

PARAMETER IDENTIFICATION AND ESTIMATION FOR STAGE-STRUCTURED POPULATION MODELS

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A stage-structured population model with unknown parameters is considered. Our purpose is to study the identifiability of the model and to develop a parameter estimation procedure. First, we analyze whether the parameter vector can or cannot uniquely be determined with the knowledge of the input-output behavior of the model. Second, we analyze how the information in the experimental data is translated into the parameters of the model. Furthermore, we propose a process to improve the recursive values of the parameters when successive observation data are considered. The structure of the state matrix leads to an analysis of the inverse of a sum of rank-one matrices.

Keywords: system identification, parameter estimation, dynamic population, discrete-time system, rank-one matrix.

1. Introduction and mathematical background

Stage-structured models are based on the assumption that a large group can be divided into smaller ones with similar parameters and in some way interconnected with one another. For example, the individuals of a population are organized in stages because of their evolution in different phases from birth to death. Although Leslie's model is quite a suitable approach for some type of animals, it does not generally conform to the analysis of the evolution of a population of many species. This is the case for some animals such as insects, turtles and even some mammals (Carnia et al., 2015), or when analyzing evolving populations of most plants. Detecting whether a plant will prosper or not depends more on the size or condition of the plant than on its age. This means that those plants that do not reach the desired size in an interval of time will remain in the same class and will not advance to the next one. This behavior does not fit into a Leslie model and in these cases the Lefkovitch model fits better since the elements of the state matrix represent the transition rate from one class of a stage (or size) to another.

When populations are structured, the birth rate is often called fertility (the number of offspring that

are produced per female of a given stage). Usually, this fertility is zero for an individual in a pre- or post-productive age and positive fertility is observed for individuals of a reproductive age. These structured systems are employed to model the changes in a population of organisms and are widely used in studies of biology, ecology and demography to determine the growth of a population, (see, e.g., Caswell, 2001; Kajin et al., 2012; Leslie, 1948; Lefkovitch, 1965). Note that this kind of dynamic process is represented by a discrete linear system with nonnegative states and nonnegative inputs. Therefore, we are considering positive systems and the study involves the use of nonnegative matrix theory and positive control theory (Kaczorek, 2002). These mathematical tools are usually used in the analysis of the evolution of several real processes (see, e.g., Cantó et al., 2014; Cao and Zhou, 2012; De La Sen and Quesada, 2003; Emmert and Allen, 2004; Li and Schneider, 2002; Li and Wang, 2006).

The notation and the basic concepts that will be used throughout the work are as follows (see Berman and Plemmons, 1994). A matrix $M=(m_{ij})$ is nonnegative if $m_{ij}\geq 0$ for all i,j, and it is denoted by $M\geq 0$. Analogously, a nonnegative vector is defined and denoted by $\mathbf{p}=(p_i)\geq 0$ if $p_i\geq 0$, for all i. From now on, we will denote by $e_i,\ i=1,\ldots,n$ the unit canonical basis of \mathbb{R}^n and by $\operatorname{col}(X_i)_{i=1}^l$ a column matrix by blocks whose

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blocks are X_i , i = 1, ..., l.

Our mathematical model considers populations in each stage as a nonnegative state variables. Sometimes the process is altered by a nonnegative entry of a new population. For instance, an inflow of elements into the first stage appears modifying the dynamic of the population (Caswell, 2001). In this way, we have the dynamics of the process represented by the discrete linear system

$$\bar{x}(t+1) = A\bar{x}(t) + B, \quad t \ge 0,$$

where $\bar{x}(t) \in \mathbb{R}^n_{\perp}$ represents the female population and the measure of a new population is given by $B = be_1$; that is, there exists only the entry of a new population at the first stage. In this model, the individuals are organized in nstage classes. Class j includes the female individuals of this stage, and, at time step t, some individuals are going from class j to j + 1 but some of them remain in class j. Many species have different stages, such as eggs, juveniles or larvae, adults, etc. Then, the population distribution entails that not all individuals reach the next stage at the same time. In this status, we have the Lefkovitch model given by

$$A = \begin{pmatrix} \tau_1 + f_1 & f_2 & \cdots & f_{n-1} & f_n \\ s_1 & \tau_2 & \cdots & 0 & 0 \\ \vdots & \ddots & \ddots & \vdots & \vdots \\ \vdots & \ddots & \ddots & \tau_{n-1} & \vdots \\ 0 & 0 & \cdots & s_{n-1} & \tau_n \end{pmatrix},$$

where the entries $f_j \geq 0$ are the fertility parameters, at least one of them nonzero, $0 < s_j \le 1$ is the survival rate growing into the next stage, and $0 \le \tau_i < 1$ the survival rate remaining in the same stage. It is clear that in these models the fertility in the first stage is usually zero. We will assume that $f_1 = 0$. From this matrix, it is possible to calculate a stable age distribution. Note that the biological interpretation of the parameters leads to a system with nonnegative matrices, $A \ge 0$ and $B \ge 0$. Hence, the system is *positive* (see Kaczorek, 2002).

On the other hand, if the models involve unknown parameters, it is essential to obtain their estimated values to predict or control the behavior of the real process.

We denote by $S(\mathbf{p})$ the class of stage-structured discrete-time linear systems $x(t+1) = A(\mathbf{p})x(t) + B$ with the parameter vector **p** belonging to a suitable subset $\mathcal{P} \subseteq \mathbb{R}^l$, and by $io(\cdot)$ the input-output response obtained from an initial condition and an input. Given a system in $S(\mathbf{p})$, we will use its Markov parameters $V(j,\mathbf{p}) =$ $A^{j}(\mathbf{p})B, j \geq 0$ to determine the input-output behavior of this system.

We say that $S(\mathbf{p})$ is globally identifiable if and only if, for any two candidate parameter vector values $\mathbf{p},\ \mathbf{q} \in$ \mathcal{P} , the same input-output behavior $io(\mathbf{p}) = io(\mathbf{q})$ implies $\mathbf{p} = \mathbf{q}$.

