Lotka, Volterra and their model

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Abstract. The chemist and statistician Lotka, as well as the mathematician Volterra, studied the ecological problem of a predator population interacting with the prey one. They independently produced the equations that give the model of this problem and discovered that, under simple hypotheses, periodic fluctuations of the populations occur. We present their lives and the derivation of the equations which bear their names.

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1. SHORT BIOGRAPHIES OF LOTKA AND VOLTERRA

The equations which model the struggle for existence of two species (prey and predators) bear the name of two scientists: Lotka and Volterra. They lived in different countries, had distinct professional and life trajectories, but they are linked together by their interest and results in mathematical modeling.

Alfred James Lotka (March 2, 1880 – December 5, 1949) was born in Lwów, Austria-Hungary, formerly part of Poland, and died in New York. His parents, Jacques and Marie (Doebely) Lotka, were US nationals and he was educated internationally. He received a B. Sc. in 1901 at the University of Birmingham, England and he did graduate work in physical chemistry (1901-1902) at Leipzig University. He received an M. A. in Physics in 1909 at Cornell University, then a D. Sc. at Birmingham University after his work there from 1909 to 1912. He worked as an assistant chemist, assistant physicist, editor of the Scientific American Supplement and staff member at Johns Hopkins University. Since 1924 until his retirement in 1947 he was statistician for the Metropolitan Life Insurance Company, New York. He married Romola Beattie in 1935 and they had no children.

Lotka's work in mathematical demography began in 1907 and continued until 1939. In 1920 he published the paper [5], where he proved by his model that undamped, permanent oscillations arise in biological systems.

In 1926 he published a paper in the field of bibliometrics, studying the number of scientific publications in specific fields. His ideas eventually contributed to scientometrics – the scientific study of scientific publications.

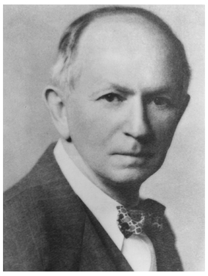

Fig. 1.1 – Alfred Lotka

Lotka published almost a hundred articles on various themes in chemistry, physics, epidemiology or biology, about half of them being devoted to population issues. He also wrote six books.

Vito Volterra (May 3, 1860 – October 11, 1940) was born in Ancona, then part of the Papal States, into a very poor Jewish family. He attended the University of Pisa, where he became professor of rational mechanics in 1883. His most famous work was done on integral equations. He began this study in 1884 and in 1896 he published papers on what is now called integral equations of Volterra type. The theory of functionals as a generalization of the idea of a function of several independent variables was developed by Volterra in a series of papers published since 1887 and was inspired by the problems of the calculus of variations. These papers initiated the modern theory of functional analysis, the name *functional* being introduced later by Hadamard. In 1892, he became professor of mechanics at the University of Turin and then, in 1900, professor of mathematical physics at the University of Rome La Sapienza. He married Virginia Almagià (1875-1968) in 1900 and they had six children, but only four lived to become adults. Their daughter Luisa married Umberto D'Ancona, a marine biologist who sparked Volterra's interest in the mathematical study of population dynamics in the Adriatic Sea.

Fig. 1.2 – Vito Volterra

Volterra had grown up during the final stages of the Risorgimento when the Papal States were finally annexed by Italy and, like his mentor Betti, he was an enthusiastic patriot, being named by the king Victor Emmanuel III as a senator of the Kingdom of Italy in 1905. On the outbreak of World War I he joined the Italian Army and worked on the development of airships. He originated the idea of using inert helium rather than flammable hydrogen and made use of his leadership abilities in organizing its manufacture.

After World War I, Volterra turned his attention to the application of his mathematical ideas to biology, principally reiterating and developing the work of Pierre François Verhulst. In the paper [7], he studied the ecological problem of a predator population interacting with the prey one. In the following years he published more results, intended to arrive at a mathematical theory of the struggle for existence.

Volterra was a plenary speaker in the International Congress of Mathematicians four times (1900, 1908, 1920, 1928).

In 1922, he joined the opposition to the Fascist regime of Benito Mussolini and in 1931 he was one of only 12 out of 1,250 professors who refused to take a mandatory oath of loyalty. As a result of his refusal to sign the oath of allegiance to the fascist government he was compelled to resign his university post and his membership of scientific academies, and, during the following years, he lived abroad, returning to Rome just before his death.

