

M1 BBS - EM8BBSEM

Simulation de Systèmes Biologiques

(#8)

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Matrice de Leslie : la récolte

Harvesting an Age-Distributed Population

Part 1: Sustainable harvesting

Recall that in any particular year, a population (e.g., a single herd of New Zealand sheep) can be represented by a *state vector* $\mathbf{x} = (x_1, x_2, \dots, x_{11}, x_{12})^T$, where x_i represents the number of female animals in the i -th age class. If absolute numbers are not known, a state may be represented equally well by a vector of *fractions* of the population in each age class, i.e., by a vector whose entries sum to 1. The *Leslie growth matrix* for the population is the transition matrix \mathbf{L} from the state in one year to the state in the next year. The entries a_1, \dots, a_{12} of the first row of \mathbf{L} represent the rates of birth for each age class, while the subdiagonal entries b_1, \dots, b_{11} represent the survival rates for each class. Thus, if \mathbf{x} is the state vector in a given year, the state vector after one year's growth is \mathbf{Lx} and the *growth* in that year (distributed in age classes) is $\mathbf{Lx} - \mathbf{x}$.

In the Leslie Growth Models module, we saw that a New Zealand sheep population will increase by about 17.6% per year -- and approach a stable age distribution -- if left alone to do nothing but reproduce (and perhaps get sheared once in a while). However, New Zealand's sheep farmers cannot live entirely on their income from wool, especially if they have to keep feeding ever more sheep. A desirable goal for management of a sheep herd (or any renewable resource) is to find a stable configuration from which one can harvest the *growth* at regular intervals -- thereby producing income and returning the population to its previous configuration.

A sustainable harvesting policy is a plan for harvesting on a regular schedule in such a way that the harvest is always the same and the state of the population after harvesting is always the same.

Suppose we let h_i be the fraction of the i -th age group that will be harvested at the end of each growth period, and we let \mathbf{H} be the diagonal matrix whose entries are the h_i 's. If we start a growth period with age-distribution state \mathbf{x} , then the state after growth will be \mathbf{Lx} . The harvest after growth will be \mathbf{HLx} , and that will reduce the population to $\mathbf{Lx} - \mathbf{HLx}$, or $(\mathbf{I} - \mathbf{H})\mathbf{Lx}$. To be sustainable, the population state after harvest must match the starting state, i.e., $(\mathbf{I} - \mathbf{H})\mathbf{Lx} = \mathbf{x}$. That is, \mathbf{x} must be an eigenvector for eigenvalue 1 for the matrix $(\mathbf{I} - \mathbf{H})\mathbf{L}$. In this part of the module, we explore some of the implications of this observation.

1. Enter the Leslie matrix \mathbf{L} in symbolic form (i.e., without specific numbers assigned to the \mathbf{a} 's and \mathbf{b} 's), and compute $(\mathbf{I} - \mathbf{H})\mathbf{L}$. You should find that $(\mathbf{I} - \mathbf{H})\mathbf{L}$ is another Leslie matrix. It differs from \mathbf{L} in that the i -th row of \mathbf{L} has been multiplied by $1 - h_i$.
2. Recall that the dominant eigenvalue λ_1 of a Leslie matrix is the unique positive eigenvalue of \mathbf{L} . Now think about the eigenvalues of the Leslie matrix $(\mathbf{I} - \mathbf{H})\mathbf{L}$, in which the i -th row of \mathbf{L} has been multiplied by $1 - h_i$. The characteristic polynomial is a single equation in 12 unknowns (the h 's) that can be satisfied in many different ways. Thus, there are infinitely many ways to construct a sustainable harvesting policy. In what follows, we consider three of those ways.

3. Before we continue, we need to recompute the dominant eigenvalue λ_1 for the Leslie matrix associated to our New Zealand sheep population. Evaluate them and specify λ_1 .
4. A *uniform* harvesting policy is one in which the same fraction h is harvested from each age group. In this case, we must have $(1 - h)Lx = x$. Explain why this means that h must satisfy $\lambda_1 = 1/(1-h)$, so $h = 1 - 1/\lambda_1$. Use this observation to find a uniform fraction of the New Zealand sheep population that can be harvested every year and leave the population distribution the same at the start of each year.
5. Explain why the harvest rate is not the same as the growth rate of approximately 17.6%.

Part 2: Harvesting the youngest class

Sheep are not all equally valuable for harvest -- in fact, in world meat markets, lamb is much more valuable than mutton. Thus, the best economic use of the herd might be to harvest only lambs and keep the mature ewes alive to breed more lambs. Is there a sustainable harvesting policy for this case?

