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Ecological monitoring in a discrete-time prey–predator model

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ABSTRACT

The paper is aimed at the methodological development of ecological monitoring in discrete-time dynamic models. In earlier papers, in the framework of continuous-time models, we have shown how a systems-theoretical methodology can be applied to the monitoring of the state process of a system of interacting populations, also estimating certain abiotic environmental changes such as pollution, climatic or seasonal changes.

In practice, however, there may be good reasons to use discrete-time models. (For instance, there may be discrete cycles in the development of the populations, or observations can be made only at discrete time steps.) Therefore the present paper is devoted to the development of the monitoring methodology in the framework of discrete-time models of population ecology. By monitoring we mean that, observing only certain component(s) of the system, we reconstruct the whole state process. This may be necessary, e.g., when in a complex ecosystem the observation of the densities of certain species is impossible, or too expensive. For the first presentation of the offered methodology, we have chosen a discrete-time version of the classical Lotka–Volterra prey–predator model. This is a minimal but not trivial system where the methodology can still be presented.

We also show how this methodology can be applied to estimate the effect of an abiotic environmental change, using a component of the population system as an environmental indicator. Although this approach is illustrated in a simplest possible case, it can be easily extended to larger ecosystems with several interacting populations and different types of abiotic environmental effects.

1. Introduction. Monitoring problems: biological needs and mathematical possibilities

The historical background of the present study is the basic dynamic Lotka–Volterra model of population ecology (Volterra, 1931; Scudo and Ziegler, 1978). Since then a huge number of studies have been devoted to this classical continuous-time model and its generalizations, the main research lines are summarized in Svirezhev and Logofet (1983). For a survey on discrete-time versions of classical population dynamics models, we can refer e.g. to Grantham and Athalye (1990). Below we set up a general approach to the monitoring of such systems.

For a sound theoretical foundation of efficient applications of biological knowledge in different fields of human activity, it is necessary to extend the traditional approach of theoretical biology focusing only on a biological object, to the study of the system "biological object – man". For instance, in a typical situation of conservation ecology, before any intervention on a population system (a set of several interacting populations), we may need the knowledge of all state variables (i.e. the densities of all species) as functions of time. However, in many cases we can observe (measure) only the densities of certain species considered indicator species. The question then arises whether from these observed densities (components of the state vector) the whole state vector can be uniquely recovered. Of course, in a static situation this is impossible, but it is often possible, if the observation is dynamic. This is one of the basic problems of *mathematical systems theory*, called *observability problem*. Let us suppose that certain projection or transform of the state vector is observed as function of time, and to different state processes there correspond different observations. Then the considered system is called *observable*, which actually means that from the observed function, in principle, the original state process can be uniquely determined. In fact, for the typically non-linear models of population biology, the adequate observability concept is local, defined near an equilibrium. From a practical point of view, in case of observability, an important question is how to effectively calculate the unknown state process from the observation.

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In order to understand the basic difficulty of the observation problem, let us consider the classical Lotka–Volterra prey–predator model. Let us suppose that we can observe only the density of the prey as function of time. We cannot proceed as in the case of a system of two algebraic equations, i.e. just substitute this known function into the system, so we obtain a single differential equation with a single unknown. The problem is that this equation cannot be uniquely solved since we do not know the initial value of the unknown function. Therefore, to recover the unknown state process we need a special method. The answer is *observer design*, a basic construction of mathematical systems theory. In fact, from the original state dynamics and the known observation, the so-called *observer system* can be constructed, the solution of which converges to the unknown state process at exponential rate. For the *continuous-time* density-dependent population system models, this observer design methodology of Sundarapandian (Sundarapandian, 2002a; Sundarapandian, 2003; Sundarapandian, 2005; Sundarapandian, 2011) has been widely applied as summarized below.

For further *biological motivation* of the present research, below we recall some successful applications of the observer design methodology to concrete state process estimation. First we mention the application of this methodology to the monitoring of the classical Lotka–Volterra prey–predator model (López et al., 2007b) and to *open and closed trophic chains*, in Varga et al. (2010), see also Gámez et al. (2010a).

In Gámez et al. (2012) observer design was applied for *stock estimation in fisheries* with reserve area, where from the catch in the free fishing area the total fish stock as function of time was estimated.

Unlike the above supra-individual examples, an *infra-individual monitoring* model is considered in Gámez et al. (2009). In fact, in the context of *radiotherapy*, under the condition of a constant irradiation we have shown that using observer design, from the total number of cells of an organ, e.g. the number of healthy cells can be estimated. Then, applying a control model the number of healthy cells can be controlled to a desired level by irradiation as control.

As for the mathematical (methodological) context of the present study we mention that in Gámez et al. (2010b), dealing with an ecological interaction chain “resource – producer – primary user –secondary consumer” we have also shown how the monitoring problem of a more complex system can be decomposed into the observation of certain subsystems, see also López et al. (2007a) and Molnár et al. (2012).

In addition we note that the observer design methodology can also be applied in environmental modelling. In fact, a change in the abiotic environment of a population system such as pollution, can be estimated using an appropriate observer system. For an example in case of continuous-time models see Gámez et al. (2008). In the present paper we will also apply a similar approach to our discrete-time model.

Unlike the above density-dependent models of ecology, a special methodological approach was necessary for the biologically very natural monitoring problem of population genetics, where from the observation of frequencies of certain phenotypes we want to recover the underlying genetic process. To cope with this problem, it was necessary to develop the above observation methodology and mathematical tools for systems with invariant manifold. In the basic case of population genetics, this invariant manifold is the simplex of allele frequencies, see Varga (1992), Gámez et al. (2003), López, (2003), López et al. (2003), López and Gámez (2004), López et al. (2005), López et al. (2008).

We emphasize that all these biological applications deal with continuous-time (i.e. differential equation) models. For overviews of monitoring of such systems applied to different biological situations see Varga, (2008), Varga et al. (2013) and Gámez (2012).

