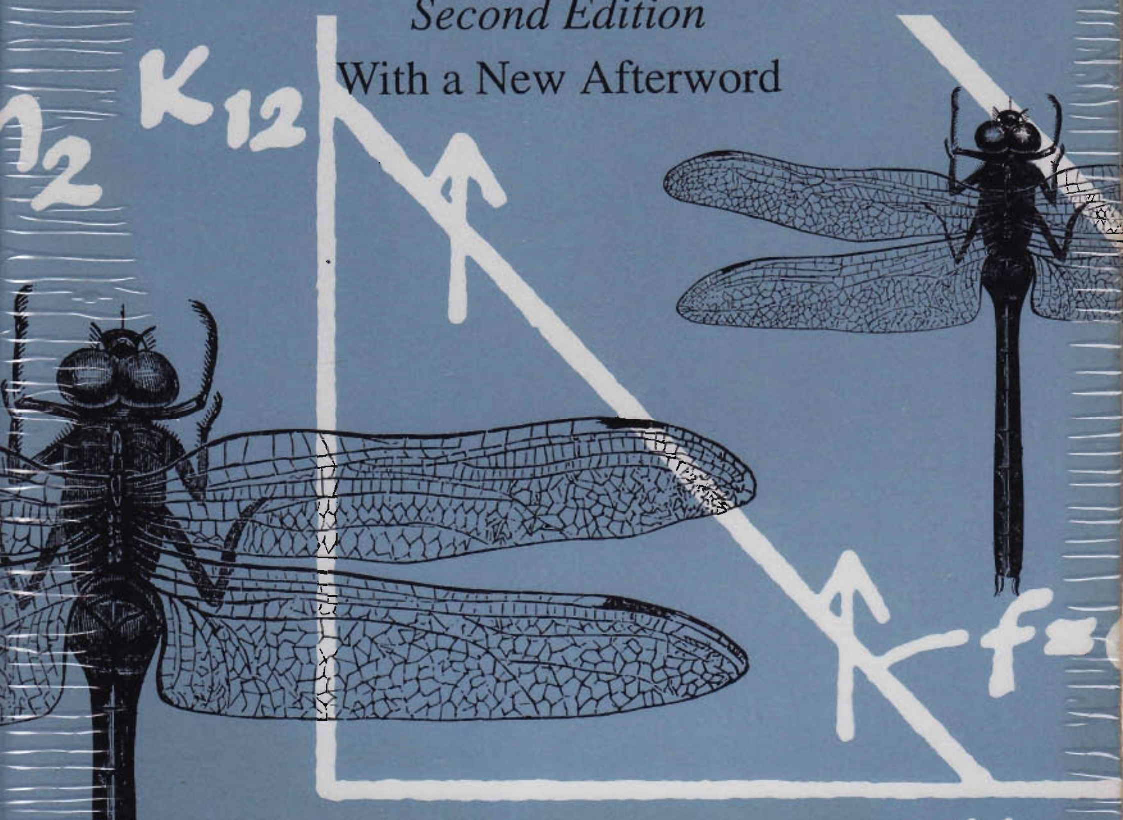
Modeling Nature

Episodes in the History of Population Ecology

Second Edition

With a New Afterword



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Modeling Nature

As more attention was paid to population dynamics in the 1920s, the one point on which there was general agreement was that this was a subject of considerable confusion and obscurity. Raymond Pearl had taken drastic steps to reduce the confusion in the biology of population growth with his bold announcement that he had discovered the law which would bring the subject to order. The storm that followed, while it caused some to distrust the crude simplicity of mathematical arguments, encouraged others to recognize the insights that seeking simplicity might offer.

Pearl's was not the only mathematical line of attack to appear during the twenties. In other areas as well, population events were being investigated with mathematical tools: these ranged from the primitive implements of the biologist to the more elaborate tools of the expert mathematician. The different approaches to population analysis reflected not only different levels of expertise, but also different perceptions of the purpose of the inquiry. On the one hand, the economic biologist wanted to predict and to control specific populations; on the other hand, the mathematician was interested in creating a general theory of the struggle for existence as an imaginative exercise. A variety of strategies sprang up within a few years of each other. These met with a mixed but polite reception at first, but then they began to foment controversy as ecologists confronted the implications of allowing mathematical thinking in this empirical discipline. In a curious twist to the story, one of the earliest advocates of mathematics in ecology, W. R. Thompson, turned out to be one of its most vigorous opponents by the mid-thirties. Before we can understand why Thompson changed his mind, it is necessary to review what these different mathematical offerings were. In this chapter, I shall discuss the main strategies which appeared in the 1920s and early 1930s; in chapter six I shall discuss their reception and the controversies they engendered.

Hosts, Parasites, and Mathematicians

The ability of mathematics to suggest conclusions not possible through observation alone had been noted early in the century, though without attracting much attention. Sir Ronald Ross, winner of the Nobel Prize in 1902 for his work on the cause of malaria, was prompted to take up a mathematical argument when he found that, even after the *Anopheles* mosquito was known to transmit the disease, there remained much popular resistance to the idea that the best way to control malaria was by controlling mosquito populations.[1] The prevailing view in the field was that the incidence of disease was not closely correlated with the numbers of mosquitoes in an area. This crude impression was summoned as an argument against the insect control measures that Ross had advocated.

Hoping to reconcile these observations with his understanding of the disease, Ross tried using a mathematical description of the relation between mosquitoes, malaria, and humans. His analysis showed that the disease would not maintain itself unless the proportion of mosquitoes was at a certain level, and that above this level a small increase in mosquitoes would cause a large increase in the incidence of malaria. Here was a possible explanation of the apparent lack of correlation between the two populations.

Ross characterized his approach as the "*a priori* method," meaning that he began by making assumptions about the cause of an epidemic; constructed a set of differential equations to describe the situation based on these assumptions; deduced the logical consequences of the mathematical argument; then tested these theoretical results by comparing them with observations. The use of the term "a priori," now commonplace for this type of modeling, can be misleading, for it suggests also that the model is constructed prior to experience, which Ross certainly did not intend. All of the theoretical treatments I shall discuss in this chapter are arguments of this type, proceeding logically from cause to effect, though their trains of reasoning are very different. Ross called his method the "Theory of Happenings," a general title intended to suggest the wide applicability of the method, not only to the quantitative study of epidemics, but also to "questions connected with statistics, demography, public health, the theory of evolution, and even commerce, politics, and statesmanship."[2] Although he began using mathematics as early as 1899, his theory of happenings appeared in 1911 as an addendum to his book *The Prevention of Malaria*. His method differed from the more usual a posteriori approach, which began with the observations; fitted analytical laws to them; and worked backward to the underlying causes. This was the method commonly used in statistics. In epidemiology it had recently been applied by John Brownlee, who built upon the researches of the nineteenth-century statistician William Farr.[3]

Whereas in epidemiology the statistics were available to support both methods of reasoning, in ecological studies the same wealth of information about life histories and populations was lacking. By the 1920s, at least one ecologist had become impatient for its accumulation. William Robin Thompson, a Canadian entomologist working for the U.S. Bureau of

Entomology, was rapidly coming to the conclusion that much order might be thrown into this confused subject by reasoning, as Ross had recommended, from a set of assumptions to their logical effects, even in the absence of a systematic body of observations.

Thompson had been hired in 1919 to do research on biological control at the bureau's European Parasite Laboratory in France.[4] He was already well known at the bureau from his student days when he had worked at the Gypsy Moth Parasite Laboratory in Massachusetts, starting in 1908. Afterward the bureau had sent him to Cornell University for graduate work, then to Italy to study the alfalfa weevil with Filippo Silvestri, one of Europe's leading entomologists. In 1913 he resigned to pursue his biological studies at Cambridge and Paris; this was followed by a stint in the Royal Navy Medical Service during the war. In 1918 he returned to Paris and was shortly rehired by L. O. Howard to study the biological control of the corn borer, a European insect that had recently become a pest in Massachusetts.

