

Mathematical models in biology, 1516Q2
Miniprojects' proposals
Block 2: Population Dynamics

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-1.1 Demographic models with age structure

[Juan Carlos, Wai Wing, Alba]

The most basic models of population growth that we considered in class do not take into account the age structure of the populations. In the case of human populations, this fact is particularly relevant since the fertility of the population varies according to the age. This project proposes to study the dynamics of population pyramids. As a reference, you should use Chapter 5 of the book by Yeagers *et al.* [14].

You are supposed to:

1. Read Chapter 5 of [14]. In particular, from Section 5.2 on (Section 5.1 is devoted to speculations having little relevance for the forthcoming sections).
2. Pay attention to the methods of population prediction in Section 5.3 and study how to obtain the von Foerster equation. To further study this equation, you can also use the Section 2.2.3 of the book [9].
3. Download from the Idescat website, <http://www.idescat>, both the age data and the fertility and mortality distributions by age (from **Data > Population > Population figures > By age group**)¹.
4. Using the Leslie matrix method, contrast the validity of the model in the last years and make a projection of the population for the forthcoming years. Compare it with available predictions and discuss the differences.
5. (optional) In the previous statement, we consider the fertility constant along the year. Is it possible to modify them by considering a linear variation between two consecutive records?

References

- [9] Jacques Istas, Mathematical modeling for the life sciences.
- [14] Edward K. Yeagers, Ronald W. Shonkwiler and James V. Herod, An introduction to the mathematics of biology: with computer algebra models.

¹You can use a database from another agency if you find more interesting data; for instance, the world population from <http://esa.un.org/unpd/wpp/Graphs/Probabilistic/POP/TOT/> provides lots of interesting segregated data.

-1.2 Predator-prey models

[Joel, Gerard, Oscar]

We consider the realistic 2-species model (see [11, Sect. 3.4])

$$\begin{cases} \frac{dN}{dt} = N \left(r \left(1 - \frac{N}{K} \right) - \frac{\kappa P}{N + D} \right), \\ \frac{dP}{dt} = P \left(s \left(1 - \frac{h P}{N} \right) \right), \end{cases}$$

where r , K , κ , D , s and h are positive constants.

1. Explain the biological meaning of the parameters r , K , κ , D , s and h .
2. Search for a suitable adimensionalisation that bring the system into:

$$\begin{cases} \frac{du}{d\tau} = u(1 - u) - \frac{a u v}{u + d}, \\ \frac{dv}{d\tau} = b v(1 - \frac{v}{u}), \end{cases} \quad (1)$$

where a , b and d are now 3 dimensionless positive parameters. Observe that it satisfies the Kolmogorov conditions (see Section 5.1. of the slides).

3. Find and classify topologically the equilibrium points of the system (1) in terms of the parameters a , b and d .
4. Detect and represent the surface in the (a, b, d) -space where a Hopf Bifurcation occurs. *Hints: A computer algebra system is required to find the HB condition. One can then plot numerically this surface restricted, for instance, to the box $\{(a, b, d) : 0 \leq a \leq 1, 0 \leq b \leq 1, 0 \leq d \leq 1\}$.*
5. Localize a specific choice of parameters where the system has a limit cycle. Prove the existence of this limit cycle from the Poincaré-Bendixson theorem. Plot the limit cycle using some numerical integrator.
6. Give a biological interpretation of the transition from having an equilibrium point to having a limit cycle. *Hint: Use bifurcation parameters that undergo the bifurcation.*
7. (optional) Obtain a bifurcation diagram in the (a, d) plane with $b = 0.06$ (this value could be different).

References

- [11] Murray, J.D., Mathematical Biology

-1.3 Chaotic dynamics in real population data

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Chaotic dynamics of populations is still a controversial issue because of the lack of both experimental works that clearly determine this regime and infinite time records. You can find a discussion by a biologist in the article (in Catalan) by Ramon Margalef that you can download from Atenea and, in general, in the book “Order and Chaos in Ecology”, which you have in the library of ETSEIB (and scanned in part in Atenea).

In this project we introduce a series of experiments that a group led by biologists and mathematicians performed in the late 90s and early 2000s to experimentally determine different types of population dynamics (from periodic to chaotic) in populations of *Triboleum castaneum*. All their publications and experimental data are collected at the following website:

<http://caldera.calstatela.edu/nonlin/>,

which we will use in the following. We will try to understand the process of modeling and trying to replicate some of their computations. The articles of reference (though you do not have to read them all) are [4], [7], [6] and [5].

