Modelling big game populations when hunting is age and sex selective[☆]

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Abstract

The main objective of this work is to model the dynamics of cynegetic populations by means of a linear control system. We want to estimate the annual corrective measures, which may be improvements or hunting, that must be implemented to take and maintain the studied population around the carrying capacity of certain area. Moreover, the model must be able to distinguish between different age-sex classes and lead the population to a desired distribution of individuals among these stage groups.

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1. Introduction

Demographic models are a powerful tool to guide decisions when managing wildlife populations. Sometimes, when studying population growth, what is especially interesting is to know the evolution of a concrete type of individuals instead of the total population. That is to say, the population is structured in different stage classes of individuals with similar characteristics and the growth of each stage class is analyzed. Hence the individuals in the population at any given time is described by a vector with as many components as the number of stage classes into which the population has been divided. Thus, each component will represent the number of individuals of a certain stage class.

Population evolution is represented by a matrix difference equation. In particular, if we assume that no migratory movement or external effect takes place, the population growth dynamics will be given by an autonomous system whose

state matrix only depends on the population attributes, i.e., natality and survival rates. Consequently, it is a nonnegative matrix [1, 2].

The equation solution and the stability study are achieved by means of the eigenvalues and eigenvectors of this nonnegative matrix, which it is known to have a dominant positive eigenvalue λ_1 with a nonnegative eigenvector $u_1 = [u_{11} \quad u_{21} \quad \ldots \quad u_{n1}]^T$ [3]. It is easy to prove that if this nonnegative matrix is diagonalizable and λ_1 is strictly dominant, the asymptotic population growth only depends on λ_1, whereas the distribution of individuals among the different stage classes tends to stabilize independently of population growth. The stable individual proportion of each stage class tends to a limit that is proportional to the components of the eigenvector u_1.

In this work we want to analyze the behaviour of a population that we have structured in different stage classes according to age and sex. We suppose that matrix A is diagonalizable, and we want to study under which conditions λ_1 is strictly dominant and consequently the stable distribution is given by u_1. After that, we will obtain the components of u_1. Analogous results have been obtained for simpler models, like the Leslie model, which distributes the population in age classes of equal time interval and only considers the female individuals. Leslie assumes that survival rates are always equal for both sexes, but this condition is not actually satisfied in real conditions, particularly in cynegetic species.

We construct a sex-specific age-at-harvest mathematical model that can analyzes the dynamic evolution of a population as a result of its intrinsic attributes and as well as external effects. The aim is to be able to estimate the annual measures (improvements or hunting) that must be executed to take a population around the carrying capacity of the studied area, guaranteeing the maximum efficiency [4]. Besides that, the model must lead the population to a given individual distribution among the different stage classes. This model could be used in the developing of the cynegetic plan of a hunting natural reserve.

2. Autonomous model

From the Lefkovitch model [5], we develop a new model that takes into account both age and sex of the individuals. Our model distinguishes between the life cycle of females and the life cycle of males, except for the youngest ones, which constitute the first stage class and where we assume the same percentage of males and females. If we divide the life cycle of females into n_f stages and the life cycle of males into n_m stages, the dynamic evolution of a population is given by:

$$N(t+1) = AN(t), \quad t \in \mathbb{Z} \tag{1}$$

where $N(t) = [N_1(t) \quad N_2(t) \quad \cdots \quad N_n(t)]^T \in \mathbb{R}_+^n$ represents the number of individuals in each stage class at instant t, with $n = 1 + n_f + n_m$.

To compute the stage-based matrix A, we must estimate, for each stage, the natality rates b_i, the probability of surviving and growing into the next stage g_i and the probability of surviving and remaining in the same stage p_i. The

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transition probabilities g_i and p_i are obtained from the stage-specific survival rates s_i and stage duration d_i by the following expressions [6]:

$$g_i = \frac{s_i^{d_i}(1 - s_i)}{1 - s_i^{d_i}} \qquad p_i = s_i - g_i = \frac{(1 - s_i^{d_i - 1})s_i}{1 - s_i^{d_i}}$$

Thus matrix A is given by:

$$A = \left[\begin{array}{ccccc|cccc} p_0 + b_0 & b_1 & b_2 & \cdots & b_{n_f} & 0 & 0 & \cdots & 0 \\ g_0/2 & p_1 & 0 & \cdots & 0 & 0 & 0 & \cdots & 0 \\ 0 & g_1 & p_2 & \cdots & 0 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & p_{n_f} & 0 & 0 & \cdots & 0 \\ \hline g_0/2 & 0 & 0 & \cdots & 0 & p_{n_f+1} & 0 & \cdots & 0 \\ 0 & 0 & 0 & \cdots & 0 & g_{n_f+1} & p_{n_f+2} & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 & 0 & \cdots & p_{n-1} \end{array}\right] = \tag{2}$$

$$= \left[\begin{array}{cc} A_{11} & O \\ A_{21} & A_{22} \end{array}\right]$$

with $b_i \geq 0$, $1 > p_i \geq 0$ and $1 \geq g_i > 0$. Actually, often $b_0 = 0$, hence for convenience, we take this value throughout this work.

