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Author(s): Sharon Kingsland
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THE REFRACTORY MODEL: THE LOGISTIC CURVE AND THE HISTORY OF POPULATION ECOLOGY

SHARON KINGSLAND

Department of the History of Science,
The Johns Hopkins University,
Baltimore, Maryland 21218 USA

ABSTRACT

The logistic curve was introduced by Raymond Pearl and Lowell Reed in 1920 and was heavily promoted as a description of human and animal population growth. In subsequent years it underwent a barrage of criticism from statisticians, economists, and biologists, a barrage directed mostly against Pearl's claim that the logistic curve was a law of growth. Nevertheless, it emerged in the mid-1930's as a central model of experimental population biology, and in its various modifications has remained an important part of modern population ecology. The history of the logistic curve reveals that its acceptance was by no means straightforward: repeated promotion of the curve by Pearl and his connections to other scientists were both important in the establishment of its place as a tool of research. The people responsible for legitimizing the logistic curve—A. J. Lotka, G. F. Gause, G. Udny Yule, and Thomas Park—all had different degrees of direct contact with Pearl in the early years of its use, and these personal contacts facilitated the acceptance of the logistic curve despite the heavy criticisms. The history of the logistic curve reveals the complicated social processes which can underlie the development of scientific disciplines.

INTRODUCTION

THE LOGISTIC CURVE stands out in the history of population ecology as one of the more fruitful and at the same time unsatisfactory models of population growth. Over the years it has given rise, in its various modifications, to a wealth of experimental data and of hypothesis regarding population interactions, especially with reference to competition. But because it forces simplicity on a complex world, it sometimes leaves the experimenter with the impression that, after all, the logistic equation has revealed little about the biology of the events it describes. This ambivalence towards models such as the logistic model was expressed in 1952 by F. E. Smith, who recognized the value of armchair thinking along deterministic lines as a way of generating concepts, but was strongly critical of the lack of correspondence between the logistic theory and the experiments which purported to verify it. He concluded, "The degree of acceptance of such concepts as, for examples, the Verhulst-Pearl logistic and the Lotka-Volterra equations, is astonishing." Smith was responding justifiably to a prolific scientific literature on the logistic curve in which the notions of what constituted a law, theory, model, or proof were frequently confused.

The logistic equation was originally put forward in 1920 not as a convenient description, but as a law of growth, and was vigorously criticized by statisticians, economists,

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and biologists over the subsequent decade and a half, before being for the most part discarded. Yet it survived and finally emerged in a different context as one of the central models of experimental population biology in the late 1930's and 1940's. The shift from rejection to acceptance was by no means a straightforward process and was not simply due to ecologists' gradual recognition of the intrinsic usefulness of the curve. To a remarkable degree the logistic curve owed its survival to two other historical factors: one was the amount of promotion given to it by its inventor, Raymond Pearl. The other was the personal contact which Pearl fostered with those people who, in different contexts, helped to establish its validity: most notably the American mathematician Alfred James Lotka and the Russian ecologist Georgii Frantsevich Gause. A more detailed look at the history of the logistic curve makes its position in the ecological literature of the 1950's seem much less astonishing, and moreover reveals the underlying processes which could influence the acceptance of scientific models.

The logistic curve describes the growth of a population over time. In its simplest form it is S-shaped, symmetrical, and is described by the equation:

$$N = \frac{K}{1 + e^{a-rt}} \qquad (1)$$

where N is the number of individuals; t the time; e the base of natural logarithms; K the upper asymptote, or limiting population; r the maximum rate of increase in an unrestricted population; and a a constant of integration. The equation can also be written in differential form, which has the advantage that it can be readily derived and more easily related to the various assumptions underlying the curve:

$$\frac{dN}{dt} = rN\left(\frac{K - N}{K}\right) \qquad (2)$$

This equation expresses more clearly the basic postulate underlying the logistic theory, that the rate of growth decreases linearly as the density of population increases toward the upper limit of K. Three assumptions of this equation are (1) that r and K are constant; (2) that there are no time lags in the response of actual rate of increase per head to the change in numbers; and (3) that all individuals are equivalent in their effect on the reduction of the actual growth rate at each density. In fact, as was recognized later, these assumptions are unrealistic (Pianka, 1978, pp. 115–16). In this paper I shall try where possible to keep to the above modern notation for the sake of uniformity and clarity, but various authors have frequently used different symbols for the variables and constants.

THE LOGISTIC'S INVENTORS

The original inventor of the logistic curve was the nineteenth-century Belgian mathematician Pierre-François Verhulst, who began work on the problem of population growth at the instigation of his mentor, Adolphe Quetelet. Quetelet had proposed in 1835 that the resistance to the growth of a population was proportional to the square of the speed with which the population increased. He found this relation appealing because he saw in it a direct physical analogy to the resistance that a medium opposes to a body travelling through it (Quetelet, 1835, v. 2, p. 277). He suggested that Verhulst submit the principle to examination and apply it to whatever population data were available.