At the European laboratory, Thompson was in charge of analyzing the relationship between the corn borer and the parasites that controlled its abundance in its native habitat. In thinking about this problem, it occurred to him that a mathematical approach might be fruitful as a way of suggesting new hypotheses. The use of mathematics to disentangle the causes that together produced a given effect had impressed him after reading D'Arcy Wentworth Thompson's new work, *On Growth and Form*, which had appeared in 1917.[5] Although these volumes had nothing to do with ecology, they showed how an understanding of mathematical relationships could be brought to bear upon a variety of problems related to the growth and structure of plants and animals. In problems of growth and form, mathematical laws could be applied with confidence because they were based upon the physical laws governing the organic and inorganic worlds. Reading these studies, Thompson carried this reasoning into his ecological problems. If ecological interactions were found to display an underlying regularity, and if this regularity could be described mathematically, then mathematics might serve as a theoretical basis for population ecology.

Thompson found the evidence of this regularity in the work of his two mentors, L. O. Howard in America and Paul Marchal in France. Both had conducted field studies of insect populations in the 1890s and had independently made the same observation: that parasite and host populations seemed to fluctuate together in definite cycles.[6] This empirical evidence gave Thompson all the excuse he needed to explore the mathematics of the case: "For he who says periodicity, regularity, rhythm, says the possibility of a mathematical representation."[7] Starting in 1920, he began to use simple algebraical expressions to describe the relations between parasites and their hosts. The idea was to find an expression for the number of hosts in each generation, taking into account the various factors which would be most important in determining the growth rate of the population (i.e., reproductive power of host and parasite, proportion of sexes in each species, and number of parasite eggs laid in each host). Assuming different initial values for the host and parasite populations, Thompson used his equations to calculate the change in the numbers of each species in successive generations and the change in the percentage of parasitism in each generation.

His equations showed that, in the early stages, the presence of a parasite did not appreciably prevent the host from increasing. The host population increased much as it would had the parasite been absent, becoming more of a nuisance with each generation. At some stage, though, the parasite population would rapidly outstrip the host and would bring about a sudden crash to extinction in the host population within a single generation. Thompson realized that this prediction was not quite right: in reality, such extinctions did not occur. Rather, the host population would merely be reduced to a low level, where it would no longer be a nuisance. But his theoretical results seemed to support observations Paul Marchal had made in the field, that changes in the numbers of insects and their parasites sometimes followed a pattern of large oscillations, each having a slow ascending period and an abrupt downward descent, with the parasite apparently causing the decline of the host.

Thompson was confident that his equations, though they simplified the biology of the interaction, did express the basic relations between host and parasite. Moreover, they offered hope for the success of future biological control programs. His findings suggested that biological control might not show any effect for several generations, but that when its effect was finally achieved, its results would be more complete and of longer duration than would be possible with mechanical or chemical means of control. He argued that, important as it was to know the details of particular cases, real progress in entomology could only be made by uncovering the general laws expressing the process underlying each particular case. Once those laws were encapsulated in formulas, it would be possible to examine particular cases and to draw conclusions of value in practical work:

> Not that these conclusions will always be rigorously in accord with the facts. Far from it. But one can at least consider them as a theme on which nature embroiders infinite variations of reality and by virtue of this they constitute a theoretical base for our work.[8]

Fifteen years later, Thompson would retract these words and confess the error of his youthful ways, but for now he plunged enthusiastically into mathematical ecology, calling upon the advice of more expert mathematicians when the problems exceeded his own abilities.

His colleagues proved to be harder to convert to mathematics than he had hoped. The officer in charge of the corn-borer research, to whom Thompson first showed his results, decided that this work was too mathematical for most entomologists. He advised Thompson that he would have trouble publishing such work in American entomological journals. Instead, Thompson wrote up his results in French and published them with Marchal's help in the *Comptes Rendus* of the Academy of Sciences in Paris.[9] Another manuscript, sent to Cambridge for publication there, came back with criticisms based not on the mathematics but on entomological problems.[10] His conversations with other entomologists revealed that their hesitation to adopt his methods was not because of the mathematics, but because his equations required biological information about the insects that was unknown; specifically, knowledge of the effective rates of reproduction of the populations in the field. His colleagues could argue from strength that it was too early yet for mathematics, that what they needed was more biological research, especially more research on the life histories of the animals under study. Thompson was sympathetic to these charges and set to work to modify his equations so that they could be used by the practical biologist.

If most of Thompson's colleagues were sluggish in responding to his mathematics, there was one mathematician who was quick to grasp the relevance of these studies to his own grand schemes. Alfred Lotka was just contemplating writing his book when Thompson's articles appeared. He had progressed steadily in working out his general method of systems analysis, with special attention to two-species interactions, and was always on the watch for concrete examples to illustrate the method's usefulness. Keeping a close eye on the literature, he found his examples, first in Ross's analysis of malaria, then in Thompson's entomological writings.

Lotka seized upon Ross's research as soon as it appeared in 1911 and incorporated the malaria example into his general study on evolution.[11] He saw in the malaria case an opportunity for a thorough study which would both illustrate his method and indicate how it might be applied: it became the focus of an exhaustive mathematical treatment, some of it written with Frank R. Sharpe, a mathematician he had met at Cornell several years before. Together they published several detailed analyses of the Ross equations in the 1920s.[12] Lotka's work sprang directly from Ross's but was refined and expanded to deal with additional problems missing from Ross's treatment; in particular, the development of the course of a malaria epidemic in its entirety (as opposed to a consideration of the equilibrium condition only), and a study of the effect of a time lag caused by a period of incubation of the malaria parasite.

These promising beginnings in mathematical epidemiology engendered few disciples. Ross expressed surprise in 1915 that so little mathematical research should have been done on such an important subject, especially given the quantity of statistics that had accumulated by then. In Edinburgh, W. O. Kermack, a biological chemist, teamed up with A. G. McKendrick, who had been interested in the mathematics of growth since the 1910s, to extend Ross's analysis in a series of papers published in the 1920s and 1930s.[13] But Lotka's efforts did not seem to impress Ross greatly, despite his desire to encourage further research in this area. Lotka sent him a copy of his book for a review in *Science Progress.* Ross had it reviewed anonymously by "an expert biometrician, who has spoken very favourably of it".[14] The review made note of all the places where Lotka had used the Ross equations, but otherwise found the theories to be "somewhat ultra-speculative."[15] As for the series on malaria that had preceded the book, Lotka had hoped that it would help him to make a connection with the Rockefeller Institute, at the time a center of experimental epidemiology, but his efforts earned him nothing in the medical field. In general, the practice of epidemiology was developing largely along laboratory, experimental lines on which the mathematical approaches of Ross and Lotka made no impact.[16]

Though the case study into which Lotka had poured so much effort finally came to nought, there were other areas where his method could be applied. When Thompson's articles appeared, Lotka accordingly brought the host-parasite example into his analysis as well. He did not fail to notice that Thompson's fluctuations provided the empirical support for the rhythmic oscillations that Herbert Spencer had deduced as the necessary outcome of the balance between the forces of increase and decrease in populations. Lotka's method differed from Thompson's in that he used a continuous-time scale, rather than the discrete-time scale with the generation as the unit of time which Thompson had used. The change gave Lotka greater flexibility but was less realistic for insect populations.

Lotka's analytical method began by describing the interactions between species as a set of simultaneous differential equations. His technique was based on methods used for the mathematical description of the dynamics of chemical reactions. For the detailed analysis of systems of differential equations, he was indebted to the researches of Henri Poincaré and Charles Emile Picard. The procedure Lotka used was an early version of what later came to be called "general system theory," which was developed by Ludwig von Bertalanffy after the Second World War. General system theory as Bertalanffy conceived it was both a point of view and a method.[17] The object was to develop mathematical techniques of analysis which could be used to model the interrelationships between the component parts comprising any sort of system. The word "system" was therefore interpreted very broadly, much more broadly than Lotka had done, so that, as a mathematical technique, systems analysis could be applied to fields as different as biology, information theory, economics, or sociology:

the idea was to make the technique applicable no matter what the particular features of the systems were themselves. Lotka did not imagine his technique as having such broad uses, but the mathematical procedure outlined in his discussion of population dynamics was identical to the one that Bertalanffy later used.

