - 0.2z_2 + 0.5z_3) \\ \dot{z}_3 = &\ z_3(3.6 - 0.8z_2 - 0.7z_3) + 2(y - z_1 - z_3 - x_1^* - x_3^*). \end{aligned}$$

For this observer system we take the initial value $z_0 = (2,\ 3.4,\ 0.8)$, near the above initial condition and see how in Figure 2 the corresponding solution z practically end up in the required solution x of the original system, for $t > t_0 = 4$.

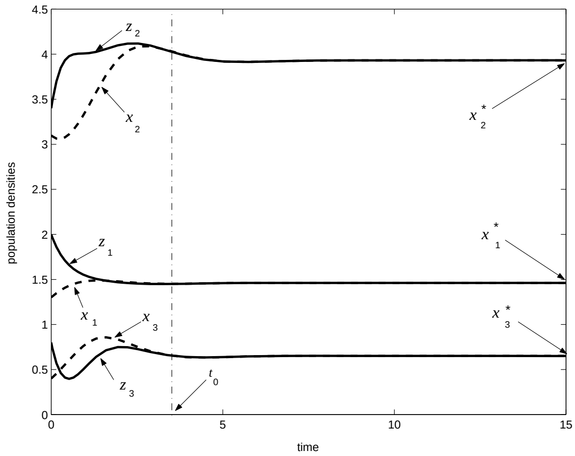

Figure 2: Solution z of the observer system, approching the required solution x

Next, if we calculate solution v of the original system, with the same initial condition z_0 we have chosen for the observer system, we can check that v practically coincides with the required solution x, only for $t > t_1 = 8$. Summing up, the example illustrates that an observer can perform better than the original system (see Figure 3).

5 Observer for a system with abiotic disturbance

In this section, based on the methodological background of Sundarapandian (2003), we consider the predator-prey model (3.1) with the presence of an

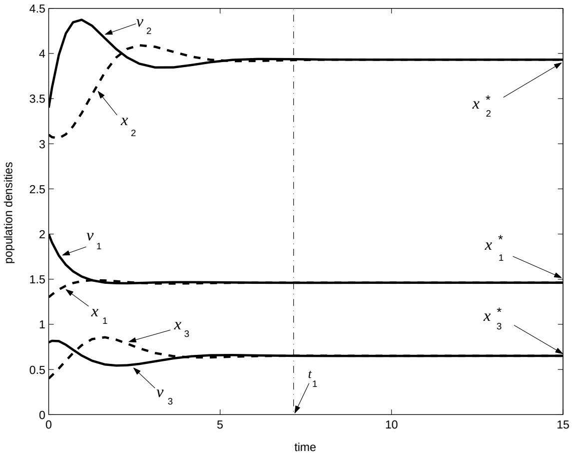

Figure 3: A solution v of the original system, approching the required solution x

unknown abiotic effect, which acts as a disturbance $w \in \mathbb{R}$, small in module, considered constant, affecting to the Malthus parameter of prey species 1 in the following way:

$$\begin{array}{rl} \dot{x}_1 = & x_1(a_1 + w - b_{11}x_1 - b_{12}x_2) \\ \dot{x}_2 = & x_2(-a_2 + b_{21}x_1 - b_{22}x_2 + b_{23}x_3) \\ \dot{x}_3 = & x_3(a_3 - b_{32}x_2 - b_{33}x_3) \\ \dot{w} = & 0 \end{array} \tag{5.5}$$

with $a_i, b_{ij} > 0$ for all $i, j = 1, 2, 3$.

It is clear that with the equilibrium $x^* > 0$ of the previous section, $(x^*, 0)$ is an equilibrium of system (5.5).

Now we have a system with two components (x, w) and our intention is to estimate the state of the population, i.e. the solution x, and the value w of the unknown parameter. To this end we shall follow the same reasoning of the above sections.