Verhulst began by reasoning that in the early states of growth, a population would increase exponentially until such time when crucial resources, in this case farmland, became limiting. He called the population existing at that moment the "normal" population: the number in excess beyond the normal population was called the "superabundant" population. Assuming that the rate of growth was retarded by some function linearly proportional to the size of the superabundant population, he obtained the differential equation for a symmetrical sigmoidal curve of growth, which he labelled the "logistic" (Verhulst, 1845). In fact, his line of reasoning did not correspond to the mathematics of his derivation of the curve: the logistic does not follow from the idea that growth shifts abruptly from an exponential rate to a slower "logistic" one at some crucial density. In any case, Verhulst realized that the logistic was only one possibility; the obstacles to growth could also be proportional to the square of the superabundant population, for example. In a second memoir, Verhulst (1847) suggested that the obstacles are proportional to the ratio of the superabundant to the total population.

Verhulst did not explain why he had chosen the term "logistique" for his first curve, but in the nineteenth century the French word was used to signify the art of calculation, as opposed to a branch of theoretical arithmetic such as the theory of proportion. It was commonly applied to a type of logarithm used in making astronomical calculations. Verhulst probably intended this term to convey the idea of a calculating device, from which one could determine the saturation level of the population and the time when it would reach that value.

When Raymond Pearl and Lowell J. Reed (1920) introduced the same curve in 1920, however, they were wholly unaware of Verhulst's memoirs. The true precursor in this case was not Verhulst, but the physiologist T. B. Robertson, who in 1908 had published two articles applying the same sigmoidal curve to various cases of individual growth in animals, plants, and man. By coincidence, he used some of Quetelet's data, without apparently being aware of Quetelet's population interests or of Verhulst's memoirs. Robertson called his curve the "autocatalytic" or self-accelerating curve, because it was the same as that used to describe certain chemical reactions, in which one of the products of the change had the property of accelerating the further progress of the reaction. On the basis of this similarity between chemical and growth curves, Robertson constructed an elaborate hypothesis to explain the changes observed in the rate of growth of individuals. He postulated that growth itself was an autocatalytic phenomenon, controlled by the secretion of an unknown catalyst, which would act to stimulate growth. The original theory applied only to the growth rate in individual organisms, but was later extended to cover growth in protozoan and bacterial populations (Robertson, 1923). Strictly speaking, the term "autocatalytic" applied only to the accelerating phase of growth, but Robertson used it to refer to the whole S-curve as well, and this rather loose designation was repeated by others, with the result that the autocatalytic curve came to be synonymous with the logistic curve.

Raymond Pearl had become interested in the growth of individual organisms as early as 1903 and published a study on the growth of the aquatic plant, *Ceratophyllum demersum*, in 1907. In 1909 he wrote a review of recent growth studies, in which he sharply criticized Robertson's use of the autocatalytic curve (Pearl, 1909). His criticism was based on two general problems in Robertson's articles: first, that his data did not in fact follow the symmetrical curves given by the theoretical equations; and second, that similarity between chemical and growth curves implied nothing about the underlying mechanisms of growth, and was therefore not sufficient to support Robertson's hypothesis. What was required, Pearl argued, was to show that there were qualitative and not merely quantitative resemblances between the two kinds of phenomena. These remarks are of interest not only because they illustrate Pearl's cautious approach to growth curves in 1909, but because, some years later, very similar criticisms were to be voiced by Pearl's own critics. The fact that they could reappear indicates how strongly Pearl had become attached to his logistic hypothesis.

Pearl's decision to investigate population growth in 1920 was partly the result of an accident. A fire in his laboratory at the Johns Hopkins University in November of 1919 completely destroyed his records of a large project which was then nearing completion, a study of tuberculosis incidence. Lacking the heart to re-do the study, he turned to a different problem, one which was suggested by his wartime work on Herbert Hoover's Food Administration program: the dynamics of population growth. In 1920, in collaboration with statistician Lowell Reed, he published an article applying Robertson's sigmoidal curve to census data for the United States. It was only after this paper was in print that they learned of Verhulst's work, and adopted his term "logistic" for their curve.

Their use of this curve was supported by certain assumptions which they believed must hold for any population. Given a limited area into which a population could expand, they argued that the rate of increase at any time was proportional to two things: the magnitude of the population at that time, and the "still unutilized potentialities of support existing in the limited area." In this case, "unutilized potentialities" could best be understood as simply the normalized difference between the existing and the limiting population (Yule, 1925, p. 4). This statement is equivalent to the assumption that the growth of a population decreases in linear fashion with the density of population. What was noteworthy in this paper was that Pearl and Reed did not derive the equation for the curve from their assumptions, as Verhulst had done using a different line of reasoning. Rather, these assumptions were tacked onto the end of the article as an extra, rational support for the use of the curve which they had adopted to fit the census figures. In other words, Pearl and Reed began with the assumption that population growth would follow a sigmoidal curve. To express the curve mathematically was a simple enough problem, and they easily found a solution in Robertson's familiar autocatalytic curve.

