5 Alfred Lotka, Vito Volterra, and Population Cycles

> Dr. Umberto D'Ancona entertained me several times with statistics that he was compiling about fishing during the period of the war and in periods previous to that, asking me if it would be possible to provide an mathematical explanation of the results that were obtained regarding the percentage of the various species in these different periods... This may justify my having permitted myself to publish this research, which is simple from an analytical point of view but which was new to me.
>
> Vito Volterra
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> *Variazioni e fluttuazioni del numero d'individui in specie animali conviventi'* (*Variations and fluctuations in the number of individuals of cohabiting animal species*), 1927

Actually, the statistics that Volterra writes above can be summarized in the following way: During the war it was observed that certain predaceous species greatly increased in numbers, when fishing had almost ceased. Opposite to it, the number of prey species was observed to decline compare to that before the war. Discussing the problem with his future father-in-law, Umberto D'Ancona asked if there could be a mathematical explanation for these changes.

Here is how this problem was solved by Vito Volterra. Consider two interacting species: a prey and a predator. The relationship between them can be expressed verbally as follows: The change in the number of prey, N, per unit of time is equal to the natural increase of the prey per unit of time minus destruction of the prey by the predator per time unit. Similarly, the change in the number of predators, P, per unit of time is equal to the increase in the predator per time, as the result of ingestion of the prey minus death of the predators per unit of time. Let me translate this verbal description into mathematical formulas as follows:

$$\begin{aligned} \dot{N} &= F_1(N) - G_1(N,P), \\ \dot{P} &= G_2(N,P) - F_2(P), \end{aligned} \tag{1}$$

where the meaning of F_1, G_1, G_2, and F_2 should be clear from the description above. Let me choose the simplest possible mathematical expressions for these functions. To wit, consider a particular case of (1):

$$\begin{aligned} \dot{N} &= aN - bNP, \\ \dot{P} &= cNP - dP, \end{aligned} \tag{2}$$

where a, b, c, d are nonnegative parameters. The interaction of a prey and a predator is described here by the bilinear function $\propto NP$, therefore, system (2) is a system of two first order autonomous equations, which in general can be written as

$$\begin{aligned} \dot{N} &= f(N,P), \\ \dot{P} &= g(N,P), \end{aligned} \tag{3}$$

for some suitable $f, g \in \mathcal{C}^{(1)}$.

Math 484/684: Mathematical modeling of biological processes by Artem Novozhilov
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Before turning to an analysis of (2), I would like to mention that exactly the same system of equations was written by Alfred Lotka, somewhat earlier than Vito Volterra. He was studying some fictional problems from *chemical kinetics*. To illustrate his approach, consider first a hypothetical chemical reaction in which reagents A and B produce a new element C:

$$A + B \to C.$$

This literally says that one molecule of A combined with one molecule of B produce one molecule of C, please remember that I speak here about *molecules*, not masses.

The *law of mass action* in chemistry states that the speed of reaction is proportional to the concentrations of the reagents. This means that for the reaction about, if I denote with the square parenthesis the concentrations of the chemicals, I can write

$$\frac{\mathrm{d}[A]}{\mathrm{d}t} = -k[A][B],$$

where k is some constant of proportionality, which is usually written above the arrow: $\xrightarrow{k}$, and the sign "minus" is taken because the arrow points "from" A. The dimensions of k are determined by the form of reaction, and for my particular example this is $concentration \cdot time^{-1}$. The same equation is true for the reagent B:

$$\frac{\mathrm{d}[B]}{\mathrm{d}t} = -k[A][B].$$

Finally, for C I have

$$\frac{\mathrm{d}[C]}{\mathrm{d}t} = k[A][B].$$

Here is an example of a reversible reaction:

$$A + B \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} C,$$

for which, following exactly the same law of mass action, I get

$$\begin{aligned} \dot{[A]} &= -k_1[A][B] + k_{-1}[C], \\ \dot{[B]} &= -k_1[A][B] + k_{-1}[C], \\ \dot{[C]} &= k_1[A][B] - k_{-1}[C]. \end{aligned}$$

Now consider a bimolecular mechanism of the form

$$2A + B \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} C,$$

which means that it is necessary to have two molecules of A and one molecule of B to produce one molecule of C. The law of mass action is this case implies that

$$\dot{[A]} = -2k_1[A]^2[B] + 2k_{-1}[C],$$

note the coefficients and power 2 in the equation. The two other equations here are

$$
\begin{aligned}
\dot{[B]} &= -k_1[A]^2[B] + k_{-1}[C],\\
\dot{[C]} &= k_1[A]^2[B] - k_{-1}[C],
\end{aligned}
$$

note the absence of the constant 2 in the equation for B.