Observation of the prey without distinction

We suppose that we observe the total quantity of population preys without doing distinction between them, i.e.,

$$y = h(x) = x_1 + x_3 - x_1^* - x_3^*.$$

Then

$$C = \frac{\partial h}{\partial x}(x^*) = [1 \quad 0 \quad 1 \quad 0]$$

and linearizing system (5.5) we obtain

$$A = \frac{\partial f}{\partial x}(x^*) = \begin{bmatrix} -b_{11}x_1^* & -b_{12}x_1^* & 0 & x_1^* \\ b_{21}x_2^* & -b_{22}x_2^* & b_{23}x_2^* & 0 \\ 0 & -b_{32}x_3^* & -b_{33}x_3^* & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}. \tag{5.6}$$

We suppose that at the equilibrium state the loss in relative rate of increase due to the intra-specific competition is the same for the two prey species (Varga et al., 2003):

$$b_{11}x_1^* = b_{33}x_3^*.$$

Then

$$det[C \mid CA \mid CA^2 \mid CA^3]^T$$

$$= (b_{21} - b_{23})x_1^*(x_2^*)^2(b_{12}x_1^* + b_{32}x_3^*)^2[-b_{11}b_{22}x_1^* + (b_{21} - b_{23})b_{32}x_3^*].$$

If we assume in addition that for the predator the increase in relative growth rate due to its predation on species 1 is smaller than the rate due to its predation on species 3

$$b_{21} < b_{23},$$

we obtain that

$$det[C \mid CA \mid CA^2 \mid CA^3]^T > 0.$$

Therefore, by Theorem 2.2, under the above hypothesis, the system is locally observable near the equilibrium: the whole system state can be monitored observing only the prey populations without distinction and moreover the unknown parameter can be estimated.

Suppose now that, contrary to the above hypothesis, the lost in relative rate of increase due to the intra-specific competition is different for the two prey species:

$$b_{11}x_1^* \neq b_{33}x_3^*.$$

Then if for the predator the increase in relative growth rate due to its predation on species 1 is the same than the rate due to its predation on species

3

$$b_{21} = b_{23},$$

keeping the same observation function of this part we obtain that

$$det[C \mid CA \mid CA^2 \mid CA^3]^T$$

$$= b_{22}b_{33}x_1^* x_2^* x_3^*(-b_{11}x_1^* + b_{33}x_3^*)[b_{32}(-b_{11}x_1^* + b_{22}x_2^*)x_3^* + b_{12}x_1^*(b_{22}x_2^* - b_{33}x_3^*)]$$

which is different to zero under one of the following hypotheses: the lost in relative rate of increase due to the intra-specific competition for the predator is bigger (or smaller) than for anyone prey species, i.e.,

$$b_{22}x_2^* > \max\{b_{11}x_1^*,\ b_{33}x_3^*\} \quad \text{or} \quad b_{22}x_2^* < \min\{b_{11}x_1^*,\ b_{33}x_3^*\}.$$

Therefore, under these hypotheses, by Theorem 2.2, the system is locally observable near the equilibrium.

Now we shall show an observation function for which no additional hypotheses is needed in order to guarantee the local observability of the system.

Observation of one prey species

Let us consider the Lotka-Volterra system (5.5). Suppose first that the density of one of the preys, say, species 1 is observed, i.e.,

$$y = h(x, w) = x_1 - x_1^*.$$

Then $C := [1\ 0\ 0\ 0]$ and linearizing the system we have matrix (5.6). Thus we obtain

$$det[C \mid CA \mid CA^2 \mid CA^3]^T = b_{12}^2 b_{23}(b_{23}b_{32} + b_{22}b_{33})(x_1^*)^3(x_2^*)^2 x_3^* > 0,$$

which by Theorem 2.2 implies local observability near the equilibrium. 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, in principle, can be uniquely recovered and it is possible therefore estimate the value of the unknown parameter. The effective calculation is illustrated in

Example 5.1

Setting the same model parameters as in (4.4), we consider the following two-prey one-predator model with the presence of an unknown abiotic effect w

$$
\begin{array}{rcl}
\dot{x}_1 = & x_1(2 + w - 1.1x_1 - 0.1x_2) \\
\dot{x}_2 = & x_2(-1 + x_1 - 0.2x_2 + 0.5x_3) \\
\dot{x}_3 = & x_3(3.6 - 0.8x_2 - 0.7x_3) \\
\dot{w} \;= & 0.
\end{array}
\tag{5.7}
$$

Then, with the equilibrium x^* of system (4.4), $(x^*, 0)$ is an equilibrium of system (5.7), which is obviously Lyapunov stable (not asymptotically).