The method itself followed from Lotka's "fundamental equation of kinetics," where the increase in a given component of the system, X_i, is expressed as a function of all the other components, X_1 to X_n, and of all the environmental parameters, P, and the genetic parameters, Q:

$$\frac{dX_i}{dt} = F_i(X_1,X_2,\ldots,X_n;\ P,Q). \tag{5.1}$$

The components, X_n, could refer, for example, to the masses of a group of species living in a biological association. To simplify the problem, the first thing he did was to assume that both the environment and the genetic constitution of the species were constant: in this way, the P's and Q's could be neglected. The fundamental equation was then applied to each component separately, X_1 to X_n, and the form of the function F (which was unknown) was approximated by means of a Taylor series expansion. This produced a series of differential equations which linked the increase of each component X_i to every other like component in the system. The next step was to solve the equations (using a mathematical technique derived largely from Henri Poincaré) and to examine the roots of the solution. From this general examination, certain conclusions could be drawn about the behavior of the aggregates under scrutiny. The value of the method, as Lotka explained, was that fairly specific distinctions could be made between different cases without having complete information about the exact functions, F.[18] When applied to single populations, the method could be used to derive the logistic curve with the appropriate assumptions following the Taylor series expansion.

In the case of the host-parasite and predator-prey relationships, which Lotka tended to lump together, he used his method to depict the interaction between the two species with much greater generality than Thompson had been able to do. For instance, he showed that under certain conditions the interaction would give rise to continual oscillations of the two populations: this was the mathematical representation of the periodic fluctuations that Thompson had noted but had not fully analyzed. A more refined analysis showed that the interaction might also take the form of a damped oscillation, where the fluctuations gradually decreased in magnitude and approached a stationary level (Figure 5.1).[19]

From these mathematical models, Lotka was able to suggest some tentative conclusions. For example, under the original assumptions it would be impossible for one species to eliminate the other, although a

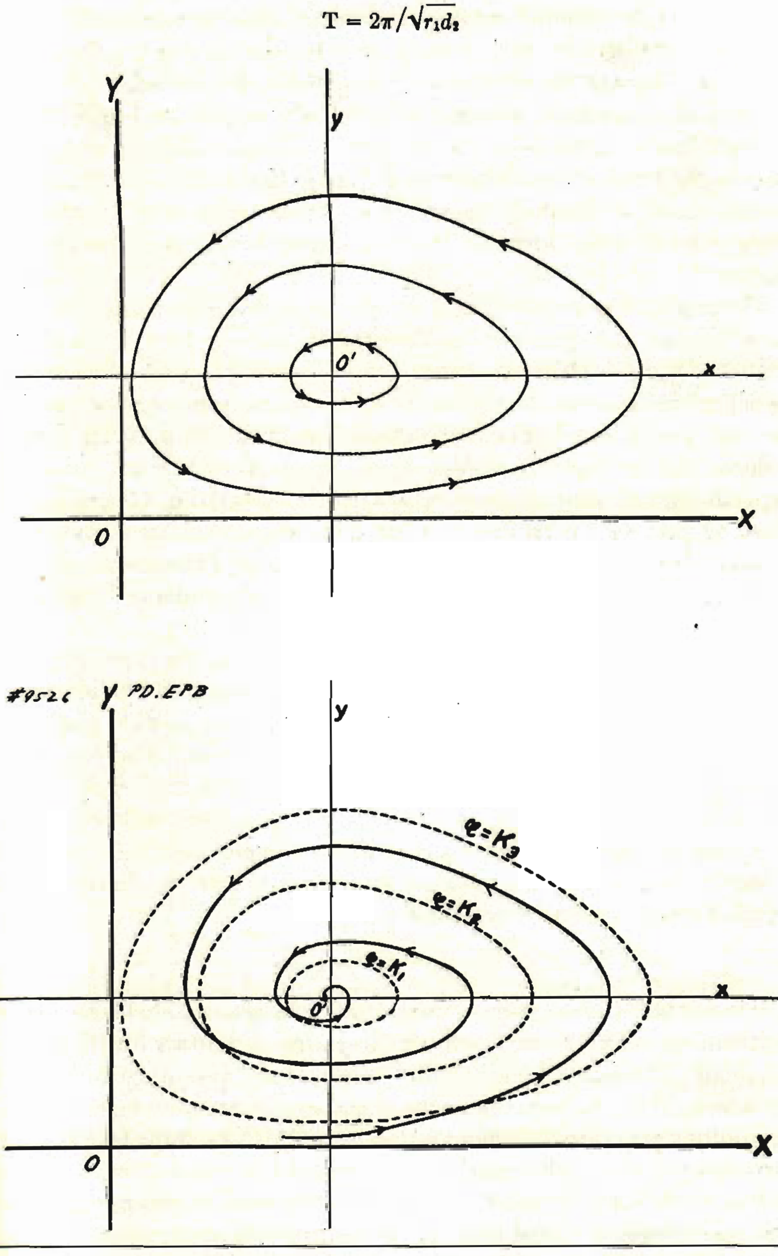

FIGURE 5.1. Curves illustrating oscillations in parasite and host populations. Each axis represents the number of one of the populations. (*a*) A cyclical process continuing indefinitely, the classic Lotka-Volterra oscillations; (*b*) Lotka's more exact treatment, resulting in a damped oscillation. (From A. J. Lotka, *Elements of Mathematical Biology*, New York: Dover Press, 1956, pp. 90, 91.)

predator might diminish its prey enough to make it vulnerable to other influences. Moreover, the addition of a second prey species would not necessarily benefit the first prey, but might to the contrary increase its chances of extinction, because the predator would no longer be constrained by the decrease of the first prey. Lotka thought this hypothetical case might have a counterpart in fisheries: heavy fishing of a common species could accidentally cause the extinction of a rarer species taken along with it, when normally the rare species would be protected by its scarcity.[20]

The predator-prey interaction and the more detailed malaria case study were but two examples used as illustrations for one part of the physical biology program. Different initial conditions could give rise to different models of interaction. Not all of these would correspond to situations in the real world, but Lotka illustrated them in his book along with the realistic models (Figure 5.2). At all times he was concerned not just to solve a specific example but to show how a general method of systems analysis could be used for any related problem. This was a fundamentally different approach from that followed by either Ross or Thompson, neither of whom specifically tried to place their studies in a broader context, mathematically or biologically.

But what was for Lotka an advantage, namely, the generality of his method, also stood as an obstacle to its acceptance, for it seemed too all-encompassing to be useful in applied research. Lotka was greatly disheartened to find that even those, such as Ross and Thompson, who might have been expected to appreciate the value of this work, failed to take much interest in it. We might speculate, then, about how he felt when he read in the pages of *Nature*, a year after the appearance of his book, that a celebrated Italian mathematician had come up with an almost identical solution to the predator-prey problem.

