

Carissimo Papà: A Great Fish Story

The Biology of Numbers: The Correspondence of Vito Volterra on Mathematical Biology. *Giorgio Israel and Ana Millán Gasca, editors, Birkhäuser Verlag, Boston, Basel, and Berlin, 2002, 414 pages, \$114.*

We first meet Volterra on the front cover of the book under review. There he is: a magnificent, full-bearded and moustached figure in full academic regalia, shown perhaps in his mid-fifties. Vito Volterra, 1860–1940, professor at the University of Rome, president of the renowned Accademia dei Lincei, member of the Royal Society, recipient of other honors too numerous to mention, scion of an Italian Jewish family whose genealogy has been traced back to the early 1400s. A crater on the Moon has been named after him. (You can check this out in *Who's Who on the Moon!*)

In 1881, at the University of Pisa, Volterra constructed a real valued function with a bounded derivative that is not Riemann integrable. (Cf. the Weierstrass continuous,

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By Philip J. Davis

non-differentiable function of 1872, and other real-variable pathologies that Poincaré railed against.) In 1882, he received a Doctor of Physics degree with a thesis in hydrodynamics. His teachers were Ulisse Dini (Dini's condition: in the theory of Fourier series) and

Enrico Betti (Betti numbers: in combinatorial topology). Over the years, first in Pisa, then in Turin, and later in Rome, Volterra worked on the general theory of integral and integro-functional equations, and I suppose that most mathematicians will recognize his name in that connection. Volterra was in the Italian air force during World War I and made contributions to the theory of air ballistics.

Volterra was also one of the first mathematicians to make tentative stabs at what would become, in the hands of Jacques Hadamard, Hans Hahn, Maurice Fréchet, Stefan Banach, and many others, the field now known as functional analysis. In fact, when I first came across his name, as a graduate student, it was in connection with the theory of analytic functionals of Luigi Fantappiè (1905–1956).

In 1931 Volterra fell afoul of the fascist regime in Italy. One of 13 state employees who refused to take an oath of loyalty to the regime, Volterra was stripped of his position. He was rehabilitated to some extent by Pius XI (Achille Ratti), a rather liberal fellow who, despite ever more stringent racial laws, appointed Volterra in 1936 to the Pontificia Accademia della Scienze.

As far as I have been able to discover, no one has written an in-depth biography of Volterra. I know that one of his sons, Edoardo Volterra (1904–1987), was a distinguished jurist and that a second son, Enrico Volterra (1905–1973), taught for many years at the University of Texas at Austin. Enrico specialized in the theory of vibrations, strength of materials, the mathematical theory of elasticity, and experimental stress analysis, producing almost a hundred papers in this field. He communicated on these topics with my late colleague Harry Kolsky, who told me that Enrico, although distinguished in his own right, suffered a bit from being in the shadow of his father.

And now to mathematical biology. Readers may have heard the old joke that mathematical talent passes from father to son-in-law. In the case of Volterra and his son-in-law, Umberto d'Ancona (1896–1964), the reverse is sort of true. D'Ancona talked to his father-in-law and got him interested in the fate of fish in the Adriatic. Here are the words of Ana Millán Gasca (co-editor, with her husband Giorgio Israel, of the volume under review), who has supplied the book under review with a 54-page introduction to the history of the early (1920s and 30s) development of population dynamics:

"D'Ancona's field of interest was extremely vast and ranged from physiology, to embryology, hydrobiology, oceanography and evolutionary theory. . . . The results of his statistical studies aroused Volterra's interest in these topics and provided a starting point for the formulation of his mathematical theories on the 'struggle for life.' . . .

"He [Volterra] tried to explain the increase in populations of Selchians [a predatory order of fish] and other predators in the Adriatic during WW I as compared with preceding and following periods. . . . There was an almost complete fishing standstill during the War."

This arousal of interest led, in 1931, to the publication of Volterra's *Leçons sur la Théorie Mathématique de la Lutte pour la Vie* (*Lectures on the Mathematical Theory of the Struggle for Life*, Marcel Brelot, editor). His preoccupation with fish is the subject of the letters in French, English, and Italian, to and from 19 different scientists, included in this volume. Each set of letters is prefaced by a short and informative scientific biography of the correspondent. There is also a short biography of Volterra himself.