Vito Volterra was a friend of Romanian mathematicians. At the First Congress of Romanian Mathematicians (Cluj, May 9-12, 1929) he was a plenary speaker presenting *On the mathematical theory of the struggle for existence*. It is worth mentioning that one of the four sections of the congress was *The History and Didactics of Mathematics*, chaired by G. Bratu (1881-1941), G. Iuga (1871-1958) and O. Onicescu (1892-1983). He was one of the eleven members of the dissertation committee, lead by Tulio Levi-Civita, who participated at the thesis defence of Gh. Pic (1907-1984), in 1932 at Rome. Volterra was the head of the examining board of Gh. Vrânceanu (1900-1979), who defended his thesis in 1924 at Rome, with Levi-Civita as supervisor. He also expressed his consideration for the Ph. D. Thesis of Gr. C. Moisil (1906-1973), defended at Bucharest and published in the same year 1929 at Gauthier-Villars, Paris.

The Accademia Nazionale dei Lincei edited five volumes of about 3000 pages ([6]), containing most of Volterra's mathematical papers, notes and memoirs (but not his books). The first paper was published in 1881, before the author was twenty-one, and the last one in 1939-1940 when Volterra was nearly eighty.

The work of Lotka and Volterra overlapped in the discussion of predator-prey interaction ([4], [1]). The problem was discussed by Lotka in 1920 and by Volterra in 1926, their conclusion being the same, that the interaction of the two species would give rise to periodic oscillation in their populations. Volterra acknowledged Lotka's priority, but he mentioned the differences in their papers. They even exchanged some respectful letters. In the case of the predator-prey interaction, the priority of Lotka was firmly established, and the equations with periodic solutions are called Lotka-Volterra equations. Volterra produced more general equations, for more than two species and considering also their interactions in the past. For worked examples of such equations see, for example, [3].

2. SIMPLE POPULATION MODELS

The simplest mathematical model of population growth assumes that the rate of increase of population is proportional to the size of population at any time. Let us denote by $P(t)$ the population at the time t and by k a positive constant. Then

$$\frac{\mathrm{d}P}{\mathrm{d}t} = kP, \tag{1}$$

which gives by integration

$$P(t) = P_0 \exp(kt),$$

where P_0 denotes the population at the time $t = 0$. This law is called the Malthusian growth model and predicts an exponential growth in the population with time. It describes pretty well what happens for certain bacteria or cultures of cells for a short time.

A more realistic model is

$$\frac{\mathrm{d}P}{\mathrm{d}t} = (B - D)\,P, \tag{2}$$

where $B(t)$ and $D(t)$ denote the birth rate and death rate per individual, respectively. The exponential law corresponds to the case $B(t) = k$ and $D(t) = 0$. Let us assume that the birth rate per individual remain constant, while the death rate per individual is directly proportional to the existing population. We obtain

$$\frac{\mathrm{d}P}{\mathrm{d}t} = (B_0 - D_0 P)\,P,$$

where B_0 and D_0 are positive constant. We can write the equation in a simpler way

$$\frac{\mathrm{d}P}{\mathrm{d}t} = r\left(1 - \frac{P}{C}\right)P, \tag{3}$$

where $r = B_0$ and $C = B_0/D_0$. Its solution is

$$P(t) = \frac{CP_0}{P_0 + (C - P_0)\exp(-rt)},$$

where $P_0 = P(0)$.

3. LOTKA-VOLTERRA EQUATIONS

The first and the simplest Lotka–Volterra model (or *predator-prey*) involves two species. One of them (the predators) feeds on the other species (the prey), which in turn feeds on some third food available around. A standard example is a population of foxes and rabbits in a woodland. The assumptions about the environment and evolution of the predator and prey populations are:

- The prey population have an unlimited food supply at all times.
- In the absence of predators, the prey population x would grow proportionally to its size, $\mathrm{d}\,x/\,\mathrm{d}\,t = \alpha x$, $\alpha > 0$. The coefficient α was named by Volterra the *coefficient of auto-increase*. (This Malthus-type equation gives by integration the geometrical law of increase $x(t) = x_0 \exp(\alpha t)$.)
- In the absence of prey, the predator population y would decline proportionally to its size, $\mathrm{d}\,y/\,\mathrm{d}\,t = -\gamma y$, $\gamma > 0$. (By integration we get in this case $y(t) = y_0 \exp(-\gamma t)$, meaning the final extinction of this population.)
- When both predator and prey are present, a decline in the prey population and a growth in the predator population will occur, each at a rate proportional to the frequency of encounters between individuals of the two species ($-\beta xy$ for prey, δxy for predators, $\beta, \delta > 0$).