As it is assumed that A is diagonalizable, we deduce from (1) that the population behaviour depends on the eigenvalues λ_i and the eigenvectors u_i of A. If moreover λ_1 is strictly dominant ($\lambda_1 > |\lambda_i|$, $i = 2, 3, \ldots, n$), then the long term evolution of the population density is:

$$\lim_{k \to \infty} N(t) = \lim_{k \to \infty} c_1(0)\lambda_1^k u_1$$

where the coefficient $c_1(0)$ is obtained from the initial conditions, whereas the percentage of individuals in each stage class is given by the vector:

$$\lim_{t \to \infty} \frac{1}{\sum\limits_{i=1}^{n} N_i(t)} N(t) = \frac{1}{\sum\limits_{j=1}^{n} u_{j1}} u_1 = v = [v_1 \; v_2 \; \ldots \; v_n]^T \tag{3}$$

consequently, the population grows indefinitely, stabilizes or becomes extinct if λ_1 is greater, equal o less than 1, respectively, although the distribution always tends to stabilize according to the eigenvector u_1 (see [1] for details).

Thus, now our two main objectives are to find the conditions that guarantee the eigenvalue λ_1 is strictly dominant and consequently the stable distribution will come to v, and to compute the expression of its components.

By (2) we have that $\sigma(A) = \sigma(A_{11}) \cup \sigma(A_{22})$. The characteristic polynomial of A_{22} is $q_{A_{22}}(\lambda) = \prod_{i=n_f+1}^{n-1}(\lambda - p_i)$, so $\sigma(A_{22}) = \{p_{n_f+1}, p_{n_f+2}, \ldots, p_{n-1}\}$, with $0 \leq p_i < 1$, $i = n_f + 1, n_f + 2, \ldots n - 1$. With respect to A_{11}, this submatrix is characterized by the following results.

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Lemma 1. *The submatrix A_{11} is primitive if the older female stage class is fertile and the newborn individuals or some females always survive and remain in the same stage, i.e., $b_{n_f} \neq 0$ and there exists at least one $p_i \neq 0$, $i = 0, 1, \ldots, n_f$.*

Proof. In [3] it is proved that a matrix is irreducible if and only if its direct graph is strongly connected. This fact happens in matrix A_{11} if $b_{n_f} \neq 0$. Moreover, an irreducible matrix is primitive if its trace is positive, which is guaranteed with one $p_i \neq 0$, $i = 0, 1, \ldots, n_f$. $\qquad\square$

Proposition 1. *If A_{11} is primitive, then $\rho(A_{11}) > max\{p_i, \ i = 0, 1, \ldots, n_f\}$.*

Proof. Consider the following function:

$$H(\lambda) = \frac{1}{2} \sum_{i=1}^{n_f} \frac{b_i \prod_{j=0}^{i-1} g_j}{\prod_{s=0}^{i}(\lambda - p_s)}$$

Hence, $q_{A_{11}}(\lambda) = 0$ if and only if $H(\lambda) = 1$ for $\lambda \neq p_i$, $i = 0, 1, \ldots, n_f$. Suppose that $p_{i_{A_{11}}} = \max\{p_i, \ i = 0, 1, \ldots, n_f\}$. $H(\lambda)$ decrease for $\lambda > p_{i_{A_{11}}} > 0$, it has a vertical asymptote in $\lambda = p_{i_{A_{11}}}$ and tends to zero when $\lambda \longrightarrow \infty$. Therefore, there exists only one $\lambda_1 > p_{i_{A_{11}}}$ such that $H(\lambda_1) = 1$. Consequently, there exists only one $\lambda_1 > p_{i_{A_{11}}}$ such that $q_{A_{11}}(\lambda_1) = 0$. As A_{11} is nonnegative and primitive then $\rho(A_{11}) = \lambda_1$. $\qquad\square$

The following result is a natural consequence of Proposition 1.