The dynamics of populations with non-overlapping generations, however, can be better described by discrete-time models, see e.g. May (1974). In Grantham and Athalye (1990), different motives are discussed why biologist may prefer discrete-time population models to continuous-time ones. The authors also consider different ways of time-discretization, also including *control problems*. In the present work, we shall deal with *observation* (or monitoring) *problems* of a prey–predator system, based on the Euler-type time discretization of the classical Lotka–Volterra model. We emphasize that in general, the discrete-time versions of a continuous-time dynamic system can display quite complex behavior such as flip bifurcation, Hopf bifurcation and chaos, see e.g. Grantham and Athalye (1990). However, as a matter of fact, we use the well-known Euler discretization of the classical continuous-time L-V model, but for our purpose we do not need the knowledge on its global behavior, *only some local properties* of this discrete dynamics are required, as discussed in details in the next two sections.

The paper is organized as follows: In Section 2, the Euler discretization of a continuous-time Lotka–Volterra prey–predator model is introduced, with the time step size as discretization parameter. Although the corresponding approximations for different discretization parameters are illustrated, we emphasize that we will study the local observability of the Euler discretization, therefore its local consistency is also addressed. Section 3 is devoted to the local stability analysis of the equilibria of the discrete-time dynamics, necessary for the study of observation. In Section 4, for the solution of the considered monitoring problem, applying the tools of Mathematical Systems Theory, the observability and the state estimation are established, observing either the predator or the prey density. For the observer design we adapt the discrete-time methodology of Sundarapandian (2002b). In Section 5, we show how this methodology can also be applied to estimate the effect of an abiotic environmental change, using a component of the population system as an environmental indicator. (For the importance of indicator species in ecological informatics see e.g. Recknagel (2013)). A Discussion section closes the main body of the paper. Certain mathematical details are included in the Appendix.

2. A discrete-time Lotka–Volterra model. Consistency and invariant sets

The simplest case of a Lotka–Volterra model describes the interaction between a prey population and a predator population, with the following system differential equations:

$$\begin{aligned} \dot{y}_1 &= ry_1 - by_1y_2 \\ \dot{y}_2 &= -dy_2 + cy_1y_2, \end{aligned}$$

where y_1 andy_2 are the densities of the prey and the predator, respectively. Let us suppose that there exists an intraspecific competition in both species. Then the previous differential equations system takes the form

$$\begin{aligned} \dot{y}_1 &= ry_1 - sy_1^2 - by_1y_2 \\ \dot{y}_2 &= -dy_2 - ey_2^2 + cy_1y_2 \end{aligned} \tag{2.1}$$

However, there are different motives why biologist may prefer discrete-time population models to continuous-time ones, see Grantham and Athalye (1990). As pointed out by May (1974), the dynamics of populations with non-overlapping generations, can be better described by discrete-time models.

In this work, applying the Euler discretization process, we shall consider the following system of difference equations describing the interaction between the two species:

$$\begin{aligned} x_1(t+1) &= (\hat{r}+1)x_1(t) - \hat{s}x_1^2(t) - \hat{b}x_1(t)x_2(t) \\ x_2(t+1) &= (1-\hat{d})x_2(t) - \hat{e}x_2^2(t) + \hat{c}x_1(t)x_2(t), \end{aligned} \tag{2.2}$$

where δ is a time step size and $\hat{r} = \delta r\,;\ \hat{s} = \delta s\,;\ \hat{b} = \delta b\,;\ \hat{d} = \delta d\,;\ \hat{e} = \delta e\,;\ \hat{c} = \delta c.$

Table 1
MSD for different time steps.

δ	MSD
1	0.1934
0.25	0.0268
0.025	0.0026

Remark 2.1. We note that model (2.2) is more general than that considered for stability in Raj et al. (2013), since we admit intraspecific competition in both species. Therefore in our illustrative examples, for the corresponding parameters we will use the same numerical values as in the quoted paper.

In order to apply any continuous or discrete-time model to describe the dynamics of a population, first of all a state space consisting of nonnegative vectors should be specified. It is well-known that the behavior of nonlinear discrete-time dynamic systems is rather complex. Concerning the Euler discretization of a general continuous-time Lotka–Volterra system, under conditions on the model parameters, a positively invariant subset of the positive orthant was given in Choo (2014). Nevertheless, the conditions needed for the construction of the invariant set, are rather implicit. Actually, for a "not too small" invariant set a very fine discretization (or in other terms, very small coefficients in the dynamics) may be necessary.

In the present paper we will consider the observation problem of a discrete-time population system near an equilibrium. Since the observer system we construct will be local, for our purpose it will be enough that the solution starting near enough the equilibrium, will not leave a neighborhood of the equilibrium, contained in the positive orthant. The latter will be guaranteed since the equilibrium turns out to be locally asymptotically stable. (For mathematical details of this reasoning see Lemma A1 of the Appendix). A simple simulation shows that, although the continuous-time dynamics (2.1) leaves the positive orthant invariant, the solutions of its discretization remain positive only near the equilibrium.

2.1. Comparison of the continuous and discrete models

For the analysis of the behavior of the discretization, let us fix system parameters $r=0.25$, $s=0.1$, $b=0.95$, $d=0.55$, $e=0.05$ and c=0.5.

Using the mean squared deviation

$$\text{MSD} = \sqrt{\frac{1}{T}\sum_{t=1}^{T} |y(t) - x(t/\delta)|^2}$$

as measure of approximation, calculating over time interval $[0,T]$ with $T=120$, we get better and better approximation by setting decreasing time steps, see Table 1 and Fig. 1.

3. Stability analysis of the equilibria of a discrete-time Lotka–Volterra dynamics

Systems (2.1) and (2.2) have the same equilibria

$$E_0 = (0,0), \quad E_1 = \left(\tfrac{r}{s}, 0\right) \text{ and } E_2 = \left(\tfrac{re+bd}{se+bc}, \tfrac{rc-sd}{se+bc}\right). \tag{3.1}$$

Equilibrium E_0 means the extinction of both species, E_1 the extinction of the predator and E_2 the coexistence of both species. In fact, equilibrium E_2 is positive, if $\frac{r}{d} > \frac{s}{c}$.

In order to analyze the local stability of these equilibria using linearization, we calculate the Jacobian of the right-hand side of system (2.2) at equilibria (3.1). From

$$J(x_1, x_2) = \begin{pmatrix} (\hat{r}+1) - 2\hat{s}x_1 - \hat{b}x_2 & -\hat{b}x_1 \\ \hat{c}x_2 & (1-\hat{d}) + \hat{c}x_1 - 2\hat{e}x_2 \end{pmatrix},$$

the Jacobian at E_0 is

$$J(E_0) = \begin{pmatrix} \hat{r}+1 & 0 \\ 0 & 1-\hat{d} \end{pmatrix},$$

having eigenvalues $\lambda_1 = \hat{r}+1$ and $\lambda_2 = 1-\hat{d}$. Obviously $|\lambda_1| > 1$, implying instability of the equilibrium point E_0.