In these works the authors modeled the population of Larvae, Pupae and Adults (L, P and A, respectively) through a system of difference equations

$$L_t = bA_{t-1} \exp(-c_{el} L_{t-1} - c_{ea} A_{t-1}), \quad (2)$$

$$P_t = L_{t-1}(1 - \mu l), \quad (3)$$

$$A_t = P_{t-1} \exp(-c_{pa} A_{t-1}) + A_{t-1}(1 - \mu a). \quad (4)$$

and explored their dynamics. In the book by Brauer *et al.* [2, Sect. 2.8] you can find a first numerical and analytical description of the model.

In this project you should:

1. Describe the biological bases of the experiments, including the *Tribolium*'s life cycle, the experimental conditions and how do they make the biological parameters of the system vary.
2. Describe the basic dynamics of the LPA-system (following firstly the indications given in Brauer-Castillo-Chavez [2]).

3. Simulate numerically some of the different transitions that can occur.
4. (optional) Can you reproduce the bifurcation diagram obtained for the experimental parameters of the system?

References

- [2] Fred Brauer and Carlos Castillo-Chávez, Mathematical models in population biology and epidemiology
- [4] Costantino, R.F., Cushing, J.M., Dennis, B. and Desharnais, R.A., Experimentally induced transitions in the dynamic behavior of insect populations
- [5] Costantino, R.F., Desharnais, R.A., Cushing, J.M., and Dennis, B., Chaotic dynamics in an insect population
- [6] Cushing, J.M., Dennis, B., Desharnais, R.A., and Costantino, R.F., An interdisciplinary approach to understanding nonlinear ecological dynamics
- [7] Dennis, B., Desharnais, R.A., Cushing, J.M. and Costantino, R.F., Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments

-1.4 Hypercycles

[Beñat, Enle, Cassius Manuel]

The hypercycle is a network of catalytically coupled self-replicating species in which each of the species enhances the reproduction of another one forming a closed loop. The abstract hypercycle theory, which was initially developed in the context of prebiotic molecular evolution, is strongly tied to the origin of life problem. The hypercycle actually models a system of entities which reproduce and cooperate among them, increasing the fitness in an altruistic way of otherwise competing species. This type of organization makes all the species to behave as a single and coherent evolutionary multimolecular unit.

The hypercycle model, see for instance [3], [13] and [8], is composed by n functional templates, x_i $i = 1, \dots, n$, with heterocatalytic connections and a pool of mutant sequences, x_e . It is given by the following set of nonlinear differential equations:

$$\dot{x}_i = F_i(x) := x_i(A_i Q + K_i x_{i-1} Q - \phi), \quad (5)$$

$$\dot{x}_e = x_e(A_e - \phi) + (1 - Q) \sum_{i=1}^n x_i(A_i + K_i x_{i-1}), \quad (6)$$

for $1 \leq i \leq n$ (we use the convention that $x_0 = x_n$), where

$$\phi(x) = \sum_{i=1}^n x_i(A_i + K_i x_{i-1}) + A_e x_e.$$

Here x_i are the population numbers of the functional hypercycle template i , while x_e corresponds to the population numbers of the pool of mutants. Parameters A_i and Q are, respectively, the Malthusian (non-catalytic) replication rate of species x_i and the average copying fidelity during replication (being $1 - Q$ the average mutation rate). Constant A_e is the Malthusian replication rate of the mutant sequences. Constants A_i, A_e, K_i are positive. The term $\phi(x)$ is a dilution outflow that keeps the total population constant and introduces competition between all the hypercycle members and the pool of mutants. The fact that the population is constant is expressed by the property that $\sum_{i=1}^n x_i + x_e = 1$ is invariant. This allows to write x_e in terms of x_i and realize that therefore the dynamics of x_i governed by (5) is independent of x_e . For that reason henceforth we focus on (5) which will be called $\dot{x} = F(x)$ in short and will be consider in the bounded domain

$$\Omega = \left\{ x \in \mathbb{R}^n \mid x_i \geq 0, \sum_{i=1}^n x_i \leq 1 \right\}.$$

We will consider the *symmetric case*, that is, we assume $A_i = A_e = a$ and $K_i = 1$, for all $i = 1, \dots, n$.