Lemma 2. *If A_{11} is primitive and the condition $max\{p_i, \ i = 0, 1, \ldots, n_f\} \geq max\{p_i, \ i = n_f + 1, n_f + 2, \ldots, n - 1\}$ is satisfied, then the spectral radius of A is the spectral radius of A_{11}, i.e., $\rho(A) = \rho(A_{11})$.*

Finally, next result is deduced directly from Lemma 1, Proposition 1 and Lemma 2, which characterizes matrix A.

Proposition 2. *Matrix A has a strictly dominant eigenvalue λ_1 if the older female stage class is fertile, the newborn individuals or some females always survive and remain in the same stage and the maximum probability of surviving and remaining in the same state in females is greater than or equal to the probability in males.*

On the other hand, as A is a nonnegative matrix, by the Perron-Frobenius theorem [3], it has a positive real eigenvalue $\lambda_1 \geq |\lambda_i|$ with a nonnegative eigenvector u_1.

Lemma 3. *The eigenvector u_1 of A associated with its strictly dominant eigenvalue λ_1 is*

$$
u_1 =
\begin{bmatrix}
\dfrac{1}{g_0} \\[2mm]
\dfrac{2(\lambda_1 - p_1)}{g_0 g_1} \\[2mm]
\dfrac{2(\lambda_1 - p_1)(\lambda_1 - p_2)}{g_0 g_1} \\[2mm]
\vdots \\[2mm]
\dfrac{2(\lambda_1 - p_1)(\lambda_1 - p_2)\cdots(\lambda_1 - p_{n_f})}{g_0 g_1 \cdots g_{n_f-1}} \\[2mm]
\dfrac{2(\lambda_1 - p_{n_f+1})}{g_0} \\[2mm]
\dfrac{2(\lambda_1 - p_{n_f+1})(\lambda_1 - p_{n_f+2})}{g_0 g_{n_f+1}} \\[2mm]
\vdots \\[2mm]
\dfrac{2(\lambda_1 - p_{n_f+1})(\lambda_1 - p_{n_f+2})\cdots(\lambda_1 - p_n)}{g_0 g_{n_f+1} \cdots g_{n-1}}
\end{bmatrix}
$$

Proof. It comes directly from the relation $Au_1 = \lambda_1 u_1$. $\qquad\square$

3. Quasi-positive system

We have just seen in Section 2 that populations tend to a stable distribution v given by the eigenvector u_1. But sometimes, it is convenient to change this distribution for economic reasons, think for instance in the case of a hunting reserve. In this section we study the way to modify the population behaviour with the aim to get a desired distribution such that the stable percentage of individuals in each stage class is given by $w = [w_1 \quad w_2 \quad \cdots \quad w_n]^T$ and the population density stands around an optimal value. For that, we use a quasi-positive control system [7], where state and output variables remain nonnegative independently of the applied control sequence. Hence, the population evolution is given by:

$$
N(t+1) = AN(t) + Bu(t), \quad t \in \mathbb{Z} \tag{4}
$$

where $Bu(t)$ shows the annual measures that must be implemented to take the population around the carrying capacity of the studied area.

3.1. Towards the desired distribution

To modify v given by (3), we apply to each stage class a control proportional to the population in this class, i.e., $Bu(t) = \operatorname{diag}(\varepsilon_1(t), \varepsilon_2(t), \ldots, \varepsilon_n(t))N(t)$. Hence, equation (4) becomes

$$
\begin{aligned}
N(t+1) &= AN(t) + \operatorname{diag}(\varepsilon_1(t), \varepsilon_2(t), \ldots, \varepsilon_n(t))N(t) = \\
&= (A + M_\varepsilon(t))N(t) = A(t)N(t)
\end{aligned} \tag{5}
$$

In consequence, the evolution of the population can be considered as an autonomous system where the nonnegativity of the variables are guaranteed by the nonnegativity of $A(t)$.