The Jacobian at E_1 is

$$J(E_1) = \begin{pmatrix} 1-\hat{r} & -\hat{b}\frac{r}{s} \\ 0 & 1+\hat{c}\frac{r}{s} - \hat{d} \end{pmatrix},$$

its eigenvalues are $\lambda_1 = 1-\hat{r}$ and $\lambda_2 = 1+\hat{c}\frac{r}{s} - \hat{d}$. Condition $|\lambda_{1,2}| < 1$ is satisfied, if $0 < \hat{r} < 2$ and $\hat{d} - 2 < \hat{c}\frac{r}{s} < \hat{d}$, implying asymptotic stability. Hence, under the latter conditions, starting from nearby states, the predator goes extinct.

At the positive equilibrium E_2 the Jacobian is

$$J(E_2) = \begin{pmatrix} 1 - \hat{s}\dfrac{re+bd}{bc+es} & -\hat{b}\dfrac{bd+er}{bc+es} \\ \hat{c}\dfrac{rc-sd}{bc+es} & 1-\hat{e}\dfrac{rc-sd}{bc+es} \end{pmatrix}. \tag{3.2}$$

Hence, for the characteristic polynomial of $J(E_2)$, we get $p(\lambda) = \lambda^2 + p_1\lambda + p_2$, where

$$p_1 = \frac{b(-2c+ds\delta) + e(cr\delta + (-2-d\delta+r\delta)s)}{bc+es},$$

$$p_2 = \frac{-e(-1+r\delta)(s-cr\delta+ds\delta) + b(c+cdr\delta^2 - ds\delta(1+d\delta))}{bc+es}.$$

We shall use the following stability criterion (Elaydi, 2005):

A necessary and sufficient condition for asymptotic stability is

$$\begin{aligned} &(i) && 1+p_1+p_2 > 0, \\ &(ii) && 1-p_1+p_2 > 0, \\ &(iii) && p_2 < 1. \end{aligned} \tag{3.3}$$

Let us check these conditions:

(i) $1+p_1+p_2 = \frac{(cr-ds)(bd+er)\delta^2}{bc+es} > 0$, if $cr > ds$
(which is also required for the positivity of equilibrium E_2).
(ii) $1-p_1+p_2 = \frac{(-2+r\delta)e(cr\delta-(2+d\delta)s)+b(c(4+dr\delta^2)-ds\delta(2+d\delta))}{bc+es} > 0$,
if $cr\delta < ds\delta + s$, $0 < \delta \le 1$ and $0 < r \le 1$.
(Here condition $cr > ds$ is also used.)
(iii) $1-p_2 < 1$ also holds under the conditions posed in (i) and (ii).

Summing up the above, we have the following theorem.

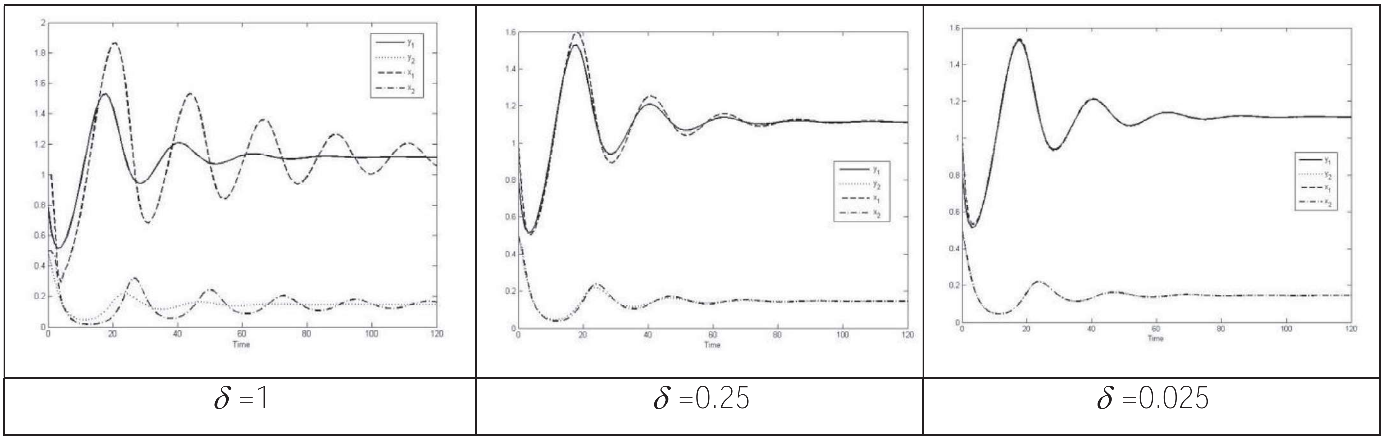
Theorem 3.1. If the model parameters satisfy conditions

$$cr > ds, \ cr\delta < ds\delta + s, \ 0 < \delta \le 1 \text{ and } 0 < r \le 1, \tag{3.4}$$

then equilibrium E_2 is positive and asymptotically stable. (In biological terms, there is a stable coexistence of both species.)