Pearl and Reed did not regard their curve as an empirical statement, in the same class as, for example, a parabola or straight line fitted to population data. Instead they considered it to be a *law* of population growth, on the grounds that the logistic curve both fitted the data and gave a reasonable picture, based on rational assumptions, of the future trend of growth. Pearl's concept of law was derived from the British biometrician Karl Pearson, with whom Pearl had studied as a post-graduate fellow in 1906. Pearson (1900) believed that scientific activity consisted of the classification of facts and the economical expression of the relationships between them by means of formulas, which acted as laws. It was in this sense that the logistic equation could be called a law, if it be assumed that it could be applied to all cases accurately. Pearl and Reed compared their curve "in a modest way" to Kepler's laws of planetary motion and to Boyle's Law (Pearl, 1924a, p. 585). Their insistence that the logistic was just such a law gave rise to a polemical and sometimes bitter dispute that was only subsiding by the time of Pearl's death, twenty years later.

The validity of calling the logistic a law rested on its ability to describe the available data. In this regard it quickly became evident that considerable modifications would be required, for not all the data conformed to the symmetrical curve. Accordingly, Pearl and Reed regarded their first equation as an approximation of the true law, not to be taken as having exact predictive value. Their caution, however, did not prevent them from giving a projected figure of the limiting population of the U.S. of around 197 million (to be reached just after the year 2000), nor from estimating the point of inflection of the curve down to the day: April 1, 1914 (Pearl and Reed, 1920).

The first adjustment of the simple curve was to postulate successive logistic cycles of growth (which were actually not true cycles, but epochs or episodes, as they did not return to the starting point). These would arise when a major change, such as an industrial revolution, created the opportunity for growth beyond the limiting value dictated under the existing system (Pearl and Reed, 1923). T. B. Robertson had also used successive cycles of growth in his own work and had been criticized by Pearl on the grounds that he had not proved that growth was actually cyclical in character. Pearl and Reed did not advance this objection in their own case, but simply assumed on common-sense grounds that population growth proceeded in this fashion, one logistic curve added onto the next through time.

The second problem was more serious, for it involved the symmetry of the curve as they had originally presented it. Pearl and Reed doubted that the curve was in reality symmetrical because they felt that such symmetry implied that the forces acting to inhibit growth in the latter half of the curve were equal in magnitude and exactly similarly distributed in time to the forces which operated to accelerate growth in the first half. "We do not believe that such rigid and inelastic postulates as these are, in fact, realized in population growth," they added (Pearl and Reed, 1920). Apart from these wholly a priori justifications, another unstated possibility was that Pearl and Reed wished to avoid the constraints of symmetry on purely empirical grounds. Their reluctance to limit themselves to a symmetrical curve may have stemmed from their desire to ensure that their "law" was flexible enough to cover all growth phenomena, in other words; that it was universally valid. A symmetrical curve clearly was not adequate to cover all the data, as Pearl had pointed out in reference to Robertson's work. Indeed, their first attempt to use an asymmetrical curve was to re-fit some of Robertson's own data, which he had earlier tried to fit to a symmetrical curve, but with poor results (Pearl and Reed, 1925).

In the process of freeing the logistic from its restrictive symmetry, Pearl and Reed generalized their original equation by adding more terms to it. Thus the original equation could be written as follows (Pearl and Reed, 1923):

$$N = \frac{K}{1 + me^{at}} \qquad (3)$$

where K, a, and m are constants. The generalized equation was then:

$$N = \frac{K}{1 + me^{a_1t + a_2t^2 + a_3t^3 + \quad + a_nt^n}} \,. \qquad (4)$$

The actual shape of the curve depended on the number of terms and the values of the constants. If all constants from a_2 to a_n were zero, the curve would reduce to the original symmetrical form. If the terms up to t^3 only were left in, the curve would be asymmetrical and sigmoidal. Apart from the difficulty of determining so many constants, the problem with this generalization was that it could be made to fit almost any set of data, and was therefore "logistic" in name only. The whole purpose of identifying a "law" would have been defeated. Pearl was aware of this type of error, for he warned against it in a 1923 textbook on statistical methods written for medical students (Pearl, 1923, p. 333). But his enthusiasm for the logistic was such that he failed to perceive the aptness of his own warning, and believed that in the expanded equation he had succeeded in setting forth a "comprehensive general theory of population growth" (Pearl and Reed, 1923). In fact, however, Pearl and Reed seldom had recourse to the generalized equation beyond the simple asymmetrical form, except as a final, if inadequate, rebuttal to criticisms that populations did not always follow a "logistic" curve.