These matrices are obtained by an iterative method from the initial matrix A of the autonomous model (1), assuming in each step that the unitary eigenvector v is equal to w. After the first iteration, the main diagonal elements of $A(1)$ are:

$$a_{ii}(1) = \lambda_1(0) - \frac{a_{i,i-1}w_{i-1}}{w_i}, \qquad i = 2, 3, \ldots, n_f + 1, n_f + 3, n_f + 4, \ldots, n$$
$$a_{n_f+2,n_f+2}(1) = \lambda_1(0) - \frac{a_{n_f+2,1}w_1}{w_{n_f+2}}$$

Proceeding in that way, we successively obtain the following matrices, in theory until computing the matrix $A(t)$ the unitary eigenvector v of which is w. Let A_k denote this matrix, and λ_{1_k} denote its strictly dominant eigenvalue, hence

$$A(t) = \begin{cases} A(t) & 0 < t < k \\ A_k & t \geq k \end{cases}$$

and since $(\lambda_{1_k}I - A_k)w = 0$, we have that

$$\lambda_{1_k} = p_0 + \frac{b_1 w_2 + b_2 w_3 + \cdots + b_{n_f}w_{n_f+1}}{w_1}$$

Nevertheless, it is not actually necessary to achieve this matrix A_k. We consider the matrix $A(t)$ invariant from an instant $t = k$ such that the relative error $|\lambda_1(t) - \lambda_{1_k}|/\lambda_{1_k}$ is less than a given tolerance *tol*. This iterative method is summarized in the following algorithm, where At denotes the successive matrices $A(t)$, D the corresponding strictly dominant eigenvalues $\lambda_1(t)$, $t = 0, 1, \ldots, k-1$, and Df the desired eigenvalue λ_{1_k}.

Algorithm 1. *Introduce A, n_f, n, w and tol.*

1. *Let $Df = A(1,1) + A(1, 2 : n_f + 1)w(2 : n_f + 1)/w(1,1)$*
2. *Obtain D*
3. *Let $At = A$*
4. *While $|D - Df|/Df > tol$*

      For $i = 2 : n_f + 1$, $At(i,i) = D - A(i, i-1)w(i-1)/w(i)$, end

      $At(n_f + 2, n_f + 2) = D - A(n_f + 1, 1)w(1)/w(n_f + 1)$

      For $j = n_f + 3 : n$, $At(j,j) = D - A(j, j-1)w(j-1)/w(j)$, end

      Obtain D

   end

From Algorithm 1, taking into account that At must be nonnegative, we conclude the next result.

Theorem 1. *Given a population dynamic (1)-(2) with stable distribution v, it is possible to modify its evolution and to reach another stable distribution w if for all $i = 2, 3, \ldots, n$ this condition holds:*

$$\min\{\lambda_1(t)\} \geq \max\left\{\frac{a_{n_f+2,1}w_1}{w_{n_f+2}}, \frac{a_{i,i-1}w_{i-1}}{w_i}\right\}.$$

This relation means that the minimum growth rate of the population must be greater than the maximum percentage of individuals that go from one group to the following one.

In the end, the annual improvement measures can be estimated taking into account equation (5) and Algorithm 1.

Remark 1. *The annual improvement measures are given by the following expressions:*

$$\varepsilon_i(1) = \lambda_1 - p_i - \frac{g_{i-1}w_{i-1}}{w_i}$$
$$\varepsilon_i(t) = \lambda_1(t) - \lambda_1(t-1)$$

with $w_{i-1} = w_1$ for $i = n$, such that for each stage class i, $i = 2, \ldots, n$, at time t, $\varepsilon_i(t) > 0$ means that new individuals must be introduced in the population or the survival rates must be improved, whereas $\varepsilon_i(t) < 0$ means that it is necessary to hunt, otherwise nothing must be done.

3.2. Towards the desired population density

Once the distribution w is achieved, the next objective is for the desired population density that we denote by P_f not to rise. Suppose that this value has been rising. In this case we must decrease the population growth applying a negative control, hence the population evolution is given by the quasi-positive system:

$$N(t+1) = A(t)N(t) - Bu(t) \tag{6}$$

where $u(t)$ is total hunting. Specifically, if we hunt in a proportional way to the population density, we take

$$u(t) = \alpha \sum_{i=1}^{n} N_i(t) = \alpha[1 \ 1 \ \ldots \ 1]N(t) = \alpha e^T N(k)$$

The next result tells us how we must distribute this negative control among the different stage classes.