Lotka and Volterra

The mathematician in question was Vito Volterra, who held the Chair of Mathematical Physics in Rome and was already known for his work on the theory of elasticity and the theory of integral and integro-differential equations.[21] He had been interested in the idea of applying mathematics to the biological and social sciences as early as 1901, but only in 1925 did he turn abruptly and with remarkable perseverence to mathematical ecology. Indirectly he came to this line of work through his daughter, Luisa, who was an ecologist and was engaged at the time to a young marine biologist named Umberto D'Ancona. D'Ancona was engaged in an analysis of some market statistics of the Adriatic fisheries around the time of the First World War. He found it odd that there appeared an unusual increase in certain predaceous species during the war years, when fishing had almost

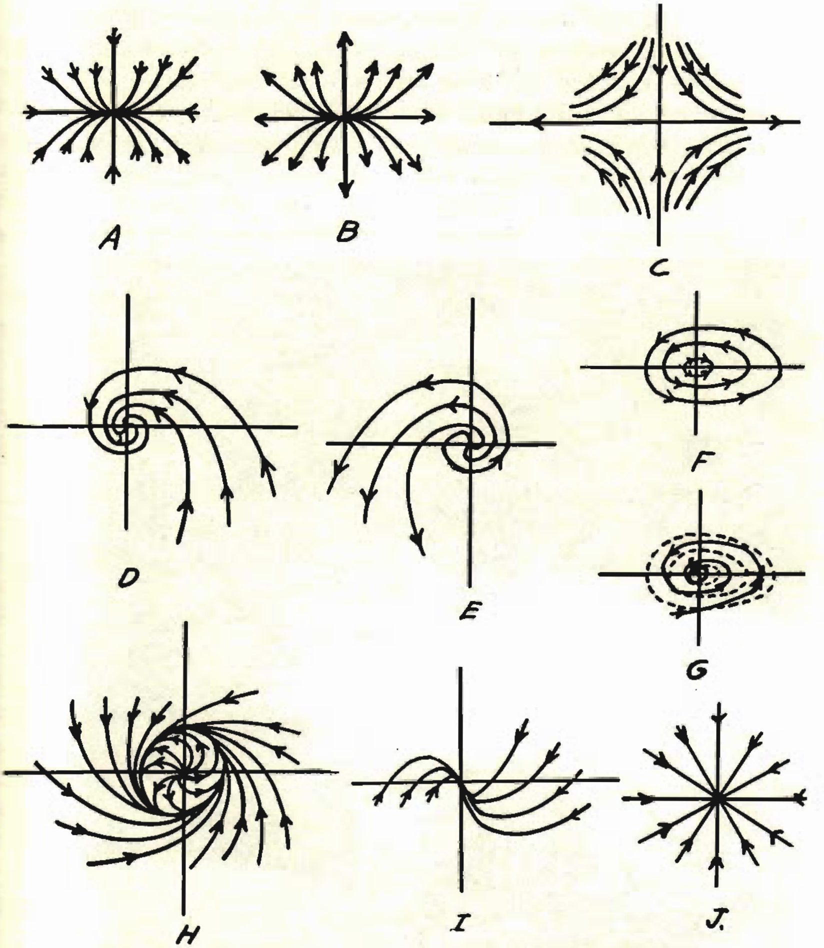

FIGURE 5.2. Lotka's diagram of integral curves, depicting different types of equilibrium, stable and unstable, in systems with two dependent variables. Cases F and G correspond to the host-parasite relations shown in Figure 5.1. The Ross malaria equations gave rise to two conditions, a stable equilibrium of type A and an unstable one of type C. The other types were included for purposes of illustration but were not associated with concrete examples. (From A. J. Lotka, *Elements of Mathematical Biology*, New York: Dover Press, 1956, p. 148.)

creased. Pondering the problem with his future father-in-law, he wondered if there could be a mathematical explanation for these changes.

Volterra took up the problem in earnest in 1925, and for the remaining fifteen years of his life became absorbed in the ramifications of this question. By 1926 he had published an elementary account in Italian of the interactions of species in a biological association.[22] A short resumé of this article published in *Nature* in the same year brought his work before the English scientific community[23] and the ever-watchful eye of Lotka. This article was the merest hint of what was to come; a light theme which was to form the basis for ever more imaginative and elaborate variations.

The article began with an analysis of a simple ecological problem, the interaction between a predator and its prey population. From there he

VITO VOLTERRA, 1860–1940
Photograph courtesy of Brandeis University Library

moved to a general analysis of population interactions, both predatory and competitive, sketching rapidly the outlines of a broad theory which would ultimately, he hoped, lead to an understanding of the dynamical behavior of the entire ecological community. Volterra considered his analysis to be part of evolutionary biology, an attempt to investigate, along mathematical lines, the day-to-day interactions of organisms as a first step toward a fully mathematical, general theory of evolution. It was, in short, the mathematical theory of the struggle for existence.

It was in the discussion of the two-species, predator-prey interaction that Lotka's and Volterra's work overlapped. With the identical problem to Lotka's, that of the numerical relations of a predator to its prey, Volterra easily derived the same equations and conclusions that the interaction would give rise to periodic oscillations in the two populations. This was the same problem Lotka had discussed in 1920 and which had first attracted Raymond Pearl's attention to his work.

It is interesting to note that the general method, apart from the applications made by Ross in epidemiology, had also been used in military strategy analysis. Frederick William Lanchester had used a similar technique to analyze combat during the First World War, and Lewis Fry Richardson independently proposed the technique to analyze combat in 1919.[24] Lotka appears not to have known of these other applications, but he certainly was aware of the parallels between the use of models in a military context and his own methods of model building. As he suggested in the *Elements*: "It is well worth considering whether interesting light may not be thrown on various problems of biological conflict, by the use of models designed to imitate the biological warfare somewhat after the manner in which the war game imitates the armed conflict of nations."[25]

For the conflict between predator and prey, Lotka expressed the relationship verbally as follows:

$$\begin{bmatrix}\text{Change in}\\ \text{number of}\\ \text{prey, } N_1\text{, per}\\ \text{unit of time}\end{bmatrix} = \begin{bmatrix}\text{Natural}\\ \text{increase of}\\ \text{prey per unit}\\ \text{of time}\end{bmatrix} - \begin{bmatrix}\text{Destruction}\\ \text{of prey by}\\ \text{predators per}\\ \text{unit of time}\end{bmatrix}. \tag{5.2}$$

$$\begin{bmatrix}\text{Change in}\\ \text{number of}\\ \text{predators,}\\ N_2\text{, per unit}\\ \text{of time}\end{bmatrix} = \begin{bmatrix}\text{Increase in}\\ \text{predators per}\\ \text{time, as result}\\ \text{of ingestion}\\ \text{of prey}\end{bmatrix} - \begin{bmatrix}\text{Deaths of}\\ \text{predators per}\\ \text{unit of time}\\ \\ \\ \end{bmatrix}. \tag{5.3}$$

These equations can be translated into differential equations for the prey species, N_1, and the predator, N_2:

$$\frac{dN_1}{dt} = r_1 N_1 - k_1 N_1 N_2, \tag{5.4}$$

$$\frac{dN_2}{dt} = k_2 N_1 N_2 - d_2 N_2, \tag{5.5}$$

where r_1 is the coefficient of increase for the prey species (births minus deaths); d_2 is the coefficient of mortality of the predator; and k_1 and k_2 are constants.

Comparing the growth of the prey species to that of the predator, we have

$$\frac{dN_1}{dN_2} = \frac{N_1}{N_2} \frac{(r_1 - k_1 N_2)}{(k_2 N_1 - d_2)}. \tag{5.6}$$

Integrating this equation and graphing the solution, a family of closed curves results, which depicts the continual oscillation of the two populations. Both Lotka and Volterra obtained the same cyclical solutions, although with slightly different reasoning: Lotka followed the reasoning of the above word-equations, whereas Volterra used what he called the "method of encounters."[26]

The method of encounters began with an analogy between physical and biological aggregations. Volterra likened the individuals in a biological association to molecules of a gas in a closed container. This comparison gave him his mathematical point of entry into the problem of how they interacted. In statistical mechanics, the number of collisions between particles of different gases is proportional to the product of their densities. In the same way, Volterra supposed that the events in a biological aggregate depended on the number of "encounters" between individuals, where the probability that one individual would encounter another would be proportional to the product of the numbers of both species. Each encounter was presumed to lead to an immediate result for each individual, which might be favorable, unfavorable, or neutral. The method of encounters was the mathematical counterpart of Lotka's method of systems analysis using Taylor series expansions, described above. It allowed Volterra to set up equations describing the course of each species and to generalize further to the case of n species.

As this summary indicates, there were a great many simplifying assumptions involved in both cases. In particular, the equations did not allow for the influence of the density of the population on its own rate of increase; that is, the populations always tended to increase exponentially and not logistically. The populations were also assumed to be homogeneous: each individual the same age and size as every other and invariable over time. Finally, each encounter between predator and prey would have an immediate effect on the individuals involved. The oscillatory behavior therefore presumed the simplest kind of interaction between the two populations, excluding other biological and environmental variables.