Alfred Lotka considered the following hypothetical reaction:

$$A + X \xrightarrow{k_1} 2X, \quad X + Y \xrightarrow{k_2} 2Y, \quad Y \xrightarrow{k_3} B,$$

where X and Y are reagents, and the supply of chemicals A and B is constant. This actually means that the system is open, and the exchange of matter with the environment should be present. I have, invoking the law of mass action, that

$$
\begin{aligned}
\dot{[X]} &= k_1[A][X] - k_2[X][Y],\\
\dot{[Y]} &= k_2[X][Y] - k_3[Y].
\end{aligned}
$$

Using the notation $N = [X]$, $P = [Y]$, $a = k_1[A]$, $b = c = k_2$, and $d = k_3$, I obtain exactly the equations of Vito Volterra (2). It is very convenient to keep in mind the chemical interpretation of equations (3) for accessing the validity of this and similar mathematical models.

This is actually why system (2) is famously known as *Lotka–Volterra model*, or *Lotka–Volterra equations*. Because of the ecological or chemical interpretations it is reasonable to set the initial conditions for this system as $N(0) = N_0 > 0$ and $P(0) = P_0 > 0$, which are positive numbers.

Lotka–Volterra system is a particular case of the general system (3), analysis of which is significantly more involved than the analysis of one autonomous equation, which we were studying in the previous lectures. However, particular form of (2) actually allows to obtain a number of results without any need of the general theory. Therefore, in this lecture I will analyze (2) by available means, but it should be clear that in more general cases I will need some additional mathematical machinery, which will be our focus for the next several lectures.

The key fact to note that if I have solutions to (2), then they define a curve $\big(N(t), P(t)\big)$ in (N, P) plane parameterized by the time t. Now, one of the basic results from Calculus states that the derivative $\frac{\mathrm{d}P}{\mathrm{d}N}$ of such a curve can be found as

$$\frac{\mathrm{d}P}{\mathrm{d}N} = \frac{\frac{\mathrm{d}P}{\mathrm{d}t}}{\frac{\mathrm{d}N}{\mathrm{d}t}} = \frac{\dot{P}}{\dot{N}}\,.$$

Therefore, two first order ODE in (2) can be replaced for one first order equation

$$\frac{\mathrm{d}P}{\mathrm{d}N} = \frac{P(cN-d)}{N(a-bP)}\,, \tag{4}$$

which is actually a separable equation, and can be integrated as

$$\frac{a-bP}{P}\,\mathrm{d}P = \frac{cN-d}{N}\,\mathrm{d}N \implies a\log P - bP = cN - d\log N + C,$$

where C is an arbitrary constant, which is determined by the initial conditions. Consider the function

$$H(N,P) := bP + cN - a\log P - d\log N.$$

I obtain that the solutions to (4) are given by the level sets of the function H:

$$H(N,P) = C.$$

I have

$$\frac{\partial H}{\partial N}(N,P) = c - \frac{d}{N}, \quad \frac{\partial H}{\partial P}(N,P) = -\frac{a}{P} + b,$$

which means that the only critical point of H is

$$(\hat{N},\hat{P}) = \left(\frac{d}{c}, \frac{a}{b}\right).$$

Also,

$$\frac{\partial^2 H}{\partial N^2}(N,P) = \frac{d}{N^2} > 0, \quad \frac{\partial^2 H}{\partial P^2}(N,P) = \frac{a}{P^2} > 0, \quad \frac{\partial H}{\partial N \partial P}(N,P) = 0,$$

which means that point $(\hat{N},\hat{P})$ is a strict minimum of the function H. Moreover, due to the fact that the second partial derivatives are negative, H is convex at any point, which implies that the only level sets of this function are closed curves that surround the point of minimum $(\hat{N},\hat{P})$ (see the figure, where the function H together with the level sets are shown).