Lemma 4. *If $B = w$, then the desired stable distribution w is preserved, independently of the applied control, that is, total hunting.*

Proof. By equations (5) and (6), from $t = k$ the population evolution is given by

$$N(t+1) = A_k N(t) - Bu(t) \tag{7}$$

Let $N = [N_1 \ N_2 \ \ldots \ N_n]^T$ be the population estimated at instant t by equation (5), that is to say, without applying the negative control, i.e., $u = 0$. At this moment, the individual distribution among the different stage classes is:

$$P = \frac{1}{\sum\limits_{i=1}^{n} N_i} N = w = [w_1 \ w_2 \ \ldots \ w_n]^T$$

Now, consider that the control is applied and u individuals are eliminated according to the class distribution given by w, i.e., $B = w$. In this case, the population estimated by (7) at instant t is:

$$N(t) = \begin{bmatrix} N_1 - w_1 u \\ N_2 - w_2 u \\ \vdots \\ N_n - w_n u \end{bmatrix}$$

But, note that for $j = 1, 2, \ldots, n$,

$$N_j(t) = \frac{N_j(\sum\limits_{i=1}^{n} N_i - u)}{\sum\limits_{i=1}^{n} N_i} \tag{8}$$

whereas the total number of individuals is

$$\sum_{i=1}^{n} N_i(t) = \sum_{i=1}^{n} N_i - u \sum_{i=1}^{n} w_i = \sum_{i=1}^{n} N_i - u \tag{9}$$

Consequently, by (8) and (9), the individual proportion in each stage class j, $j = 1, 2, \ldots, n$, at instant t is:

$$P_j(t) = \frac{N_j(t)}{\sum\limits_{i=1}^{n} N_i(t)} = \frac{N_j \left(\sum\limits_{i=1}^{n} N_i - u \right)}{\sum\limits_{i=1}^{n} N_i \left(\sum\limits_{i=1}^{n} N_i - u \right)} = w_j$$

$\square$

Therefore,

$$\begin{aligned} N(t+1) &= A(t)N(t) - Bu(t) = (A(t) - \alpha w e^T)N(t) = \\ &= AN(t) + (M_\varepsilon(t) - \alpha w e^T)N(t) = AN(t) + U(t) \end{aligned} \tag{10}$$

with $U(t) = (M_\varepsilon(t) - \alpha w e^T)N(t)$. We set the coefficient α in such a way that both the desired distribution and density are reached at the same time.

Remark 2. *For each stage class i, $i = 1, 2, \ldots, n$, at time t, $U_i(t) > 0$ means that new individuals must be introduced in the population or the survival rates must be improved, whereas $U_i(t) < 0$ means that it is necessary to hunt.*

Finally, suppose that the population has reached the optimal stable distribution w and the optimal density P_f, which correspond to a population density less than the carrying capacity of the studied area, so that population growth must stop. For that, we must hunt, that is, we must apply a negative control $u(t)$, which is estimated from the equation,

$$N(t+1) = A_k N(t) - wu(t) \tag{11}$$

solving by less squares approximation so that $u(t)$ is given by:

$$u(t) = (w^T w)^{-1} w (A_t N(t) - wP_f). \tag{12}$$

4. Example

The population of Spanish wild goat (*Capra pyrenaica*) in the Valencian natural reserve of "Muela de Cortes" has been selected to illustrate the usefulness of the quasi-positive systems shown in the previous sections. In Table 1 we can find the main attributes of this population.

Age	Males		Females		
	Initial population	Survival rate	Initial population	Survival rate	Natality rate
0-1	133	0.79	132	0.79	0
2-3	90	0.90	152	0.97	0.65
4-6	105	1.00	156	0.91	0.85
7-9	49	0.90	80	1.00	0.75
10-14	14	0.90	58	0.85	0.50

Table 1: Attributes of the Spanish wild goal population from "Muela de Cortes"

From Table 1, we see the population is divided in nine stage classes: newborn individuals (where we consider the same percentage of males and females), the remainder four stage classes of females and the remainder four stage classes of males. The population evolution can be represented by the autonomous model (1), which has a state matrix A with a strictly dominant eigenvalue $\lambda_1 = 1.1102$. This value means that, without any external influence, the population tends to grow in an indefinite manner, reaching the stable distribution

$v = [0.3423\ 0.0966\ 0.0970\ 0.0602\ 0.0771\ 0.0938\ 0.0901\ 0.0627\ 0.0802]^T.$

Nevertheless, this situation can not be supported by the reserve [8], which admits a carrying capacity of 1756 individuals with the optimal distribution

$w = [0.2580\ 0.1196\ 0.1002\ 0.0849\ 0.0421\ 0.1344\ 0.1384\ 0.0712\ 0.0513]^T.$

Hence, the natural stable distribution v differs with the optimal distribution w by 12%.

To modify the stable population distribution we apply the quasi-positive model (5), where matrices $A(t)$ are obtained by Algorithm 1 with a tolerance of 5%. The relative errors and deviation of the corresponding dominant eigenvalues $\lambda_1(t)$ and eigenvectors $v(t)$ from λ_{1_k} and w, respectively, are shown in Table 2, whereas the total population estimated at each time can be found in Table 3.

