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On the Contribution of Volterra and Lotka to the Development of Modern Biomathematics*

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ABSTRACT – The birth of modern biomathematics took place in the 1920s and was characterized by two significant new facts: the systematic use of mathematics in biology not as a technical aid but as a conceptual tool, and the attempt to apply a determinist or a mechanist conception to biology. In this paper we deal with the developments of population dynamics and with the main contributions to this trend, i.e. the works of Vito Volterra and Alfred J. Lotka. The purpose is to show that these contributions are representative – in different and sometimes contrasting ways – of the new developments of biomathematics. The analysis of the priority question concerning the discovery of the 'Volterra-Lotka' equations and the analysis of the Volterra-Lotka correspondence show that Volterra's approach was strictly adherent to the classical physico-mathematical paradigm, while Lotka's point of view was more eclectic and open-minded as regards the new developments of physics, and somewhat skeptical about formal statements. We could say that while Volterra followed the 'mechanical analogy' Lotka had an inclination for the 'thermodynamic analogy' and had a great interest for the energetic problems in population dynamics.

The 1920s were a period of rapid growth and change in modern biomathematics. This does not of course mean that before this (even many decades before), biomathematics had not made considerable progress of decisive importance for its subsequent development.[1] Nevertheless, the 1920s were characterized by two significant new facts. The first of these was a kind of *invasion* of biology by mathematics; mathematics was no longer used merely as a technical aid but as a conceptual tool for investigation purposes. It was no longer a question of using a few formulae of carrying out an occa-

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[1] On the introduction of mathematical modelling in theoretical biology see Scudo (1971; 1984) and the recent first complete history of population ecology by S.E. Kingsland (Kingsland, 1985). These works contain an accurate analysis of the contributions of Volterra and Lotka to mathematical biology. The aim of the present paper is to emphasize the analogies and the differences between Volterra's and Lotka's approaches and to show that their 'reductionist' views are different on many points. Our analysis is based on a reinterpretation of the priority dispute and of the content of the correspondence between Volterra and Lotka. This correspondence is unpublished, except for some quotations which can be found in Kingsland (1985). We shall quote also part of a letter of Volterra to D'Arcy W. Thompson. These correspondences are conserved in the Volterra Archive at the Accademia Nazionale dei Lincei, Rome (see Israel, 1982 a).

sional calculation, but of bringing into action the whole vast array of sophisticated theorems of mathematical analysis. The second novelty was conceptual in nature. It was during this period that the most determined attempts were made to apply the determinist conception, in particular, mechanism, to biology. The concepts and methods used in classical mathematical physics were seen as the most appropriate model to imitate in order to achieve this aim.

The contributions of Vito Volterra and Alfred J. Lotka are representative (albeit in different, and sometimes contrasting ways) of the developments mentioned above. It is no coincidence that Ludwig von Bertalanffy, in his *General System Theory*,[2] makes frequent reference to the contributions of Volterra and Lotka, whom he actually considers as precursors of system theory in biology.

In 1925 Lotka published his famous treatise on *Elements of Physical Biology*,[3] while the first of the long series of papers devoted by Volterra to the mathematical study of population dynamics[4] saw the light in 1926. Indeed, the discovery of the famous prey-predator equations (later known as the 'Volterra-Lotka equations')[5]

$$\frac{dx}{dt} = Ax - Bxy$$

$$\frac{dy}{dt} = Cxy - Dy$$

gave rise to a priority dispute between the two scientists. Priority questions always have an important and serious nucleus which is related to the occurrence of simultaneous discovery. Furthermore, the occurrence of simultaneous discoveries is almost always indicative of the fact that a given scientific development has reached an almost 'objective' degree of maturity. I have discussed the controversy on priority between Volterra and Lotka elsewhere.[6] However, I shall briefly outline the main points,

[2] Bertalanffy von (1968).

[3] Lotka (1925); republished in 1956 as *Elements of Mathematical Biology*.