Despite recognition of these unrealistic simplifications, Volterra expressed his conclusions in the form of three "laws." The first, the "law of the periodic cycle," stated that the fluctuations of the two species were periodic in nature and depended only on the initial conditions and the various coefficients of increase and decrease. The second, the "law of conservation of the averages," provided for the constancy of the average numbers of the two species, all else being constant, no matter what their initial numbers were. The third, "the law of the disturbance of the averages," stated that, if an attempt were made to destroy the individuals of the two species of predator and prey uniformly and in proportion to their numbers, the average number of the prey species would increase and that of the predator would decrease. This last law would imply, for instance, that a temporary halt in fishing would benefit the predator, a prediction which seemed to be borne out by D'Ancona's independent observations based on the statistics from the Italian markets. The apparent confirmation of theory by observation suggested to Volterra that he was on the right track.

When Volterra's article appeared in 1926, Lotka had settled into his job at the Metropolitan Life Insurance Company and was pursuing his demographic studies with energy and satisfaction. He had little time left over to devote to physical biology, but Volterra's piece stirred him to write a letter to the editor of *Nature*, pointing out areas of overlap with his book.[27] The letter was published with a reply from Volterra acknowledging Lotka's priority in certain areas, but indicating quite rightly that there were still important differences between them. From this polite exchange there began a brief but mutually respectful correspondence between the two, from which Lotka drew a welcome measure of moral support:

> Your very kind interest and good wishes are of material assistance to me in renewing my energies on a topic in which there has not always been much encouragement for my work and in which I had almost come to feel that I would not be able to do much more hereafter, but I feel differently since reading your letter.[28]

For all Lotka's satisfaction that a mathematician of Volterra's rank should have indirectly endorsed his results, the problem of priority worried him. He decided to write a review article discussing the relation between his and Volterra's contributions. Raymond Pearl promised him space for it in *The Quarterly Review of Biology*. The manuscript began with a justification of the use of a chemical viewpoint in biology; dwelt at length on the competition and predation cases as discussed by Volterra, with supplemental analysis by Lotka; moved to a consideration of energy relationships; and finally ended with a philosophical discussion of perception and consciousness and their relation to physics.[29] For the most part, the intended article was a condensed version of the *Elements*, with more detail on the areas pertinent to Volterra's investigations. As Lotka worked on the manuscript, Volterra himself was busy elaborating and publicizing his own work: he expanded the early treatment with a detailed study published in 1927 in Italian, while shorter articles and translations of the 1926 paper appeared in French, English, and Russian.[30]

Slowly Lotka's discussion took shape. By mid-year in 1928 he had decided to publish some of the technical details ahead of time, for reasons he explained to Pearl: "The fact is that I am somewhat in fear of anticipation of my other work at the hands of Volterra. So far he has barely touched on the phase of the matter which I am taking up, but there is always a risk that he might branch out in that direction."[31] Apart from this short piece, hidden in a mathematical journal, nothing of more general interest appeared for three years. In 1931 Lotka had written only one short article on the mathematical theory of capture,[32] similar to his earlier mathematical paper. Beginning with the predator-prey equations, he considered the conditions under which a predator found and captured its prey in a given territory. This was an extension of the discussion in the *Elements* in which he had used the chess-game analogy, and it resembled in its details and tone a problem in military strategy. The article, published in 1932, was to be followed by two others, on "frequency of capture" and "influence on inter-species equilibrium of modification in the characteristics of competing species."[33] These were never published, but a companion article on Volterra's competition equations, also published in 1932, may have been a preliminary version of the third part.[34] In the meantime, Pearl was still awaiting the review article for his journal.

In 1931 the appearance of a book by Volterra, *Leçons sur la théorie mathématique de la lutte pour la vie*,[35] increased Lotka's sense of urgency to publish. The book was compiled from a lecture series Volterra had given in the winter of 1928–1929 at the new Institut Henri Poincaré in Paris. Here Volterra elaborated some of the ideas he had introduced in the earlier papers, with new refinements to make up for the lack of realism of the early models. He had early on made a distinction between two types of biological associations, conservative and dissipative ones. Conservative systems were analogous to frictionless systems in mechanics: in a biologically conservative system the oscillations set up by the interactions of the species remained constant, with none of the species going extinct or increasing indefinitely in a finite time. This was the situation represented by the predator-prey oscillation described above.

But Volterra believed that absolutely conservative systems were ideal cases, which only approximated the natural situation. It was more likely that natural associations were dissipative, that is, the fluctuations of the species were damped and the association tended toward an equilibrium state, analogous to the effect of internal friction in material systems. The main difference between the two systems was that the dissipative system took account of the effects of a population's size on its own growth (as, for instance, if the populations grew logistically, rather than exponentially). These effects would tend to dampen the oscillations between the different species. The distinction therefore introduced a more realistic modification to the idealized system of continual oscillations.

The *Leçons* developed the mathematical distinctions between these two systems and included a chapter discussing time lags as well. Volterra referred to these time-lag effects as "hereditary phenomena"; heredity referring not to descent, but to the fact that a population's history could influence its present behavior. This meant that an encounter need not have an immediate effect, but might be noticeable only after a certain time interval; the analogy here was with conditions of retardation or drag in mechanics.

Although these modifications were meant to make the models more realistic, the book was essentially an elaborate mathematical argument, based on the principles of mechanics as they might be applied to biological aggregations. Even in their more sophisticated form, the models were based on many unrealistic assumptions, from which some rather far-reaching conclusions had been deduced. But as Volterra fully admitted, this was to be seen as a work in pure mathematics, even if it was couched in biological language. It was, as he wrote, the rational phase of the study of biological associations. Those who would embark on the applied phase would require more profound discussion, based on fact and experience, of the initial hypotheses.

Although Lotka found the discussion in the book admirable, he was disappointed to find his own work given superficial treatment in the historical chapter, written by D'Ancona, concluding it. His grievance was directed not so much at Volterra, who had conscientiously mentioned Lotka's work in all his publications after 1926. Rather, Lotka was concerned that other writers, influenced by Volterra's brief references, were perpetuating the impression that Lotka's work was insignificant in comparison with Volterra's. His feelings were aggravated by the appearance of several publications which favored Volterra's work and seemed to be influenced by personal connections to Volterra himself.

One of these was a review article on mathematical biology published in 1927 by Joseph Pérès, a mathematician who had helped W. R. Thompson a few years earlier.[36] Pérès was also a former student of Volterra and a later collaborator, so it was not surprising that his article reflected Volterra's contributions overwhelmingly. Lotka was dismayed when he came across the article a year later, as he wrote to Pearl:

> He gives eleven pages to Volterra's work and three or four footnotes to mine. I think you will agree with me that this is definitely a case of displacement of the center of gravity. After reading his paper, which is very good as

> far as it goes, I was more pleased than ever at the opportunity which you are kindly offering me of coming out before American Readers with a statement of the situation as viewed from our side of the issue.[37]

Each discussion of mathematical ecology that appeared seemed to compound the injury Lotka felt. Karl Friederichs, a German entomologist, included a discussion of the researches of Thompson, Lotka, and Volterra in his zoological text published in 1930.[38] All Lotka saw was that he had given Volterra's work much greater prominence. Feeling by now wholly exasperated, yet remaining strangely silent despite his acute sense of being neglected, Lotka explained his actions to Friederichs:

> Perhaps I might add that when I allowed the correspondence relating to the Volterra matter to close after a very brief letter from me, this was not because I acquiesced in the position that Volterra had taken, but because I have a very strong personal aversion to priority disputes. . . . Through the kindness of the editors of one of our journals I have been given an opportunity to express myself at length on the matter and I hope to do so in due course; but as I have already stated, my time is greatly occupied and I prefer to give my efforts to productive work rather than to squabble about priority. Nevertheless, the occasion seems to call for some action on my part if I can possibly get down to it.[39]

Lotka never did fulfill his plans to publish an assessment of Volterra's work in relation to his own. Neither the review article for Pearl, nor a review of Volterra's book which he had intended to write for Pearl, were ever completed. Just at that time, however, a new opportunity to express his ideas was offered to him through the mediation of a Russian geophysicist and mathematician, Vladimir Aleksandrovich Kostitzin. Lotka made use of the offer, not to debate with Volterra, but to summarize his physical-biology point of view for a different audience and to gather his latest results in demography into one book.

