

Monitoring of population systems*

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Abstract

This is a *selected overview* of a research line initiated and mostly developed by the three authors over the last three decades. Applying the state space paradigm of Mathematical Systems Theory, monitoring means that from the observation (a transform) of an unknown state process, the latter should be recovered. Since most of the dynamic models of population biology are nonlinear, for solving the monitoring problem, tools of nonlinear analysis are applied in different contexts. This approach to monitoring has found different applications ranging from population ecology to radiotherapy, from stock estimation in fisheries to monitoring of solar thermal heating systems.

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1 Introduction

In this paper we survey certain typical results from a research line initiated and mostly developed by the listed coauthors over the last three decades. The reviewed results range from the very beginning [32] to a just submitted manuscript [24].

Throughout this paper, by a population system we mean either a single population where the individuals are classified according to some equivalence relation, or a community of several interacting populations, see Figure 1.

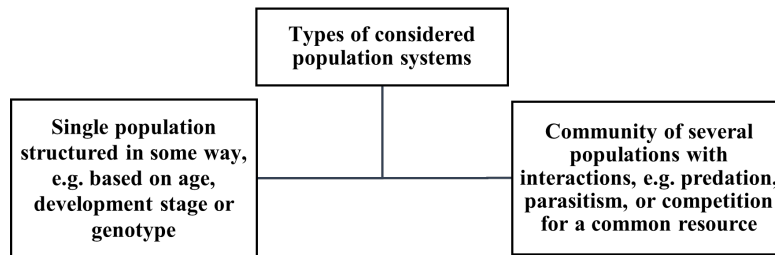


Figure 1: Combinations of both types provide more complex population systems.

The basic idea proposed at the beginning of the research line of *monitoring of population systems*, was the application of the state space paradigm of Mathematical Systems Theory. In this framework, monitoring means that from a transform (observed function) of an unknown state process, the latter should be recovered. Intuitively, *observability* means that different state processes imply different observed functions.

Of course, invertibility of the mentioned transformation obviously implies observability. However, when the transformation in question is not invertible, e.g. it is a projection (i.e. we observe only certain component(s) of the state vector), the "movement" due to the dynamics may make it possible for us to recover the state process from its projection.

Furthermore, in case of observability, under certain stability conditions, the so-called *observer design* procedure makes it possible to effectively estimate the unknown state process. Since most of the dynamic models of population biology are nonlinear, for solving the monitoring problem, tools of nonlinear analysis are applied in different contexts, both to continuous-time and discrete-time dynamics, see Figure 2. This approach to monitoring has found different applications ranging from population ecology to radiotherapy, from stock estimation in fisheries to monitoring of solar thermal heating systems.

Considering Figure 3, we emphasize a sufficient condition for the observability in the case of frequency-dependent dynamics should be weaker than in the case when there is no invariant manifold.

Figure 4 shows a general control-observation system, in the present paper however, for the sake of simplicity we deal only with monitoring (i.e. observa-

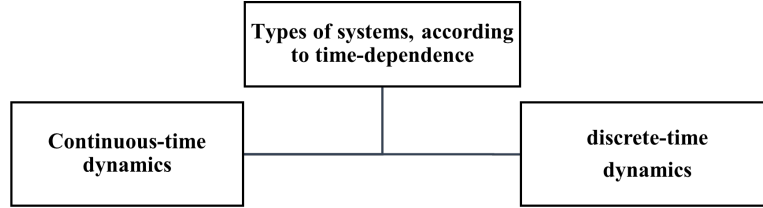


Figure 2: In most cases there is a natural way to choose one of the types of time-dependence.

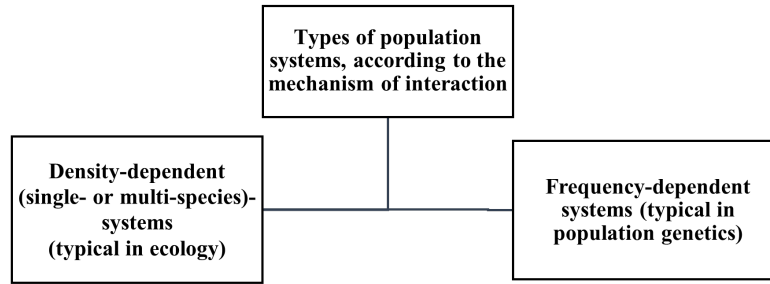


Figure 3: In the frequency-dependent case, the observability problem is particular, since the simplex of frequency vectors is an invariant manifold for the dynamics.

tion) of population systems without control. (For the control aspects of population systems we can refer e.g. to our Remark 2 below.)