Thus, while the identifiability of the model guarantees that the parameter vector can uniquely be determined by the knowledge of the input-output behavior of the model, the estimation responds to how the information in the experimental data is translated into the model parameters. The identifiability guarantees that the model parameters can be estimated under ideal conditions. Usually, the solution of the estimation problem is obtained through minimization of a least squares function. Accordingly, the estimation problem is usually addressed by fitting model simulations to the observed experimental data set $\{ob(i) \in \mathbb{R}^n, i =$ $1, \ldots, K$. To solve this problem, the system x(t+1) = $A(\mathbf{p})x(t) + B$ is rewritten as

$$x(t+1) = M(t)\mathbf{p} + N(t), t > 0,$$

and the objective is to minimize the quadratic cost function

$$J_K(\mathbf{p}) = \frac{1}{2} \sum_{i=1}^K e(i)^T e(i) = \frac{1}{2} \mathbf{e}_K^T \mathbf{e}_K,$$

where $e(i)=(ob(i)-x(i)),\ i=1,\ldots,K,\ \mathbf{e}_K=(e(i))_{i=0}^{K-1},$ with $\{ob(t),\ t=1,\ldots,K\}$ being a data set of K observations and $\{x(t), t = 1, ..., K\}$, the system response starting from an initial condition x(0).

Several studies on parameter estimation and structure identification can be found in the literature. The main problem of these models is to determine techniques to adjust the parameters from experimental data. An analysis of experimental data errors due to parameter sensitivity is given by Boyadjiev and Dimitrova (2005). In the work Verdière et al. (2005) a nonlinear pharmacokinetic model is used and it is analyzed how only one output polynomial provides information on the identifiability of the model; this information is used in numerical parameter Finally, a good review of identifiability estimation. problems and the estimation process is given by Chou and Voit (2013).

This paper is organized as follows. In the next section, we present the stage-structured population model and a background on the mathematical tools used throughout the work. In Section 3, we obtain theoretical results on the identifiability of the parameters involved in the process. Then, we board the estimation problem establishing conditions in order to ensure an estimated value of the parameter from a data set. In Section 4, the analysis of our model leads us to study properties of a sum of rank-one matrices. Then, we establish a recursive process to improve the values of the parameters by addition of more observed data. The results are illustrated with an example.

2. Identifiability and estimation of parameters in stage-structured models

We consider the stage-structured population model including a controlled inflow of elements represented by (1). The transformation matrix

$$S = \operatorname{diag}(1, s_1, s_1 s_2, \ldots, s_1 \cdots s_{n-1})$$

leads us from the model (1) to a similar system, with $x(t) = S^{-1}\bar{x}(t)$, given by

$$x(t+1) = A(\mathbf{p})x(t) + B,\tag{2}$$

with

$$A(\mathbf{p}) = S^{-1}AS = \begin{pmatrix} a_1 & a_2 & \cdots & a_{n-1} & a_n \\ 1 & \tau_2 & \cdots & 0 & 0 \\ \vdots & \ddots & \ddots & \vdots & \vdots \\ \vdots & \ddots & \ddots & \tau_{n-1} & \vdots \\ 0 & 0 & \cdots & 1 & \tau_n \end{pmatrix},$$
(3)

where $a_1 = \tau_1$, $a_j = f_j \prod_{i=1}^{j-1} s_i$, j = 2, ..., n. Note that the transformation matrix S preserves the matrix

$$B = (b \ 0 \cdots \ 0)^T. \tag{4}$$

The parameter vector \mathbf{p} is given by $\mathbf{p} = (\bar{\mathbf{p}}^T \mid \bar{\bar{\mathbf{p}}}^T)^T = (a_1 \cdots a_n \mid \tau_2 \cdots \tau_n)^T \in \mathcal{P}$, where $\mathcal{P} = \bar{\mathcal{P}} \oplus \bar{\bar{\mathcal{P}}}$, with $\bar{\mathcal{P}} = \{(\bar{\mathbf{p}}, O) / \bar{\mathbf{p}} = (\bar{p}_i) \in \mathbb{R}^n_+, \ 0 \leq \bar{p}_1 < 1\}$ and $\bar{\bar{\mathcal{P}}} = \{(O, \bar{\bar{\mathbf{p}}}) / \bar{\bar{\mathbf{p}}} = (\bar{p}_i) \in \mathbb{R}^{n-1}_+ / 0 \leq \bar{p}_i < 1\}$.

It is of interest to accurately estimate these parameters. As a first step, we propose to study the identifiability of the system.

It is known that a model is globally identifiable if and only if there exists a single input-output behavior for every parameter set. Therefore, from a fixed structure, we want to test whether the relationship between the parameter sets and the response of the model is unique.

The class of positive structured models $S(\mathbf{p}) = (A(\mathbf{p}), B)$ given in (2) has the response

$$x(t) = A(\mathbf{p})^t x(0) + \sum_{i=0}^{t-1} V(i, \mathbf{p}), \quad t \ge 0,$$

given by the Markov parameters $V(i, \mathbf{p}) = A(\mathbf{p})^i B$, $i \ge 0$, with matrices $A(\mathbf{p})$ and B given in (3) and (4).

From now on, we consider the initial-value problem

(IVP)
$$\begin{cases} x(t+1) = A(\mathbf{p})x(t) + B, \\ x(0) = x_1(0)e_1 \in \mathbb{R}^n_+, \text{ with } x_1(0) > 0. \end{cases}$$

In the following theorem, we analyze its response.

Theorem 1. For (IVP) the response $x(i) = (x_j(i))_{j=1}^n$, for all $1 \le i < n$, satisfies $x_j(i) \ge 0$ if $1 \le j \le i$, $x_{i+1}(i) > 0$ and $x_j(i) = 0$, $i+1 < j \le n$.

Proof. The solution of the system (2) is given by

$$x(i) = A^{i}(\mathbf{p})x(0) + \sum_{l=0}^{i-1} A^{l}(\mathbf{p})B.$$

From the structure of $A(\mathbf{p})$ and $B=be_1$ given in (3) and (4), choosing $x(0)=x_1(0)e_1$, we obtain that x(i) is in a polyhedral cone. Specifically, it is a linear combination with nonnegative scalars of the kind

$$x(i) = \alpha_1 e_1 + \dots + \alpha_{i+1} e_{i+1},$$
 (5)

with $\alpha_j \geq 0, \ j = 1, \ldots, i$, and $\alpha_{i+1} > 0$. Then, $x_j(i) \geq 0$ for $j = 1, \ldots, i$, $x_{i+1}(i) > 0$ and $x_j(i) = 0$, for $j = i+1, \ldots, n$.