Having presented the general theory, it remained to test it against the data. In 1924, Pearl and Reed fitted census figures of sixteen countries, the world as a whole, and one city to logistic curves (Pearl, 1924a, pp. 584–637). In only one case, however, that of the city of Baltimore, were the data extensive enough to cover most of the S-curve, a consideration which Pearl and Reed simply disregarded. In their first paper of 1920, the U. S. census data covered less than half the curve, not even showing a tendency to saturate, since they had not used the 1920 census results which would have brought the curve to the point of inflection (Fig. 1). The entire upper half of the curve was extrapolated. For Germany (Fig. 2) and Japan, two cycles had to be used to fit the data, on the justification that both countries had undergone major industrial changes in the recent past. The observations on Denmark filled less than a third of the curve, yet they remarked that "the fit of theory to observations is well-nigh perfect" (Pearl, 1924a, p. 596). To be sure, the fits were perfect in that the points lay close to the curve, but this did not diminish the fact that in most cases the data were not sufficient to warrant the use of the logistic, as opposed to a different curve, in the first place.

Pearl and Reed did not rely solely on census data to prove the correctness of their curve, however. They assembled figures from other sources showing that growth in general, whether on the individual or the population level, followed a logistic path. As a result of T. B. Robertson's work, the autocatalytic curve had been applied to a wide variety of cases of individual growth by the mid-1920's. Other biologists had independently used the same curve to describe the growth of microorganisms and yeast populations (Lloyd, 1967). Pearl and Reed both cited and reproduced the results of these studies in their papers as support of the logistic curve hypothesis.

In his own laboratory, Pearl and his assis-

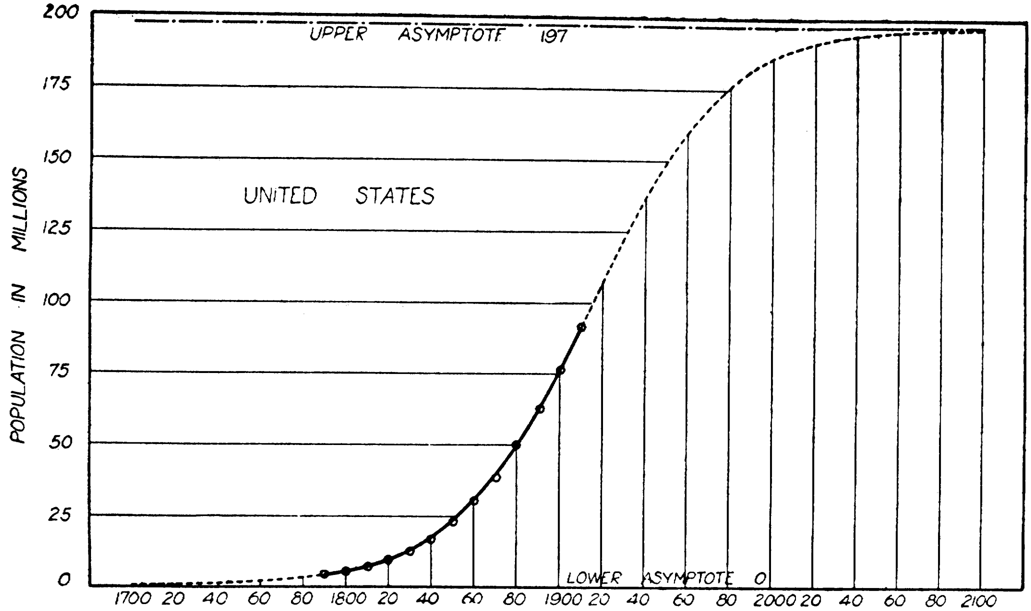

FIG. 1. SYMMETRICAL LOGISTIC CURVE FITTED TO U.S. CENSUS DATA
From Pearl, 1924c.

tants were engaged in a series of studies on populations of the fruit-fly, *Drosophila*, which they found also followed the logistic curve in the initial stages of growth (Pearl, 1925, chap. 2). The accumulated evidence, although accepted by Pearl somewhat uncritically, was abundant enough for him to proclaim in 1924: "In the matter of population growth there not only 'ought to be a law' but five years' research has plainly shown that there is one" (Pearl, 1924b, p. 302). By 1927 he confidently asserted that "It is an observed *fact*, which at this stage of the discussion involves no theoretical implications whatever, or postulates special to it, that the growth of populations of the most diverse organisms follows a regular and characteristic course" (Pearl, 1927, p. 533). Pearl had come full circle: having assumed logistic growth from a priori principles in order to fit his initial data, he now believed that the empirical evidence proved the truth of the logistic "law."

Pearl was skilled at publicizing his own theories. From 1920 to 1927 he published, either alone or with Lowell Reed, over a dozen articles devoted to the logistic curve, which appeared in a wide array of scientific and popular journals. These included his own journal, *The Quarterly Review of Biology*, and that of his good friend H. L. Mencken, *The American Mercury*. Although a few of the articles dealt with specific modifications of the theory, for the most part they were almost identical statements of the basic theory and application of the curve.