[4] Volterra (1926 a).

[5] In these equations x represents the number of preys (measured in real quantities), y the number of predators (also a real number) and t time. The growth rate of preys is assumed to be constant ('malthusian' growth). The effect of predation is represented by the two terms Cxy and − Dxy. Volterra described the mechanism of predations by the so-called 'method of encounters' (the ecosystem is considered as the system of the molecules of a perfect gas in a closed container). This reference to the concepts of statistical mechanics is absent in Lotka's approach (see on this point Kingsland, 1985, p. 110).

[6] See Israel (1982 b). The importance of the priority controversy between Volterra and Lotka with respect to their conceptions of mathematical modelling in biology, is underestimated in Kingsland (1985). In our opinion, the importance of this priority controversy is evident if one takes account of Lotka's papers concerning the law of mass action and a model of an oscillating chemical reaction (Lotka, 1920 a, b).

because I consider it to be of great historiographic interest. The reader is referred to the cited article for more details.

In 1926 Vito Volterra published his paper on 'variations and fluctuations in the number of individuals in cohabiting animal species'.[7] Almost at the same time, an article appeared in the journal *Nature*,[8] summarizing the theories of population dynamics set out in the first work. The article in *Nature* attracted the attention of A.J. Lotka, who claimed priority in formulating the differential system describing 'predator-prey' ecology, on the grounds of the results already published in his book *Elements of Physical Biology*.[9] It is significant that the equations in question had already been formulated by Lotka in 1920 in two papers on oscillating chemical reactions.[10] The original inspiration actually dates back to a paper he wrote in 1910.[11] Also in the contemporary mathematical literature the date of the first formulation of Volterra and Lotka's equations is customarily associated with the above works. Oddly enough, however, Lotka does not refer to his 1920 papers when claiming priority. Volterra acknowledges Lotka's priority in formulating the simpler two-dimensional case, but claims that his own results are more general and far-reaching. He also maintains that there is a clear-cut difference between the point of view on which his work is based and that of Lotka. In order to explain this difference, Volterra actually cites Lotka's 1920 work, from which – in his point of view – Lotka derived the equations *by analogy* and applied them to the case of biology. In a letter to Lotka in French at the height of the controversy, Volterra writes:

> Je vous suis très reconnaissant de votre aimable lettre et de l'important recueil de vos mémoires que vous avez eu l'obligeance de m'envoyer. J'en ai parcouru la plus grande partie, j'ai lu les deux mémoires n. 3 et n. 13 et j'ai compris la voie que vous avez suivie pour obtenir les équations dans le cas de deux espèces. C'est l'analogie du cas biologique avec la question chimique qui vous a guidé. Pour ma part j'ignorais la question chimique et c'est pour repondre à la question que M. D'Ancona me posait que j'ai obtenu les mêmes équations au § 3.[12]

And again in a letter to D'Arcy W. Thompson:

> Je viens de recevoir un volume du Prof. Lotka ayant pour titre 'Physical Biology' où je vois qu'il avait traité en partie le cas de deux espèces en arrivant jusqu'au dia-

[7] Volterra (1926 a).
[8] Volterra (1926 b).
[9] See Lotka (1925) (reprint 1956, pp. 88-94). See also Kingsland (1985), pp. 109-110.
[10] Lotka (1920 a, b).
[11] Lotka (1910).
[12] 'I am very grateful for your kind letter and the large collection of your notes you so kindly sent me. I have browsed through most of them. I have read notes no. 3 and no. 13, and can see the path you followed to obtain the equations in the case of the two species. It is the analogy between the biological case and the chemical question that has guided you. As for me, I was unaware of the chemical