For linear models there are many well established techniques for analyzing identifiability; see, e.g., the works of Boyadjiev and Dimitrova (2005) or Dion *et al.* (2003) and the references therein. In our case, to identify the parameters, we consider an initial state x(0) and two parameters $\mathbf{p}, \mathbf{q} \in \mathcal{P}$, and we suppose that $V(j, \mathbf{p}) = V(j, \mathbf{q})$. Then, we want to prove that $\mathbf{p} = \mathbf{q}$, that is, the identifiability of the system class $S(\mathbf{p})$. This result is given in the following theorem.

Theorem 2. Consider the stage-structured system class $S(\mathbf{p}) = (A(\mathbf{p}), B)$ given by (3) and (4) with $\mathbf{p} \in \mathcal{P} \subseteq \mathbb{R}^{2n-1}_+$. The Markov parameters $V(j, \mathbf{p}) = (v(j, \mathbf{p})_{\alpha})_{\alpha=1}^n$, $j = 1, \ldots, n$, satisfy

$$v(j, \mathbf{p})_{1} = \sum_{l=1}^{j} a_{l}v(j-1, \mathbf{p})_{l},$$

$$v(j, \mathbf{p})_{\alpha} = v(j-1, \mathbf{p})_{\alpha-1} + \tau_{\alpha}v(j-1, \mathbf{p})_{\alpha},$$

$$\alpha = 2, \dots, j,$$

$$v(j, \mathbf{p})_{j+1} = b,$$

$$v(j, \mathbf{p})_{\alpha} = 0, \quad \alpha = j+2, \dots n,$$

$$(6)$$

and the stage-structured system class $S(\mathbf{p}) = (A(\mathbf{p}), B)$ is identifiable.

Proof. Exploiting the form of matrix $A(\mathbf{p})$, we obtain

$$V(j, \mathbf{p}) = A^{j}(\mathbf{p})B = A(\mathbf{p})V(j-1, \mathbf{p})$$

$$= \left(\sum_{l=1}^{n} a_{l}v(j-1, \mathbf{p})_{l}, v(j-1, \mathbf{p})_{1} + \tau_{2}v(j-1, \mathbf{p})_{2}, \cdots, v(j-1, \mathbf{p})_{n-1} + \tau_{n}v(j-1, \mathbf{p})_{n}\right)^{T}.$$

$$(7)$$

In addition, a straight recursive calculation allows us to check the expression established in (6). Then, if we consider $V(j,\mathbf{p})=V(j,\mathbf{q})$, we can identify all parameters following the steps of Algorithm 1.

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Algorithm 1. Identification of the parameter p.

Step 1. Input data: b, input variable parameters **p** and **q** such that

$$\mathbf{p} = (\bar{\mathbf{p}}^T \mid \bar{\bar{\mathbf{p}}}^T)^T = (a_1 \cdots a_n \mid \tau_2 \cdots \tau_n)^T, \mathbf{q} = (\bar{\mathbf{q}}^T \mid \bar{\bar{\mathbf{q}}}^T)^T = (\hat{a}_1 \cdots \hat{a}_n \mid \hat{\tau}_2 \cdots \hat{\tau}_n)^T,$$

where $\bar{\mathbf{p}}$, $\bar{\mathbf{q}} \in \bar{\mathcal{P}}$ and $\bar{\bar{\mathbf{p}}}$, $\bar{\bar{\mathbf{q}}} \in \bar{\bar{\mathcal{P}}}$.

Step 2. Construct $A(\mathbf{p})$, $A(\mathbf{q})$ and B as in (3) and (4).

Step 3. Set i = 1:

Step 3.1. Construct the Markov parameters $V(i, \mathbf{p})$ and $V(j, \mathbf{q})$ of the system (2).

Step 3.2. Solve $V(j, \mathbf{p}) = V(j, \mathbf{q})$. From (7), it is obtained that $a_i = \hat{a}_i$ and $\tau_i = \hat{\tau}_i$ (when j = 1 only $a_1 = \hat{a}_1$).

Step 3.3. Make j = j + 1. If $j \le n$ then return to Step 3.1. Otherwise, go to Step 4.

Step 4. All parameters are identified, $a_i = \hat{a}_i$ and $\tau_i =$ $\hat{\tau}_i$, for all j. Then $\mathbf{p} = \mathbf{q}$.

Having checked that all the parameters are identifiable, we attack the estimation of their values. Parameter estimation is an important issue in biological and dynamic population systems because it is necessary in order to know the behavior of the dynamic process.

Given the observed experimental data set $\{ob(i) \in$ \mathbb{R}^n , $i = 1, \ldots, K$, we consider e(i) = (ob(i) - x(i))as the error between the observed value and the obtained value by the simulation of the given model at time i, i = $1, \ldots, K$. Rewriting the system (2),

$$x(t+1) = M(t)\mathbf{p} + N(t), \quad t \ge 0.$$
 (8)

From d(i) = ob(i) - N(i-1), i = 1,...,K and $M(i), i = 0, \dots, K-1$, we construct the following stacked matrices:

$$d_K = \operatorname{col}(d(i))_{i=1}^K, \quad H_K = \operatorname{col}(M(i))_{i=0}^{K-1}.$$

We look for the value of the parameter which minimizes the quadratic error

$$J_K(\mathbf{p}) = \frac{1}{2} \sum_{i=1}^K e(i)^T e(i)$$
$$= \frac{1}{2} \mathbf{e}_K^T \mathbf{e}_K = \frac{1}{2} (d_K - H_K \mathbf{p})^T (d_K - H_K \mathbf{p}).$$

This minimizer **p** satisfies

$$\frac{\partial J_K(\mathbf{p})}{\partial \mathbf{p}} = H_K^T H_K \mathbf{p} - H_K^T d_K = 0.$$

Note that the vector \mathbf{p} that minimizes the function $J_K(\mathbf{p})$ is given as follows. If $H_K^T H_K$ is nonsingular, then $\mathbf{p} =$ $(H_K^T H_K)^{-1} H_K^T d_K$, and if it is singular, then $\mathbf{p} = H_K^{\dagger} d_K$, where † denotes the Moore-Penrose generalized inverse matrix.