Pearl also had close ties with the British statistician G. Udny Yule, who presented Pearl's theory at the British Association meeting held in Toronto in 1924. In expanded form, as Yule's presidential address to the Royal Statistical Society (Yule, 1925), it provided a complete discussion of the theory as developed by Verhulst and by Pearl and Reed. Yule emphasized that the curve could not be used for long-term prediction, due to the uncertainties caused by wars and other disruptions, but he was otherwise very supportive of Pearl's work. His article, which Pearl cited often in later papers, was important for explaining and lending stature to the logistic theory.

Pearl himself discussed his theory in a session of the World Population Conference held in Geneva in 1927, later publishing the talk in *The Quarterly Review of Biology* (Pearl, 1927). Finally, the logistic curve was a

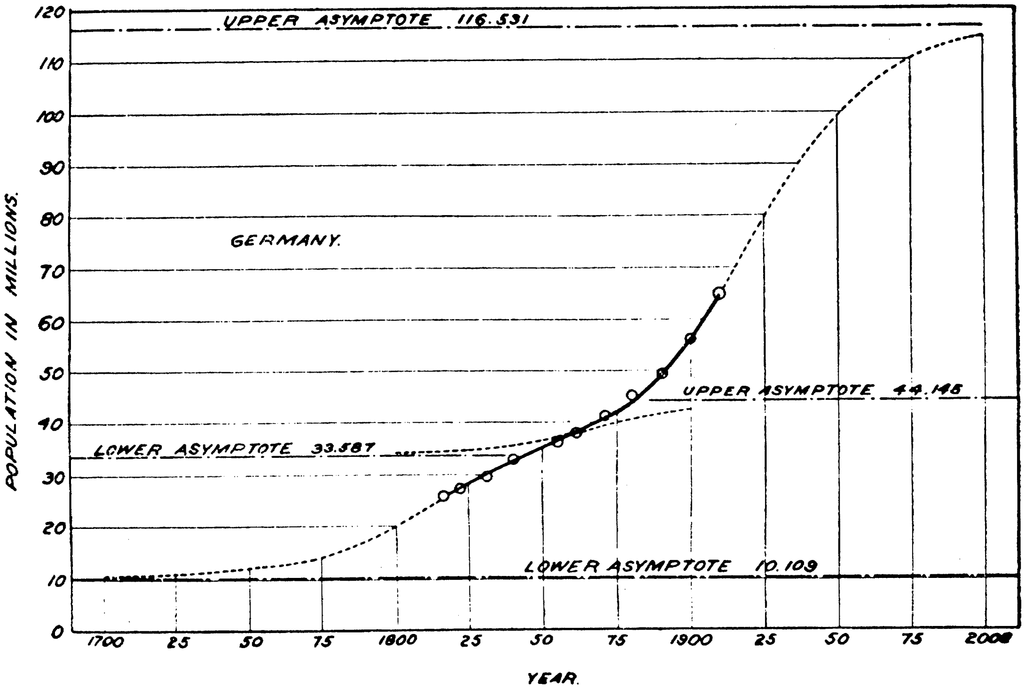

FIG. 2. GERMAN CENSUS DATA FITTED TO TWO LOGISTIC CURVES
From Pearl, 1924c.

prominent feature of three books which Pearl published during this period, *The Biology of Death* (1922), *Studies in Human Biology* (1924a), and *The Biology of Population Growth* (1925). With this amount of publicity, Pearl's logistic curve attracted a great deal of attention and, inevitably, a great deal of criticism.

THE LOGISTIC HYPOTHESIS DISCREDITED

The first to subject the logistic curve to scrutiny were economists and statisticians. Those involved in demographic problems were essentially concerned with making predictions, which then became the basis for specific planning proposals. Because statistics was an applied science, the statistician tended to view his ability to predict with caution. The nature of this work, its attention to detail, instilled an acute awareness of the complexity of events and an accompanying hesitation to venture far beyond the facts. For this reason, the most frequent criticism of the logistic curve was that there were too many uncertainties even to attempt to use a regular curve like the logistic, let alone to have any confidence in its predictions. The logistic was not a useful curve.

Pearl clearly placed great value on the ability of his curve to indicate long-term trends, but to forestall this objection he began to backtrack, deemphasizing the criterion of predictability as a test of his theory: "The extrapolated portions of the curve have no bearing whatsoever upon the adequacy of the curves to describe the *known facts* of population growth. It is upon the success or failure of the attempt to demonstrate this adequacy, *and upon this alone,* that the judgment of the scientific validity of the hypothesis must rest" (Pearl, 1924a, pp. 586–7). Expressing the economist's point of view, A. B. Wolfe (1927) pointed out that such a statement was hardly in accord with Pearl's insistence that his curve expressed a rational law. "For if the formula is a rational law, that is, if it somehow reflects the mechanism—a mechanism explainable or describable in terms of known principles—by which human population growth is what it is, it should also reflect what that growth will be" (p. 573). If the curve did not have any predictive value, then the other curves commonly used for short-term projections were equally useful.