1. Prove that system (5) can have at most 3 equilibrium points: $(0, \dots, 0)$ and two points on the line $x_1 = \dots = x_n$. Give their expression and study their stability (that is, give a formula for the eigenvalues of the corresponding Jacobian matrices). *Hint: note that DF is a circulant matrix.*
2. For $n \leq 4$, prove that if the equilibrium points with $x_1 = \dots = x_n$ do not exist, then there are no periodic orbits for system (5). *Hint: study the flow on the hyperplanes $\sum_{i=1}^n x_i = \alpha$, with $\alpha \leq 1$.*
3. Consider the case $n = 5$ and $a = 0.1$. Starting with $Q = 0.9$, try to find, numerically, a stable periodic orbit. Then, decrease Q until you reach a Q_{PO} such that the limit cycle does not exist. For the smallest Q having a limit cycle, compute the eigenvalues of the associated Poincaré map.
4. (optional) Still in the above case, fix any $Q \in (Q_{PO}, 0.9)$, add a small stochastic perturbation (white noise) to every equation in system (5), and study the dynamics of the system for different realizations of the noise process.
5. Discuss the biological interpretation of the previous statements.

References

- [3] Campos, P.R.A., Fontanari, J.F., Stadler, P.F., Error propagation in the hypercycle
- [8] A. Guillamon, E. Fontich and J. Sardanyés, Bifurcations analysis of oscillating hypercycles
- [12] Josep Sardanyés, The hypercycle: from molecular to ecosystems dynamics
- [13] Silvestre, D.A.M.M., Fontanari, J.F., The information capacity of hypercycles

-1.5 Rabies pest

[Marc, Felix, Anna]

In 1979, a rabies pest, coming from East Europe, arrived in France from the Eastern border. Foxes were the main vehicle of the rabies.

1. We consider the foxes to be divided into two groups, infective I and susceptible S . The proposed model is:

$$\begin{cases} \frac{dS(t)}{dt} = r(S(t) + I(t)) \left(1 - \frac{S(t)}{K}\right) - \beta S(t) I(t), \\ \frac{dI(t)}{dt} = \beta S(t) I(t) - u I(t), \end{cases}$$

where all the parameters are positive.

- a) Justify this model.
 - b) Find the stability of the steady state $(S, I) = (K, 0)$, give conditions on the parameters that allow an outbreak of the pest. Discuss these conditions. You can adopt the point of view of the rabies virus! What is your best strategy?
2. A first method to eradicate the rabies pest consists in killing the foxes, for instance by giving a bonus to the hunters. This method is modeled by:

$$\begin{cases} \frac{dS(t)}{dt} = r(S(t) + I(t)) \left(1 - \frac{S(t)}{K}\right) - \beta S(t) I(t) - c S(t), \\ \frac{dI(t)}{dt} = \beta S(t) I(t) - u I(t) - c I(t), \end{cases}$$

where c is the hunting parameter; hunting is done both on infective and susceptible. Give conditions on the parameters that prevent the rabies pest.

3. A second method to eradicate the rabies pest consist in vaccinating the foxes. This method is modeled by:

$$\begin{cases} \frac{dS(t)}{dt} = r(S(t) + I(t)) \left(1 - \frac{S(t)}{K}\right) - \beta (1 - v) S(t) I(t), \\ \frac{dI(t)}{dt} = \beta (1 - v) S(t) I(t) - u I(t), \end{cases}$$

where v is the vaccinating parameter. Give conditions on the parameters that prevent the rabies pest.

4. Give a biological interpretation of the three above systems.
5. Which method would you choose? Would a combination of the two methods give some advantage?

-1.6 Epidemic models with seasonal infectivity

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We want to consider how seasonally varying parameters act as a forcing mechanism and examine their dynamical consequences. We aim at proving how such temporally forced models allow us to better capture the observed pattern of recurrent epidemics in contrast to unforced models, which predict oscillations that are damped toward equilibrium.

Consider the following system that Bailey proposed to model measles:

$$\begin{cases} dX/dt = \mu N - \beta(t) X Y N, \\ dY/dt = \beta(t) X Y N - \gamma Y, \end{cases} \quad (7)$$

where μ is the per capita birth rate and γ is the recovery rate from the infection. These equations ignore the death of susceptible and infectious individuals, and also the age structure. Therefore, the model assumes that all individuals contract the infection during their lifetime, which is a reasonable approximation for measles.