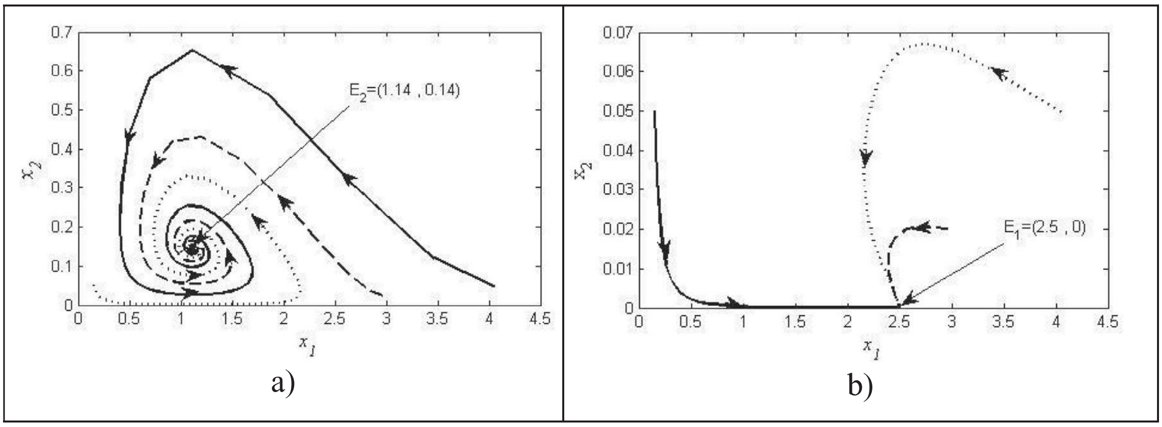
Remark 3.1. We note that if condition (3.4) holds, but the sufficient condition for the asymptotic stability of E_1 does not, then it really happens that E_2 is asymptotically stable, but E_1 is not, see Fig. 2(a). Fig. 2(b) shows that the opposite behavior can also occur, when (3.4) does not hold: there is no stable coexistence (even there is no positive equilibrium), but asymptotic stability of E_1 is observed.

In the rest of this work we suppose that condition (3.4) on the parameters holds to guarantee the asymptotic stability of the positive equilibrium E_2 given by (3.1).



δ =1 δ =0.25 δ =0.025

Fig. 1. Discrete-time approximation of the solution of system (2.1), with different time steps δ.



a) b)

Fig. 2. Different stability behavior of different equilibria in system (2.2). a) For $r=0.25$, $s=0.1$, $b=0.95$, $d=0.55$, $e=0.05$, c=0.5 and δ=0.25, (3.4) holds, E_0 is a repulsor E_2 is an attractor. b) Changing only parameter c to 0.2, (3.4) does not hold, and we get a different picture: E_0 is a repulsor E_1 is an attractor.

4. Observability analysis and observer design

In this section we summarize the methodology we will apply to the monitoring problem of a prey–predator system described by a discrete-time model. This problem consists in recovering the complete state process from the observation of one of its components (in our case either the prey or the predator density). In order to apply the tools of Mathematical Systems Theory, let us consider a general discrete-time dynamics

$$x(t+1) = f(x(t)),\ (t = 0,\ 1, \ldots), \tag{4.1}$$

and an observation equation

$$w(t) = h(x(t)), \qquad (t = 0,\ 1, \ldots), \tag{4.2}$$

where f: $D \to D$ (with an open set $D \subset R^n$) and h: $D \to R^p$ are smooth (continuously differentiable) functions, $x^* \in D$ is an equilibrium for dynamics (4.1): $f(x^*) = x^*$, furthermore $h(x^*) = 0$. Sequence $w(t) \quad (t = 0,\ 1, \ldots)$,is called the observation, corresponding to the state process $x(t) \quad (t = 0,\ 1, \ldots)$,

Remark 4.1. Observation Eq. (4.2) expresses the fact that instead of the state sequence $x(t) \quad (t = 0,\ 1, \ldots)$,we can observe only a transform of it. In the case of a system of several interacting populations, when the components of the state vector $x(t)$ are the densities of the single populations, function h may be a projection that with every vector associates certain components of it, e.g. $h(x) = x_2$. More precisely, to satisfy the technical condition the deviation of the density of population 2 from its equilibrium value should be considered: $h(x) = x_2 - x_2^*$. (Then $w(t) = x_2(t) - x_2^*$.) Another example may be the undistinguished observation of populations 1 and 2: $h(x) = x_1 + x_2 - (x_1^* + x_2^*)$.

Definition 4.1. Observation system (4.1)–(4.2) is said to be *locally observable near equilibrium* x^* over the discrete time interval $\{0,\ 1, \ldots,\ n-1\}$ if in a certain neighborhood of x^* from the observation $w(t)$ the state process $x(t) \quad (t = 0,\ 1, \ldots, n-1)$ (or equivalently,$x(0)$) can be uniquely recovered. (A more formal definition of local observability is given in the Appendix, see Definition A1.)

In the next section, we will find sufficient conditions for the local observability of our system near the equilibrium of coexistence $x^* = E_2$, in different monitoring situations, when we can only observe one species at a time, either the prey or the predator.

To this end, we will apply a linearization method analogous to that proved for continuous-time observation systems in Lee and Markus (1967), see Theorem A.1 of the Appendix. Local observability, together with the stability results of the previous section will be used for the effective estimation of the state process $x(t)$, in the knowledge of the observation $w(t)$, applying the observer design methodology we recall below from Sundarapandian (2004), in an equivalent form, appropriate for our model analysis.

Definition 4.2. Let $G = h(D)$ and g: $D \times G \to D$ be a smooth function with $g(x^*, 0) = x^*$. The discrete-time nonlinear system described by

$$z(t+1) = g(z(t), w(t)), \qquad (t = 0,\ 1, \ldots), \tag{4.3}$$

is called a *local exponential observer* for system (4.1)–(4.2), if the composite system (4.1)–(4.3) satisfies the following two requirements: There exists a neighborhood $G(x^*)$ of x^*such that for all $x(0)$, $z(0) \in G(x^*)$

(A) $x(0) = z(0)$ implies $x(t) = z(t)$, $(t = 1, 2, \ldots)$.
(B) $z(t) - x(t)$ tends to zero exponentially, as $t \to \infty$.

Let us consider the linearization of observation system (4.1)-(4.2) at equilibrium x^*, defining

$$A = f'(x^*), \quad C = h'(x^*). \tag{4.4}$$

For the construction of the observer, we will use the following theorem:

Theorem 4.1. (Sundarapandian, 2004) Suppose that system dynamics (4.1) is Lyapunov stable at equilibrium x^*, and for some $n \times p$ matrix H, all the eigenvalues of $A - HC$ lie inside the open unit disc of the complex plane. Then system

$$z(t+1) = f(z(t)) + H[w(t) - h(z(t))] \; (t = 0, 1, \ldots) \tag{4.5}$$

is a local exponential observer for system (4.1)-(4.2). If the following rank condition holds:

$$rank \begin{pmatrix} C \\ CA \\ \vdots \\ CA^{n-1} \end{pmatrix} = n, \tag{4.6}$$

then there always exists a local exponential observer of form (4.5) for system (4.1)-(4.2).