Again to forestall the same objection, Pearl (1924a, p. 587) stressed that the logistic curve could only be used on the assumption that no fundamentally new factor influencing the population should come into play in the period under observation. Arguing that it was impossible to make this kind of assertion with respect to human populations where social, economic, political, or religious changes were highly unpredictable, Wolfe accused Pearl of not taking his own proviso seriously enough. "One would be tempted to the inference that Pearl is driven by the fine frenzy of pure intellectual play, did he not in his later writings broadly hint that he feels himself to be on the trail of a great discovery—a 'rational,' 'mathematico-biological' law of population growth, universally valid" (p. 576).

A similar objection was raised by demographer George H. Knibbs, whose monumental analysis of the Australian census had failed to disclose any general law of population growth (Knibbs, 1917). Knibbs' attacks on the logistic hypothesis were based on what he perceived to be an erroneous assumption of the theory: that the "reproductive impulse" of a population was constant in time, but was prevented from expressing itself completely by the effects of population density and limitation of resources (1925, 1926–27). He argued that other kinds of factors, such as social, ethical, or economic changes, could lead to an intensification or diminution of the "impulse to increase." He meant by this that a group's standard of living, including its whole attitude toward reproduction, was determined by its social and ethical outlook, which could possibly change over time as a result of social evolution. Therefore a change in the basic "character" of the people, a change acting independently of population density, could cause consequent changes in the rate of increase. Whatever the results of this change, it could not be subject to law, and the use of the logistic curve was seen as a misleading exercise in curve-fitting which could not be considered as proof of the theory.

Knibbs did not mention it himself, but the question he had raised about alterations in character, to be understood as referring to a group's attitude towards reproduction, tied in with the controversial issue of birth control as a factor in population decline. Pearl's theory seemed to imply that the decrease in rate of growth was an automatic response of a population growing to a certain level, rather than a result of conscious human intervention. The hypothesis that birth control was causing the modern decline in birth-rate was therefore advanced as an alternative to Pearl's hypothesis (Hogben, 1931). This distinction was reasonable on the part of Pearl's critics, for he did conceive population growth to be a biologically self-regulated process, without specifying what he meant by self-regulation. However, it really misrepresented his point of view, for he was an advocate of birth control, which he regarded as "an intelligent adaptive response to an environmental force, population pressure" (Pearl, 1925, p. 212).

For those, like Wolfe and Knibbs, who had been accustomed to view the complexity of human society as proof that growth could not be reduced to a simple law, Pearl's apparently casual neglect of environmental and social factors seemed wholly wrong-headed. Actually, Pearl did believe that major changes such as industrial revolutions had a measurable impact on population growth, and he did not hesitate to employ these explanations when he needed to postulate two or more cycles of growth to fit a given set of data. In most cases, however, he discounted the notion that anything short of catastrophic turmoil could shift a population from its logistic path. Economic conditions and social factors, such as birth control, had an effect, but their effect was to make the population follow the logistic curve.

Eventually, though, his manner of expression, if not his attitude, altered in response to these criticisms. In his earlier writings he tended simply to exclude the actions of external circumstances from consideration with respect to the logistic curve, but by 1927 he was arguing that the logistic equation did indeed take these factors into account. Their effect was not measured independently, however, but in terms of what he called the "primary biological factors" of natality, mortality, and migration (migration in this case being considered unimportant). The logistic equation included environmental variables, Pearl argued, "in the sense that it describes the integrated end effect upon population size of the aggregated forces tending towards increase on the one hand, and decrease in numbers on the other hand" (Pearl, 1927, p. 541). Ignoring his own use of a priori reasoning, Pearl countered the arguments of critics who claimed otherwise in a manner not designed to placate them: "This argument is rubbish, born out of the conservative resistance to any new idea which the established order of learning has always shown, by that wind-broken and spavined old stallion, faith in *a priori* logic as against plain facts of experience" (1927, p. 541).

Pearl's vehemence on this issue, and the inability of his critics to grasp his argument, can only be understood with reference to his particular conception of the population as a discrete entity, analogous to an individual organism, though of course lacking the organism's organization. This perception was essentially a carry-over from his earlier work on plant growth (1907), but was later influenced by the supra-organismic viewpoint of his friend William Morton Wheeler. Although the idea that the population was a discrete entity was entirely artificial in this case, it allowed Pearl to make, for the purposes of argument, a clear separation between what he called the biological, or "internal," environment and the physical, or "external," environment of the population, just as he had earlier drawn the distinction between hereditary and environmental factors determining the growth of the individual plant. His critics, however, did not view populations in this way, and although this conception was contained in Pearl's earlier work (1925), he did not really make it explicit until 1927. "Populations of whatever organisms are, in their very nature, aggregate wholes, and behave in growth and other ways as such," he wrote in 1927 (p. 541). The assumption behind this statement, that the population behaves like the individual organism, meant that it was permissible to examine growth exclusively in terms of the "biological" environment, or in terms of the attributes, such as birth-rate and death-rate, which belonged to the population itself, rather than to the external world. The "physical" environment, with its intractable variables, could be conveniently given second place.