From the system (2) and the structure of matrix $A(\mathbf{p})$ given in (3), we obtain

$$M(t) = \begin{pmatrix} x^T(t) & O \\ O & D_t \end{pmatrix},$$

$$N(t) = (b x_1(t) x_2(t) \cdots x_{n-1}(t))^T,$$

with

$$x(t) = (x_i(t))_{i=1}^n,$$

 $D_t = \text{diag}(x_2(t), \dots, x_n(t)).$

Then.

$$H_K^T H_K = \left(\begin{array}{cc} X_k X_K^T & O \\ O & Y_K^T Y_K \end{array} \right), \quad d_K = \left(\begin{array}{c} \bar{d}_K \\ \bar{\bar{d}}_K \end{array} \right),$$

with

$$X_{K} = (x(0) \cdots x(K-1)),$$

$$Y_{K} = \operatorname{col}(D_{i})_{i=0}^{K-1},$$

$$\bar{d}_{K} = \operatorname{col}(d_{1}(i))_{i=1}^{K},$$

$$\bar{d}_{K} = \operatorname{col}((\bar{d}_{K})_{i})_{i=1}^{K},$$
(9)

with $(\bar{d}_K)_i = \operatorname{col}(d_j(i))_{j=2}^n$.

Taking into account the structure of above matrices and $\mathbf{p} = (\bar{\mathbf{p}}^T \mid \bar{\mathbf{p}}^T)^T$, we have the matrix equation $H_K^T H_K \mathbf{p} = H_K^T d_K$, which is uncoupled into two matrix equations:

$$S_K \bar{\mathbf{p}} = X_K \bar{d}_K$$
 with $S_K = X_K X_K^T$, (10)
 $T_K \bar{\bar{\mathbf{p}}} = Y_V^T \bar{d}_K$ with $T_K = Y_V^T Y_K$. (11)

$$T_K \bar{\mathbf{p}} = Y_K^T \bar{d}_K$$
 with $T_K = Y_K^T Y_K$. (11)

The analysis of the solutions of these equations leads to the following results. First, we consider the estimation problem only referring to the structure of the coefficient matrices $A(\mathbf{p})$ and B:

(PEP1) Parameter estimation problem without restrictions on p:

Find $\mathbf{p} = (\bar{\mathbf{p}}^T \mid \bar{\bar{\mathbf{p}}}^T)^T$ satisfying the system of equations (10) and (11).

(PEP1) has a solution for any number of observations K. Construct the matrix $X_K = (x(0) \cdots x(K-1))$. Using the form of x(i) given in (5), matrix S_K is singular if K < n and nonsingular if $K \ge n$. When K < n, we are using the Moore-Penrose inverse of S_K to solve the estimation problem $S_K \bar{\mathbf{p}} = X_K \bar{d}_K$, and S_n^{-1} when K = n. We give only the result for the case when the number of observations K exceeds n.

Theorem 3. Consider (IVP) and an observed data set $\{ob(i)\}_{i=1}^K$ with $K \ge n$. Then (PEP1) has a unique solution given by

$$\bar{p} = S_K^{-1} X_K \bar{d}_K,
\bar{p} = T_K^{-1} Y_K^T \bar{d}_K.$$
(12)

Proof. Construct the matrix

$$X_K = (x(0) \cdots x(K-1)).$$

Using the form of x(i) given in (5) we can ensure that X_K is of full row rank. Hence, matrix $S_K = X_K X_K^T$ is nonsingular. Then $\bar{\mathbf{p}} = S_K^{-1} X_K \bar{d}_K$.

From Theorem 1, for all time indices $i, 1 \leq i \leq n$, we have that, for $j=2,\ldots,n$, the entry $x_j(i+1)$ is positive. Then, we can assure that Y_K is of full column rank. Thus, $T_K = Y_K^T Y_K$ is nonsingular and the assertion follows. That is, $\bar{\mathbf{p}} = T_K^{-1} Y_K^T \bar{d}_K$.

Note that the parameter estimation problem associated with our model is more restrictive. In particular, we need a parameter vector $\mathbf{p} = (\bar{\mathbf{p}}^T \mid \bar{\mathbf{p}}^T)^T$ which satisfies the necessary conditions to represent the evolution of a structured population by stages. Thus, the problem will be formulated as follows:

(PEP2) Parameter estimation problem with $p \in \mathcal{P}$:

Find $\mathbf{p} = (\bar{\mathbf{p}}^T \mid \bar{\mathbf{p}}^T)^T$ satisfying the system of equations (10) and (11), and fulfilling $\mathbf{p} = (\bar{\mathbf{p}}^T \mid \bar{\bar{\mathbf{p}}}^T)^T \in \mathcal{P}$, with $\mathcal{P} = \bar{\mathcal{P}} \oplus \bar{\bar{\mathcal{P}}}$,

$$\bar{\mathcal{P}} = \{ (\bar{\mathbf{p}}, O) / \bar{\mathbf{p}} = (\bar{p}_i) \in \mathbb{R}^n_+, \ 0 \le \bar{p}_1 < 1 \},
\bar{\bar{\mathcal{P}}} = \{ (O, \bar{\mathbf{p}}) / \bar{\bar{\mathbf{p}}} = (\bar{p}_i) \in \mathbb{R}^{n-1}_+, \ 0 \le \bar{\bar{p}}_i < 1 \}.$$

Lemma 1. Consider (**IVP**) and an observed data set $\{ob(i)\}_{i=1}^K$ with $1 \le K \le n$. Then the equation $S_K \bar{p} = X_K \bar{d}_K$ has a solution $\bar{p} = (\bar{p}_i)_{i=1}^n$, satisfying $\bar{p}_i \ge 0$ and $0 \le \bar{p}_1 < 1$ if and only if the following conditions are satisfied:

(i)
$$\sum_{j=1}^{i} (-1)^{i-j} M_{i-j} (j-1) x_1(0)^{j-1} d_1(j) \geq 0$$
, $i=1,\ldots,K$, with $M_{\alpha}(\beta)$ given in (13) and $M_0(\beta)=1$.