4.1. Observation of the predator

In this subsection we consider the case when we observe the density of the predator population, and we want to estimate the prey population in function of time. We note that in the typical situation of biological pest control, where the released agent is a predator, it is normal to suppose that the density of the latter is observed. (In fact, its initial value is exactly known.)

In order to analyze the observability of model (2.2), we shall observe the density predator in function of time. Therefore, the observation equation corresponding to (4.2) is

$$w(t) = h(x_1(t), x_2(t)) = x_2(t) - x_2^* \; (t = 0, 1, \ldots), \tag{4.7}$$

where x_2^* is the second coordinate of the positive equilibrium point E_2, that is the predator density at the asymptotically stable equilibrium. (For technical reason the observed quantity is the deviation of the number of the predator species at stage t from its equilibrium value.)

Linearizing observation system (2.2)–(4.7), we get

$$A = J(E_2) \text{ given in } (3.2), \text{ and } C = h'(E_2) = \begin{pmatrix} 0 & 1 \end{pmatrix}.$$

Now, for the linearized system we have $rank[C|CA]^T = 2$, if $\frac{rc-sd}{bc+es} \neq 0$. Since all parameters are positive and $\frac{r}{d} > \frac{s}{c}$ has already been supposed to guarantee the positivity of equilibrium E_2, this rank condition is verified. Therefore, the rank condition of Theorem A1 of the Appendix is fulfilled, so we obtain that observation system (2.2)-(4.6) is locally observable near the positive equilibrium. This means that the whole system state can be uniquely recovered, observing only the predator species. Summing up, we have

Theorem 4.2. Under parameter conditions (3.4), observation system (2.2)-(4.7) is locally observable near the asymptotically stable positive equilibrium E_2.

To construct an observer system for observation system (2.2)–(4.7), we shall suppose that condition (3.4) holds. In order to apply Theorem 4.1, we have only to find a matrix H such that $A - HC$ is convergent. This is illustrated by the following example.

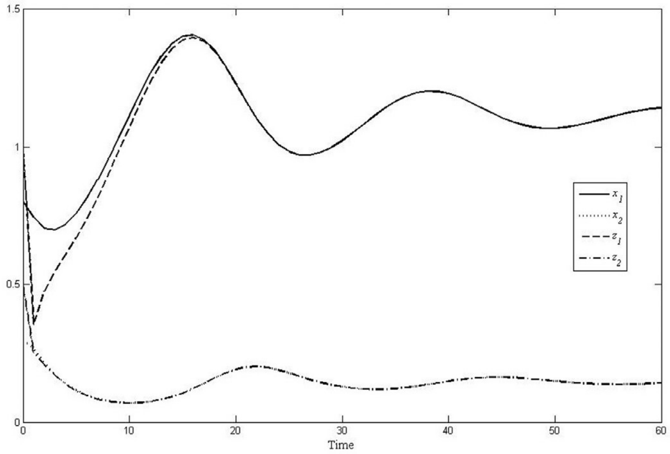


Fig. 3. Estimation of the state process from the observation of the predator density.

Example 4.1. We consider the prey–predator system (2.2) with system parameters of Section 2.1: $r = 0.25$, $s = 0.1$, $b = 0.95$, $d = 0.55$, $e = 0.05$ and $c = 0.5$, and time step size $\delta = 0.25$:

$$\begin{aligned} x_1(t+1) &= (0.0625 + 1)x_1(t) - 0.025x_1^2(t) - 0.2375x_1(t)x_2(t) \\ x_2(t+1) &= (1 - 0.1375)x_2(t) - 0.0125x_2^2(t) + 0.125x_1(t)x_2(t), \end{aligned} \tag{4.8}$$

observing the predator species with observation equation given in (4.7).

Now conditions (3.4) hold. Therefore this system has an asymptotically stable positive equilibrium$E_2 = (1.115\;,\; 0.146)$, and it is easy to check that e.g. for matrix

$$H = \begin{pmatrix} 3 \\ 1 \end{pmatrix}$$

we have that $A - HC$ is convergent. Therefore, by Theorem 4.1, we can construct the following observer system:

$$\begin{aligned} z_1(t+1) &= (0.0625 + 1)z_1(t) - 0.025z_1^2(t) - 0.2375z_1(t)z_2(t) \\ &\quad +3(w(t) - h(z(t))) \\ z_2(t+1) &= (1 - 0.1375)z_2(t) - 0.0125z_2^2(t) + 0.125z_1(t)z_2(t) \\ &\quad +(w(t) - h(z(t))). \end{aligned} \tag{4.9}$$

In order to see how a solution of the observer estimates the solution of the original system, let us calculate the solution $x(t)$ $(t = 0, 1, \ldots)$of system (4.8) with initial condition $x(0) = (0.8, 0.3)$ near the positive equilibrium, to be considered “unknown”. In Fig. 3 we can see how the solution $z(t)$ $(t = 0, 1, \ldots)$ of the observer system (4.9), calculated with the observation $w(t) = h(x(t))(t = 0, 1, \ldots)$ and with a nearby initial condition $z(0) = (1, 0.5)$, approximates the “unknown” solution of the original system.

4.2. Observation of the prey

In the case when the prey is easier to observe, we can consider an observation function defined by

$$w(t) = h(x_1(t), x_2(t)) = x_1(t) - x_1^*, \tag{4.10}$$

associated with the same dynamics (2.2), with the same parameter values as in the previous subsection, where x_1^* is the first coordinate of the positive equilibrium E_2, that is the prey density at the asymptotically stable positive equilibrium.

Now, for the linearization of observation system (2.2)-(4.10), we obtain the Jacobian of the right-hand side of (2.2) at the positive equilibrium point:

$$A = J(E_2)$$

described in (3.2), and the observation matrix

$$C = h'(E_2) = \begin{pmatrix} 1 & 0 \end{pmatrix}.$$

Now, condition $\frac{r}{d} > \frac{s}{c}$ again implies rank condition $rank[C|CA]^T = 2$. Hence, by Theorem A1 of the Appendix, we obtain

Theorem 4.2. Under parameter condition (3.4) for the asymptotic stability of the positive equilibrium, the observation system (2.2)-(4.10) is locally observable near the positive equilibrium E_2.