The fact that both individual organisms and populations followed the same logistic path was circumstantial evidence that they were fundamentally alike. But, as Pearl had argued in response to T. B. Robertson, quantitative evidence was not sufficient to prove qualitative similarity. In order to prove that a population did behave like an individual, he needed to show that the shape of the growth curve could be explained by some mechanism "internal" to the population, that is, one involving the intrinsic "biological" attributes of the aggregate. He found this evidence in his studies of the fruit-fly, *Drosophila*.

Starting in 1921, Pearl and his associates had been conducting an intensive series of studies on the duration of life, using fruit-flies as experimental subjects. In the course of these studies, they found that density of population influences the death-rate of the flies (Pearl and Parker, 1922), and more surprisingly, that it affects the rate of reproduction as well, by inhibiting the fertility of the female flies (Pearl, 1925, pp. 134–41). Here, Pearl felt, was a solution to the problem of the mechanism behind the logistic curve, a vera causa to explain why the rate of growth decreases in the upper portion of the curve. He also noticed a similar connection between density and egg-laying in populations of rock fowl, with which he had worked more than a decade earlier. Impressed by these results, he then went a step further, and claimed in 1925 to have demonstrated that human populations also show a definite density effect on birth rate, and he suggested that the relationhsip was of the same character, fundamentally, as that found in hens and flies (Pearl, 1925, pp. 146–56).

His critics viewed this connection between density and rate of growth as being of a somewhat mystical character, especially when applied to humans. The British biologist Lancelot Hogben (1931) discounted the idea that fruit-fly and human populations could be compared in this manner, and in so doing he echoed Pearl's own criticisms of T. B. Robertson:

> The mere fact that the same type of equation can be used for two different sets of variables does not necessarily denote the same intrinsic mechanism. . . . Pearl's conception of density, as applied to human populations, remains a purely statistical abstraction devoid of specifiable biological significance. The mere fact that an assumption can be tested in a biological laboratory does not of itself confer on it the status of a biological hypothesis. If, and only if, its biological significance can be clearly envisaged, is it permissible to assign any theoretical meaning to a correspondence between the growth of human populations in successive cycles and the single cycle experimental curves of *Drosophila* or yeast (p. 167).

The problem of establishing the biological significance of these results was an important one. Pearl had first published these conclusions, with his heroic extrapolations to human society, without any suggestion as to how density might influence the growth rate. In 1932 he tried to remedy this flaw by publishing a study of the mechanism behind the density effect he had uncovered in *Drosophila* (Pearl, 1932). Using the analogy of gas molecules colliding randomly in an enclosed space, he interpreted the reduced fecundity as an interference effect of the flies on each other, one caused by space limitation, which altered three activities, food intake, energy output in muscular activity, and oviposition.

As Thomas Park (1937) later pointed out, these experiments were important in showing how density could influence growth by acting on the behavior mechanisms of individuals in a population. Pearl's error was to link this interference effect exclusively with the logistic curve. If the logistic equation is comparable to Boyle's Law, as Pearl thought, then the interference effect is analogous to the underlying explanation of Boyle's Law provided by the kinetic theory of gases. It was not until 1944 that F. W. Robertson and J. H. Sang, working in Lancelot Hogben's department, tested these results thoroughly and arrived at a different interpretation (Robertson and Sang, 1944). They discovered that changes in the quality and quantity of the food were the most important factors influencing the rate of egg-laying in *Drosophila*. The crowding effect that Pearl had postulated was in fact the result of competition for food. If the flies were adequately fed, the same crowding produced only a slight decrease in fecundity. Therefore the rate of growth was affected very simply by environmental changes, observed as changes in the food supply, rather than by a more complicated physiological interference. The implication was that the logistic curve was an empirical statement that bore no particular relevance to biological processes.

The density experiments could not, as Pearl thought, be seen as providing the underlying mechanism which proved that the logistic equation was in fact the law of growth. Economists, demographers, and biologists alike were justified in remaining sceptical in the light of Pearl's haste to employ analogies, based on meager evidence, between individual organisms and populations, and between human and animal populations. The criticisms recounted so far were mainly directed toward the gaps in Pearl's reasoning. They called attention to the factors he had not included, the interpretations he had not considered, and the analyses he had not performed. But his mathematical methods were equally under attack, and nowhere with greater fervor than from the Harvard physicist turned statistician, Edwin Bidwell Wilson.