gramme 2 qui est pareil au mien.[13] Je ne connaissais pas le travaux de M. Lotka, c'est pourquoi je n'ai pas pu les citer... M. Lotka part d'une analogie, qui existe avec un problème chimique déjà traité[14] et se borne à intégrer les deux équations qu'on a dans le cas de deux espèces que j'ai designé par III et IV, mais il n'en déduit pas les trois lois que j'ai trouvées[15] ni aucune des conséquences que j'ai tirées. Il ne traite non plus tous les autres cas de deux espèces que j'ai examiné dans le § 4.[16] En outre il n'envisage pas le cas de *n* espèces c'est pourquoi il ne connait pas les fluctuations générales ni l'existence des associations conservatives et dissipatives. D'autre part son volume se rapporte à des questions très générales de statistique de manière que l'on peut dire qu'il y a dans nos recherches un petit domaine commun mais elles s'en détachent complètement dans tout le reste. Quoique ce domaine soit à mon avis assez restreint, je regrette de n'avoir pas cité dans mon travail des Lincei qu'il m'avait precedé au sujet d'une partie de la matière.[17]

On the basis of these quotations it is possible to give an answer to the following questions: why did Lotka raise the priority controversy on the basis of his 1925 book and not on the basis of his 1920 work, which established the priority much more clearly? Why were the latter works mentioned *by Volterra*, and for the purpose of diminishing the value of Lotka's priority? The reason for the paradox lies, in my opinion, in the fact that Lotka's 1920 papers (on oscillating chemical reactions) could be used as a proof of priority only within a mathematical modelling or system theory conception (based on the concept of the isomorphism of laws). However,

question and it was in answer to the question Mr. D'Ancona asked me that I obtained the same equations in § 3'. (Volterra to Lotka, draft of a letter, undated, probably November 1926, Volterra Archive at the Accademia Nazionale dei Lincei).

[13] Volterra's reference is to the phase diagram of 'Volterra-Lotka equations' (see also Lotka, 1925, reprint 1956, p. 90).

[14] Lotka (1920 a).

[15] The first law ('law of the periodic cycle') states the periodicity of the fluctuations of the two species. The second law ('law of the conservation of the averages') states that the average numbers of the two species in a period of fluctuation are constant and equal to the values of the coordinates of equilibrium. The third law ('law of the perturbation of the averages') solved the D'Ancona problem (which in turn was the first motivation of Volterra's research): if we destroy (i.e., if we fish) the two species uniformly and in proportion to their numbers, the average number of the prey species would increase and the average numbers of predator species would decrease.

[16] In particular, the case of limited (logistic) growth, which may be interpreted as the consequence of an 'internal friction'. Volterra's reference is to § 4 of Volterra (1926 a).

[17] 'I have just received a book from Prof. Lotka entitled *Physical Biology* in which I see that he has partially treated the case of two species, going as far as to obtain diagram 2, which is similar to mine. I was not familiar with the works of Mr. Lotka, which is why I was unable to cite it... Mr. Lotka starts off from an analogy with a previously treated chemical problem and limits himself to integrating the two equations obtained in the case of the two species, which I have denoted as III and IV. However, he has not derived the three laws, nor any of the consequences, that I have found. Moreover, he does not treat any of the other cases of two species that I have examined in § 4. Furthermore, he does not envisage the case of *n* species, which is why he is not aware of general fluctuations or of the existence of conservative and dissipative associations. On the other hand, his book refers to very general statistical matters, so that our researches may be said to have a small area in common but to be quite different as far as all the rest is concerned. Although this area is, in my opinion, a quite narrow one, I nevertheless regret not having mentioned in my work for the Lincei that he had preceded me with regard to a part of the topic'. (Volterra to D'Arcy Thompson, draft of a letter, undated, probably November 1926, Volterra Archive at the Accademia Nazionale dei Lincei).

not even Lotka (much less Volterra), subscribed to any conception of this kind, so that both of them viewed the 1920 papers in a setting that is quite different to that of the work on population dynamics of 1925 and 1926.

