Population Dynamics

I. Linear Models

Consider a population of annual plants, that produce an average of f seeds per plant in the summer and die in the winter. A fraction of the seeds also die during the winter and, of those that survive, only another fraction germinates in spring and produce new plants. The number of plants in the year n+1 can be written as

$$P_{n+1} = \underbrace{\alpha}_{\substack{\text{fraction of}\\ \text{seeds that}\\ \text{germinate}}} \underbrace{\sigma}_{\substack{\text{fraction that}\\ \text{survives the}\\ \text{winter}}} \underbrace{f}_{\substack{\text{Average number of}\\ \text{seeds per}\\ \text{plant}}} P_n \equiv r P_n \qquad (1)$$

r = effective growth rate

This equation can be solved very easely by iteration : give the population at year zero we obtain

$$P_1 = r P_0$$

$$P_2 = r P_1 = r(r P_0) = r^2 P_0$$

$$P_3 = r P_2 = r^3 P_0$$

and

$$P_n = r^n P_0 = P_0 e^{n \ln r} . \qquad (2)$$

If $r > 1$ $(\ln r > 0)$ we have an exponential growth of the population. If $r < 1$ the population gets smaller and smaller, going extinct. Only for $r = 1$ we obtain equilibrium, $P_n = P_0$.

In this first lecture we are going to explore a set of equations that are very similar to eq. (1), in which the variables describing the populations occur only linearly (no P_n^2, $\cos P_n$, etc.). Although these equations are simple and can always be solved, they involve some important aspects that we need to know in some detail.

I am going to modify eq. (1) step by step so as to construct more interesting (and slightly more complicate) systems.

MIGRANTS - Suppose that besides the plants growing from last year seed's a number m of plants germinate from extra seed brought by the wind. The equation becomes

$$P_{n+1} = r P_n + m \tag{3}$$

This is a non-homogeneous equation and can be solved by adding to the homogeneous solution (for $m=0$) any particular solution of the full equation. The homogeneous equation is solved by eq. (2)

$$P_n = \tilde{P}_0 \, r^n$$

and a particular solution of eq. (3) is obtained by setting $P_n = P_{n+1} = \bar{P}$:

$$\bar{P} = r\bar{P} + m \implies \bar{P} = \frac{m}{1-r}$$

The complete solution is

$$P_n = \tilde{P}_0 \, r^n + \frac{m}{1-r}$$

As you can check by substituting this into eq. (3).

Finally, setting $n=0$

$$P_0 = \tilde{P}_0 + \frac{m}{1-r} \longrightarrow \tilde{P}_0 = P_0 - \frac{m}{1-r}$$

And

$$P_n = \left(P_0 - \frac{m}{1-r}\right) e^{n \ln r} + \frac{m}{1-r} \qquad (4)$$

Exercises

1) Plot the function $P_n \times n$ for $r<1$. Why the population does not go extinct?

2) Solve the equation (3) for $r=1$.

3) Set $r = 1+\varepsilon$ in eq. (4), take the limit $\varepsilon \to 0$ and compare with your previous solution.

SECOND ORDER EQUATIONS

Suppose now that part of the seeds that did not germinate go through another winter and then have a second chance to do so. Our equation becomes

$$P_{n+1} = \alpha \sigma f P_n + \alpha' \sigma (1-\alpha) \sigma f P_{n-1}$$

where $(1-\alpha)$ = fraction that did not germinate

α' = fraction of those two-years old seeds that germinate

and the extra σ appears because the seeds have to survive another winter.

This can be re-written as

$$P_{n+1} - \beta P_n + \gamma P_{n-1} = 0 \qquad (5)$$

where I am using $\beta = \alpha \sigma f$ and $\gamma = -\alpha' \sigma^2 (1-\alpha) f$.

This is a linear equation of the second order because it needs P_n and P_{n-1} to find P_{n+1}. There are two ways of solving this equation:

1- DIRECT solution — Since the equation is linear we try something similar to eq. (2):

$$P_n = C\lambda^n$$

where C and λ are unknowns. Substituting in (5):

$$C\lambda^{n+1} - \beta C\lambda^n + \gamma C\lambda^{n-1} = 0$$

or

$$C\lambda^{n-1}(\lambda^2 - \beta\lambda + \gamma) = 0 .$$

This is a good solution if

$$\lambda^2 - \beta\lambda + \gamma = 0 \tag{6}$$

otherwise $C=0$ or $\lambda=0$ which is not what we are looking for. Solving for λ we find two solutions

$$\lambda_\pm = \frac{\beta}{2} \pm \frac{1}{2}\sqrt{\beta^2 - 4\gamma} \tag{7}$$

And

$$P_n = C_+\lambda_+^n + C_-\lambda_-^n \tag{8}$$

This is very similar to eq. (2) but now we need not only P_0, but also P_1 to find the two constants C_+ and C_-

Exercise: obtain expressions for C_+ and C_- in terms of the initial conditions P_0 and P_1.