(ii)
$$0 < d_1(1) < x_1(0)$$
.

Proof. For the observed data set in question and from the initial state $x(0) = x_1(0)e_1 \in \mathbb{R}^n_+$ with $x_1(0) > 0$, the matrix X_K given in (9) is

$$X_K = \left(\begin{array}{c} U_K \\ O \end{array}\right),$$

with

$$U_K = \begin{pmatrix} x_1(0) & x_1(1) & \cdots & x_1(K-1) \\ 0 & x_2(1) & \cdots & x_2(K-1) \\ \vdots & \vdots & \cdots & \vdots \\ 0 & 0 & \cdots & x_K(K-1) \end{pmatrix},$$

nonsingular. When K < n, we are using the Moore–Penrose inverse of S_K to solve the estimation problem $S_K \bar{\mathbf{p}} = X_K \bar{d}_K$, and S_n^{-1} when K = n,

$$S_K^{\dagger} X_K = (X_K^T)^{\dagger} = \begin{pmatrix} (U_K^T)^{-1} \\ O \end{pmatrix},$$

$$S_n^{-1} X_n = U_n^{-1}.$$
(14)

From Theorem 1, $K \leq n$, and from the expressions given in (14), we consider the inverse matrix of $(U_K^T)^{-1}$, which is a lower triangular matrix. Then, to calculate its inverse matrix, we can use the explicit formula given by Baliarsingh and Dutta (2015), obtaining its (i,j)-th entry given by

$$((U_K^T)^{-1})_{ij} = \begin{cases} \frac{(-1)^{i-j} M_{i-j} (j-1)}{(x_1(0))^{i-j+1}}, & 1 \le j < i, \\ \frac{1}{x_1(0)}, & j = i, \\ 0, & j > i, \end{cases}$$

for i, j = 1, ..., K, with $M_{\alpha}(\beta)$ given in (13).

Denoting by \bar{p}_i the *i*-th entry of $\bar{\mathbf{p}}$ and by $((U_K^T)^{-1})_i$ the *i*-th row $(U_K^T)^{-1}$, we observe that

$$\bar{p}_{i} = ((U_{K}^{T})^{-1})_{i}\bar{d}_{K}$$

$$= \sum_{j=1}^{i-1} (-1)^{i-j} \frac{M_{i-j}(j-1)}{(x_{1}(0))^{i-j+1}} d_{1}(j)$$

$$+ \frac{1}{x_{1}(0)} d_{1}(i), \quad i = 1, \dots, K,$$
(15)

$$\bar{p}_i = 0, \quad i = K + 1, \dots, n.$$

Then, the condition (i) is satisfied if and only if $((U_K^T)^{-1})_i \bar{d}_K \geq 0$, that is, $\bar{p}_i \geq 0$, for $i=1,\ldots,n$. Moreover, we have that

$$((U_K^T)^{-1})_1 = \left(\frac{1}{x_1(0)} \cdot 0 \cdots 0\right).$$

Then $\bar{p}_1 = d_1(1)/x_1(0)$ and $0 \le \bar{p}_1 < 1$ if and only if the condition given in (ii) holds.

Lemma 2. Consider (**IVP**) and an observed data set $\{ob(i)\}_{i=1}^K$ with $K \geq 1$. Setting $x_K^{(i)} = \operatorname{col}(x_i(j))_{j=0}^{K-1}$ and $d_K^{(i)} = \operatorname{col}(d_i(j))_{j=1}^K$ $i = 2, \ldots, n$, we have that $T_K \bar{\bar{p}} = Y_K^T \bar{d}_K$ has a solution $\bar{\bar{p}}$ satisfying $0 \leq \bar{\bar{p}}_i < 1$, with $\bar{\bar{p}} = (\bar{\bar{p}}_i)_{i=1}^{n-1}$ if and only if

(iii)
$$0 \le (x_K^{(i)})^T d_K^{(i)} < ||x_K^{(i)}||_2^2$$
.

Proof. From the definition of matrix Y_K in (9), we have

$$Y_K^{\dagger} = \operatorname{diag}\left(\|x_K^{(2)}\|_2^{-2}, \dots, \|x_K^{(K)}\|_2^{-2}\right) Y_K^T.$$

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$$M_{\alpha}(\beta) = \begin{vmatrix} x_{\beta+1}(\beta+1) & x_{\beta+2}(\beta+1) & 0 & \cdots & 0 \\ x_{\beta+1}(\beta+2) & x_{\beta+2}(\beta+2) & x_{\beta+3}(\beta+2) & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ x_{\beta+1}(\beta+\alpha) & x_{\beta+2}(\beta+\alpha) & x_{\beta+3}(\beta+\alpha) & \cdots & x_{\beta+\alpha}(\beta+\alpha) \end{vmatrix},$$
(13)

Then, from Eqn. (11), we have that $\bar{p}_i, i=1,\ldots,n-1,$ is given by

$$\bar{\bar{p}}_{i} = \|x_{K}^{(i+1)}\|_{2}^{-2} \sum_{j=0}^{K-1} x_{i+1}(j) d_{i+1}(j+1)$$
if $i = 1, \dots, K-1$,
$$\bar{\bar{p}}_{i} = 0$$
if $i = K, \dots, K-1$,
$$(16)$$

when K < n. If $K \ge n$, the expression (16) holds for i = 1, ..., n-1. Then, $0 \le \bar{p}_i < 1$ if and only if

$$0 \leq (x_{i+1}(0)\cdots x_{i+1}(K-1))^{T} \begin{pmatrix} d_{i+1}(1) \\ \vdots \\ d_{i+1}(K) \end{pmatrix}$$
$$< (x_{i+1}(0)\cdots x_{i+1}(K-1))^{T} \begin{pmatrix} x_{i+1}(0) \\ \vdots \\ x_{i+1}(K-1) \end{pmatrix}.$$

Writing

$$x_K^{(i)} = \operatorname{col}(x_i(j))_{j=0}^{K-1}, \quad d_K^{(i)} = \operatorname{col}(d_i(j))_{j=1}^K,$$
 $i=2,\ldots,n,$ we have the condition given in (iii).