Suppose now that we observe the density of species prey 1, i.e.,

$$y = h(x, w) = x_1 - x_1^*.$$

Then

$$C := [1\ 0\ 0\ 0].$$

For a generic system of this kind, for this observation, in last subsection, we have just guaranteed the local observability of model. Now we shall see graphically that from the observation of prey 1 it is possible to recover the state of the whole population and to estimate the unknown parameter. For example, let us suppose that the actual disturbance parameter is $w = 0.2$. Now, we construct a local observer for system (5.7) near equilibrium $(x^*, w^*) = (1.4608,\ 3.9307,\ 0.6506,\ 0)$. We also suppose that the initial condition for system (5.7), near the equilibrium is $(x_0, w_0) = (1.3,\ 3.1,\ 0.4,\ 0.2)$. The corresponding solution of (5.7) is represented in Figure 4. Linearizing system (5.7) at equilibrium $(x^*, 0)$ we obtain the following matrix corresponding to (5.6) and substituting the corresponding coefficients we have

$$A = \begin{bmatrix} -1.6069 & -0.1461 & 0 & 1.4608 \\ 3.9307 & -0.7861 & 1.9654 & 0 \\ 0 & -0.5205 & -0.4554 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}.$$

For matrix $K \in \mathbb{R}^{4\times 1}$ with coefficients $k_1 = 0,\ k_2 = 0,\ k_3 = 0,\ k_4 = 1$ we obtain that matrix $A - KC$ is stable because it has only eigenvalues with

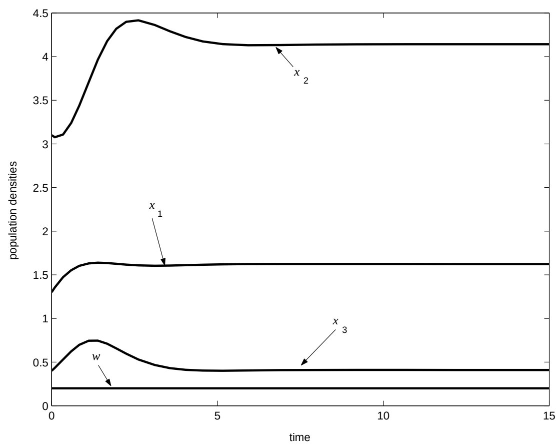

Figure 4: Solution of system (5.7)

negative real part. Then, by Theorem 4.3, we construct the observer system

$$\begin{aligned} \dot{z}_1 &= z_1(2 + z_4 - 1.1z_1 - 0.1z_2) \\ \dot{z}_2 &= z_2(-1 + z_1 - 0.2z_2 + 0.5z_3) \\ \dot{z}_3 &= z_3(3.6 - 0.8z_2 - 0.7z_3) \\ \dot{z}_4 &= 0 + y - (z_1 - x_1^*) \end{aligned} \tag{5.8}$$

We take an initial value near to the above initial condition, for example, $(\overline{x}_0, \overline{w}_0) = (1.8,\ 3.5,\ 0.7,\ 0.4)$ and we can see in the Figure 5 as the solution of observer system tends to the solution of the original system. The construction of the solution z of the observer is now important, because if we obtain the solution $(\overline{x}, \overline{w})$ of the original system for the same initial condition as for the observer system, $(\overline{x}, \overline{w})$ does not tend to the required solution (x, w), as we can see in Figure 6. (The reason is that the considered equilibrium $(x^*, 0)$ of (5.7) is only Lyapunov stable, but not asymptotically).