2 Monitoring of a frequency-dependent population system

Let us suppose that in a large, panmictic Mendelian population, at an autosomal locus alleles A_1, \dots, A_n ($n \geq 2$) determine a trait. In this model the genetic state of the population is described in terms of the time-dependent relative allele frequencies x_i ($i = 1, \dots, n$). Let $w_{i,j}$ denote the fitness of genotype $A_i A_j$. Then the dynamics of the genetic state of the population, also called Fisher's model of natural selection, is

$$\dot{x}_i = x_i \left(\sum_{j=1}^n w_{i,j} x_j - \sum_{k,l=1}^n w_{k,l} x_k x_l \right) \quad i = 1, \dots, n \quad (2.1)$$

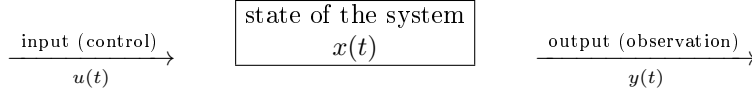


Figure 4: Control–observation or input–output system.

and the relative interior of the standard simplex $\overset{\circ}{S}_n \subset \mathbb{R}^n$ is positively invariant for (2.1). Therefore, to check observability, an appropriate sufficient condition was needed for the case of nonlinear systems with invariant manifold.

2.1 Observability of systems with invariant manifold

In general terms, let $m, n \in \mathbb{N}$, $f \in C^1(\mathbb{R}^n, \mathbb{R}^n)$, $h \in C^1(\mathbb{R}^n, \mathbb{R}^m)$ and consider *observation system*,

$$\dot{x} = f(x) \quad (2.2)$$

$$y = h(x). \quad (2.3)$$

Assume that $x^* \in \overset{\circ}{S}_n$, $f(x^*) = 0$, $h(x^*) = 0$, and there exists $T > 0$ such that any solution of the system (2.2), starting close enough to equilibrium x^* is defined on $[0, T]$.

DEFINITION 1 *For some $k = 1, \dots, n$, a subset $M \subset \mathbb{R}^n$ is said a regular k -dimensional submanifold, if there is an open set $G \subset \mathbb{R}^n$ and a function $\Phi \in C^1(G, \mathbb{R}^{n-k})$ such that for every $x \in G$ we have $R_{\Phi'(x)} = \mathbb{R}^{n-k}$, and $M = \Phi^{-1}(0)$.*

For the rest of this subsection we supposed that for some $k = 1, \dots, n$, a subset $M \subset \mathbb{R}^n$ is a regular k -dimensional submanifold, positively invariant for system (2.2), and $x^* \in M$ is an equilibrium of this system. In particular, the relative interior $\overset{\circ}{S}_n \subset \mathbb{R}^n$ of the standard simplex is a regular $(n-1)$ -dimensional submanifold, positively invariant for system (2.1).

DEFINITION 2 *We shall say that observation system (2.2)-(2.3) is locally observable in M , near equilibrium x^* , on $[0, T]$, if there exists $\varepsilon > 0$ with the property that*

$$\left. \begin{array}{l} x^i \in M, |x^i(0) - x^*| < \varepsilon \quad i = 1, 2 \\ \dot{x}^i(t) = f(x^i(t)) \quad t \in [0, T] \\ h \circ x^1 = h \circ x^2 \end{array} \right\} \implies x^1 = x^2.$$

Since for $k < n$, local observability in an invariant manifold is a weaker requirement than the usual local observability, for the weaker case it is reasonable

to find a weaker sufficient condition than the classical one, where there is no invariant manifold [15].

Considering the linearization of observation system (2.2)-(2.3), define

$$A = f'(x^*), C = h'(x^*), \text{ and } Q = \begin{pmatrix} C \\ CA \\ \vdots \\ CA^{n-1} \end{pmatrix}.$$

Now, denoting by $T_{x^*}(M)$ the tangent space of M at x^* , from [32] we recall the following sufficient condition:

THEOREM 1 *Let Q correspond to the linearization of (2.2)-(2.3). Then transversality condition $T_{x^*}(M) \cap \ker Q = \{0\}$ implies that observation system (2.2)-(2.3) is locally observable in M , near equilibrium x^* , on $[0, T]$.*

REMARK 1 It is easy to see that Theorem 1 can be considered as an extension of the sufficient condition well-known for observation systems without invariant manifold. [15].