Note that, under the conditions (i)–(iii), the parameter $\mathbf{p} = (\bar{\mathbf{p}}^T \,|\, \bar{\mathbf{p}}^T)^T$ belongs to \mathcal{P} , with $\mathcal{P} = \bar{\mathcal{P}} \oplus \bar{\mathcal{P}}$, $\bar{\mathcal{P}} = \{(\bar{p}_i) \in \mathbb{R}^n_+ \,/\, 0 \leq \bar{p}_1 < 1\}$ and $\bar{\mathcal{P}} = \{(\bar{p}_i) \in \mathbb{R}^{n-1}_+ \,/\, 0 \leq \bar{p}_i < 1\}$. As a direct consequence of the previous lemmas, we give the following result.

Theorem 4. Consider (**IVP**) and an observed data set $\{ob(i)\}_{i=1}^K$ with $1 \le K \le n$. The parameter vector $\mathbf{p} = (\bar{\mathbf{p}}^T \mid \bar{\mathbf{p}}^T)^T$ given in (15) and (16) solves (**PEP2**) for $K \le n$ if and only if the conditions (i)–(iii) given in Lemmas 1 and 2 hold.

Remark 1. When k > n, the matrix X_K is a full-rank matrix, and we move to the next section the study of that case.

3. Recursive process using inversion of a sum of rank-one matrices

The matrix $S_i = X_i X_i^T$ with $X_i = (x(0) \cdots x(i-1))$ is a sum of rank-one matrices,

$$S_1 = x(0)x^T(0),$$

$$S_{i+1} = X_{i+1}X_{i+1}^T$$

$$= \sum_{l=0}^{i} x(l)x^T(l) = S_i + x(i)x^T(i), \quad i \ge 1.$$

This fact motives the study of the inverse of a sum of rank-one matrices. It is known (Ljung and Soderstrom, 1983) that, given $S \in \mathbb{R}^{n \times n}$ and $v \in \mathbb{R}^n$, if S is nonsingular, then $S + vv^T$ is also nonsingular and its inverse matrix is given by

$$(S + vv^T)^{-1} = S^{-1} - \frac{S^{-1}vv^TS^{-1}}{1 + v^TS^{-1}v}$$

We are now able to establish a recursive process in order to improve the estimated value of the parameter vector **p** by successive construction of an inverse of a matrix, which is formed as a sum of rank-one matrices.

We assume that $K \ge n$, and we study (**PEP2**) when a new observed data piece ob(K+1) is obtained.

Given a K observed data set, $\{ob(i), i = 1, \ldots, K\}$, we have an estimated value, \mathbf{p}_K , of the parameter vector and we construct the system (2) with matrices $A(\mathbf{p}_K)$ and B given in (3) and (4), and define the following matrices:

$$A_K = \frac{S_K^{-1}x(K)}{1+\alpha_K}, \quad \mathcal{B}_K = (I + D_K^2 T_K^{-1})^{-1} D_K,$$
 (17)

with $\alpha_K = x^T(K)S_K^{-1}x(K)$. To improve the approximated value of parameter \mathbf{p} , we add one observation ob(K+1) and fit the mathematical model to the (K+1)-element observed data set.

Theorem 5. Let K ($K \ge n$) be an observed data set $\{ob(i)\}_{i=1}^K$. Consider the assumptions of Theorem 3 and $\boldsymbol{p}_K = (\bar{\boldsymbol{p}}_K^T \mid \bar{\boldsymbol{p}}_K^T)^T$ as the parameter solving (**PEP1**) for K. Given a new observed data piece ob(K+1), the parameter vector $\boldsymbol{p}_{K+1} = (\bar{\boldsymbol{p}}_{K+1}^T \mid \bar{\boldsymbol{p}}_{K+1}^T)^T$ given by

$$\bar{\boldsymbol{p}}_{K+1} = (I - \mathcal{A}_K x^T(K))\bar{\boldsymbol{p}}_K + \mathcal{A}_K d_1(K+1), \quad (18)$$

$$\bar{\bar{p}}_{K+1} = \mathcal{B}_K D_K^{-1} \left(\bar{\bar{p}}_K + T_K^{-1} D_K \begin{pmatrix} d_2(K+1) \\ \vdots \\ d_n(K+1) \end{pmatrix} \right)$$

solves (PEP1) for K+1.

Proof. Given the observed data $\{ob(i)\}_{i=1}^{K+1}$, we have that $\mathbf{p}_{K+1} = (\bar{\mathbf{p}}_{K+1}^T \mid \bar{\bar{\mathbf{p}}}_{K+1}^T)^T$ solves (**PEP1**) for K+1 if it is the solution of the system

$$S_{K+1}\bar{\mathbf{p}} = X_{K+1}\bar{d}_{K+1},\tag{19}$$

$$T_{K+1}\bar{\bar{\mathbf{p}}} = Y_{K+1}^T \bar{\bar{d}}_{K+1}.$$
 (20)

By construction of matrices S_i , X_i and \bar{d}_i , we have

$$\begin{split} \bar{\mathbf{p}}_{K+1} &= S_{K+1}^{-1} X_{K+1} \bar{d}_{K+1} \\ &= \left(S_K^{-1} - \frac{S_K^{-1} x(K) x^T(K) S_K^{-1}}{1 + \alpha_K} \right) \\ &\times (X_K \, x(K)) \left(\begin{array}{c} \bar{d}_K \\ d_1(K+1) \end{array} \right) \\ &= \left(I - \frac{S_K^{-1} x(K) x^T(K)}{1 + \alpha_K} \right) \underbrace{S_K^{-1} X_K \bar{d}_K}_{\bar{\mathbf{p}}_K} \\ &+ S_K^{-1} x(K) d_1(K+1) \\ &- \underbrace{S_K^{-1} x(K) x^T(K) S_K^{-1} x(K)}_{1 + \alpha_K} d_1(K+1) \\ &= \left(I - \frac{S_K^{-1} x(K) x^T(K)}{1 + \alpha_K} \right) \bar{\mathbf{p}}_K \\ &+ \underbrace{S_K^{-1} x(K)}_{1 + \alpha_K} d_1(K+1). \end{split}$$