Example: the Fibonacci Rabbits. You are given a couple of rabbits. It takes them one month to mature and, starting the second month they give birth to one new couple every month. Assuming every couple behaves the same way the number of rabbits each month, F_n, becomes:

$F_0 = 0$

$F_1 = 1 \rightarrow$ first couple

$F_2 = 1 \rightarrow$ " " mature

$F_3 = 2 \rightarrow$ first couple + second newly born couple

$F_4 = 3 \rightarrow$ 1st couple + 2nd mature couple + 3rd newly born

$F_5 = 5$

$F_6 = 8$

$\vdots$

$$F_{n+1} = F_n + F_{n-1} \qquad (9)$$

Comparing with eq. (5) we find $\beta = 1$, $\gamma = -1$

$$\lambda_{\pm} = \frac{1 \pm \sqrt{5}}{2}$$

Using $F_0 = 0$ and $F_1 = 1$ we find

$$C_+ = \frac{1}{\sqrt{5}} \; ; \quad C_- = -\frac{1}{\sqrt{5}}$$

and

$$F_n = \frac{1}{\sqrt{5}}\left(\frac{1+\sqrt{5}}{2}\right)^n - \frac{1}{\sqrt{5}}\left(\frac{1-\sqrt{5}}{2}\right)^n .$$

The Fibonacci numbers are very famous and the ratio between successive numbers is known to tend to the "golden mean", a proportion used in the Renaissance paintings and sculptures. It is defined as the way to divide a segment at x

so that the three parts x, $1-x$, 1 have the same ratio:

$$\frac{1}{x} = \frac{x}{1-x} \implies x^2 + x - 1 = 0$$

$$x = \frac{\sqrt{5}-1}{2}.$$

<u>Exercise</u>: show that

$$\lim_{n\to\infty} \frac{F_n}{F_{n+1}} = \lambda_+ = \frac{1}{x}$$

2- Solution by Eigenvalues and Eigenvectors

Eq. (5) can be re-written if we define $q_n = p_{n-1}$:

we obtain

$$\begin{cases} p_{n+1} = \beta p_n - \gamma q_n \\ q_{n+1} = p_n \end{cases}$$

which is a set of 2 equations of the first order. This is analogous to Newton's equation rewritten as Hamilton's equations.

Conversely, given any system of equations

$$\begin{cases} p_{n+1} = a_{11} p_n + a_{12} q_n \\ q_{n+1} = a_{21} p_n + a_{22} q_n \end{cases}$$

it can be rewritten as eq. (5) with

$$\beta = a_{11} + a_{22} \qquad (10)$$

$$\gamma = a_{11} a_{22} - a_{12} a_{21} .$$

In matrix form

$$X_{n+1} = A X_n \qquad (11)$$

with

$$X_n = \begin{pmatrix} p_n \\ q_n \end{pmatrix} \; ; \quad A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} . \qquad (12)$$

$\beta = tr(A)$ = trace of A

$\gamma = \det(A)$ = determinant of A.

If A is "well behaved" it has two special vectors v_+ and v_-, called eigenvectors, such that

$$A v_+ = \lambda_+ v_+ \qquad (13)$$

and

$$A v_- = \lambda_- v_-$$

where the eigenvalues λ_i satisfy

$$\det(A - \lambda \mathbb{1}) \equiv (a_{11} - \lambda)(a_{22} - \lambda) - a_{12} a_{21} = 0.$$

This is exactly eq (6) with the definitions (10). Once λ_+ and λ_- are calculated, eqs. (13) can be solved for v_+ and v_-.