When the interaction rate is adjoined to the natural rate, the prey equation becomes

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \alpha x - \beta xy$$

and may be interpreted as: the change in the prey's numbers is given by its own growth minus the rate at which it is preyed upon. Similarly, the predator equation becomes

$$\frac{\mathrm{d}y}{\mathrm{d}t} = -\gamma y + \delta xy,$$

where δxy represents the growth of the predator population. Hence the equation expresses the change in the predator population as growth determined by the food supply, minus natural death.

The predator-prey equations ([5], [7]) are

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \alpha x - \beta xy \qquad \frac{\mathrm{d}y}{\mathrm{d}t} = -\gamma y + \delta xy, \tag{4}$$

with $\alpha, \beta, \gamma, \delta > 0$. Equations (4) allow for the equilibrium point with nonzero components $P(\gamma/\delta, \alpha/\beta)$.

Equations (4) cannot be solved analytically, but we can plot the solutions using Maple. For $\alpha = 2$, $\beta = 1.1$, $\gamma = 1$ and $\delta = 0.9$ we get the equations

$$\frac{\mathrm{d}x}{\mathrm{d}t} = 2x - 1.1xy \qquad \frac{\mathrm{d}y}{\mathrm{d}t} = -y + 0.9xy, \tag{5}$$

and we choose the initial conditions $x(0) = 1$, $y(0) = 0.5$ (the predator population is half of the prey one). In this case the equilibrium point is $P(10/9, 20/11)$. In Fig. 3.3 we use blue for the prey population and red for the predator one.

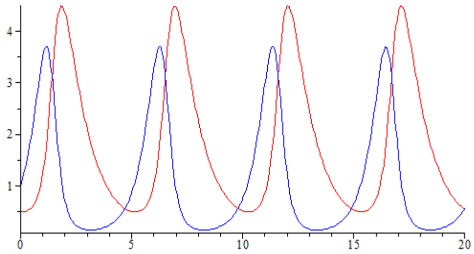

Fig. 3.3 – Prey (blue) and predators (red) for (5)

In Fig. 3.4 we plot the trajectory and note again the periodicity of the phenomenon.

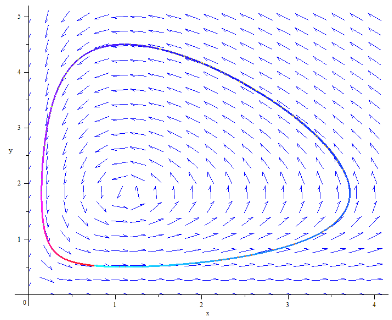

Fig. 3.4 – The trajectory prey-predators for (5)

Equations (4) were validated by Gause ([2]) whose experiments (for example on *Paramecium bursaria* - predator and the yeast *Schizosaccharomyses pombe* - prey) established that periodic fluctuations of the Lotka-Volterra type actually occur under controlled experimental conditions. Volterra has proved that the periodicity is not a consequence of external circumstances, as seasons or human interference, but a consequence of the species interaction itself.

In [8], Volterra developed a general theory of n species. For $n = 2$, equations (4) are modified to

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= \alpha x - \lambda x^2 - \beta xy \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= -\gamma y - \kappa y^2 + \delta xy, \end{aligned} \tag{6}$$

where $\alpha, \beta, \gamma, \delta, \lambda, \kappa > 0$. In equations (6) the fluctuations of x and y are damped, which means that their amplitude diminish and in time they tend to the equilibrium state.

As an example, we consider, beside the parameters in (5), $\lambda = 0.1$ and $\kappa = 0.1$ and the same initial conditions $x(0) = 1$, $y(0) = 0.5$. The equations

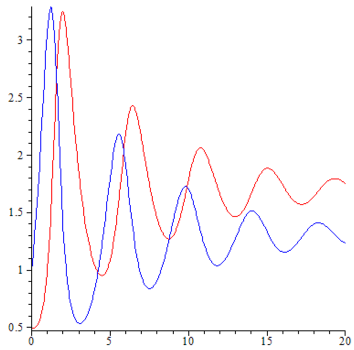

Fig. 3.5 – Prey (blue) and predators (red) for (7)

become

$$(7)\qquad \begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= 2x - 0.1x^2 - 1.1xy \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= -y - 0.1y^2 + 0.9xy. \end{aligned}$$

In this case the variation of prey and predators is no more periodic, as it can be seen in Fig. 3.5.