2.2 Application of the sufficient condition

Now we illustrate the application of Theorem 1 to the phenotypic observation of the genetic state process in Fisher's model of selection. To this end, first we need a so-called *polymorphic equilibrium*, that is, an allele frequency vector $x^* \in \overset{\circ}{S}_n$ of (2.1), where

$$(Wx^*)_i = \langle x^*, Wx^* \rangle \quad i = 1, \dots, n.$$

The latter condition means that every allele has the same marginal (or potential) fitness. Intuitively, if the marginal fitness of an allele A_i is higher than the average fitness of the population, then the frequency of A_i will increase, and in the opposite case this frequency will decrease.

Let us suppose that W is invertible, and $\langle W^{-1}\mathbf{1}, \mathbf{1} \rangle \neq 0$ holds with $\mathbf{1} = (1, \dots, 1) \in \mathbb{R}^n$, and

$$x^* = \frac{W^{-1}\mathbf{1}}{\langle W^{-1}\mathbf{1}, \mathbf{1} \rangle} > 0. \quad (2.4)$$

Then x^* is the unique polymorphic equilibrium, and hence also an interior equilibrium of system (2.1).

EXAMPLE 1 *Consider a Fisher type 1-locus 3-allele selection model, i.e. system (2.1) with $n = 3$, and suppose that a polymorphic equilibrium (2.4) exists. Furthermore, between alleles A_1, A_2, A_3 the dominance relationships are the following: both A_1 and A_2 are dominant over A_3 , while A_1 and A_2 are codominant. In other words, denoting by $\overline{A_i A_j}$ the phenotype corresponding to genotype $A_i A_j$,*

we have $\overline{A_1A_3} = \overline{A_1A_1}$, $\overline{A_2A_3} = \overline{A_2A_2}$, $\overline{A_1A_2}$ is a phenotype different from the previous ones, and the fourth phenotype is $\overline{A_3A_3}$. (We note that for this genotype–phenotype correspondence a well-known example is the ABO blood group system.)

Now the frequencies of the four phenotypes, calculated from allele frequencies x_i are, respectively

$$\overline{A_1A_1} : x_1^2 + 2x_1x_2; \overline{A_2A_2} : x_2^2 + 2x_2x_3; \overline{A_1A_2} : 2x_1x_2; \overline{A_3A_3} : x_3^2.$$

Assume that, instead of the time-dependent allelic state x , the time-dependent frequency of phenotype $\overline{A_3A_3}$ is observed. For observation system (2.2)-(2.3) we define $f \in C^1(\mathbb{R}^3, \mathbb{R}^3)$ and $h \in C^1(\mathbb{R}^3, \mathbb{R})$ as follows:

$$f_i(x) = x_i \left(\sum_{j=1}^3 w_{i,j}x_j - \sum_{k,l=1}^3 w_{k,l}x_kx_l \right) \quad i = 1, 2, 3. \quad (2.5)$$

$$h(x) = x_3^2 - x_3^{*2}, \quad (2.6)$$

and let w^* be the equilibrium value of the mean fitness, $w^* = \sum_{k,l=1}^3 w_{k,l}x_k^*x_l^*$.

For the application of Theorem 1, let us take $M = \overset{\circ}{S}_3$, and based on (2.5)-(2.6) calculate the corresponding Jacobians $A = f'(x^*)$ and $C = h'(x^*)$ to get

$a_{i,j} = x_i^*(w_{i,j} - 2w^*)$ ($i, j = 1, 2, 3$), $C = [0, 0, 2x_3^*]$, and $Q = \begin{pmatrix} C \\ CA \\ CA^2 \end{pmatrix}$. Now we

can apply Theorem 1 with $M = \overset{\circ}{S}_3$, and $T_{x^*}(\overset{\circ}{S}_3) = \{z \in \mathbb{R}^3 | z_1 + z_2 + z_3 = 0\}$.

Hence a straightforward checking provides the following:

THEOREM 2 Suppose that $x_1^*(w_{1,1} - w_{1,2}) + x_2^*(w_{2,1} - w_{2,2}) \neq 0$ and $w_{3,1} \neq w^*$. Then observation system (2.2)-(2.3) as given by (2.5)-(2.6), is locally observable in $\overset{\circ}{S}_3$, near equilibrium x^* , on $[0, T]$.

REMARK 2 First we note that Theorem 1 was also applied to models of reaction kinetics in [1]. Furthermore, for an outlook we also note that if some of the fitness parameters are considered as control functions, we obtain a model of artificial selection, where controllability is also an issue, see e.g. [31], [18], [21] and [8].