I knew just a bit about five of the correspondents and had read two of their books (those named here): Marcel Brelot (1903–1987); potential



Vito Volterra, in full academic regalia. From *The Biology of Numbers: The Correspondence of Vito Volterra on Mathematical Biology*.

theory. Joseph Larmor (1857–1942), Cambridge University; electromagnetics, optics, analytical dynamics. Alfred J. Lotka (1880–1949), statistician for the Metropolitan Life Insurance Company. Raymond Pearl (1879–1940), biomathematician and statistician, Johns Hopkins Medical School; author of *The Biology of Population Growth*. D’Arcy W. Thompson (1860–1948), morphologist, University of St. Andrews; author of the classic *On Growth and Form*.

The 94 letters to and from Volterra’s son-in-law Umberto d’Ancona, about whom I knew nothing, take pride of place in this book. The d’Ancona letters are concerned mostly with the passage from the zoological facts to the formation of appropriate mathematical models.

A clip from one of them, kindly translated for me by Professor Franco Preparata (who years ago used to play bocce with Enrico!) gives a bit of the flavor of this correspondence:

Sienna, 25-XI-1929

Carissimo Papà:

• • •

I also feel that to leave in the word “heredity” will not greatly bother the biologists. It will be appropriate, however, to add a note explaining what you mean by “heredity” and saying that you use this word in a sense quite different from the conventional one.

• • •

Among the three titles you propose [for your book] I believe that the second one, *Théorie mathématique de la lutte pour la vie*, is the best. The first too could go, *Principes mathématiques de la lutte pour la vie*. On the other hand, I don’t like the third, *Principes mathématiques de biologie*. The part of biology that your work refers to is ecology or ethology, that is, the study of customs and of the environment. This being the case, it would perhaps be preferable even to mention to which part of ecology you refer, and specifically the study of biological associations or biocenosis of the relations among species.

In the case in which, of three species, the 1st simultaneously eats the 2nd and the 3rd, I don’t think that one may separately consider the 1st and the 2nd, and then the 1st and the 3rd. The more the 1st species eats of the 2nd, the less it eats of the 3rd, and vice versa. On the other hand, the nutritional values of the 2nd and the 3rd species will be different. But I believe that one could analyze [lit.: calculate] this case by taking the sum of the numbers of individuals of species 2 and 3, each multiplied by a coefficient. Don’t you think?

What you mention of plant parasites seems to agree fully with your theory. Indeed, the plant parasite *Icerya* (the one that one finds in Ariccia [a town near Rome] on the mimosa trees) has not been destroyed by *Novius*, although the presence of the latter keeps the former in proportions that are not greatly damaging.

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In what way should one carry out this analysis using a series of statistical data over some number of years? This I believe should be the first practical item to solve.

I am glad to hear that you are well and you like it there. Mamma [Umberto’s mother-in-law] will join you in a few days. Today we were down there for lunch. We are all well.

Tanti saluti affettuosi:
Umberto

Reading the letters (assuming you can get through the French and Italian) gives an idea of Volterra’s extensive scientific contacts. More importantly, it gives an idea of the birth pangs of a relatively new and problematic application of mathematics. You will get whiffs of the struggles between the deterministic and the probabilistic approaches; between continuous and discrete models; among models in either category; between holistic (empirical and experimental) and mathematical approaches; between closed-form solutions and numerical solutions; between the qualitative and the quantitative. You will also read about the struggle between the realists and the idealists as regards what the goals of the inquiry should be. Gasca’s introduction fleshes out these various antagonisms.

While it is true that Volterra stepped in where most mathematicians of the day feared to tread—one section of Gasca’s introduction is titled “Volterra’s Biomathematics, or the Daring of a Conservative”—the application of mathematics to living organisms had a history going back more than a century. Morbidity databases were compiled in the 1600s. In 1798, Thomas Malthus published *An Essay on the Principle of Population*. Then there was Adolphe Quetelet, who in 1835 titled his work *A Treatise on Man, and the Development of His Faculties*. This was a lengthy account of the influence of probability on human affairs, and here the normal curve rears its (currently contentious) head. In 1846, Pierre Verhulst produced a nonlinear equation for population growth embodying the assumption that growth is proportional to population size but is inhibited proportionally by its difference from a supposed upper limit (the “logistic equation,” the normal form of which is $dx/dt = rx(1 - x)$). Later came Francis Galton, Karl Pearson, et al. Think also of Lewis Fry Richardson, a Quaker and, paradoxically, the father of mathematical war gaming, who in his 1919 *The Mathematical Psychology of War* came up with a set of linear differential equations to describe the arms race between nations. Surely an instance of “la lutte pour la vie.”