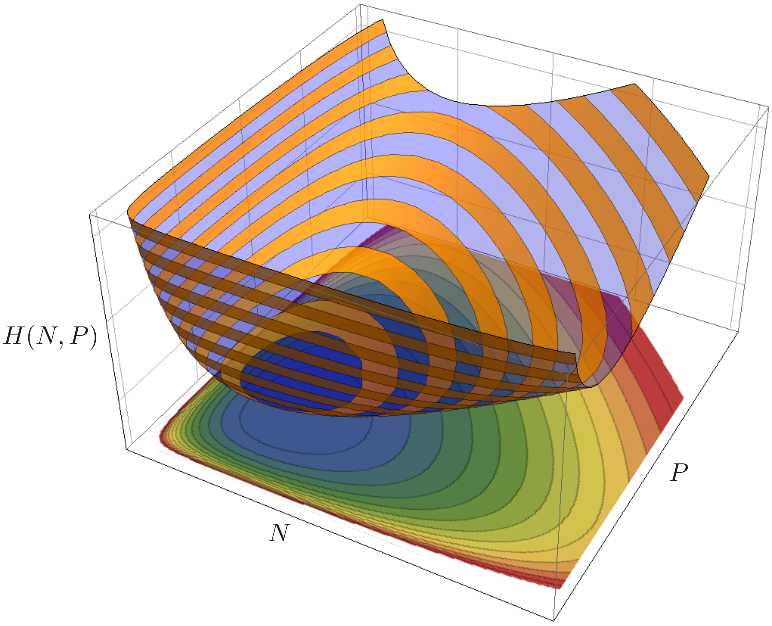

Figure 1: The surface $H(N,P)$ together with the level sets $H(N,P) = C$

So, what kind of information about the original function N and P I got, and what was lost? I now know that the curves are closed (apart from the point $(\hat{N},\hat{P})$, which is actually an *equilibrium point* of (2)), but I do not know the direction of movement along these curves when t increases. This is a kind