Further, using the definitions of T_i , Y_i , D_i and \bar{d}_i , as

$$T_{K+1}^{-1} = \left((Y_K^T D_K) \begin{pmatrix} Y_K \\ D_K \end{pmatrix} \right)^{-1}$$
$$= (T_K + D_K^2)^{-1} = (I + T_K^{-1} D_K^2)^{-1} T_K^{-1},$$

we obtain

$$\begin{split} &\bar{\mathbf{p}}_{K+1} \\ &= T_{K+1}^{-1} Y_{K+1}^T \bar{d}_{K+1} \\ &= (I + T_K^{-1} D_K^2)^{-1} T_K^{-1} (Y_K^T D_K) \begin{pmatrix} \bar{d}_K \\ d_2(K+1) \\ \vdots \\ d_n(K+1) \end{pmatrix} \\ &= (I + T_K^{-1} D_K^2)^{-1} \\ &\times \left(\underbrace{T_K^{-1} Y_K^T \bar{d}_K}_{\bar{\mathbf{p}}_K} + T_K^{-1} D_K \begin{pmatrix} d_2(K+1) \\ \vdots \\ d_n(K+1) \end{pmatrix}\right). \end{split}$$

Hence, using the matrices \mathcal{A}_K and \mathcal{B}_K defined in (17), the parameter vector $\mathbf{p}_{K+1} = (\bar{\mathbf{p}}_{K+1}^T \mid \bar{\mathbf{p}}_{K+1}^T)^T$ given in (18) solves (**PEP1**) for K+1.

Analyzing the expressions given in (18), if the parameter $\bar{\mathbf{p}}_K \in \mathcal{P}$, we can prove that the conditions

(iv)
$$\bar{\mathbf{p}}_K + \mathcal{A}_K \beta_K \geq O$$
,

(v)
$$-\bar{p}_{K,1} \leq (A_K)_1 \beta_K < 1 - \bar{p}_{K,1}$$
,

guarantee that $\bar{\mathbf{p}}_{K+1}$ is nonnegative with the first entry less than 1, where $\beta_K = (d_1(K+1) - x^T(K)\bar{\mathbf{p}}_K)$. Also, the condition

(vi)
$$\frac{(d_{i+1}(K+1) - x_{i+1}(K))x_{i+1}(K)}{\|x_K^{(i+1)}\|_2^2} < (1 - \bar{p}_{K,i}),$$
 for all $i = 1, \dots, n-1$,

is equivalent to $0 \le \bar{p}_{K+1,i} < 1, i = 1, ..., n-1$.

Thus, under these conditions, the parameter vector given in (18) also solves (**PEP2**) for K+1. This fact is expressed in the following theorem.

Theorem 6. Let K ($K \ge n$) be an observed data set $\{ob(i)\}_{i=1}^K$. Under the assumptions of Theorem 3 let $\boldsymbol{p}_K = (\bar{\boldsymbol{p}}_K^T \mid \bar{\boldsymbol{p}}_K^T)^T$ be a parameter solving (**PEP2**) for K. Given a new observed data piece ob(K+1), \boldsymbol{p}_{K+1} given in (18) solves (**PEP2**) for K+1 if and only if the conditions (iv)–(vi) are satisfied.

Last, using the 2-norm, we show some conditions to ensure the closeness between the two approaches. From (18) we have

$$\|\bar{\mathbf{p}}_{K+1} - \bar{\mathbf{p}}_{K}\|_{2}$$

$$= \|(I - \mathcal{A}_{K}x^{T}(K))\bar{\mathbf{p}}_{K} + \mathcal{A}_{K}d_{1}(K+1) - \bar{\mathbf{p}}_{K}\|_{2}$$

$$= \|\mathcal{A}_{K}\left(-x^{T}(K)\bar{\mathbf{p}}_{K} + d_{1}(K+1)\right)\|_{2}$$

$$\leq \|\mathcal{A}_{K}\|_{2}|-x^{T}(K)\bar{\mathbf{p}}_{K} + d_{1}(K+1)|$$

$$= \|\mathcal{A}_{K}\|_{2}|ob_{1}(K+1) - x_{1}(K+1)|, \tag{21}$$

and

$$\|\bar{\mathbf{p}}_{K+1} - \bar{\mathbf{p}}_{K}\|_{2}$$

$$= \|((I + T_{K}^{-1}D_{K}^{2})^{-1} - I)\bar{\mathbf{p}}_{K}$$

$$+ (I + T_{K}^{-1}D_{K}^{2})^{-1}T_{K}^{-1}D_{K}\bar{d}(k+1)\|_{2}$$

$$= \|\mathcal{B}_{K}T_{K}^{-1}\left(-D_{K}\bar{\mathbf{p}}_{K} + \bar{d}(k+1)\right)\|_{2}$$

$$\leq \|\mathcal{B}_{K}T_{K}^{-1}\|_{2}\| - D_{K}\bar{\mathbf{p}}_{K} + \bar{d}(k+1)\|_{2}$$

$$= \|\mathcal{B}_{K}T_{K}^{-1}\|_{2}\|\bar{x}(K+1) - \bar{ob}(K+1)\|_{2}, \qquad (22)$$

with $\bar{\sigma}(K+1) = \text{col}(\sigma_i(K+1)))_{i=2}^n$, and $\sigma = x, d, ob$. Thus, given $\epsilon > 0$ and a new observed data piece ob(K+1) such that

$$|x_{1}(K+1) - ob_{1}(K+1)| < \frac{\epsilon}{2\|\mathcal{A}_{K}\|_{2}},$$

$$\|\bar{\bar{x}}(K+1) - \bar{ob}(K+1)\|_{2} < \frac{\epsilon}{2\|\mathcal{B}_{K}T_{K}^{-1}\|_{2}},$$
(23)

we have

$$\|\mathbf{p}_{K+1} - \mathbf{p}_{K}\| \le \|\bar{\mathbf{p}}_{K+1} - \bar{\mathbf{p}}_{K}\| + \|\bar{\bar{\mathbf{p}}}_{K+1} - \bar{\bar{\mathbf{p}}}_{K}\|_{2} < \epsilon.$$

From now on we shall write

$$m_K = \max\{\|\mathcal{A}_K\|_2, \|\mathcal{B}_K T_K^{-1}\|_2\},$$
 (24)

with A_K and B_K given in (17).