From the point of view of contemporary mathematical modelling the first place is occupied by the *mathematical pattern*. This consists of a formal structure capable of representing a large number of *isomorphic* phenomena. From this point of view, a chemical model and a biological model described by the same equation are fundamentally homogeneous. They are like two concrete, specific manifestations of the same 'abstract phenomenon'. In our case, they are two concrete examples of *non-linear oscillators*. This is more or less how von Bertalanffy sees the contribution of Volterra and Lotka.[18] However, the point of view of the precursors of modern biomathematics is quite different: for them, although based on the same equations, a chemical model and a biological model are quite different because they have been obtained from completely different empirical bases. The procedure of *analogy* (which von Bertalanffy correctly refers to as one of the conceptual procedures typical of modern mathematical modelling) was considered by Volterra as a rather inadequate approach (as the letters cited above confirm). Lotka, on the other hand, does not object on this point, and apparently agrees with it. In our opinion, Volterra was quite right in saying that it was the analogy between the biological case and the chemical question that suggested to Lotka the choice of this kind of equations. But Lotka refers to his equations as deduced from the empirical analysis of a parasite-host ecosystem and does not mention the analogy with the chemical model.

Therefore, both Volterra's and Lotka's approaches are of the 'classical' type: they accord central importance to the relationship between the empirical analysis of data, mathematical formalization and experimentation.

But this is where the analogies end and the differences begin. And, however interesting the analogies may be because they help us understand the various features of Volterra's and Lotka's scientific paradigm, the differences are even more significant and illuminating.[19]

The analysis of these differences leads us to an issue of capital importance, i.e., the influence exerted by the model of classical physics (and by determinist and mechanist conception in general) on the formalization of disciplines such as biology, which were previously refractory to mathematical analysis. The more or less complete acceptance of the determinist (or even

[18] See Bertalanffy von (1968), *passim*.

[19] See also the interesting analysis concerning some aspects of these differences developed in Kingsland (1985), pp. 123-6. Kingsland's thesis is that 'it was in the use of analogies that [Volterra's] methods were in greatest conflict with Lotka's' (*ibid.*, p. 124). We shall return to this point later.

strictly mechanist) paradigm of classical physics had a powerful effect on the way biomathematics grew up. Volterra did not take a purely traditionalistic attitude, otherwise he would simply have rejected the possibility of developing a mathematical biology, as would have been done by a Painlevé and, to a lesser extent, by Poincaré (which is proved by the attitude they actually did take over the quite analogous question of the mathematization of economics).[20] Nevertheless, Volterra was always of the idea that the only way to ground a new science on a solid basis was to introduce into it the concepts and methods of classical physics, in short, to follow the path of mechanical analogy. Volterra's proposed aim of extending the scope of classical determinism became evident as early as the famous 1901 conference[21] in which he claimed that the application of mathematics to biology did not seem to be have progressed as far as its application to economics. For the sake of brevity, we shall limit our description of Volterra's point of view concerning the relationship between the methods used in physics and the formalization of 'new' sciences, using his own apt words:

> Le concept de l'*homo oeconomicus*, qui a donné lieu à tant de discussions, qui a soulevé tant de difficultés et qui trouve toujours des cerveaux rebelles à l'accepter, semble à notre savant[22] chose si naturelle, qu'il éprouve une véritable surprise de l'étonnement plein de défiance suscité chez quelques-uns par cet être idéal et schématique. Il voit dans l'*homo oeconomicus* un concept analogue à ceux qu'une longue habitude lui a rendu familiers. Il est en effet accoutumé à idéaliser, en regardant les surfaces comme sans frottement, les fils comme inextensibles, les corps solides comme indéformables et il a l'habitude de substituer aux fluides de la nature les liquides et les gaz parfaits.
>
> Et non seulement il a l'habitude de tout cela, mais il connait l'avantage que présentent ces conceptions.
>
> S'il continue à s'avancer, il s'aperçoit que, aussi bien dans sa science qu'en économie, tout se réduit à un jeu de tendances et de liaisons, celles ci limitant l'action des premières qui, par réaction, engendrent des tensions. De cet ensemble naît, tantôt l'équilibre, tantôt le mouvement, d'où une statique et une dynamique dans l'une et l'autre science.
>
> Nous avons déjà touché aux vicissitudes traversées par l'idée de force en mécanique: des sommets de la métaphysique elle est descendue dans le domaine des grandeurs mesurables. En économie l'heure est passée de parler avec Jevons d'expression mathématique de grandeur non mesurable. M. Pareto, au lieu de partir directement du concept d'*ophélimité*, comme il faisait dans son *Cours d'économie politique*, propose maintenant de partir d'une notion purement quantitative par les courbes d'indifférence, qui correspondent assez bien aux courbes de niveau et aux surfaces equipotentielles de la mécanique.
>
> Les théories moleculaires et atomiques conduisent à concevoir comme discontinue la constitution intime des corps; Cauchy, Lamé et tous ceux qui ont établi la

