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History of Mathematics: Mathematical Ecology

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The German publishing house Springer-Verlag puts out a continuing series of volumes on biomathematics, the application of mathematics in a biological context of one kind or another. Volume 22 of this series, published in 1978, was entitled *The Golden Age of Theoretical Ecology: 1923-1940.* It is a collection of papers from this era, reprinted with comments by the editors, F. M. Scudo and J. R. Ziegler. The dates themselves are somewhat arbitrary; they depend on the choice of the papers they decided to include. Those papers are the work of five authors: A. N. Kolmogorov, V. A. Kostitzin, A. J. Lotka, F. R. Sharpe and Vito Volterra.

Some years later, the rival publishing house Birkhser Verlag published a related volume, *The Biology of Numbers*, a collection of Vito Volterra's correspondence on such matters, edited by G. Israel and A. M. Gasca. I was fortunate to be asked to write up the entry on this work for the journal *Mathematical Reviews*, and I now treasure the copy I received in consequence. The first chapter of this book is a splendid recounting of much of the material I will cover in this paper but, because its focus is rather different, I include material Israel and Gasca leave out, and vice versa.

Mathematical approaches to some aspects of biology are not really new, although they have multiplied enormously in recent years. But quite early last century, the mathematical expression and analysis of Mendel's laws of inheritance greatly aided their understanding. I wrote on this in my History column in *Function* in June 2004. Earlier (April 1987) I had written on the work of Sir Ronald Ross on the deadly disease malaria. For this work, Ross was awarded a Nobel Prize in 1902. In the course of his investigations, he derived a pair of equations (the Ross malaria equations) that enabled the mathematical analysis of the spread of this disease. That analysis was carried out in great detail by the US mathematician A. J. Lotka. It was published by the *American Journal of Hygiene* as a special supplement dated 1923. (A section of this work was co-authored with Sharpe.) It is this event that provides Scudo and Ziegler with their first date. (Their second is the date of Volterra's death.) Lotka and Sharpe's work would not usually be described as ecological, but rather epidemiological. However, it *is* concerned to discuss the interaction between two species, humans and mosquitoes, and so on this basis can properly claim the ecological mantle.

The mathematical model Ross developed comprised two simultaneous differential equations, that is equations involving two unknown functions and their derivatives. All the models to be discussed in this present paper are of this general form, although the number of equations is sometimes greater than two. (If n species interact, then there

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are n equations.) This foray into interspecific interaction must have whetted Lotkas appetite for such analysis, for in 1925 he published a book which dealt in part with this and similar matters, and in 1932 he considered in detail the situation in which two separate species compete for a common resource. Researches along these same lines were being conducted, independently but at the same time, by the very great Italian mathematician Vito Volterra (1860-1940). Volterra was a prolific mathematician, active in many fields. I wrote of him in my *Function* column for August 2003. His interest in biomathematics has been dated as far back as 1901, but his first sustained effort was a very lengthy (over 170 pages!) paper appearing in 1927. In this he considered two different types of interaction between two species. The first was the same as that analysed by Lotka. The situation with two competing species results in four different cases:

1. Species 1 necessarily becomes extinct.
2. Species 2 necessarily becomes extinct.
3. One of the species does become extinct, but which one it is depends on the initial numbers.
4. The two species continue to co-exist.