The solution of equation (11) is given by

$$X_n = a_+ \lambda_+^n v_+ + a_- \lambda_-^n v_- \qquad (14)$$

PROOF

$$A X_n = a_1 \lambda_+^n A v_+ + a_- \lambda_-^n A v_-$$

$$= a_1 \lambda_1^{n+1} v_1 + a_- \lambda_-^{n+1} v_-$$

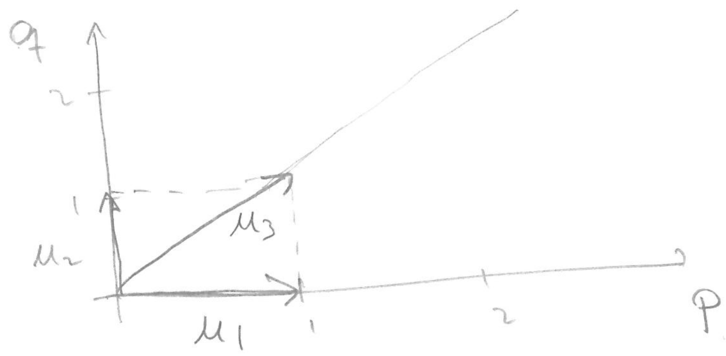
$$= X_{n+1}$$

It is important to understand this structure. The plane $p-q$ is usually called the "phase space". A point in this plane represents the populations at a given moment.

Vectors represent directions in the plane. The vector

$$u_1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$$

for example, is in the p-direction



The set of points $a u_1$ for $0 < a < \infty$ span the entire p-axis. The vector

$$u_2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$$

is in the q-direction. Finally consider

$$u_3 = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$$

and the set of points $a \cdot u_3$ for $0 < a < \infty$. It spans the line passing through the origin and the point $(p, q) = (1, 1)$.

Similarly the eigenvectors v_+ and v_- represent special directions in this plane. If the initial condition are chosen so that $a_- = 0$ in eq. (14) then

$$X_{n+1} = a_+ \lambda_+^{n+1} v_+$$

and the solution moves along the line defined by v_+. If $a_+ = 0$, the points y_n move along v_-. The type of motion depends on whether λ_+ and λ_- are positive, negative, smaller or larger than 1, real or complex.

The behaviour of the solutions (8) or (14) can be studied if we focus on the contribution of each term separately. Therefore we take

$$P_n = C \lambda^n$$

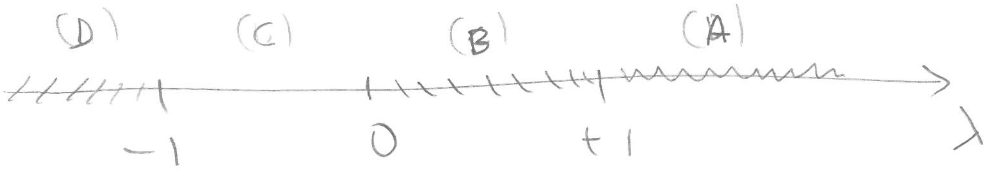
or

$$X_n = a v \lambda^n$$

where λ is one of the two solutions λ_+ or λ_-.

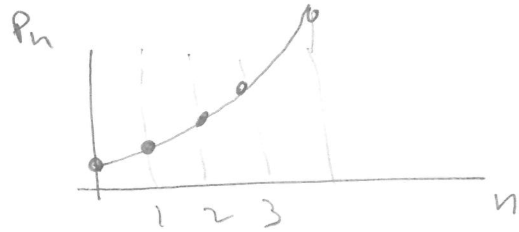
The following cases may appear according to eq. (7)

I – λ is real ; $\beta^2 > 4\gamma$



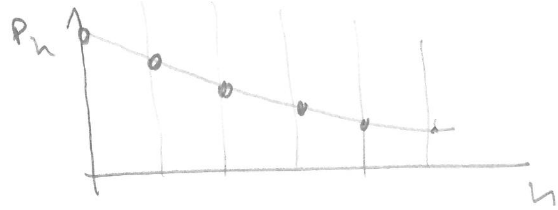
(A) $\lambda > 1$, $P_n = c\lambda^n$.

Exponential growth



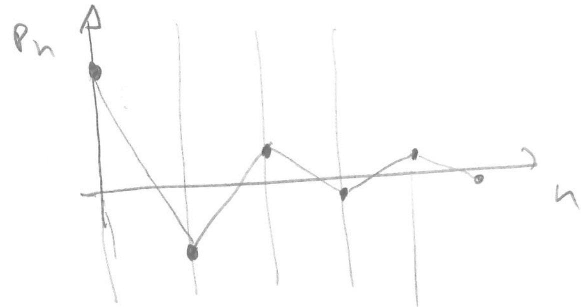
(B) $0 < \lambda < 1$

Exponential damping



(C) $-1 < \lambda < 0$

dumping with oscillation



(D) $\lambda < -1$

growth with oscillations

II – λ is complex ; $\beta^2 < 4\gamma$

(therefore $\gamma > 0$)

In this case $\lambda_+ = \lambda_-^*$ and we need to take both term into account. Consider eq. (8) ; because P_n is real we need to choose $C_+ = C_-^*$.