[20] See, on this topic, Israel and Ingrao (1985 a) and Israel and Ingrao (1987), Chapter 6.

[21] Volterra (1901). The following quotations are taken from the revised French edition of this conference (Volterra, 1906).

[22] 'Un savant abitué à la mécanique' (Volterra, 1906, p. 9).

théorie mathématique de l'élasticité, dont la grande portée et les applications pratiques se révèlent tous les jours, ne purent parvenir à leur but qu'en passant, par un trait de génie, du discontinu au continu. Or, comme les créateurs de la théorie de l'élasticité ou comme Fourier dans la théorie de la chaleur, les économistes supposent que la quantité des biens dont chacun peut disposer, quantité discontinue par sa nature, varie par degrés continus.

Finalement, notre savant reconnaîtra dans le procédé logique employé pour obtenir les conditions de l'équilibre économique, le raisonnement par lequel il établit le principe du travail virtuel, et quand il se trouvera devant les équations différentielles de l'économie, il éprouvera le désir de leur appliquer les méthodes d'intégration qu'il connaît.[23]

It must be emphasized that, in Volterra's point of view, the mechanical analogy in economics – and, as we shall see, in biology – leads to the use of differential equations as *the* fundamental mathematical tool.

Volterra rapidly lost interest in economics for reasons that we cannot detail here.[24] In 1925, when his son-in-law, Umberto D'Ancona submitted to him the well known problem of the fluctuation in the number of predatory fishes in the Upper Adriatic, he threw himself body and soul into the study of problems involving the mathematical description of competing animal populations.

The theories developed by Volterra in fifteen or so years of activity (until his death in 1940) clearly show how closely he followed the mechanical analogy. I shall mention only a few aspects. In the first place, he

[23] 'The notion of *homo oeconomicus* which has given rise to much debate and created so many difficulties, and which some people are still loth to accept, appears so easy to our mechanical scientist that he is taken aback at other people's different surprise at this ideal, schematic being. He sees the concept of *homo oeconomicus* as analogous to those which are so familiar so him as the result of long habitual use. He is accustomed to idealizing surfaces, considering them to be frictionless, accepting lines to be nonextendable and solid bodies to be indeformable, and he is used to replacing natural fluids with perfect liquids and gases. Not only is this second nature to him: he also knows the advantages that derive from these concepts. If the mechanics scholar pursues this study, he will see that in both his own science and in economics everything can be reduced to an interplay of trends and constraints – the latter restricting the former which react by generating tensions. It is from this interplay that equilibrium or movement stems, one static and one dynamic, in both these sciences. We have already referred to the vicissitudes of the idea of force in the history of mechanics: from the peaks of metaphysics, we have descended into the sphere of measurable things. In economics, for example, we no longer speak as Jevons did about the mathematical expression of non-measurable quantities. Even Pareto seems to have given up his idea of *ophelimity*, which was the cornerstone of his original edifice, and is moving to purely quantitative concepts with his indifference curves which so beautifully match the level curves and equipotential surfaces of mechanics. Molecular and atomic theories suggest that the intimate constitution of bodies is discontinuous; Lamé, Cauchy and all the others who established the mathematical theory of elasticity, whose great scope and continuous practical application are emerging every day, were only able to do so by moving from the discontinuous to the continuous, by a stroke of sheer genius. Now, as the creators of the theory of elasticity did, and as Fourier did with the theory of heat, the economists assume that the quantities of goods of which each person may dispose, and which by their nature are assumed to be discontinuous, vary by continuous degrees. Lastly, our mechanical scientist sees in the logical process for obtaining the conditions for economic equilibrium the same reasoning he himself uses to establish the principle of virtual work, and when he comes across economic differential equations he feels the urge to apply to them the integration methods which he knows work so well'. (Volterra, 1906, pp. 9-10).