Stimulated by his son-in-law, Volterra took a flyer with considerable gusto into a new (for him) field. He didn’t bother to inform himself about its current status; even as he was modeling the struggle for life, he was scooped by Lotka, and this led to some professional rancor between the two men. Their result, now known as the Lotka–Volterra nonlinear model (Lotka 1925, Volterra 1926), reads as follows:

$$\begin{aligned} dx/dt &= Ax - Bxy \\ dy/dt &= Cy + Dxy. \end{aligned}$$

It makes frequent appearances in elementary courses in mathematical modeling.

Do these equations reproduce accurately what goes on out there in predator–prey situations? Here is what ecologist Peter Turchin told me:

“Lotka–Volterra is not a very realistic model of real resource–consumer systems. To my knowledge there has been no successful application of it to any field or laboratory population system. But this is all beside the point because the Lotka–Volterra model seems to get at some extremely basic features of trophic interactions [i.e., relating to nourishment]: their inherent proneness to oscillations. In fact the Lotka–Volterra model predicts a rather special kind of oscillation . . . in which the amplitude of oscillation depends on initial conditions.”

Still, there is no doubt but that Volterra’s great mathematical prestige lent legitimacy to the whole program of population dynamics, and he and his predecessors left a rich legacy. These equations were merely the starting point for a new generation of biomathematicians who suggested and worked with a variety of modifications. There is, to name just one example, the Rosenzweig–MacArthur model, which has certain rational functions of x and y on its right-hand side. Population dynamicists now seem to have more competing models than Detroit auto makers!

Since Gasca’s introduction does not really take us into the computer age, I wanted to update my own knowledge. As all of my readers surely know, the field of dynamical systems—and in particular population dynamics—embraces people, animals, cells, molecules. It extends to molecular biology, genetics, epidemiology, and ecology.

Today, population dynamics is big business, engaging all sorts of mathematicians, statisticians, biologists, economists, technologists, sociologists, whose work feeds into that of strategists, decision makers, management executives, politicians, philosophers, and cranks. Turchin has been applying mathematical models to the rise and fall of nations. I have yet to direct my reading to a general discussion of problems attendant on the techniques used in counting numbers of fish, wolves, larch budmoths, people, and so forth. After all, the U.S. Census figures released and applied must now conform to Supreme Court rulings. How sensitive to ball-park estimates of the parameters are the conclusions derived from models?

Questions are often raised about which of the population models have quantitative or predictive value, which lead to policy decisions, which have merely heuristic value, which are useful in setting goals for empirical studies, and which are simply mumbo-math. A recent and still mysterious phenomenon of interest to coastal New Englanders is that lobsters are now found in abundance in the waters of Maine, but are very scarce south of Cape Cod (*The New York Times*, August 7, 2005). As I read this I wondered whether the spirit of Volterra was hovering over these waters. Professor Stan Cobb, a lobster biologist at the University of Rhode Island, answered my question:

“There has been quite a bit of modelling of the population dynamics of lobsters. The current minimum legal size and the definition of over-fishing of lobsters are based on a so-called yield-per-recruit model. One of the issues for many of the models is that they require knowledge of the distribution of ages in the population, an as yet impossible task in arthropods, which have no key to age such as tree rings or otolith ring, requiring the use of stage-structured instead of age-structured models. Newer approaches include matrix projection models and individual-based models. . . . The Lotka–Volterra equation has dominated ecological thinking for many years.”

Adoption or modification of a model-based public policy of any sort, of course, can put current and future livelihoods at risk.



In reading about the current status of population dynamics, I’ve found the following three books useful:

David Tilman and Peter Kareiva, editors, *Spatial Ecology*, Princeton University Press, Princeton, New Jersey, 1997.

William W. Murdoch, Cheryl J. Briggs, and Roger M. Nisbet, *Consumer–Resource Dynamics*, Princeton University Press, Princeton, New Jersey, 2003.

Peter Turchin, *Complex Population Dynamics*, Princeton University Press, Princeton, New Jersey, 2003.

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