6 Discussion

In the paper we have shown how the concepts and methods of mathematical systems theory are appropriate to solve certain monitoring problems of population ecology. For a one predator-two prey system, observing e.g. the two prey populations without distinction, under simple biological conditions,

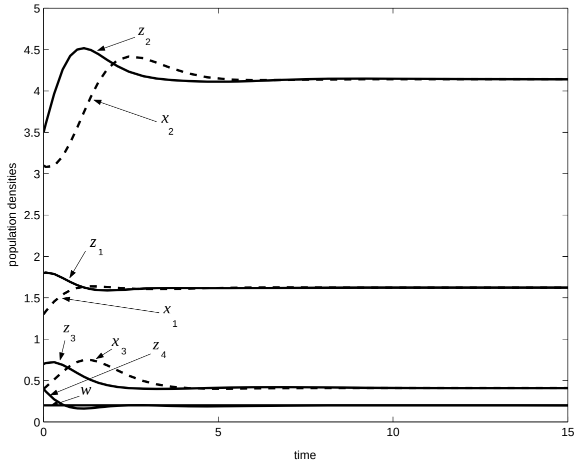

Figure 5: Solution z of the observer system (5.8), approching the required solution (x, w) of (5.7).

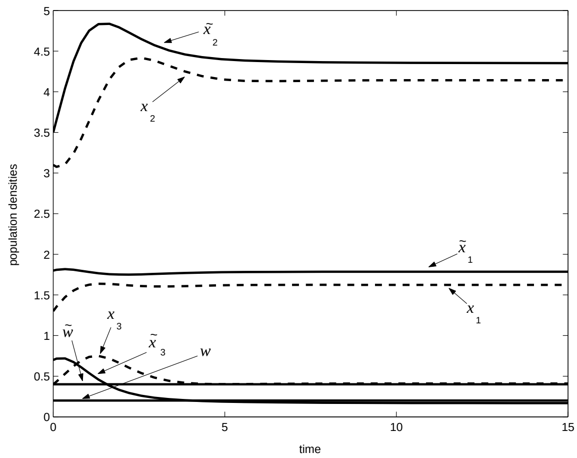

Figure 6: A nearby solution $(\overline{x}, \overline{w})$ of the original system (5.7) that does not approach the required solution (x, w).

constructing an observer system, the whole process of the population system can be recovered asymptotically in an efficient way. Observer systems can also be applied to estimate unknown abiotic effects appearing in the Malthus parameters, which is also illustrated by a numerical example. For an outlook we point out that, in principle, this approach to monitoring abiotic effects can also be applied to time-varying abiotic effects, described by a differential system (exosystem).

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8 References

Bernard, O., Gauthier, S. and Sciandra, A., (1998). Nonlinear observers for a class of biological systems: application to validation of a phytoplanktonic growth model. IEEE Transactions on Automatic Control, Vol. 43, No. 8, 1056-1065.

Kalman, R.E., Falb, P.L. and Arbib, M.A., (1969). Topics in Mathematical System Theory. New York: McGraw-hill.

Lee, E.B. and Markus, L., (1971). Foundations of Optimal Control Theory. New York-London-Sydney : Wiley.

López, I. (2003). Observabilidad y controlabilidad en modelos de evolución (Tesis doctoral). Almería: Servicio de Publicaciones de la Universidad de Almería. ISBN: 84-8240-683-3.

López, I., Gámez, M., Carreño, R. and Varga, Z., (2003). Recovering genetic processes from phenotypic observation. En V. Capasso (Ed.), Mathematical

Modelling and Computing in Biology and Medicine, 5th ECMTB Conference 2002 (pp. 356-361); Milán: miriam.

López, I., Gámez, M. and Carreño, R. (2004). Observability in dynamic evolutionary models. Biosystems, 73, 99-109.

Shamandy, A. (2005). Monitoring of trophic chains. Biosystems, Vol. 81, Issue 1, 43-48.

Sundarapandian, V. (2002). Local observer design for nonlinear systems. Mathematical and computer modelling 35, 25-36.

Sundarapandian, V. (2003). Exponential observer design for nonlinear systems with real parametric uncertainty. Mathematical and computer modelling, 37 (1-2), 177-190.

Varga, Z. (1992). On observability of Fisher's model of selection. Pure Math. and Appl. Ser. B, 1, 15-25.

Varga, Z., Scarelli, A. and Shamandy, A., (2002). An observability problem of population ecology. In V. Capasso (Ed.), Mathematical Modelling and Computing in Biology and Medicine, 5th ECMTB Conference 2002 (Abstracts, p.189). Milán: miriam.

Varga, Z., Scarelli, A. and Shamandy, A., (2003). State monitoring of a population system in changing environment. Community Ecology 4 (1), 73-78.