If we harvest only from the youngest group, then $h_1 = h$, the fraction harvested from that group, and all the other h 's are zero. In step 2 of Part 1, we asked you to think about the algebraic condition on h 's in order to have 1 as an eigenvalue of $(I - H)L$. With only the first h different from zero, that condition simplifies to

$$(1 - h)(a_1 + a_2b_1 + a_3b_1b_2 + \dots + a_{12}b_1b_2b_3\dots b_{11}) = 1$$

or

$$(1 - h)R = 1,$$

where

$$R = a_1 + a_2b_1 + a_3b_1b_2 + \dots + a_{12}b_1b_2b_3\dots b_{11}.$$

The quantity R is called the *net reproduction rate* of the population -- it is, in fact, the average number of daughters born to a ewe in her expected lifetime.

1. Calculate the net reproduction rate \mathbf{R} for the New Zealand sheep population.
2. To have a sustainable harvesting policy with only lambs being harvested, we must have $(1 - h)\mathbf{R} = 1$. Find the number h that satisfies this condition. What fraction of the lambs should be harvested each year?
3. Find the stable population distribution \mathbf{x} for this harvesting policy. What fraction of the total population should be lambs at the start of the growth period? At the end of the growth period? What fraction of the total population is harvested after the growth period? How does this compare with uniform harvesting?

Part 3: Optimal harvesting

We have now considered two sustainable harvesting policies: harvesting the same fraction from every age group, and harvesting only from the youngest age group. The latter probably produces a much smaller harvest in pounds of meat, but possibly a more valuable harvest for the sheep farmer. We now ask: What sustainable harvesting policy would produce the largest possible harvest in terms of numbers of animals? Another way to ask the question: What combination of harvesting fractions h_1, h_2, \dots, h_{12} results in the largest fraction of the total population being harvested -- while still maintaining sustainability?

On the face of it, this is a very difficult question. However, there is a theorem from linear programming theory that simplifies the question considerably:

Optimal Sustainable Yield

If a sustainable harvesting policy is optimal, it harvests only from one or two age classes. If two age classes are harvested, then the older class is completely harvested.

[C. Rorres, "Optimal Sustainable Yield of a Renewable Resource," *Biometrics*, Vol. 32, 1976, pages 945-948.]

1. For the New Zealand sheep population, it can be shown (by techniques beyond the level of this course) that the optimal yield is achieved when $h_1 = 0.522$, $h_9 = 1$, and all the other h 's are zero. Find the sustainable age distribution for this policy, both before and after growth.
2. What fraction of the total population is harvested each year? How does this compare with uniform harvesting and with lambs-only harvesting?

Points to ponder:

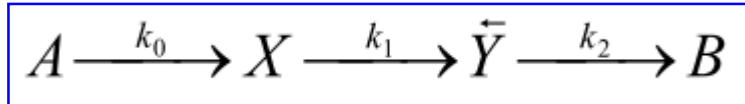
1. Describe in your own words the meaning of "sustainable harvesting policy." How does a second Leslie matrix for a given population arise in this context? What is the significance of 1 as an eigenvalue for that matrix? What is the significance of an eigenvector for the eigenvalue 1?
2. If a sustainable harvesting policy takes the same fraction from every age group, how is that fraction calculated from the original Leslie matrix? How is a stable age distribution calculated?
3. If a sustainable harvesting policy takes only a fraction of the youngest age group, how is that fraction calculated from the original Leslie matrix? How is a stable age distribution calculated?
4. Can either uniform harvesting or youngest-only harvesting be an optimal sustainable policy in the sense of harvesting the largest number of individuals? Explain.

Processus périodiques

A periodic kinetic equation has been described for the first time by Lotka (1925). A purely hypothetical reaction serves as a didactic model for studying periodic processes. It is given by the following schema:



The molecules of the substrate **A**, which is in excess, convert to the substance **X** with a constant rate **k₀** (reaction of the zeroth order). **X** is converted to **Y** in a second order reaction (the reaction rate **k₁** depends on the concentrations of both **X** and **Y**, which is denoted by a reverse arrow above **Y**). **Y** undergoes an irreversible decay, forming product **B** with the rate **k₂**.



The mathematical model of this system is described by the following set of equations:

$$\frac{dX}{dt} = k_0 - k_1 XY$$

$$\frac{dY}{dt} = k_1 XY - k_2 Y$$

$$\frac{dB}{dt} = k_2 Y$$

The first two equations do not depend on **B**, hence they can be analyzed independently of the third one. We shall proceed as usual, beginning with the determination of stationary points in the phase plane of the studied system, which are obtained by solving the algebraic equations, resulting from equation all derivatives to zero.