[24] See Ingrao and Israel (1985 a, b) and Ingrao and Israel (1987).

attempts to strike an analogy between friction in mechanics and the interaction between individuals of the same species; he then neglects this in order to derive the simplest form of the 'frictionless' equations. Then he introduces friction, after which he constructs a function analogous to energy. Depending on whether it remains constant or decreases during the evolution of the biological system, this function allows the latter to be classified as *conservative* or *dissipative*. The model of the interaction between individuals that compete with, or prey on, each other is that of a perfect gas in which collisions between molecules occur at random. And *dulcis in fundo*, after deriving the more general form of his equations, Volterra attempts to re-derive them as the 'eulerian' of a variational principle; by imitating the principle of minimal action, he obtain a 'principle of minimal vital action'.

Alfred J. Lotka, supervisor of the Statistical Bureau of the Metropolitan Life Insurance Company of New York, had a completely different background to Volterra. Not only his previous training but also his professional activities had caused Lotka to become deeply involved in *population statistics*, on the subject of which he was a great expert. In other words, Lotka's background was far more eclectic and less ridigly centered around the paradigm of classical physics, than was Volterra's. Of course, this does not mean that Lotka was insensitive (as was partly inevitable at that time) to what, paraphrasing the title of a movie by Luis Buñuel could be called 'the discrete fascination of classical physics'. A glance at the contents of his book *Elements of Mathematical Biology* is enough to appreciate this. An introductory chapter on the 'General Principles' is followed by three chapters, respectively devoted to the kinetics, statics and the dynamics systems. However, this initial impression is quite superficial because under this traditional, almost scholastic, expository scheme of things, one can find ideas and problems that are anything but traditional. In Chapter 1, for instance, he tackles the problem of irreversibility and its statistical significance. In the chapter on statistics, he studies the problem of equilibrium states in a way that, in many respects, anticipates many contemporary ideas regarding the qualitative analysis of dynamical systems. In the final chapter, he examines energy problems, treating biological subjects as 'energy transformers of Nature'.

So far it may be said that Lotka has not limited himself to a strictly 'mechanical' type of analysis, but is still open to other approaches (particularly of a thermodynamic type). In fact, we could define the difference between Lotka's and Volterra's approaches by saying that Volterra follows the 'mechanical analogy' while Lotka has an inclination for 'thermodynamic analogy'.[25] But there is a deeper difference concerning the conception of the role of physics. In fact, Volterra's point of view was strictly

[25] See note 19.

adherent to the classical physico-mathematical paradigm, a tradition that goes back to the work of Joseph Fourier and has its outstanding expression in the works of Henri Poincaré.[26] It is well known that Volterra was sceptical about the possibility of developing physics as a branch distinct from mathematical physics and was therefore sceptical about the new developments of theoretical physics. Lotka's point of view wasn't at all restricted to a so rigid paradigm; it was more eclectic and open-minded as regards the new developments of physics, and sceptical about formal statements.[27] But there are also other differences between Lotka's and Volterra's views. I am referring here to the attention that Lotka pays to the 'vitalistic' arguments albeit from a non-vitalistic point of view. From this standpoint, the pages he devotes to the role of consciousness in living organisms are both interesting and original. The following quotation shows how he tries to avoid any restrictively deterministic approach:

> It seems that even the most trivial voluntary action involves the interference of consciousness in the course of physical events, and of such more or less trivial voluntary acts our waking consciousness is filled to the brim. A certain interest may therefore attach to an alternative point of view which has been developed by the writer elsewhere, and which is based on the following considerations.
>
> A quantity which does not appear in the working equation describing the laws of action of a physical system may nevertheless play a significant role in the world's events. So, for example, a mathematical theory of wealth, covering at any rate certain aspects of economics, can be built up in terms of prices and sales alone, without pushing the analysis of fundamentals beyond this point; that is to say, without examining the human emotions and motives that, presumably, find their numerical expression in prices. On such basis as this, for example, Cournot founded his admirable 'Researches into Mathematical Theory of Wealth'.
>
> But to most of us it will appear quite evident that such a treatment as this is necessarily a very incomplete presentation of the actual events, however exactly it may represent the resultant effects observed. For it wholly ignores our desires and purposes, which to us appear very real and important constituents of the course of nature.
>
> This example should open our eyes to the possibility, with which we must be prepared to reckon, that the equations of dynamics, however perfectly they may picture the course of certain physical events, may fail entirely to reveal or to give expression to underlying agency that may, in fact, be of fundamental significance. The interference of consciousness in mechanics may be very real, and yet the course of events may appear fully determined by the laws of dynamics.[28]

There is obviously no doubt about the topicality of these issues.

The comparison between Volterra's biomathematical work and that of Lotka reveals, on the one hand, an extremely comprehensive and mathe-

[26] See Israel (1984).

[27] We agree on this question with the analysis of S. E. Kingsland (Kingsland, 1985, pp. 124-6), except for the assertion that Volterra and Lotka come from the same tradition in physics. See also note 31 below.

[28] Lotka (1925), reprint 1956, pp. 408-9.

matically rigorous edifice constructed with reference to the idea of the mathematics-experiment relationship on which classical physics is based and, on the other, a 'seminal work' that is much less organized as far as its methods and approach are concerned, but nevertheless abounds in ideas and concepts of great interest and potential.

It is no wonder that using such different approaches, Volterra and Lotka had such trouble in understanding each other, as we can see from their correspondence. In his desire to discuss the substance of the matter with Volterra, Lotka immediately tackles the issues he is interested in, emphasizing the restricted nature of the problems touched upon by the mathematical model over which the question of priority has risen:

> ...it seems that the main interest does not lie so much in the kinetics as in the dynamics of systems composed of a large number of energy transformers having certain characteristic properties. In the final part of my book I have endeavoured to develop this branch of science. Here the discussion leads to a study of the apparatus by means of which these transformers manage to capture the free energy they need in order to function. This brings in certain partial derivatives $\partial r_i / \partial X_j$ that I have related back to the 'economic value'. On the basis of the principles of Spencer and Jevons according to which the feeling being tends to maximize his pleasure, at the same time as he is acting in the interest of the species, there is found to be a relationship between the economic value and the partial derivatives $\partial r_i / \partial X_j$. This relationship would be perfect in a perfectly adapted species. It differs to varying degrees from this ideal in the present species. These reflections automatically spring to mind when I read your article. I should be very happy to believe that they are of some interest to you.[29]

And he insists in a subsequent letter, whose arguments emphasize the difference between the two points of view:

> I have, of course, found in your longer monograph many things of prime importance. I will not now enter into a discussion of the matter; only one point I might speak of in passing, namely, that I have been particularly interested in Section 4 in which you broach the question of encounters between individuals of the two species. I believe that here is the starting point for some further developments. The problems of the statistical mechanics of systems of energy transformers (for that is what animals and plants are), hinge just on this question of the collisions or encounters between the individual organisms. All these encounters are determined, not, as in the comparatively simple case of gaseous molecules, merely by velocities and positions, but by an elaborate mechanism comprising sense organs, motor organs and adjustor faculties.[30] If you have been turning over the leaves of my book, you may have found that I have a little to say on the question of collisions on page 359.