Setting

$$\lambda_\pm = \frac{\beta}{2} \pm \frac{i}{2}\sqrt{4\gamma - \beta^2} \equiv r e^{\pm i\varphi}$$

$$r = \sqrt{\gamma}$$

$$tg\,\varphi = \frac{\sqrt{4\gamma - \beta^2}}{\beta}$$

$$C_+ = \frac{A - iB}{2} \quad ; \quad C_- = \frac{A + iB}{2}$$

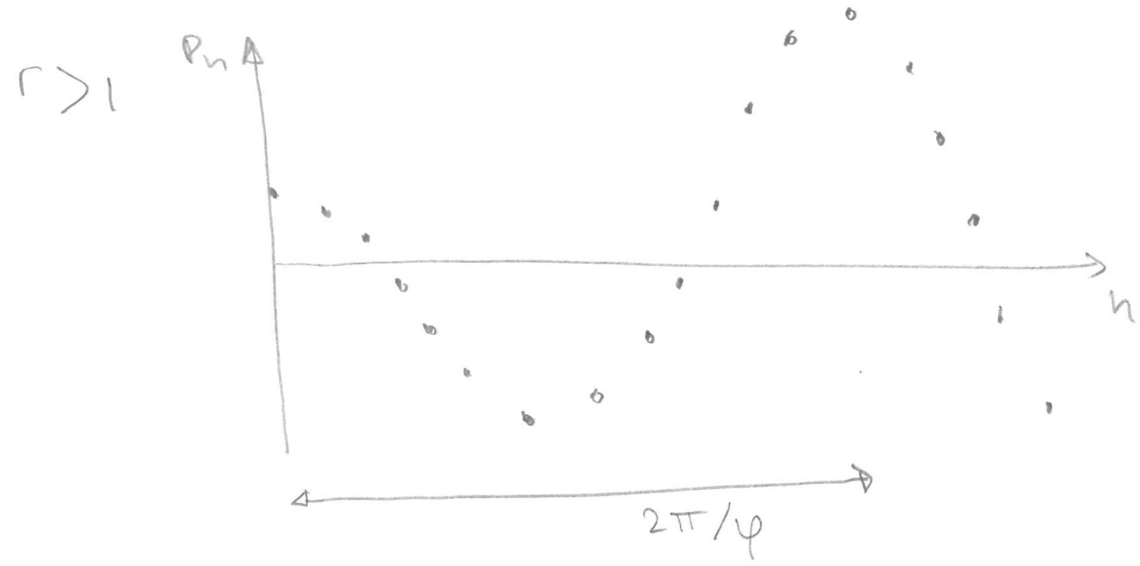
we get

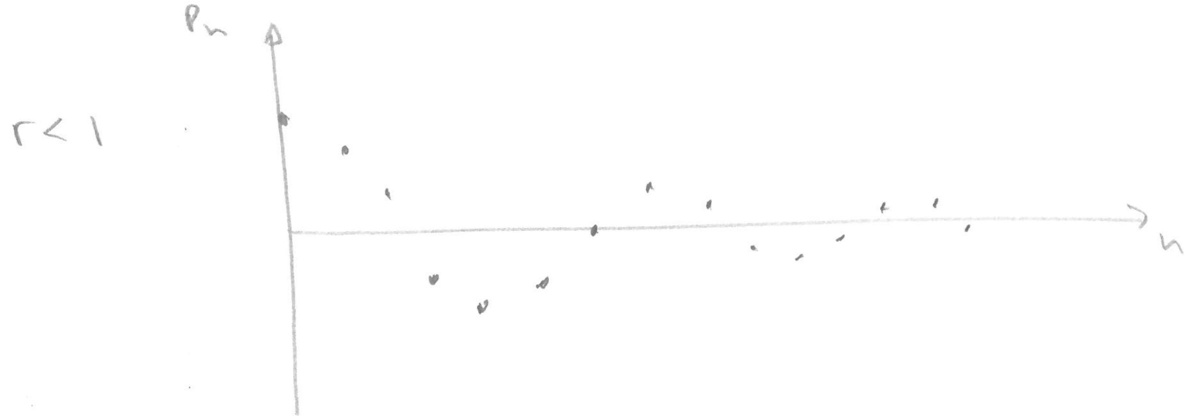
$$P_n = \frac{(A - iB)}{2} r^n e^{in\varphi} + \frac{(A + iB)}{2} r^n e^{-in\varphi}$$

or

$$P_n = A r^n \cos(n\varphi) + B r^n \sin(n\varphi) .$$

This is illustrated for $r > 1$ and $r < 1$:





The period of these oscillations can be estimated by setting

$$\bar{n}\varphi = 2\pi \longrightarrow \quad \bar{n} = \frac{2\pi}{\varphi}$$

which implies that after $\frac{2\pi}{\varphi}$ steps the sine and cossine return to their initial values.