Kostitzin, originally trained as a geophysicist, left Russia for Paris in the late 1920s, whereupon he came into contact with Volterra, who was giving a lecture series at the Sorbonne, and developed an interest in mathematical biology. He maintained close ties with Volterra throughout the 1930s.[40] In 1933 he was working on a mathematical study of symbiosis and parasitism (his wife was a parasitologist), which was to be published as part of a series on biometry and statistical biology edited by the French geneticist Georges Teissier.[41] Kostitzin's own work had been influenced by Lotka's extensions of Thompson's results, and in connection with this series he contacted Lotka to see if he would be interested in contributing to it. Lotka immediately suggested a two-part treatment of biological aggregations, the first to be devoted to demographic phenomena in a single population, the second treating of mixed populations comprising several species, the whole to be tied to the principle of "evolution."[42]

The final product, published as *Théorie analytique des associations biologiques*,[43] was somewhat narrower in scope. The first part, which appeared in 1934, was an overview of the issues and general methods described in the *Elements*. One noteworthy change was Lotka's more explicit appeal to ecologists, with references to the relevant writings of R. N. Chapman and Charles Elton. His discussion of Volterra was minimal, confined to a single footnote correcting a historical error of priority in the case of *n* species interacting. The second part did not appear until 1939 and was entirely demographic, focusing on human populations. His intended treatment of mixed populations of several species never appeared, except in so far as it was included in the general discussion of the first part. But Volterra and D'Ancona had subsequently published a monograph on biological associations in 1935 as part of the same series,[44], and it is possible that Lotka (or the editors) felt that his treatment of the same problem would be redundant.

Lotka's worry that the promotion of Volterra's work was threatening his own position was excessive. The mild priority dispute, which ensured Lotka at least a footnote, however brief, in Volterra's articles, helped to disseminate news of Lotka's research to the proper audience. The tendency to lump Lotka and Volterra together, however, also helped to obscure the differences between them. On the whole, Lotka's emphasis on energy relationships and the economic tone of his writings continued to be overlooked by biologists. But in the case of predator-prey interactions, at least, his priority was firmly established, and the equations with oscillatory solutions describing the changes in the two populations came to be known as the Lotka-Volterra equations.

By the late 1930s the differences which stemmed from Lotka and Volterra's different ideas of physical biology became more apparent. Lotka had become totally involved in demography (although he did keep abreast of the biological literature relevant to population studies), and this emphasis came to dominate his later work. The English revision of the *Théorie analytique*, to be called *Analytic Demography*,[45] was to be even more restricted to human populations, with analysis of certain demographic problems which he had not considered in the French version. He died in 1949 before completing this work. Whereas Lotka was focusing ever more closely on the case of single-species populations, trying to extract as much specific information as was possible through demographic analysis, Volterra was moving toward a more sweeping statement of the principles of mathematical biology. This involved the more conspicuous use of physical analogy, to the extent that he defined mathematically a quantity called "demographic energy" (actual and potential), which was conserved in the same way that the energy of physics was conserved.[46] He also defined "demographic work" and the "principle of least vital action," all of which was a direct transfer of the methods and concepts of physics into biology. These were merely more exaggerated uses of the same analogical reasoning which Volterra had employed in his early articles.

Concurrently with these highly mathematical studies, which had by the late 1930s covered enough paper to be widely known, if imperfectly understood, in the ecological community, there arose yet another mathematical strategy to add to the range of choices available to ecologists. This one appeared independently from the far side of the globe—Australia. It bore some resemblance to Thompson's and Volterra's approaches, and some important differences. It grew from a student's rude remark, and before the decade was out, it had lit the fire of one of the most heated controversies in population ecology.

The Balance of Nature

While Thompson, Lotka, and Volterra were pursuing their different courses in mathematical ecology, an entomologist working in Australia, Alexander John Nicholson, was beginning to work through his own puzzled thoughts on population regulation. He had been lecturing in entomology since 1921 at the University of Sydney, his first academic position following his studies in zoology, chemistry, and botany at the University of Birmingham, England, where he received his B.Sc. and M.Sc. degrees.[47] At Sydney he found little time for research, for he had first to organize a whole new subdepartment of entomology. At the start there was neither equipment nor material suitable for teaching, and he had to spend much of his time collecting and photographing insects for class use.

One of the rewards of teaching surely comes when students express skepticism about the established truths they are handed in the classroom, for it is by such rude queries that teachers are sometimes jolted to reconsider familiar arguments. So it was with Nicholson. He had taught that one of the means by which populations were limited was through the limitation of the food supply. One of his students, having answered an examination question as he had been taught, finished by asserting that, nevertheless, he did not believe it: the worst pests did not consume all of their food supply, even without artificial control measures. This observation was not new to Nicholson, but it caused him to think more carefully about how populations were controlled in nature.

He reasoned that an increase in a population of insects would bring about an increase in its enemies as well, which would prey more heavily on the first population. A species and its enemies would therefore tend to reach a balance at which the number of prey was just sufficient to support as many predators as would destroy the surplus number of prey produced. This idea resembled the earlier arguments of Stephen A. Forbes, especially his suggestion that species and their enemies would tend to develop a "common interest" which would produce a balance in nature. Nicholson then concluded that a population may, in a sense, be thought to limit *itself*, because it would induce greater opposition to further multiplication as it grew. From these ideas he developed a theory of population regulation based on the importance of competition within a species as the main regulating mechanism.

His first opportunity to apply these ideas came in 1927, when he was faced with the duty of writing an address as the retiring president of the Zoological Society of New South Wales. He had collected a large number of slides illustrating mimicry and protective coloration, and he decided to give the address on that topic. This talk soon grew into a larger study of mimicry which, along with other manuscripts dealing with population regulation, became his thesis for the Doctor of Science degree.[48]

By 1930 he had expanded this work into a massive, but still largely speculative, account of the possible mechanisms of population regulation. His efforts to publish it as a book came to an abrupt end when the referee turned it down. He picked what he thought were the most salvageable sections for separate publication: these dealt with the host-parasite interaction, which had been developed more precisely than other examples in the manuscript.

Nicholson's initial argument was nonmathematical, but like a mathematical argument it was deductive in nature, based on a set of simplifying assumptions, to which were added a few arithmetical computations. The computations were not based on field data, but were hypothetical numerical examples that helped him to depict his argument graphically in the absence of exact information. The hypothetical examples led to unexpected conclusions. His reasoning suggested that the interactions between host and parasite populations would lead to a system of oscillations that increased over time. That is, as a population began to swing back to its equilibrium position, it would tend to go too far, producing an unstable situation of ever-increasing oscillations.

Nicholson was disconcerted by this result. He appealed to a physicist colleague at the university, Victor Albert Bailey, for some mathematical help. Bailey converted Nicholson's verbal arguments into mathematical form and came up with the same conclusions, although he was able to state them with greater precision. Together they worked out more details of the argument, considering various initial assumptions and showing how different conclusions could be derived. The basic theory was summarized in two articles published in 1933 and 1935: the first, written by Nicholson, gave the verbal and arithmetical argument, while the second covered much the same ground with the addition of Bailey's mathematical proofs.[49]

Bailey's point of view reflected that of a physicist, just as Volterra's had. He considered the movement of parasites in search of hosts to be analogous to Maxwell's theory of the mean free path of a particle in a gas. In keeping with the comparison to the dynamic theory of gases, he assumed that density was uniform, and that search proceeded randomly in the population as a whole. Because Nicholson had based his argument on discrete-time intervals—that is, assuming a definite succession of generations (as opposed to the continuous-time models of Lotka and Volterra)—Bailey's mathematical verifications also used the same method. On his own, however, he extended the study to continuous interaction and worked out some further mathematical details in separate articles.[50]

Quite apart from Bailey's use of physical analogies to construct the

ALEXANDER JOHN NICHOLSON, 1895–1969
Photograph courtesy of Commonwealth Scientific and Industrial Research Organization Archives, Australia

basis of the mathematical argument, Nicholson's conception of the problem made use of an analogy which depended on the idea that there existed in nature a balance. This was based on the observation that population densities changed in response to changes in the environment. To convey his ideas, he employed the image of a population functioning like an instrument or a machine. The balance was conceived to be analogous to that of a balloon floating in the atmosphere. As the ambient temperature changed from day to night, the balloon would undergo changes in height and volume, continually rising and falling as its position of equilibrium with the surrounding air moved. In the same way, Nicholson thought that population densities were continually tending toward a stable level in relation to fluctuating environmental conditions. Experimental studies of the kind carried out by Pearl, Chapman, and others seemed to support the impression of balance gained from field observation; after a period of growth, a laboratory population would attain a certain steady density which represented its position of balance in the laboratory environment.