We consider a sinusoidal transmission rate as a function of time:

$$\beta(t) = \beta_0(1 + \beta_1 \cos(\omega t)). \quad (8)$$

1. Compute the basic reproductive ratio, R_0 , for system (7).
2. Assuming that the amplitude of seasonality is small ($\beta_1 \ll 1$), transform system (7-8) into the second order differential equation

$$\frac{d^2 y}{dt^2} + \mu R_0 \frac{dy}{dt} + \mu \beta_0 y = -\beta_1 \omega \gamma \sin(\omega t). \quad (9)$$

3. Prove that the amplitude of the solutions of (9) is given by:

$$M = \beta_1 \omega \gamma \left((\mu \beta_0 - \omega^2)^2 + (\omega \mu R_0)^2 \right)^{-1/2}.$$

4. In the case of measles, available data allow to set $1/\gamma = 2$, $\mu R_0 \approx 0.014$ and $\omega = \pi/26$, taking a week as unit time. Prove that the above analysis predicts an 8-fold amplification of the oscillation amplitude of the seasonal input.

5. Add an equation to the model with the Exposed subpopulation so that we achieve a SEIR model with $\mu = 0.02$ per year, $\beta_0 = 1250$, $1/\sigma = 8$ days, and $1/\gamma = 5$ days. Plot the time series for different levels of seasonality β_1 (0.025, 0.05, and 0.25, respectively).
6. For $\beta_1 = j * 0.3/N$, with $j = 0, \dots, N$, $N = 1000$, run the solutions of the SEIR system for 150 years and then plot the maxima of the trajectories in the next 50 years against β_1 . You are obtaining a *bifurcation diagram* indicating the infection peaks.
7. Read Section 5.2 from [10] and give an overall interpretation of the above results.

- [1] N.T.J. Bailey, The Mathematical Theory of Infectious Diseases and its Applications
- [3] Campos, P.R.A., Fontanari, J.F., Stadler, P.F., Error propagation in the hypercycle
- [10] Matt J. Keeling and Pejman Rohani, Modeling Infectious Diseases in Humans and Animals

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- [1] N.T.J. Bailey. *The Mathematical Theory of Infectious Diseases and its Applications*. London: Charles Griffin and Company., 1975.
- [2] Fred Brauer and Carlos Castillo-Chávez. *Mathematical models in population biology and epidemiology*, volume 40 of *Texts in Applied Mathematics*. Springer-Verlag, New York, 2001.
- [3] P. R. A. Campos, J. F. Fontanari, and P. F. Stadler. Error propagation in the hypercycle. *Phys. Rev. E*, 61:2996–3002, 2000.
- [4] R. F. Costantino, J. M. Cushing, Brian Dennis, and Robert A. Desharnais. Experimentally induced transitions in the dynamic behaviour of insect populations. *Nature*, 375:227–230, 1995.
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- [7] Brian Dennis, Robert A. Desharnais, J. M. Cushing, and R. F. Costantino. Nonlinear demographic dynamics: Mathematical models, statistical methods, and biological experiments. *Ecological Monographs*, 65:261–282, 1995.

- [8] Antoni Guillamon, Ernest Fontich, and Josep Sardanyés. Bifurcations analysis of oscillating hypercycles. *Journal of Theoretical Biology*, 387:23 – 30, 2015.
- [9] Jacques Istas. *Mathematical modeling for the life sciences*. Universitext. Springer-Verlag, Berlin, 2005.
- [10] Matt J. Keeling and Pejman Rohani. *Modeling Infectious Diseases in Humans and Animals*. Princeton University Press, 2008.
- [11] J.D. Murray. *Mathematical biology (vol. 1)*. Springer Verlag, 2003.
- [12] J. Sardanyés. The hypercycle: from molecular to ecosystems dynamics. In A. Dupont and H. Jacobs, editors, *Landscape Ecology Research Trends*, chapter 6. Nova Publishers, 2008.
- [13] A. M. M. Silvestre and J. F. Fontanari. The information capacity of hypercycles. *J. Theor. Biol.*, 254:804–806, 2008.
- [14] Edward K. Yeagers, Ronald W. Shonkwiler, and James V. Herod. *An introduction to the mathematics of biology: with computer algebra models*. Boston: Birkhäuser. x, 417 p. 862.00 , 1996.