The equations:

$$0 = k_0 - k_1 \bar{X}\bar{Y}$$

$$0 = k_1 \bar{X}\bar{Y} - k_2 \bar{Y}$$

have two solutions. The trivial one ($\mathbf{Y=0}$) is not interesting and will not be discussed. The other one is:

$$\bar{X} = \frac{k_2}{k_1}$$

$$\bar{Y} = \frac{k_0}{k_2}$$

To analyze the type of stability associated with this stationary point we will introduce small perturbations $x(t)$ and $y(t)$ about the equilibrium:

$$X(t) = \bar{X} + x(t)$$

$$Y(t) = \bar{Y} + y(t)$$

Substituting the above relations to the original equations we obtain the expressions for the perturbations:

$$\begin{aligned}\frac{dx}{dt} &= -\frac{k_0 k_1}{k_2} x - k_2 y - k_1 xy \\ \frac{dy}{dt} &= \frac{k_0 k_1}{k_2} x + k_1 xy\end{aligned}$$

Neglecting small terms of the second order (xy) we get a linearized system of equations:

$$\begin{aligned}\frac{dx}{dt} &= -\frac{k_0 k_1}{k_2} x - k_2 y \\ \frac{dy}{dt} &= \frac{k_0 k_1}{k_2} x\end{aligned}$$

Introducing the following denotations:

$$\frac{k_0 k_1}{k_2} = 2\delta, \quad k_0 k_1 = \omega_0^2$$

we get:

$$\begin{aligned} \frac{dx}{dt} &= -2\delta x - \frac{\omega_0^2}{2\delta} y \\ \frac{dy}{dt} &= 2\delta x \end{aligned}$$

with the characteristic equation:

$$\lambda^2 + 2\delta\lambda + \omega_0^2 = 0$$

The determinant Δ is given by:

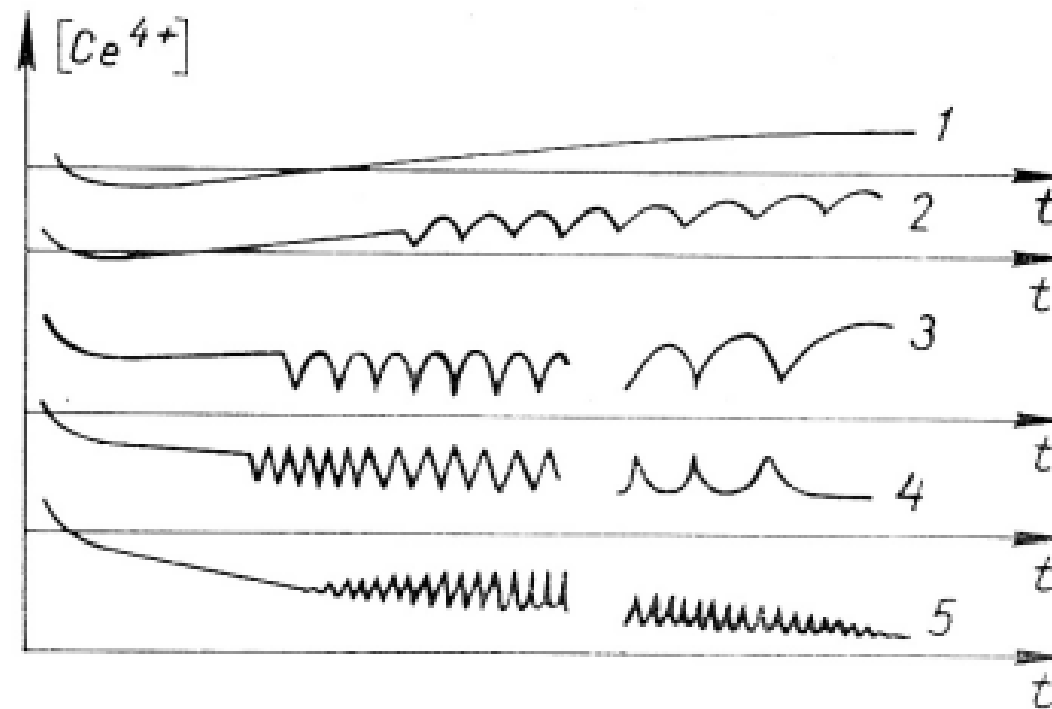
$$\Delta = 4(\delta^2 - \omega_0^2)$$

Periodic oscillations occur when $\Delta < 0$, i.e. when:

$$\delta^2 < \omega_0^2, \quad 4k_2^2 > k_0k_1$$

Experimental confirmation of the occurrence of periodic reactions in nature has been obtained in the 1960s (Zhabotynski *et al.*). Oxidation of malonic acid **C₃H₄O₄** with a mixture of **KBrO₃** and **Ce(SO₄)₂** led to observation of changes in the color of the solution, roughly once per second. It has been shown that the color changes resulted from periodic creation of **Ce⁴⁺** ions in the solution.