It is still a matter of some debate whether this fourth possibility can actually occur in nature. The equations in their most general form allow it, however, some ecologists espouse to a general law (the Competitive Exclusion Principle) which it seems to violate. The second (and by far the longer) section of Volterra's paper discussed the situation where one species (the predator) feeds on the other (the prey). In this case, suppose that x is the number of prey individuals and y the number of predators. Both these quantities are functions of t, the time, and Volterra was able to demonstrate that both were exactly periodic functions of t, and that if one plotted one against the other, the plots were closed curves. Volterra's model of the predator-prey interaction has been much criticized on precisely this ground. We can best see why by comparing it with a more familiar case. The simple pendulum can be modelled by equations that, when solved, lead to a position x and a velocity v that are both exactly periodic in t. If we plot x against v, then we see a closed curve, an ellipse. (If we choose the units of measurement carefully, we can make this ellipse into a circle, physicists call it the reference circle.) So there is a strong analogy between the two models. But we are all well aware that the simple pendulum is not really as simple as it seems. As time goes by it swings through ever smaller arcs and eventually stops completely. This is the result of friction, which is always present. The simple analysis of pendulum motion ignores this and so, to that extent, is unrealistic. It was Lotka who demonstrated that Volterra's exactly periodic solutions no longer applied if one of the constants it involves is found (in real life) to vary, even ever so slightly. Both the simple pendulum and the Volterra predator-prey equations are said to be structurally unstable, because these small alterations (inclusion of friction, tiny variation in a constant) radically change the long-term behavior of the system being analyzed. There is a school of thought that regards structural instability as a defect in a mathematical model. However, this is not the end of the matter. The simple pendulum may be analyzed in terms of the frictionless equations just as long as we do not press matters too far. (A grandfather clock works fine just as long as we remember to wind it, and so counteract the effect of friction!) Essentially this was Volterra's answer to his critics. He saw his predator-prey equations as giving an account of real-life ecology, but one that was an excellent approximation rather than the full story. There is a third possible way in which two species can interact. The cases outlined so far deal with either the case in which neither species benefits from the presence of the other, or the case in which one species does benefit from the presence of the other. The third possibility, that was omitted, was the case in which both species benefit from the presence of the other. This third type of interaction goes by a number of names. In modern usage, the most common is *mutualism*, but other words have been used. In particular symbiosis a term now used to imply close association. (Lichens are symbiotic associations between algae and fungi. The relations between us humans and our domestic animals are nowadays more likely to be described as mutualist, rather than symbiotic.) This case was studied most intensively by Kostitzin, who devoted a large part of a 1934 book to it. What particularly interested Kostitzin was the evolutionary pressure for mutualism to develop from predation.

The same equations that describe predator-prey interaction can also be used to analyze the relation between host and parasite, with the host as the prey and the parasite as the predator. But it is not really in the parasite's best interest to kill its host. Thus there is an evolutionary pressure on the parasite to adapt towards more benign, nonlethal (and even further to beneficial) forms. It is widely believed that the mitochondria (those sub-cellular organelles that provide power to animals and are necessary to their survival) began their life as parasitic creatures. Similarly, humans today no longer hunt cattle or sheep, although we presume that our remote ancestors *did* hunt theirs! Thus, by the middle of the 1930s, models had been proposed and analyzed for all the possible interactions between two species.

An obvious line for further research was the extension to three or more species. Perhaps the most enduring legacy of this work is the theorem saying that if one species predates two or more prey species, then all but one of these prey species will be driven to extinction. (This may be viewed as an example of the Competitive Exclusion Principle.) We see this effect in practice. Were it not for rigid protocols and strict enforcement, all whales other than Minkes would by now have been wiped out. This result was discovered by Volterra in the course of his collaboration with a fisheries biologist, Umberto D'Ancona. D'Ancona was particularly interested in the maintenance of fish stock in the Adriatic Sea. There was some evidence in this study for the oscillations predicted by Volterra's two-species predator-prey model, but recent analysis casts doubt on this interpretation. (The same is true of other claimed verifications, notably the fluctuating numbers of lynx and hare pelts listed in the records of the Hudsons Bay Company.)

Volterra published extensively on interspecific interaction. He developed a model applying to n species, and examined conservative cases of this. The conditions under which these exist are so restrictive that biologists treat them with great skepticism.