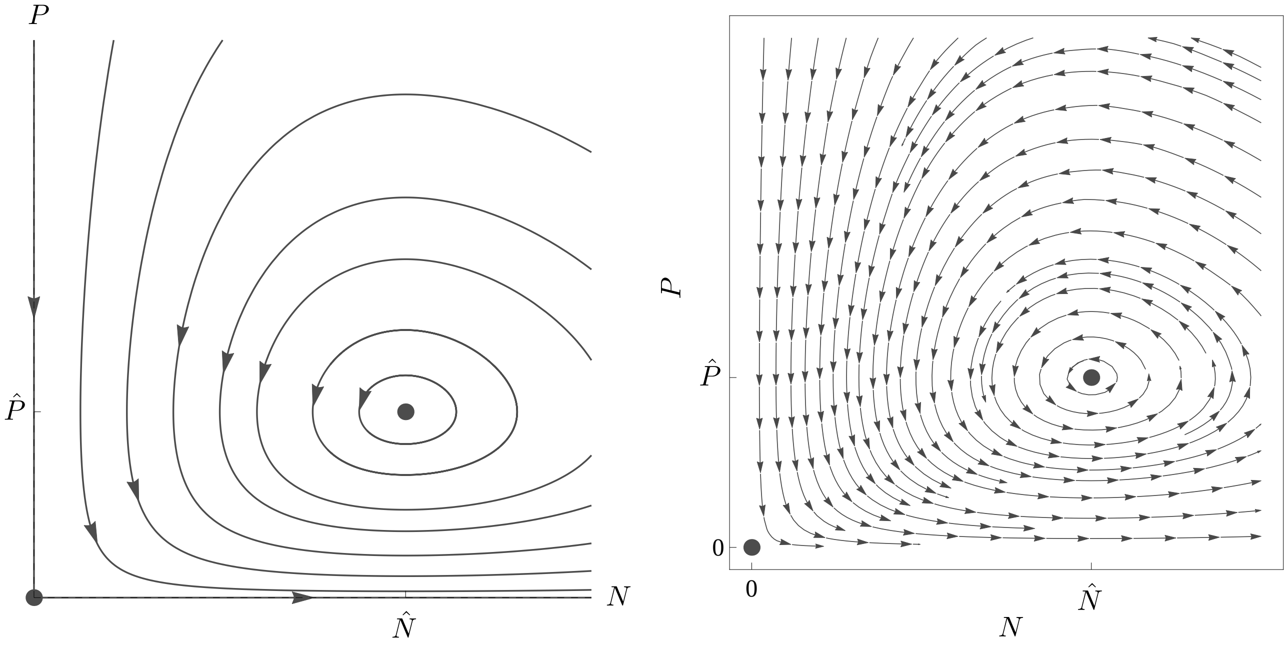

Figure 2: The level sets of H together with time directions specified by the vector field $(\dot{N}, \dot{P})$. The bold points denote the nontrivial equilibrium $(\hat{N}, \hat{P})$ and the origin, which is also an equilibrium. On the right I show the direction field (f, g)

of information I lost when jumping from (2) to (4). However, it is quite straightforward to figure out the directions looking at the vector field given by $f(N, P) = aN - bNP$, $g(N, P) = cNP - dP$ (recall that a *vector field* means that at each point of the plane I have a prescribed vector). Note, e.g., that along the N-axis the direction is positive, and along the P-axis the direction in negative (though this should be clear from just looking at (2)). Therefore, I can put the directions on the curves as shown in the figure.

Now to one of the main conclusions: Since the solutions are represented by the closed curves on the plane (N, P) and nowhere $(\dot{N}, \dot{P}) = 0$ except for the equilibrium, then there exists $T > 0$ such that $\big(N(t; N_0), P(t; P_0)\big) = \big(N(t + T; N_0), P(t + T; P_0)\big)$ and since the vector field $(\dot{N}, \dot{P})$ does not depend on t (it does not change with t), then I conclude that the solutions to (2) are periodic functions with period T (see their graphs in the figure below). Moreover, consider the average values of the prey and predator populations over one period:

$$\frac{1}{T}\int_0^T N(\xi)\,\mathrm{d}\xi, \quad \frac{1}{T}\int_0^T P(\xi)\,\mathrm{d}\xi.$$

To find them I notice that equations (2) can be written as

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}\log N &= a - bP,\\ \frac{\mathrm{d}}{\mathrm{d}t}\log P &= cN - d.\end{aligned}$$

I integrate these equalities over one period and find, since

$$\int_0^T \log N(\xi)\,\mathrm{d}\xi = \log N(T) - \log N(0) = 0,$$

that

$$\frac{1}{T}\int_0^T N(\xi)\,\mathrm{d}\xi = \frac{d}{c} = \hat{N}, \quad \frac{1}{T}\int_0^T P(\xi)\,\mathrm{d}\xi = \frac{a}{b} = \hat{P}.$$

That is, the average prey and predator populations do not depend on the initial conditions or the period of oscillations, and coincide with the coordinates of the nontrivial equilibrium.

Now assume that I start fishing for both prey and predator populations. It means that the growth rate of preys will decrease by some amount δ_1, and the death rate of the predators will increase by some amount δ_2, i.e., new parameters will be $a-\delta_1, d+\delta_2$, and new equilibrium point will be

$$\hat{N}_{\text{new}} = \frac{d+\delta_2}{c} > \hat{N}_{\text{old}}, \quad \hat{P}_{\text{new}} = \frac{a-\delta_1}{c} < \hat{P}_{\text{old}}.$$

In other words I proved

Proposition 1 (Volterra's principle)**.** *If in a system "prey–predator" both species are destroyed uniformly and proportionally to their total amounts, then the average prey population increases and the average predator population decreases.*

Another extremely important from ecological point of view conclusion of the analysis of the Lotka–Volterra model is that in the system "prey–predator" it is possible to observe *endogenous* oscillations, i.e., the oscillations that are inherent to the system and not caused by any external circumstances (see in the figure time dependent solutions to (2) obtained numerically).