The equilibrium point $(1.3, 1.7)$ is approached when the time increases, as it is shown in Fig. 3.6.

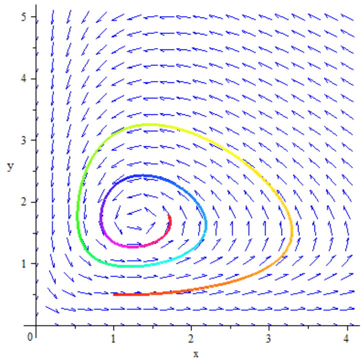

Fig. 3.6 – The trajectory prey-predators for (7)

Volterra continued the study considering more realistic hypotheses. For example, for a single population (as the prey one), the simple equation $\mathrm{d}\,x/\,\mathrm{d}\,t = \alpha x$, $\alpha > 0$ was improved as

$$(8)\qquad \frac{\mathrm{d}x}{\mathrm{d}t} = \left(\alpha - \lambda x + \mu \sin \nu t - \int_0^t f(t-\tau)x(\tau)\,\mathrm{d}\tau\right) x + \iota,$$

where the coefficient of auto-increase α is corrected with the effect of competition within the species $-\lambda x$, with a periodic term $\mu \sin \nu t$ due to the seasonal variations of the environment and an integral representing some delayed effects as the intoxication of the environment with waste products; at last ι is added to indicate immigration at a constant rate.

Volterra improved also the model in equations (6), and obtained one which consists in two integro-differential equations. In [9], he considered the reasoning that leads to the first equation in (6) not satisfactory, because the nourishment received by individuals of the second species in a time interval is not what produces the increase in species in the same time interval; in fact the nourishment received in the preceding time affects the increasing of the species. The same change is made in the second equation in (6), and the better version has the form

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= \left(\alpha - \lambda x - \int_{-\infty}^{t} F_1(t-\tau) y(\tau)\,\mathrm{d}\tau\right) x \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= \left(-\gamma - \kappa y + \int_{-\infty}^{t} F_2(t-\tau) x(\tau)\,\mathrm{d}\tau\right) y. \end{aligned} \tag{9}$$

The functions F_1 and F_2 are nonnegative continuous delay kernels defined and integrable on $[0, \infty)$, representing the contribution of the predation occurred in the past to changing the rate of the prey and predators, respectively.

The extension of the study of delayed effects to n species was done in the last paper [10] dedicated by Volterra to this subject. There he considers n given populations of the various species N_1, N_2, ..., N_n, with ε_1, ε_2, ..., ε_n the coefficients of auto-increase. The coefficient A_{sr} measures that unitary action (per individual) which the species s exercises upon the species r, while A_{rs} denotes the inverse action that species r exercises upon the species s; and as it is supposed that these actions are such that, while one species injures the other, the latter profits from the first (for example, one species devours the other) the coefficients A_{sr}, A_{rs} may be assumed to have opposite signs. They will not however be of equal absolute value. The equations in this case are

$$\frac{\mathrm{d}N_r}{\mathrm{d}t} = \left(\varepsilon_r + \sum_{s=1}^{n} A_{sr} N_s\right) N_r, \quad r = 1, ..., n. \tag{10}$$

We end by presenting the case in [10] where historical interaction is considered too. Volterra denotes a (unitary) action by $F_{sr}(t-\tau)$ when it is exercised by the species s in the infinitesimal interval of time $(\tau, \tau + \mathrm{d}\tau)$ and is manifested on the species r at time t. If the historical actions may be prolonged indefinitely in the past, the equations read

$$\frac{\mathrm{d}N_r}{\mathrm{d}t} = \left(\varepsilon_r + \sum_{s=1}^{n} \left(A_{sr} N_s(t) + \int_{-\infty}^{t} F_{sr}(t-\tau) N_s(\tau)\,\mathrm{d}\tau\right)\right) N_r(t), \quad r = 1, ..., n,$$

otherwise the limit below in the integral can be chosen to be finite.

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