But the fact that a population would tend to stabilize at a given density under given conditions did not imply that populations were actually controlled by external conditions, such as climate. If, as Nicholson argued, the existence of balance implied the existence of a controlling factor, then it was also the case that such a controlling factor had to be responsive to changes within the population itself. Climatic effects usually were felt irrespective of the density of the population. A true control had to act with increasing severity as the population density increased. Nicholson felt that there was only one factor which met this requirement of density-dependent action, and this was competition. Competition by its very nature became more severe as density increased; it therefore had to be the mechanism behind population regulation. Organisms could not be thought of as having direct and immediate rapport with the environment at all times, rather they were indirectly responsive through the mediating influence of competitive relations with members of the same species. This was not to deny that sudden climatic changes did at times kill off portions of the population, but only to assert that such effects were not responsible for the balance of populations. The existence of competition was therefore inseparable from the idea of regulation.

COMPETIT.

In another metaphor, Nicholson compared the controlling function of competition to that of the governor on a steam engine.[51] Just as the governor responded to the weight of different loads on the engine by adjusting the steam output and thereby varying the power, in the same way a change in environmental stress caused the level of competition to rise or fall, until the density was again adjusted to balance the stress. Competition was not as sensitive as the governor of an engine, however, with the result that fluctuations in density would occur as the balance was readjusted. These metaphors did not always clarify Nicholson's reasoning. Competition was a vague and broadly defined concept. Without a clear connection to practical work, this deductive method would strike many as excessively abstract. Concrete experiments which would help to put the ideas into context would follow only after a delay of several years.[52]

The purpose of his theory was not just to contribute to economic entomology, however, but to clarify the role of natural selection in relation to the balance of nature. In his earlier study of mimicry, he had been struck by the fact that well-camouflaged species seemed to be no more successful than their relatives that lacked this adaptive property. This observation suggested that the success of a species (as seen by its numbers) was somehow independent of its possession of a given adaptive trait. Natural selection was responsible for producing adaptive characteristics, such as mimicry, but it was not responsible for the success of the species.

To modern ears this argument sounds odd. Nicholson imagined that competition acted as a counterforce to natural selection in the fixing of genetic traits during the course of evolution. He argued as follows: when individuals with advantageous characteristics appeared, they would tend to be preserved by natural selection. But their preservation would cause a population increase as well, until competition was so intense that some of the members of the original population would be destroyed. Gradually the new, favored type would come to replace the original type. Natural selection (preservation of new types) was seen as a disturbing influence which disrupted the balance of nature; whereas competition restored and maintained balance during and after "selection," enabling new types to replace old ones.[53] This was a rather literal interpretation of natural selection. Some adaptations therefore were of little value to the species as a whole, because they arose completely by competition within the species. This conclusion seemed compatible with his studies of mimicry in butterflies, because the degree of mimetic resemblance appeared to reach a level of perfection far beyond its effect on the general viability of the species.

This argument threw a strange twist into Darwin's discussion of natural selection. For Darwin, the corollary to the struggle for existence was that the structure of an organism was related, often in subtle ways, to that of all others with which it had to compete, or on which it fed, or from which it had to escape. Both intra- and interspecific competition could determine given adaptive structures. But whereas for Darwin natural selection acted through competition as part of one process, Nicholson made a sharp distinction between natural selection as a disruptive mechanism and competition as a regulatory mechanism.

Nicholson was trying to explode what he took to be a common but wrong belief, that natural selection had two functions: to select and to produce balance among populations. He felt that this idea of natural selection was an unfortunate example of teleological thinking. He argued, to the contrary, that natural selection functioned only to select and not to produce balance; that is, it improved adaptation but had nothing to do with the regulation of populations. He did not say where this common view originated, but recalling Stephen Forbes's nineteenth-century merger of Darwinian natural selection with Spencerian arguments about balance, it is possible that the view to which Nicholson objected was the product of a similar combination of Darwin and Spencer that went into early ecological theory. Nicholson believed that the view that natural selection created a balance in nature was caused partly by an erroneous concept of adaptation as the fairly close adjustment of animal to environment. But Nicholson did not think that ecological studies really supported this view of adaptation. Once it was understood that adaptation did not imply a precise balance of organism and environment, he felt, it would follow that an improvement in adaptation would be seen as having nothing to do with the balance or limitation of populations. His argument is at times difficult to unravel, but it illustrates the complexity and diversity of opinion surrounding the interpretation of natural selection, adaptation, and population regulation in the decade leading up to the modern synthesis.

Nicholson and Bailey were interested mainly in animal populations. For practical purposes they narrowed their view of competition to include only that occurring when animals were engaged in a search for essential resources: for instance, a parasite in search of its host. Under these conditions, competition depended on two basic properties: first, the species' power of increase; second, the individual's ability to exploit the surrounding territory to gain what it needed for survival. The density at which competition would be felt would depend on these two properties. The second property included a wide category of specific traits, such as the efficiency of organisms at finding, capturing, and utilizing resources, as well as the efficiency of their prey at avoiding capture.

Their discussion reflected the same awareness that Lotka had shown of the need to consider the detailed behavior schedule of the individuals, interpreted in energetic terms, before species relationships could be properly understood. Lotka was hampered by lack of data and was not able to carry his analysis very far. Nicholson and Bailey experienced the same obstacle, but they tried to overcome it by gathering all these behavioral and energetic terms into a single measure. These were summed up in the characteristic which Nicholson called the "area of discovery." This was defined as the area effectively explored by an average parasite individual, but it was intended to represent all the things that affected the efficiency of animals as they searched for resources over a given territory in their lifetimes. Without knowing exactly what these efficiencies were, species could still be compared by measuring their respective areas of discovery.

The rest of the theory followed from a detailed consideration of this problem, analyzed under a variety of hypothetical circumstances which might be expected to approximate real situations.

Nicholson and Bailey first considered the types of parasitism under which a steady state would be produced. They then moved to an analysis of the situation where a population was removed from its equilibrium position and would tend to return to its steady state level. Interpreted as a problem of competition while searching for food, and based on discontinuous interaction, the host-parasite relation took on a fundamentally different aspect than that given it by Lotka and Volterra. The "Lotka-Volterra equations" did not take into consideration the effect of competition from members of the same species. Moreover, although Volterra had later considered the effects of time lags in the results of an encounter, neither had included the delays which would result from the age distribution of the populations. That is, they assumed that individuals were born mature. In Bailey's analysis, both sorts of delays were taken into account. He found that when the age distribution in particular was considered, he did not obtain the steady state oscillations of the Lotka-Volterra model, but rather the unstable system of increasing oscillations that Nicholson had first found so disconcerting.[54] Nicholson and Bailey knew that these increasing oscillations were not found in nature. They suggested that the result of these oscillations would be the breaking up of the population into many widely separated groups, each group waxing and waning, finally disappearing and being replaced by new groups. In the predator-prey interaction, Nicholson concluded that, although the same conditions necessary for oscillations existed, they would likely be less violent in nature and would tend to produce a stable system of oscillations, rather than the unstable one of the host-parasite interaction.