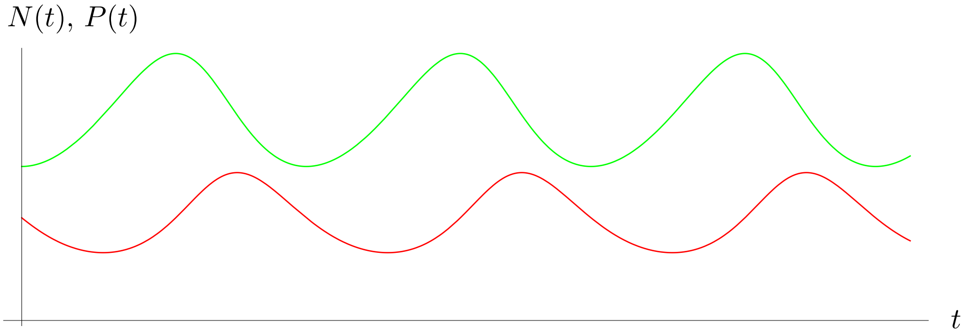

Figure 3: Solutions to (2) versus time t. The prey population is in green, and the predator population is in red. Note that the prey oscillations precede the predator oscillations

The fact that the populations of prey and predator oscillate was well known for quite a while. Here is an example of the historical record taken over 90 years for a population of lynxes versus a population of hares (actually, this is the data on sales of the hunting companies, but it is believed that the number of sales reflect the total populations): These data show that the wild populations do experience oscillations, and the Lotka–Volterra model provides an explanation for these oscillations such that we do not need to invoke other additional reasons such as climate, or something else.

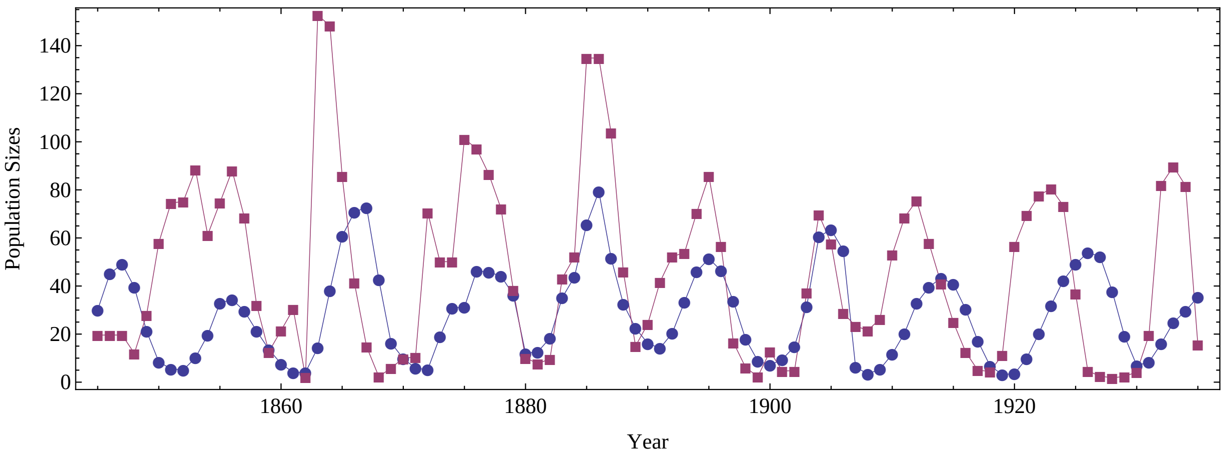

Figure 4: Historical data on lynxes and hares populations in Canada. Source: Odum, E. P., Odum, H. T., & Andrews, J. (1971). Fundamentals of ecology. Philadelphia: Saunders.

There are a lot of drawbacks of model (2) (can you think of any?), which I will discuss later. For now it should be clear that systems of autonomous differential equations are of great value in modeling interacting populations (or, for that matter, chemical reactions), and in the next several lectures I will present the elements of the mathematical analysis of such systems.