REMARK 3 We emphasize that observability only means that from the observation the underlying state process, *in principle*, can be uniquely recovered. The next step in the modelling-methodological development was the effective estimation of the state process, based on observer design, initially proposed by [25] and further developed by [28]. As a matter of fact, this approach does not deal with systems with invariant manifold, therefore we had to cope with

this problem in [22], where the phenotypic selection process is described by an evolutionary game. To avoid this complication, in the next section we recall the monitoring of a density-dependent population system, using an appropriate observer system.

3 Monitoring of a density-dependent population model

In this section, first we show how a general scheme of [28] leads to an effective estimation of an unknown state process: First find an equilibrium, then check its Lyapunov stability, finally, using the observed function, construct the so-called observer system, the solutions of which asymptotically estimate the unknown state process.

3.1 Local observability

Similarly to Section 2, let $m, n \in \mathbb{N}$, $f \in C^1(\mathbb{R}^n, \mathbb{R}^n)$, $h \in C^1(\mathbb{R}^n, \mathbb{R}^m)$, $x^* \in \mathbb{R}^n$, $f(x^*) = 0$, $h(x^*) = 0$; and consider observation system,

$$\dot{x} = f(x) \tag{3.1}$$

$$y = h(x). \tag{3.2}$$

where (3.2) defines a transform of the state. Here it is again supposed there exists a $T > 0$ such that any solution of system (3.1), starting close enough to equilibrium x^* is defined on $[0, T]$. Since in typical density-dependent population models, invariant manifold is not an issue, we can apply the "straight" observability concept, obtained from Definition 1 by dropping the condition that the involved solutions initially belong to an invariant manifold:

DEFINITION 3 *We shall say that observation system (3.1)-(3.2) is locally observable near equilibrium x^* on $[0, T]$, if there exists $\varepsilon > 0$ with the property that*

$$\left. \begin{array}{l} |x^i(0) - x^*| < \varepsilon \quad i = 1, 2 \\ \dot{x}^i(t) = f(x^i(t)) \quad t \in [0, T] \\ h \circ x^1 = h \circ x^2 \end{array} \right\} \implies x^1 = x^2.$$

Defining $A = f'(x^*)$ and $C = h'(x^*)$, from [15] we recall

THEOREM 3 *If $\text{rank } Q = n$, then system (3.1)-(3.2) is locally observable at x^* on $[0, T]$.*

3.2 Observer system

DEFINITION 4 Given a function $G \in C^1(\mathbb{R}^n \times \mathbb{R}^m, \mathbb{R}^n)$, we say that

$$\dot{z} = G(x, y) \quad (3.3)$$

is a local (exponential) observer for system (3.1)-(3.2) at x^* , if for the joint system (3.1)-(3.2)-(3.3) we have

$$i) \ x(0) = z(0) \implies x(t) = z(t) \quad t \in [0, +\infty),$$

$$ii) \ \text{there exists a neighborhood } V \text{ of } x^* \text{ such that } x(0), z(0) \in V \implies \lim_{\infty} (z - x) = 0 \text{ (exponentially).}$$

Now from [28] we recall

THEOREM 4 Assume that an equilibrium x^* of system (3.1) is Lyapunov stable (in particular, solutions starting near x^* are defined on $[0, +\infty)$), and K is a real $n \times m$ matrix, called gain matrix, such that $A - KC$ is a stable matrix (i.e. all its eigenvalues have negative real parts). Then system

$$\dot{z} = f(z) + K[y - h(z)] \quad (3.4)$$

is a local exponential observer for observation system (3.1)-(3.2).

The above observer design method has been applied to the monitoring of different Lotka-Volterra type population systems e.g. in [19]. Below, as an example, we shortly present the observer design for a non-Lotka-Volterra type trophic chain model, based on [34]. The considered trophic chain is of type *resource – producer – primary consumer*, where the resource, the 0th trophic level can be solar energy or inorganic nutrient (x_0) with constant supply, the 1st trophic level (producer) is a plant population (of density x_1), the 2nd trophic level (primary consumer) is a herbivorous population (of density x_2). With the obvious meaning of the coefficients

$$Q, \alpha_0, \alpha_1, m_1, m_2 > 0; \quad k_1, k_2 \in (0, 1); \quad \beta_1, \beta_2 \in [0, 1);$$