$\lambda_1(1)$	$\lambda_1(2)$	$\lambda_1(3)$	$\lambda_1(4)$	$\lambda_1(5)$	$\lambda_1(6)$
0.2077	0.1648	0.1321	0.1067	0.0866	0.0706
$v(1)$	$v(2)$	$v(3)$	$v(4)$	$v(5)$	$v(6)$
0.1199	0.0665	0.0514	0.0403	0.0321	0.0257

Table 2: Characteristics of the sequence of matrices $A(t)$ obtained by Algorithm 1.

Year 0	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
969	1218	1508	1908	2473	3268	4059

Table 3: Population evolution estimated by the model (5).

Note that after six years we have achieved the desired distribution but the population density is too high, more than twice the reserve carrying capacity. Hence, we must decrease population growth. For that, we apply the quasi-positive model (10), with $A(t)$ obtained by Algorithm 1. Now, we get the desired population density and distribution in six years if a hunting strain of 8% and a tolerance of 5% are considered. From time $t \geq 6$, we consider $A(t) = A(6)$ and apply equations (11) and (12) to keep the population in this conditions. All these results are summarized in Figure 1. After 5, 10 and 15 years the population distribution differs with the optimal w by less than 5%.

5. Conclusions

Quasi-positive linear control systems can be used to manage the big game population of a natural reserve where environmentally sustainable development must be guaranteed. These models allow us to estimate the measures that must be implemented to take and maintain the studied population around the carrying capacity of the reserve, with an individual distribution that leads to maximum efficiency.

References

[1] H. Caswell, Matrix Population Models: construction, analysis and interpretation, Sinauer Associates, Inc. Publishers, Massachusetts, 2001.

[2] E. Flipse, J. M. Veling, An application of the Leslie matrix model to the population dynamics of the hooded seal, *Cystophora cristata* erxleben, Ecological Modelling 24 (1984) 43-59.
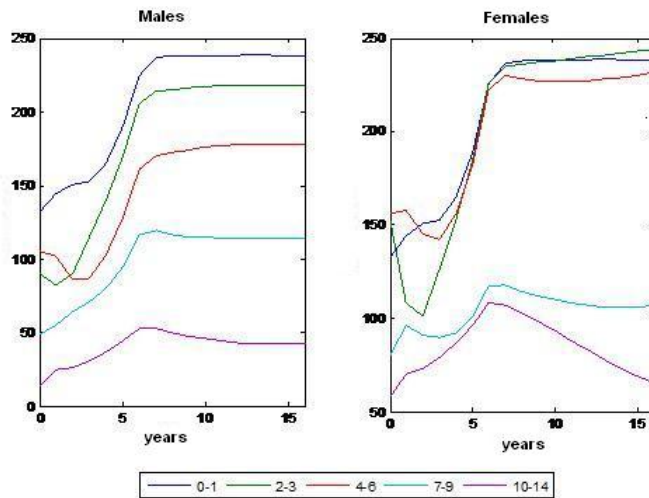
Figure 1: Population evolution estimated by the model (10).

[3] A. Berman, R. J. Plemmons, Nonnegative Matrices in the Mathematical Sciences, Computer Science and Applied Mathematics, Academic Press, New York, 1979.

[4] G. Bastin, A. Provost, Feedback stabilisation with positive control of dissipative compartmental systems, Proceedings of the 15th International Symposium on Mathematical Theory of Networks and Systems, Notre-Dame, USA, 2002.

[5] L. P. Lefkovitch, The sudy of population growth in organisms grouped by stages, Biometrics 21 (1965) 1-18.

[6] D. T. Crouse, L. B. Crowder, H. Caswell, A stage-based population model for loggerhead sea turtles and implications for conservation, Ecology 68(5) (1987) 1412-1423.

[7] R. Cantó, B. Ricarte, A. M. Urbano, Definición y aplicación de los sistemas de control lineales quasi-positivos. Actas del VI Congreso: La investigación ante la sociedad del conocimiento. Sostenibilidad y medioambiente, pp. 75-78, SPUPV, Alcoi, Alicante, 2009.

[8] M. Selma, Aplicación de un sistema lineal de control para la elaboración del plan especial de aprovechamiento cinegético de caza mayor de la reserva valenciana de caza de la "Muela de Cortes", Trabajo Final de Carrera de Ingeniero de Montes, 2009.