Now, analogously to the previous subsection, with the same illustrative system parameters as in Example 4.1, we show how to asymptotically recover the state process from the observation of the prey density, by constructing an observer system.

Example 4.2. We consider the same system of difference Eq. (4.8) describing the interaction between one prey and one predator species, but now we observe the prey species as defined by the observation Eq. (4.10). The numerical values of the system parameters and the time step size are the same as in Example 4.1.

As we have seen in Example 4.1, system has an asymptotically stable positive equilibrium$E_2 = (1.115\ ,\ 0.146)$, and now condition $rank[C|CA]^T = 2$ also holds. Therefore the existence of a local exponential observer is guaranteed by Theorem 4.1. Furthermore, for the construction of a concrete observer system, it is enough to check that e.g. with matrix

$$H = \begin{pmatrix} 0.8 \\ -0.2 \end{pmatrix},$$

$A - HC$ is a convergent matrix. Therefore, by Theorem 4.1 we can construct the following observer system

$$\begin{aligned} z_1(t+1) &= (0.0625+1)z_1(t) - 0.025z_1^2(t) - 0.2375z_1(t)z_2(t) \\ &\quad +0.8(w(t) - h(z(t))) \\ z_2(t+1) &= (1-0.1375)z_2(t) - 0.0125z_2^2(t) + 0.125z_1(t)z_2(t) \\ &\quad -0.2(w(t) - h(z(t))). \end{aligned} \tag{4.11}$$

Now we calculate the solution of system (4.8), with initial state $x(0) = (0.8,\ 0.3)$, near the positive equilibrium $E_2 = (1.115\ ,\ 0.146)$. This is the "unknown" solution to be estimated from the observation of the prey density as given in (4.10). Fig. 4 shows how the solution of the observer system (4.11) with the nearby initial condition $z(0) = (1,\ 0.5)$ approximates the "unknown" state process.

5. Monitoring of an environmental change in the prey–predator system

5.1. The extended population system

In this section, based on the methodological background of the previous section (see also (Sundarapandian, 2003)), we consider the discrete-time prey–predator model (2.2) with the presence of an unknown abiotic effect, which acts as an unknown small disturbance $v \in R$, considered constant, affecting the Malthus parameter of the prey species in the following way:

$$\begin{aligned} x_1(t+1) &= (\hat{r} + 1 + v(t))x_1(t) - \hat{s}x_1^2(t) - \hat{b}x_1(t)x_2(t) \\ x_2(t+1) &= (1-\hat{d})x_2(t) - \hat{e}x_2^2(t) + \hat{c}x_1(t)x_2(t) \\ v(t+1) &= v(t). \end{aligned} \tag{5.1}$$

It is clear that under conditions (3.4), for v small enough, not only E_2 is a positive equilibrium of (2.2), but $(E_2,0)$ is an equilibrium of system (5.1), too.

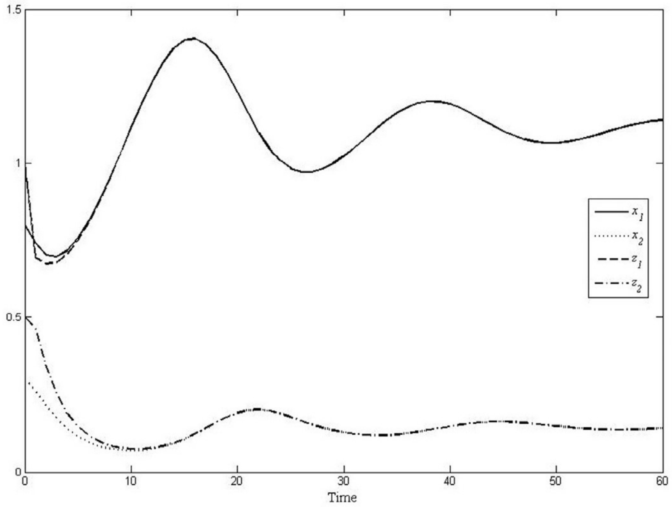


Fig. 4. Estimation of the state process from the observation of the prey density.

For the application of the methodology of Section 2, some mathematical considerations are necessary. First, to see the consistency of model (5.1), under conditions (3.4) of Theorem 3.1, we note that E_2 is asymptotically stable. Fixing a time step size $0 < \delta \le 1$ and $0 < r < 1$, asymptotic stability is robust against a small additive change v in the Malthus parameter of the prey, and hence the solution of the first two equations of system (5.1) for its discretization remains positive near equilibrium $E_{2,}$ for $v(0)$ small enough in module (see Appendix, Definition A1 and Lemma A1.)

For the construction of the observer, we will also need the Lyapunov stability of equilibrium $(E_2,0)$. It is obviously the case, since for $v(0)$ small enough, under conditions (3.4), E_2 is asymptotically stable for the x-part of system (5.1), in particular, it is also Lyapunov stable. The zero equilibrium of the third component of system (5.1) is obviously Lyapunov stable, implying the Lyapunov stability of equilibrium $(E_2,0)$ for the extended system (5.1).

Now, for the estimation of the unknown change v it will be enough to construct an observer for system (5.1), observing one of the species, say the predator. Then the third coordinate of the solution of the observer will tend to the unknown value of v.

5.2. Parameter estimation from the observation of an indicator species

Suppose that the density of the predator is observed, i.e. the observation equation is

$$w = h(x, v) = x_2 - x_2^*. \tag{5.2}$$

For the Jacobian of the right-hand side of (5.1) at equilibrium $(E_2,0)$ we get

$$A = \begin{pmatrix} 1 - \hat{s}x_1^* & -\hat{b}x_1^* & 0 \\ \hat{c}x_2^* & 1 - \hat{e}x_2^* & 0 \\ 0 & 0 & 1 \end{pmatrix}, \tag{5.3}$$

and from the linearization of the observation (5.2) we obtain

$$C = h'(E_2, 0) = (0, 1, 0). \tag{5.4}$$

Thus we obtain

$$\operatorname{del}\begin{pmatrix} C \\ CA \\ CA^2 \end{pmatrix} = \hat{c}^2 x_1^* x_2^* > 0,$$

and hence the rank condition (4.6) is satisfied, which by Theorem A.1 of the Appendix implies local observability near the equilibrium. Thus, if this system is not far from the equilibrium, it is