[29] Lotka to Volterra (Letter, November 2, 1926), Volterra Archive at the Accademia Nazionale dei Lincei.

[30] Here the difference with Volterra's approach appear quite evident. 'Volterra's massive entrance into the field consisted first in a systematic exploration of all the reasonable analogies between ecology and classical statistical mechanics' (Scudo, 1984, p. 21).

What I have then said I would like to modify only in one minor particular. The discussion is there conducted as if the notion of the organism extended over the twenty-four hours of the day. In actual fact, of course, only certain fractions K of the twenty-four are so employed, and this fraction should enter in obvious manner into the discussion. The discussion will further have to take into account the kind of thing that is discussed on pages 346 to 358. I am at present giving my thoughts to this phase of the subject and I am hoping that perhaps in a little while I may have something in readiness for publication. There is something unsatisfactory in the rather extreme degree of idealization, of conventionalization, which is necessary to introduce into the discussion at the present stage of this very new science. I believe that it is necessary for us to deliberately overcome a certain repugnance which one feels towards such extreme conventionalization and to proceed with the work in the hope that the first crude steps may turn out in time to have been necessary preliminaries for a more perfect treatment of the subject.[31] Owing to the immense complexities of the physical systems presented to us in living nature it is necessary, I believe, in order to be able to progress at all, to begin with modest and greatly simplified examples. From your monograph it appears to me that you entertain somewhat similar thoughts. Naturally, I should be greatly interested in an expression of your views.[32]

Volterra's reply to these considerations is rather laconic and somewhat cool:

Dans votre lettre vous me parlez de la question la plus importante: la question dynamique et énergétique. Elle prime naturellement toutes les autres. J'y avais beaucoup songé et j'y songerai encore. Vous qui avez des idées si vastes et qui avez approfondi un domaine si étendu vous pouvez obtenir là dessus des résultats d'une grande portée.[33]

Even a cursory examination of the work produced in the field of biomathematics over the past few decades would show that Volterra's approach was (and still is, in part) the most influential. Of course, we are speaking of a Volterrian approach that has been transformed from the mathematical modelling standpoint, i.e. 'freed' from any need for the empirical verification typical of Volterra's classical conception and from any strict adherence to the paradigm of mechanical analogy. I think that the reasons for this lay in the force of attraction that can be exerted by the model of a consolidated dis-

[31] It is quite clear from all Volterra's writings that he did not suffer from such a repugnance. It is true that Volterra considered of vital importance the requirement of empirical reliability of the mathematical models in biology and considered very important the problem of empirical validation. But, in his views, the reductionist approach was utmost reliable. Could a 'mechanical reductionist' feel repugnance towards 'extreme conventionalizations' as the frictionless pendulum? In fact, the Volterra-Lotka oscillator is the non-linear biological counterpart of the linear oscillator in mechanics.

[32] Lotka to Volterra (Letter, December 1, 1926), Volterra Archive at the Accademia Nazionale dei Lincei.

[33] 'In your letter you speak of the most important issue: the dynamics and energy question. It obviously comes before all the others. I have given much thought to it and will continue to do so. In view of your wide-ranging ideas and the broad scope of your studies, you should obtain some very significant results'. (Volterra to Lotka, Draft of a letter, undated, probably December 1926, Volterra Archive at the Accademia Nazionale dei Lincei).

cipline (as classical physics). This influence can also be seen in the prevailing use of classical techniques of differential equations in biomathematics of our century, as a consequence of the influence of Volterra's work. The influence of Lotka's work in the specific field of biomathematics can certainly be detected in the work of scientists like Rashevsky, von Bertalanffy and Prigogine, i.e., in the development of research that had (and to some extent still has) difficulty in establishing itself as 'normal science'.

In conclusion, the case study outlined above appears to be very interesting also with regard to the different trends in present-day biomathematics.

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