Theorem 7. Let $K \geq n$ and the assumptions of Theorem 3 hold. Consider observed data $\{ob(i)\}_{i=1}^K$ and \mathbf{p}_K solving (**PEP2**) for K. Given $\epsilon > 0$ and a new observed data piece ob(K+1) such that

$$||x(K+1) - ob(K+1)||_2 < \frac{\epsilon}{m_k},$$
 (25)

with m_K given in (24) we have, $\| \boldsymbol{p}_{K+1} - \boldsymbol{p}_K \|_2 < \epsilon$, \boldsymbol{p}_{K+1} being the estimated value given in (18).

Proof. Joining expressions given in (18) and rewriting as in (21) and (22), we obtain

$$\begin{split} &\|\mathbf{p}_{K+1} - \mathbf{p}_{K}\|_{2} \\ &= \| \left(\begin{array}{cc} \mathcal{A}_{K} & O \\ O & \mathcal{B}_{K}T_{K}^{-1} \end{array} \right) \left(ob(K+1) - x(K+1) \right) \|_{2} \\ &\leq m_{K} \|x(K+1) - ob(K+1) \|_{2} < \epsilon. \end{split}$$

The recursive process to improve the estimated value of the parameter vector, fulling also the restrictions of (PEP2) is shown as Algorithm 2.

Algorithm 2. Estimation of the parameter p.

Step 1. Input data: $b, x_1(0) > 0$, the observed data $\{ob(i)\}_{i=1}^n$, an initial estimate of parameter vector \mathbf{p}_n , and $K (K \ge n)$.

Step 2. Construct the vector $x(0) = (x_1(0) \ 0 \ \cdots \ 0)^T$, $A(\mathbf{p}_n)$ and B as in (3) and (4).

For i = 1 to n, we construct $x(i) = A(\mathbf{p}_n)x(i-1) + B$.

Step 3. Calculate $X_n, Y_n, \bar{d}_n, \bar{d}_n, S_n$ and T_n as in (9).

Step 4. Set i = 1.

Step 5. Input observed data ob(n + j).

Step 5.1. Calculate $\bar{\mathbf{p}}_{n+j}$ and $\bar{\bar{\mathbf{p}}}_{n+j}$ as in (18).

Step 5.2. Check the conditions (iv)–(vi). If some of them do not hold, then go to Step 6. Otherwise, go to Step 5.3.

Step 5.3. For i = 1, ..., n + j, construct x(i) = $A(\mathbf{p}_{n+j})x(i-1) + B \text{ and } X_{n+j}, Y_{n+j}, \bar{d}_{n+j}, \bar{d}_{n+j},$ S_{n+i} and T_{n+i} .

Step 5.4. Set j = j + 1. If $n + j \le K$, return to Step 5.1. Otherwise, go to Step 6.

Step 6. The process is finished.

3.1. Illustrative example. The aim of this part is to discuss estimation of the parameters for an element of $S(\mathbf{p})$ in the particular case of a population with three stages. In this model, the individuals that do not reach

the desired maturity in a step of time will remain in the same class and will not advance to the next one.

We start from the fact that the initial observed data are known and we have simulated an observed data set to analyze the reliability of the above algorithm.

In our population model, f_i : the fertility parameters, s_i : the survival rates growing into the next stage and τ_i the survival rates remaining in the same stage, are given by $f_1 = 0$, $f_2 = 0$, $f_3 = 3$, $s_1 = 0.6$, $s_2 =$ $0.7, \ \tau_1 = 0.17, \ \tau_2 = 0.25, \ \tau_3 = 0.86.$ Taking into account the discussion of the previous sections and making the relevant transformations, we have that \mathbf{p} (0.17, 0, 1.26, 0.25, 0.86). We consider an initial condition which only has individuals of the first class, in particular, given by $x^{T}(0) = (4000, 0, 0)$, and we suppose the process is altered, in each step, by an entry of b = 400 individuals of new population at the first stage. Then we simulate the process established in the above algorithm. Starting from the fact that the estimated value of the parameter from three observations obtained is

$$\mathbf{p}_3 = (0.1625, \ 0.0105745, \ 1.24467, \ 0.247957, \ 0.8625),$$

new observations are added. The obtained results are displayed in Fig. 1. These represent the evolution of the parameter estimates for the first K=15 observations. The difficulty of finding approximations to specific data is well known, especially when there are some altered data. Nevertheless, our observed data set satisfies the conditions of the theorems given in the last section. Therefore, using the 2-norm, it is observed how close two consecutive estimates of the parameter are.

Conclusions

A class S(p) of stage-structured population models with unknown parameters was considered. We proposed an iterative method to analyze if the parameters can be uniquely recovered from the observed data. Using this method, we ensured the identifiability of the models in S(p). This fact guarantees that the model parameters can be estimated under ideal conditions. We solved the estimation problem with or without restrictions on the parameters by minimizing the least squares criterion. The novelty that our proposal presents is the use of the structure of the matrices that describe the models of the S(p) class. Thus, these matrices were analyzed and results were obtained that allow us to improve the estimation procedure. In the analysis of the estimation of parameters, we gave some conditions to ensure the restrictions on the parameters, both for a number of observations smaller and larger than the size of the state vector. Finally, we solved the problem of adjusting the parameters from experimental data given a boundary that ensures that two consecutive approximations are sufficiently close.

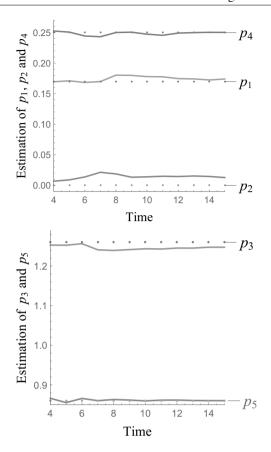


Fig. 1. Estimated values of the parameter $\mathbf{p} = (p_i)_{i=1}^5$ from the iterative process when K = 15.

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