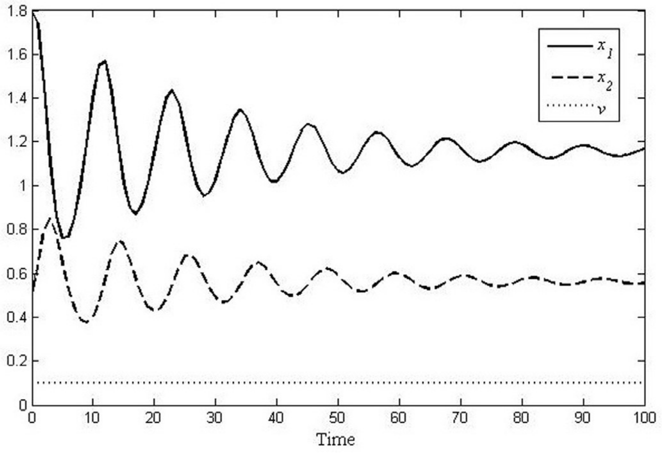


Fig. 5. Solution of system (5.5) to be estimated by the observer.

enough to observe the density of predator over a time interval, and the prey density, in principle, can be uniquely recovered, and it is therefore possible to estimate the value of the unknown parameter. Furthermore, the same rank condition, together with the Lyapunov stability of the equilibrium will guarantee the existence of a local exponential observer for system (5.1)-(5.2), to be illustrated below:

Example 5.1. Setting the same model parameters as in the above Section 2, we consider the following discrete-time prey–predator model with the presence of an unknown abiotic effect v:

$$\begin{aligned} & x_1(t+1) = (0.25\delta + 1 + v(t))x_1(t) - 0.1\delta x_1^2(t) - 0.95\delta x_1(t)x_2(t) \\ & x_2(t+1) = (1 - 0.55\delta)x_2(t) - 0.05\delta x_2^2(t) + 0.5\delta x_1(t)x_2(t) \\ & v(t+1) = v(t), \end{aligned} \tag{5.5}$$

where δ is a time step size. For δ=0.25 we have a positive equilibrium E_2 system (2.2) (see Remark 3.1), and (E_2,0) is an equilibrium of system (5.5). Suppose now that we observe the density of the predator species, i.e. the observation equation is (5.2), and its linearization is (5.4).

The general reasoning of the previous subsection also applies to this illustrative example. In particular, observation system (5.5)-(5.2) is not only locally observable near equilibrium (E_2,0)=(1.114, 0.14, 0), but it also admits the construction of an appropriate observer system near this equilibrium. For instance, let us suppose that the disturbance parameter is $v = 0.1$, considered "unknown" . Let us suppose that the initial condition for the "unknown" solution of the system near the equilibrium is $(x_1(0), x_2(0), v(0)) = (1.8, 0.5, 0.1)$. The corresponding solution of system (5.5) is shown in Fig. 5.

Linearizing system (5.5) at equilibrium (E_2, 0), for the Jacobian of the right-hand side we get

$$A = \begin{bmatrix} 0.972 & -0.265 & 1.114 \\ 0.018 & 0.998 & 0 \\ 0 & 0 & 1 \end{bmatrix}.$$

For matrix $K \in R^{3x1}$ with entries $k_1 = 2$, $k_2 = 0.9$, $k_3 = 0.05$, we can easily check that matrix A-KC has only eigenvalues with module less than one. Therefore, by Theorem 4.1, we can construct an observer system:

$$\begin{aligned} & z_1(t+1) = (0.0625 + 1 + v(t))x_1(t) - 0.025\delta x_1^2(t) \\ & \quad -0.2375x_1(t)x_2(t) + 2(w(t) - h(z(t))) \\ & z_2(t+1) = (1 - 0.1375)x_2(t) - 0.0125x_2^2(t) + 0.125x_1(t)x_2(t) \\ & \quad +0.9(w(t) - h(z(t))) \\ & z_3(t+1) = v(t) + 0.05(w(t) - h(z(t))). \end{aligned} \tag{5.6}$$

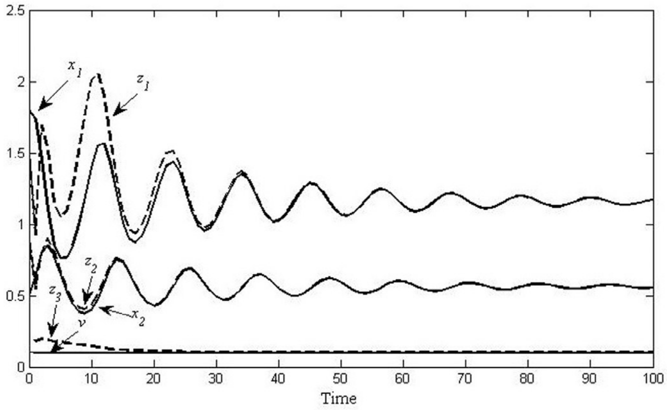


Fig. 6. Simultaneous estimation of the state process and the unknown parameter change.

Now we take an initial value near to the above initial condition, for example, $(z_1(0), z_2(0), z_3(0)) = (1.5, 0.9, 0.2)$. We can see in Fig. 6, how the solution of the observer system tends to the solution of the original system.

6. Conclusions and discussion

6.1. Some methodological conclusions

As it is discussed e.g. in Grantham and Athalye (1990), discrete-time versions of classical population dynamics models can display behaviors quite different from those of the corresponding continuous-time models. From the modelling point of view, neither the invariance of the non-negative orthant of the solutions can be guaranteed. On the example of a discrete-time Lotka–Volterra prey–predator model, we have shown that locally, near an equilibrium, under simple conditions on the system parameters, local positivity near the positive equilibrium holds.

On illustrative numerical examples we have demonstrated that the observer design methodology developed in engineering context for continuous-time systems, may be efficiently applied to discrete-time models of population ecology, providing a good estimation of the whole state process, based on its partial observation. (Some necessary mathematical details have been also worked out.)

We can also conclude that the same methodology can be also appropriate to the estimation of abiotic environmental changes.

6.2. Discussion of possible extensions

For the sake of simplicity, we have presented the offered methodology in the framework of a minimal but not trivial discrete-time population system, namely the Euler discretization of the classical Lotka–Volterra prey–predator model with intraspecific interaction in both populations. The proposed methodology, however, can be extended in several directions.