In general, Nicholson and Bailey hoped for a more exact treatment of the problem of population regulation than any of their predecessors, with more careful consideration of the alternative outcomes that would result from different biological assumptions. But apart from the differences in their orientation and in the nature of their specific conclusions, their results were of the same character as those of Lotka and Volterra. They found that the interactions between species would, all else being equal, produce oscillations in the two populations, as distinct from oscillations caused by external environmental conditions. These conclusions were not meant to be exact representations of nature, but to indicate the ideal behavior of populations under simplified conditions. As theoretical predictions, they were intended to serve as guides for experiment and observation.

Nicholson and Bailey planned to write a series of five articles on the subject, of which Nicholson's 1933 paper was a summary, but only the first part of the joint series was published. Bailey sent it to Lotka in 1933 in manuscript form, with a request for Lotka's help in finding a suitable publisher for the series.[55] Lotka was irritated to find that his own work was hardly discussed, but he complied with the request and sent it to Raymond Pearl, though coupled with a testy letter to Pearl expressing his annoyance at not receiving proper credit.[56] Pearl sided with Lotka and rejected the article, adding that it appeared far too speculative for his journal,[57] but more likely feeling that it was too mathematical. Lotka sent the manuscript back to Bailey with a long letter explaining his dissatisfaction that his priority and contributions to biology had been overlooked in recent literature.[58] The article finally appeared in 1935 in the *Proceedings* of the Zoological Society of London. It began with a paragraph summarizing Lotka's work, but made the point that Lotka's equations seemed too general to yield the specific kinds of conclusions which Nicholson and Bailey were after. Moreover, they had not been able to derive their theory from Lotka's fundamental equations. In general, they felt a greater affinity toward Volterra's methods, which mirrored Bailey's own image of the population in analogy with the theory of gases.

Differences and Similarities

The researches of Thompson, Lotka, Volterra, Nicholson, and Bailey represented the principal lines along which theoretical population ecology developed in the 1920s and 1930s. Each was guided by a different method of reasoning, reflecting the different backgrounds and different goals of the authors.

Thompson's strategy was by far the most cautious and the most realistic. He believed in formulating a problem strictly in biological terms first, using mathematics only to simplify the statement of the problem. Given the lack of biological information on the populations he studied, his analysis did not take him very far. Nevertheless, he began optimistically, trusting that the use of mathematical models would give entomology the predictive ability of the physical sciences and would in turn guide the applied strategies of economic entomologists.

Nicholson shared many of Thompson's goals for applied science, though he had broader interests in evolutionary biology as well. He was on the whole much more prone to speculation than was Thompson, for although he had not had time for much research, he had time to teach and to think. He had an imaginative, metaphorical perception of the population, one that would later give Thompson much cause for complaint. But with Bailey's help, he hoped to create models which were both precise and realistic, incorporating better assumptions based on what was known of the behavior of host and parasite populations. They perceived the increased realism of their models to be a major improvement over Volterra's models.[59]

Volterra, on the other hand, came to the mathematical theory of the struggle for existence from his background in classical mechanics. His ways of thinking, his ideas of science, were those of classical mechanics. "All of us in our generation," he wrote in 1907, "were raised with those principles that a modern world calls mechanicist; and indeed, that all phenomena, at least those under the domain of physics, could be reduced to phenomena of motion and could be brought within the orbit of classical mechanics, was a dogma adhered to by every school and whose origin is lost in the remote Cartesian philosophy."[60] In 1925, through a chance inquiry, he seized the opportunity to extend this worldview to biology; it was natural that he would try to create, in essence, a biological mechanics.

The success of mechanics was in turn due to the use of the techniques of calculus. A few starting hypotheses, though not very realistic, would allow the problem to be represented mathematically with calculus. By seeing how well the mathematical predictions accorded with reality, the initial hypotheses could be adjusted to make them more realistic. The method that Volterra used therefore began with generality and worked toward greater realism. It started with a coarse view of nature and by a series of steps approached the fine reasoning of the geometer.[61] But in order to create this first, coarse view, Volterra had drawn heavily upon analogies taken from physics and used as heuristic devices. He had let his imagination run. If the metaphors were too abstract from a biological point of view, he could calm the reader with the assurance that he was, after all, engaged in a work of pure mathematics.

It was in the use of analogies that his methods were in greatest conflict with Lotka's. Lotka had come from the same tradition in physics, but he developed his analogies differently. He saw physical biology as being based on identity of type between physical and biological systems: this led him directly to the study of matter and energy transformations. When Lotka spoke of "energy" it was in the same sense as that understood by physicists; his use of the term "dynamics" denoted the study of energy transfers through the biological system. For Volterra, "biological dynamics" meant the enunciation of energetic principles in biology analogous to the ones in physical dynamics, such as the conservation of energy and the principle of least action. He did not look at energy exchanges in the population, but at the transformation of a wholly metaphorical "demographic energy." Lotka's particularly careful habit of thought, his attention to the meaning of words, his precision in the use of analogies, and his skepticism of metaphorical entities taken as realities, reflected the training in science which he had received from John Henry Poynting. These were

Lotka - fundamental equivalence with physics (principles

Volterra - formal equivalence

Poynting's habits of reasoning, which had so inspired Lotka in his student days and had guided him in the development of his ideas.[62]

Lotka was interested in uncovering laws of nature, following the model of physics, but he did not adopt Volterra's course. He was aware that the equations which he and Volterra had developed independently were formal statements which need not have any deeper significance. He felt it necessary to go beyond formal expressions in order to deduce necessary relations from known principles. In this way, it might be possible to arrive at a law which was not merely an empirical rule, but "a law of nature that brooks no exception."[63]

Analysis of this kind had to be based on a realistic perception of the individual, which for Lotka meant treating it as an energy transformer capable of a wide range of adaptive strategies to ensure its survival. But his analysis was not conducted with reference to an *actual* individual, species, or population; rather, the individual itself was idealized to represent a general class of energy transformer, for which there might be many examples in nature. As Lotka explained:

> It will not be necessary or even desirable to deal primarily with specific living organisms, but with transformer *types* possessing properties characteristic of the physical *modus operandi* of living organisms. The kind of problem then to be studied will be the relation between the distribution of matter in the system on the one hand, and on the other the particular properties and variation in properties of the several types of transformers of which the system is composed.[64]

By idealizing the organism in this way, precision was lost but generality increased. A problem dealing with the interaction between a "pursued" transformer and a "pursuing" transformer, for example, could be reduced to a problem of geometry. Using mathematical techniques of analysis, one could then discuss, for instance, the influence of density and distribution of refuges in the territory on the probability that the "pursuer" would capture the "pursued." The hypothetical organism was a model in an analogous sense to the Carnot heat engine in physics. Carnot's engine, which existed only on paper, was composed of perfectly conducting and insulating parts through which heat was transferred and work performed. Though an ideal case, it illustrated the underlying physical reality later expressed in the second law of thermodynamics. In the same way, Lotka imagined that his models of energy transformers would lead to general principles, based on physical and biological reality, which would govern all transformers of that type.[65] An example of one such principle was his "law" that evolution proceeded in such direction as to maximize energy flow through the whole system.

Max. power law

The result of this point of view was that his predictions were qualitative and were framed as comparisons between types of situations. Such predictions were furthest removed from the goals of applied science; it is no wonder that they were the least used and appreciated at the time. Lotka came to recognize the inevitable gap in communication between himself and biologists, but he did not try to close it. In 1945 he still referred to his work as a special branch of physics and not of biology. But his demographic work fared better, as will be seen in chapter six.

Despite the radically different strategies represented in the glut of theories that emerged in these years, they all had the same underlying objective: to show that theoretical, mathematical approaches had a place in biology. Put even more strongly, they wanted to show that theory could *guide* experiment and research, and that it was not worth waiting until all the facts were in before engaging in speculation with the help of mathematical models. As Lotka wrote to Volterra, knowing he would have the latter's full support, "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."[66]

In the next chapter I shall describe how biologists responded to these choices of style and these grand claims. There were treasures here to satisfy many wants, and to provoke many jealousies. The range of responses extended from enthusiastic acceptance to hostile rejection. Many steered a middle course and remained interested but aloof, adopting, as Bacon had remarked of an earlier age, the prudent mean between "the arrogance of dogmatism and the despair of skepticism."[67]