the ecological model is

$$\dot{x}_0 = Q - \alpha_0 x_0 x_1 + \beta_1 m_1 x_1 + \beta_2 m_2 x_2 \quad (3.5)$$

$$\dot{x}_1 = x_1 (-m_1 + k_1 \alpha_0 x_0 - \alpha_1 x_2) \quad (3.6)$$

$$\dot{x}_2 = x_2 (-m_2 + k_2 \alpha_1 x_1) \quad (3.7)$$

In [27] it was shown that for resource supply Q high enough, there exists a unique equilibrium $x^* > 0$, and both in systems with no recycling (with $\beta_1 = 0$ and $\beta_2 = 0$) and with partial recycling (i.e. at least one of inequalities $0 < \beta_1 < 1$ and $0 < \beta_2 < 1$ holds), x^* is asymptotically stable, implying stable ecological

coexistence of the system. Suppose that the resource (its deviation from its equilibrium value) is observed:

$$h(x) = x_0 - x_0^*. \quad (3.8)$$

Then for the corresponding Jacobians we have

$$A = \begin{pmatrix} -\alpha_0 x_1^* & -\alpha_0 x_0^* + \beta_1 m_1 & \beta_2 m_2 \\ k_1 \alpha_0 x_1^* & 0 & -\alpha_1 x_1^* \\ 0 & k_2 \alpha_1 x_2^* & 0 \end{pmatrix}, C = h'(x^*) = (1 \ 0 \ 0).$$

Now, for k_1 large enough, with $K = \begin{pmatrix} k_1 \\ 0 \\ 1 \end{pmatrix}$, matrix $A - KC$ is stable. Therefore, applying Theorem 4, an observer system can be constructed, as illustrated in the following

EXAMPLE 2 *Let us consider the above model with parameter values $Q = 10; \alpha_0 = 0.3; \alpha_1 = 0.1; \beta_1 = 0.2; \beta_2 = 0.3; m_1 = 0.1; m_2 = 0.4; k_1 = 0.5; k_2 = 0.5$. In this case the considered system (3.5)-(3.7) has a positive equilibrium $x^* = (4.52, 8, 5.78)$, which is asymptotically stable. The observer system we obtain is*

$$\begin{aligned} \dot{z}_0 &= 10 - 0.3z_0z_1 + 0.2 \cdot 0.1z_1 + 0.3 \cdot 0.4z_2 + 10[y - (z_0 - x_0^*)] \\ \dot{z}_1 &= z_1(-0.1 + 0.5 \cdot 0.3z_0 - 0.1z_2) \\ \dot{z}_2 &= z_2(-0.4 + 0.5 \cdot 0.1z_1) + 1[y - (z_0 - x_0^*)]. \end{aligned} \quad (3.9)$$

The respective solutions of the original system and the observer system are shown in Figure 5.

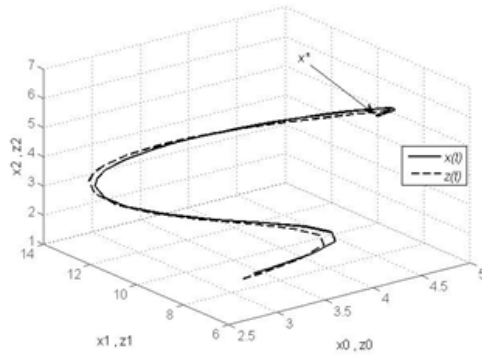


Figure 5: Solution of the observer system, starting from $z(0) = (2.9, 7.2, 1.8)$, estimates the "unknown" solution of the original system (3.5)-(3.7), starting from $x(0) = (3, 7, 2)$.

4 Further developments and outlook

4.1 Monitoring of frequency-dependent population systems

As a continuation of our results, first we report on the further developments on observers for frequency-dependent population systems. First, in the Ph.D. thesis [16] the results of subsection 2.2 have been extended to a selection-mutation model, see also [21], [26] and [17]. In addition, in [16] the case when in a single-locus sexual population, a phenotypic selection process is considered in terms of an evolutionary game (see also [3]). In [22], similar sexual population was studied using the standard continuous-time evolutionary game dynamics. Here the observer design was adapted to a frequency-dependent case, where the relative interior of the frequency simplex turned out to be long-term invariant for the observer system. (The latter means that for the solution z of the observer system, for t large enough, $z(t)$ can be interpreted as a frequency vector.) For a parametrized evolutionary game Hopf bifurcation was also obtained.