The figure below presents some of the results, concerning the observed variations of the Ce^{4+} ions in time. The different curves have been obtained for different initial conditions of the experiment, i.e. for different ratios of concentrations of substrates. The character of the curves varies from sinusoidal (5) to relaxational (2, 3).



Systèmes proie-prédateur

Lotka (1925) and, independently, Volterra (1926) proposed a simple model for the population dynamics of two interacting species. This model was meant to treat the ***predator-prey interactions***.

Let's assume that hares and lynxes populate an ***isolated area***. Hares eat plants, available without limitations. Lynxes (predators) eat hares (prey). Suppose the numbers of the hares and lynxes are X and Y , respectively.

With food freely available, hares multiply with the growth rate proportional to their number. However, they perish proportionally to the number of their encounters with lynxes.

Lynxes profit from encounters with the hares, but in the absence of prey, which is their only food, they die out with the rate proportional to their numbers.

Mathematically, we can describe this situation with the help of the following set of equations:

$$\frac{dX}{dt} = rX - aXY$$

$$\frac{dY}{dt} = -mY + bXY$$

where the coefficients ***r***, ***a***, ***m*** and ***b*** are positive constants.

Stationary points of this system can be found if all derivatives are equated to zero:

$$0 = \bar{X}(r - a\bar{Y})$$

$$0 = \bar{Y}(-m + b\bar{X})$$

The first obvious solution is the stationary point **(0,0)**. Analysis of small perturbations about this point leads to the following system of equations:

$$\left. \begin{aligned} \frac{dx}{dt} &= rx - axy \\ \frac{dy}{dt} &= -my + bxy \end{aligned} \right\} \xrightarrow{\text{linearization}} \left\{ \begin{aligned} \frac{dx}{dt} &= rx \\ \frac{dy}{dt} &= -my \end{aligned} \right.$$

The characteristic equation has the form:

$$\lambda^2 + (m - r)\lambda - rm = 0$$

The solution is:

$$\lambda_1 = -m$$

$$\lambda_2 = r$$

Hence, the solutions [perturbations about the point $(0,0)$] are linear combinations of the following exponentials:

$$x(t) = Ae^{-mt} + Be^{rt}$$

$$y(t) = Ce^{-mt} + De^{rt}$$

According to the theory, when two roots have different signs the stationary point is a **saddle**.

The other (non-trivial) solution is:

$$\bar{X} = \frac{m}{b}, \quad \bar{Y} = \frac{r}{a}$$

Since all parameters are positive, the stationary point is located in the first quadrant of the system's phase plane. Introducing small perturbations $\mathbf{x}(t)$ and $\mathbf{y}(t)$ about this point and linearizing the system gives us the following equations:

$$\frac{dx}{dt} = -\frac{am}{b}y$$

$$\frac{dy}{dt} = \frac{br}{a}x$$

The characteristic equation in this case has the form:

$$\lambda^2 + rm = 0$$

with two imaginary roots:

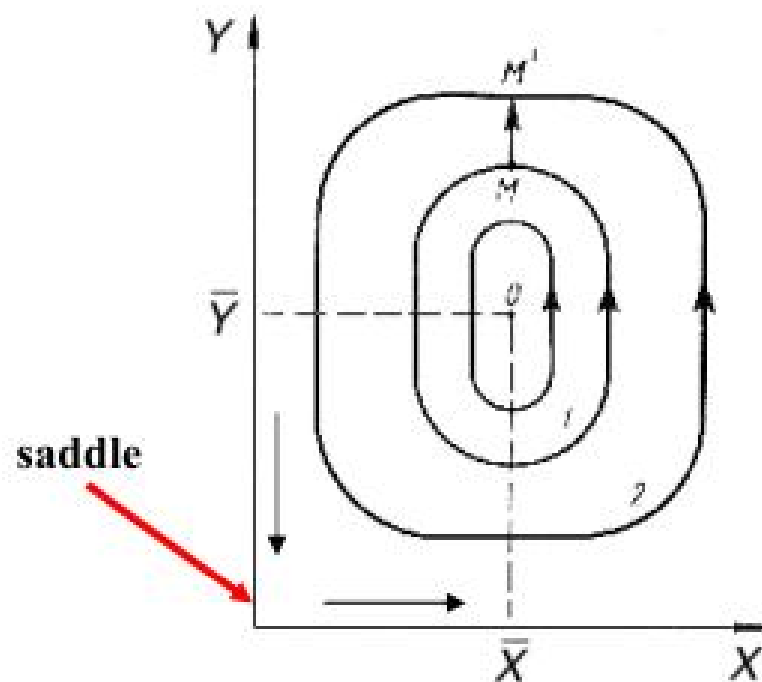
$$\lambda_{1,2} = \pm i\sqrt{rm} = \pm i\omega$$