(In particular, they reject a theorem claiming that the number of species in a climax (i.e. mature) ecosystem is necessarily even!) Even Volterra had qualms about this one; however, he was more interested in the mathematics than in its biological origins. To this end, he developed a complex theoretical structure analogous to the highly ramified and sophisticated elaborations of Newtonian mechanics discovered in the 18$^{\text{th}}$ and 19$^{\text{th}}$ centuries. Of these investigations, Volterra's biographer, Sir Edmund Whittaker, made this comment:

> "It would be rash to say whether [they] will remain what they appear to be at first, and certainly are, *at least*, a clever and remarkable *tour de force* or whether they will eventually be seen as the germs of a profound biodynamics, essential to the theoretical and economic biology of the future ..."

Time has passed since these words were written in 1941, and we may now make the judgment that Whittaker withheld. The biological significance of these investigations is limited, however, they turned out to tell us a lot about systems of differential equations.

Another direction taken by research into theoretical ecology was first explored by the Russian mathematician Andrey Kolmogorov (1903-1987). Kolmogorov was one of the 20$^{\text{th}}$ century's greatest mathematicians. He is best remembered today for his contributions to the understanding of probability theory. His one venture into theoretical ecology was published (in 1936) in an obscure Italian journal and attracted little or no notice until Aldo Rescigno (then working at the University of New South Wales) and his American associate, I. W. Richardson, drew attention to it in 1967. What Kolmogorov did was to take Volterra's predator-prey model and to generalize it. Where Volterra had explicit forms for the rates of growth of the two species, Kolmogorov used instead very general functions, subject only to very obvious constraints. He was able to demonstrate oscillatory behavior, but without the structural instability. This was, in part, because he fed into his equations a realistic assumption that Volterra had overlooked: *In the absence of predators, the number of prey cannot increase indefinitely*. Rescigno and Richardson not only drew attention to Kolmogorov's paper, but they also extended his analysis to the cases of competition and mutualism. Later, Rescigno (who by then had moved to ANU) went further and considered the case of three species in competition with one another. He discovered cases in which one or two of the species necessarily became extinct; other cases in which one or two of the species became extinct, but which ones they were depended on the initial numbers; and a further case in which all three species continued to coexist. This last case and those others that result in the continued coexistence of two of the species all violate the Competitive Exclusion Principle, but there is no reason *in the mathematics itself* why they cannot occur. This line of research was perhaps becoming somewhat profitless anyway, because it seemed that it was difficult to arrive at any firm testable conclusions, but the *coup de grace* was delivered in 1967 by Stephen Smale. Smale (1930–) is another of the mathematical superstars to figure in our story. Among the areas he investigates is dynamical systems theory, which embraces the study of systems of differential equations. Smale considered the case of competition between n species, along the lines pioneered by Kolmogorov and extended by Rescigno and Richardson. The n differential equations of this case were written in very general form and subjected only to those conditions of biological plausibility that Kolmogorov and the others had imposed. However, Smale found that when $n > 4$, *any* behavior is possible. In other words, nothing at all useful could be said. This is because chaos intervenes. This was not a consideration with the early work, because when n is 2 (or even 3 for such systems) chaos cannot occur. This was the final knell for mathematical ecology's golden age, which is not to say, however, that mathematical ecology itself is not alive and well. It has just learned to be less ambitious and to look more closely to the actual biology involved before embarking upon the process of mathematical modeling. There is today much less emphasis on grand general theories and much more concentration on specific models. These more specific models are directed to some immediate purpose, usually to do with conservation or economic matters.

Further Reading

A Google search under mathematical ecology will lead directly to modern research in the area. Biographies of Kolmogorov, Volterra and Smale are all to be found at the St Andrews MacTutor site:

http://www-history.mcs.st-and.ac.uk/

The introductions to the two works mentioned at the beginning of this article are also highly informative, and could be read by *Parabola*'s audience. They are unlikely to be held by school or municipal libraries, but many university libraries hold them. I should also mention a journal article by Scudo. It is entitled 'Vito Volterra and Theoretical Ecology' and was published in the *Journal of Theoretical Biology*, Volume **2** (1971), pp. 1–23. This also should be widely held by university libraries. It does contain material which will be beyond *Parabola*'s readers at this stage, but if they are prepared to bleep through these, there is much of interest to be