4.2 Monitoring of density-dependent population systems

In [35] the observability study (the sufficient condition for local observability) was extended to the case when a changing environment is also included in the model in terms of known time-dependent additive control functions in the Malthus parameters and in the interaction coefficients, in case of a one-predator-two-prey system and a trophic chain.

The effective estimation of a state process from an observation, as presented in subsection 3.2, was applied in [11]. In fishery, for a sustainable management, a reserve area is often separated. In the considered fishing effort model, a single-species population dynamics is considered, where one subpopulation lives in a reserve area, the other part of the population in a free area for fishing, and there is a two-way migration between the two areas. The biomass harvested in the unreserved area in unit time is the observation, and the observer system provides a *deterministic estimate of the stock in the reserve area*. (In the studied case, our approach provided a better estimate of the stock than the global observer of [12]).

In [9] special ecological interaction chains are studied that are of the type resource–producer–primary user–secondary consumer. They turn out to be of *verticum type*; intuitively, they consist of a sequence of "subsystems" to which the observation problem can be decomposed. (See also [20] and [9]).

A further issue concerning observer design, is that it may be applied to *estimate the unknown effect of an abiotic change in the environment of a population system*. In [11] already cited above, it is also supposed that there is an unknown change in the migration rates (depending on an abiotic factor) of the form of additional terms c_1w and c_2w , respectively, where constants c_1 and c_2 are known. Then completing the fishery model with a further, trivial differential equation $\dot{w} = 0$, to the extended system the observer design method of [28] can also be

applied. The solutions of the obtained observer system not only estimate the state process (the stock in both areas), but also approximate the unknown value of the parameter w . We also note that similar parameter estimation was applied in [6] and [5].

Robust observer design method was proposed in [23]. In the usual observer design, as recalled in subsection 3.2, a gain matrix K must be found that guarantees that the solutions of the corresponding observer system approach the unknown solution of the original system at exponential rate. In [23] multi-species population systems displaying stable coexistence are considered, where the asymptotic stability is obtained by the stability of the Jacobian A of the right-hand side of the system dynamics at an equilibrium. Let us suppose that the stable matrix A is *sign-stable* in the sense that it remains stable whenever we change its entries without violating its sign pattern $\text{sgn } a_{i,j}$. Under the condition of sign-stability of A we have shown that in the process of observer design the same gain matrix can be applied even if, in the meanwhile, due to some changes in the environment, certain interactions suffer a quantitative change. We note that sign-stability can be checked in terms of the *signed directed graph associated with the above matrix A* . The proposed robust observer design is illustrated with examples of a trophic chain and a Lotka-Volterra type system with vertical structure.

We also mention that in [10], for competitive Lotka–Volterra systems, an *iterative scheme* was proposed *for the construction of an observer system*. Furthermore, for control-observation systems shown in Figure 4, in [30] a new nonlinear system inversion method was applied for the reconstruction of time-dependent abiotic environmental changes, from the observation of certain indicator species.

Finally, we recall some further applications from the research line of monitoring by observer design. In [4], observer design was applied in the field of radiotherapy, for the case when the total number of cells is observed, without distinction between healthy and affected cells. The constructed observer system made it possible to estimate the population of both the healthy and the affected cells. A quite different application field was in engineering of solar thermal heating systems. In [13] with some modification of the methodology of subsection 3.2, a real-time version of the state observer design for solar thermal heating systems was proposed, estimating some unmeasured state variables. Based on real data, the proposed state estimation method was also applied to a concrete solar heating system.

Furthermore, in [14] a *global nonlinear state observer* was constructed for a solar domestic water heating system. Global here means that the solution of the observer system can start from any initial state.

4.3 Monitoring of discrete-time density-dependent population models

There is a discrete-time analogue of the observer design presented in subsection 3.2, for its description we refer to [29]. In [7] the monitoring problem of the

Euler discretization of the classical continuous-time Lotka–Volterra predator-prey model was studied. By and large, the observer design can be carried out similarly to the continuous case, but the parallel between the two cases is not straightforward. In the submitted paper [24] the *monitoring problem of a Leslie type, discrete-time, age-specific but nonlinear population model* is considered, where the time-dependent size of certain age class(es) is observed, and the time-dependent total age distribution should be recovered (see Figure 1 above). This issue (also its version to be developed, where instead of age classes, development stages are involved) is obviously important in population ecology. Of course, monitoring of multi-species versions of these models would also be interesting.

Finally, we note that surveys [33], [35] and [2] were interim reports on the current state of art of the research line of monitoring of population systems.

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