First of all, we note that for the generalization to multi-species Lotka–Volterra type population systems, formally it is enough to discretize the continuous-time systems-theoretical population-ecological model of Varga et al. (2003). In fact, it is expected that the reasoning of the present paper concerning local positivity, Lyapunov stability and local observability can be adapted to the discretization of this continuous-time multi-species model, at least if the Lotka–Volterra system is either conservative or dissipative.

A further extension of our results concerns the interspecific interaction. In the Lotka–Volterra model, for the sake of simplicity, the number of prey consumed by a predator in unit time (i.e. the functional response) is proportional to the prey density, and the conversion of prey into predator is proportional to the consumed prey (providing the numerical response), for these concepts see e.g. Holling (1959) and Solomon (1949). Our approach can also be applied to the case of more general functional and numerical responses.

Finally, an extension is also possible concerning the estimation of environmental effects on the biological parameters of the population system. Abiotic changes like pollution may affect not only Malthus parameters, but also interaction coefficients, see e.g. Gragnani (2002). Our approach also applies to the latter situation. Furthermore, suppose that in the abiotic environment there is a continuous change obeying a known dynamic law (exosystem), which affects certain parameters of the population system model. This abiotic effect may be e.g. pollution produced by an industrial plant, a periodical (seasonal) change of temperature, or a monotonous increase of the mean temperature due to global warming, etc. To the corresponding discrete-time population model extended with the dynamics of the exosystem, our monitoring approach may also be applied. For the mathematical background of the observer design for discrete-time systems with exosystem we refer to Sundarapandian (2004).

Appendix

Let n be a positive integer, $n > 1$, f: $R^n \to R^n$ an arbitrary function, and consider the discrete-time system

$$x(t+1) = f(x(t)) \quad (t = 0,\ 1, \ldots). \tag{A.0}$$

Definition A.1. System (A.0) is said to be locally positive at $x^* \in R^n$, $x^* > 0$, if there exists $\delta > 0$ such that

$$x(0) \in G_\delta(x^*) \Rightarrow x(t) > 0 (t = 1, 2, \ldots).$$

Suppose that $x^* \in R^n$ $x^* > 0$ is an equilibrium for dynamics (A.0): $f(x^*) = x^*$, which is asymptotically stable. This means that

(a) for every $\varepsilon > 0$ there exists a $\delta > 0$ with $\delta < \varepsilon$, such that for the corresponding neighborhoods $G_\varepsilon(x^*)$ and $G_\delta(x^*)$ we have $x(0) \in G_\delta(x^*) \Rightarrow x(t) \in G_\varepsilon(x^*) (t = 1, 2, \ldots)$;

(b) there exists a $\delta_1 > 0$such that for every $x(0) \in G_{\delta 1}(x^*)$ we have $\lim\limits_{t\to\infty} x(t) = x^*$.

Using only part a), and setting the above $\varepsilon > 0$ such that $G_\varepsilon(x^*) \subset \mathrm{int}R^n_+$, with the corresponding $\delta > 0$ we obtain that

$$x(0) \in G_\delta(x^*) \Rightarrow x(t) > 0 (t = 1, 2, \ldots).$$

Hence we obtain the following

Lemma A1. If $x^* > 0$ is an asymptotically stable equilibrium of system (A.0), then system (A.0) is locally positive at x^*.

Let $D \subset R^n$ be an open set, f: $D \to D$ and h: $D \to R^p$ continuously differentiable (smooth) functions, and consider

$x(t+1) = f(x(t))$,(A.1)

$w(t) = h(x(t))$, $\quad (t = 0,\ 1, \ldots)$.(A.2)

Suppose that $x^* \in D$ is an equilibrium for dynamics (A.1), $f(x^*) = x^*$, and $h(x^*) = 0$.

Definition A.2. System (A.1) – (A.2) is called locally observable (on the discrete time interval $\{0,\ 1, \ldots,\ n-1\}$), if there exists a neighborhood $G(x^*)$ of x^* such that

$$\left.\begin{array}{lll} x(0) \in G(x^*), & x(t+1) = f(x(t)) & (t = 0, \ldots, n-1) \\ v(0) \in G(x^*), & v(t+1) = f(v(t)) & (t = 0, \ldots, n-1) \\ & h(x(t)) = h(v(t)) & (t = 0, \ldots, n-1) \end{array}\right\} \Rightarrow x(0) = v(0).$$

For the linearization of system (A.1) – (A.2), let us introduce the Jacobians

$$A = f'(x^*), \quad C = h'(x^*).$$

Now we can easily obtain a sufficient condition for local observability, which is a discrete-time analog of a similar theorem of Lee and Markus (1967).

Theorem. A.1. If

$$rank \begin{pmatrix} C \\ CA \\ \vdots \\ CA^{n-1} \end{pmatrix} = n, \tag{A.3}$$

then system (A.1) – (A.2) is locally observable at x^*.

Proof. Introducing the $(n-1)$-iteration of f,

$$f^{[n-1]} = \underbrace{f \circ f \circ \ldots \circ f}_{(n-1)\ times},$$

we have to prove that mapping

$$H = \begin{pmatrix} h \\ h \circ f \\ \vdots \\ h \circ f^{[n-1]} \end{pmatrix}$$

is locally injective. We have

$$H'(x^*) = \begin{pmatrix} h'(x^*) \\ h'(f(x^*))f'(x^*) \\ h'(f(f(x^*))) \cdot f'(f(x^*))f'(x^*) \\ \vdots \\ h'(\underbrace{f(f(\ldots f}_{(n-1)\ times}(x^*)))) \cdot f'(\underbrace{f(f(\ldots f}_{(n-2)\ times}(x^*)))) \end{pmatrix}$$

$$= \begin{pmatrix} h'(x^*) \\ h'(x^*)f'(x^*) \\ h'(x^*)f'(x^*)f'(x^*) \\ \vdots \\ h'(x^*)(f'(x^*))^{n-1} \end{pmatrix} = \begin{pmatrix} C \\ CA \\ CA^2 \\ \vdots \\ CA^{n-1} \end{pmatrix}.$$

Since by condition (A.3), $H'(x^*)$ has full rank, mapping H is locally injective, implying local observability of system (A.1) – (A.2).

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