Example : production of red blood cells

R_n = number of blood cells on day n

M_n = number of cells produced by marrow on day n

f = fraction of cells removed by spleen

γ = production constant (# of cells produced per cell removed)

$$R_{n+1} = (1-f)R_n + M_n$$

$$M_{n+1} = \gamma f R_n$$

(a) $$R_{n+1} = (1-f)R_n + \gamma f R_{n-1}$$

(b) $$\begin{pmatrix} R_{n+1} \\ M_{n+1} \end{pmatrix} = \begin{pmatrix} (1-f) & 1 \\ \gamma f & 0 \end{pmatrix} \begin{pmatrix} R_n \\ M_n \end{pmatrix}$$

Using (a) with $R_n = c\lambda^n$ leads to

$$\lambda^2 - (1-f)\lambda - \gamma f = 0$$

$$\lambda_\pm = \frac{1-f}{2} \pm \frac{1}{2}\sqrt{\Delta}$$

$$\Delta = (1-f)^2 + 4\gamma f > (1-f)^2$$

$$\Rightarrow \quad \begin{array}{l} \lambda_+ > 0 \\ \lambda_- < 0 \end{array} \quad \text{and} \quad |\lambda_+| > |\lambda_-|$$

$$R_n = c_1 \lambda_+^n + c_2 \lambda_-^n$$

For large n the behavior is dominated by λ_+.

To maintain a constant number of red blood cells we need to have $\lambda_+ \sim 1$:

$$1 = \frac{1-f}{2} + \frac{1}{2}\sqrt{\Delta} \rightarrow \sqrt{\Delta} = 1+f$$

or $$(1-f)^2 + 4\gamma f = (1+f)^2 \Rightarrow \boxed{\gamma = 1}$$

i.e., for each cell destroyed we need exactly one cell produced.

Exercise: In the case of annual plants, eqs (1) and (2), the plants thrive if the number of seeds produced per plant satisfies

$$f > \frac{1}{\alpha \sigma},$$

so that $r > 1$. If seeds from the previous year also contribute to the population, as in eqs. (5) and (8), show that this condition becomes

$$f > \frac{1}{\alpha\sigma + \alpha^2\sigma^2(1-\alpha)}$$

and less seeds are needed. Hint: impose $\lambda_+ > 1$.

Other examples

1) Insects. Each female has $\underline{f}$ offspring; a fraction $\underline{m}$ dies before maturity; a fraction $\underline{r}$ of the offspring are females

$P_n \equiv$ number of adult females in generation n

$$P_{n+1} = r(1-m) f P_n$$

2) Predators p_n and preys q_n

$$p_{n+1} = d\, p_n + a\, q_n$$
$$q_{n+1} = r\, q_n + b\, p_n$$

$d < 1$ (predators die if there are no preys)

$r > 1$ (prey thrive without predators)

Solve the problem assuming

$d = 1/2$, $r = 3/2$, $b = 3/2$, $a = 5/6$

write your solution in terms of q_0, p_0.

<u>solution</u>: $\lambda_+ = 5/2$ $\lambda_- = -1/2$

$$v_+ = \begin{pmatrix} 2/3 \\ 1 \end{pmatrix} \qquad v_- = \begin{pmatrix} -4/3 \\ 1 \end{pmatrix}$$

$$u_n = \begin{pmatrix} p_n \\ q_n \end{pmatrix}$$

$$u_n = \left(p_0 + q_0/3\right)\left(\frac{5}{2}\right)^n v_+ + \left(\frac{2q_0}{3} - p_0\right)\left(-\frac{1}{2}\right)^n v_-$$

or, explicitly,

$$p_n = \frac{2}{3}\left(p_0 + \frac{q_0}{3}\right)\left(\frac{5}{2}\right)^n - \frac{1}{3}\left(\frac{2q_0}{3} - p_0\right)\left(-\frac{1}{2}\right)^n$$

$$q_n = \left(p_0 + \frac{q_0}{3}\right)\left(\frac{5}{2}\right)^n + \left(\frac{2q_0}{3} - p_0\right)\left(-\frac{1}{2}\right)^n$$

The populations grow and, for $n \to \infty$, the ratio between preys and predators tend to

$$\lim_{n \to \infty} \frac{q_n}{p_n} = \frac{3}{2}$$