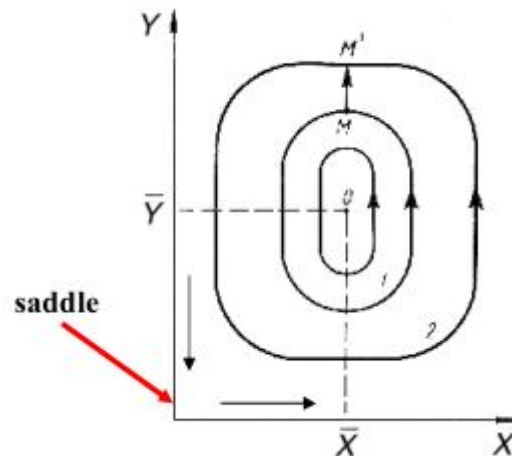
The solutions are given by the following equations:

$$x(t) = Ae^{i\omega t} + Be^{-i\omega t} = A'\cos(\omega t) + B'\sin(\omega t)$$

$$y(t) = Ce^{i\omega t} + De^{-i\omega t} = C'\cos(\omega t) + D'\sin(\omega t)$$

Imaginary values of the roots indicate that the stationary point is a **center**. Trajectories close to this point are concentric ellipses. Strictly speaking, however, a center is not a stable point (a center is at the border of a stable and an unstable manifold). Look at the graph below.



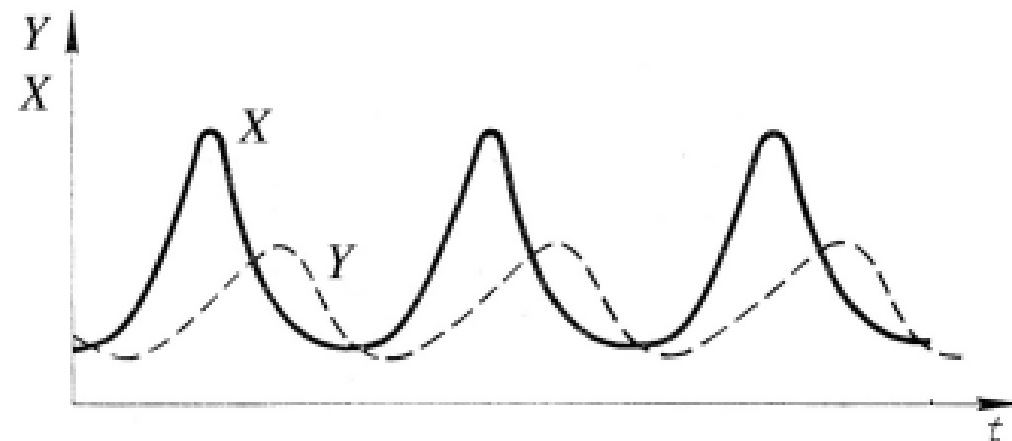


Suppose that the system moves along trajectory **1**. When it reaches the point **M**, a certain number of predators are added to the system. As a result, the system's state jumps to the point **M'**. If no further perturbations occur, oscillations of **X** and **Y** will continue with larger amplitudes. The new trajectory is now described by curve **2**.

This is a typical case of a **neutral equilibrium**. Oscillations are unstable because their characteristics change irreversibly under the influence of even small perturbations. A similar type of equilibrium is exhibited by a ball on a flat surface.

Note: *an unstable state cannot describe a **real** biological system. Hence, despite its simplicity, the Lotka-Volterra model is of limited use.*

In the figure below are shown the temporal changes of X and Y , obtained by numerical integration. Both functions are periodic. Maximal number of prey X always precedes the maxima of predators Y .



And here are some experimental data. The Hudson Bay Company clerks have kept logs of animal skins supplied by Canadian trappers beginning with 1845. As can be seen, oscillations occur with periods of about 9 – 10 years. The maximum number of hares usually precedes the maximum number of lynxes by one year. The real-life curves are not as smooth as the simulated ones for obvious reasons: our model does not take into account other predators and/or prey, nor climactic changes.