Pearl had come to know Wilson when both were serving in an editorial capacity on the *Proceedings of the National Academy of Sciences*. Over the years he developed a high regard for Wilson's abilities and considered him one of his closest friends, a feeling that quickly dissipated when Wilson launched a line of attack that soon resembled a crusade to destroy Pearl's credibility in the scientific community. This debate was considerably aggravated by differences of personality between the two and by Wilson's tendency to resort to sarcasm in criticism.

In February of 1924, Wilson (1926) delivered a talk on statistical inference at Pearl's home ground, the School of Hygiene and Public Health at the Johns Hopkins University. With Pearl almost certainly expected to be in the audience, he attacked those people "who seem for some reason to believe that a mathematical formula is eternally true." "Their attitude is Shamanistic. They go through with magic propitiatory rites, idolatrous of mathematics, ignorant of what it can and can not do for them. And I am not quite sure that the high priests of this pure and undefiled science do not somewhat aid and abet the idolatry" (pp. 290–91).

But the real blow was struck in 1925 when Wilson, prompted by annoyance at Udny Yule's exposition of the logistic theory at the British Association meeting in Toronto, sarcastically poked fun at Pearl in an article in *Science* (Wilson, 1925a). Using Canadian census data, he fitted them to an equation having the algebraic form of a logistic, but in this case he rather unfairly chose constants that produced a curve having an accelerated, not a retarded, rate of growth. Wilson's form of the equation predicted that "on some day apparently in the year 2020 the Canadian population will become infinite." The logistic, he argued, clearly led to absurd results! Wilson openly admitted that it was "pushing the formula pretty hard" to distort it in this fashion, but he felt strongly that the logistic had no underlying justification and was, moreover, inadequate to describe a rapidly growing population like the Canadian.

He reserved his serious criticism for a second article devoted to a pamphlet Pearl and Reed had written on the future population of New York City (Wilson and Luyten, 1925). Wilson's argument was based on what he though was a logical fallacy. The logistic curve could never be applied to a whole region and to its parts separately, because two logistic curves when added together did not give a logistic curve. Therefore, at any time, the sum of the component logistic curves would be out of line with the result predicted by a logistic independently calculated for the whole area. Wilson (1925b) supplemented this article by an announcement that he had had special graph paper made up, on which the logistic curve could be plotted as a straight line. He offered the paper at small cost to the members of the National Academy of Sciences, presumably so that they might discover the deficiencies of the logistic equation for themselves. His criticism in this case was somewhat beside the point, for as Wilson knew, the exponential curve was also non-additive. Besides, as Udny Yule (Stevenson, 1925, p. 89) explained, the objection really applied only if one were interested in using the logistic equation to predict populations both in parts and in whole. As a general description of growth, the logistic curve could still be useful under the right conditions.

Pearl, however, indeed intended his curve to have predictive value, and he clearly felt the sting of the criticism, for it was one of the few that he took time to answer carefully. Rather than back down on this issue, Pearl and Reed (1927) wrote a rebuttal to Wilson in which they showed that if the curves to be summed had the same rate of growth and were synchronous, their addition would give a logistic curve. Otherwise, the sum would not be logistic but some other winding curve. Unable to disregard this eventuality, they appealed to the generalized form of their equation to represent the summation. In view of the inadequacies of the generalized logistic equation, this line of reasoning was more an evasion than a solution of the problem posed by Wilson.

Irritated by the printing of what he saw as Pearl and Reed's "egregious errors of theory and practice," Wilson continued his criticisms in a lengthy and technical paper (Wilson and Puffer, 1933). His argument was an expansion and generalization, with numerous examples, of the criticisms made in the earlier articles. After detailed analysis of the simple logistic equation, Wilson concluded that, although it might be useful for fitting census data, it could not be interpreted as a rational law, nor could it be made the basis for forecasts. In short, he agreed with Verhulst's conclusion in 1845, that until more observations were assembled, the law of population remained unknown.

Along the way, Wilson also succeeded in blocking Pearl's transfer to Harvard as the replacement for William Morton Wheeler, the retiring head of the Bussey Institute. Assured of support both from Wheeler and President Lowell of Harvard University, Pearl had conditionally accepted the appointment in the spring of 1929. When news of this reached Wilson, who was statistician at the Harvard School of Public Health, he mounted a vigorous campaign among the

Harvard faculty to discredit Pearl. By midsummer, his criticisms of Pearl's statistical methods had attracted enough attention to put serious doubts in the minds of the Harvard Overseers, who had to approve the nomination. Despite intense lobbying by Pearl's supporters—L. J. Henderson, Thomas Barbour, and W. M. Wheeler—the Overseers rejected the nomination in September, 1929. Recognizing that this was a likely eventuality, Pearl had already indicated his determination not to accept the Harvard position, even if finally offered to him. Pearl remained at the Johns Hopkins University until his death in 1940.

In addition to the clamor created by Wilson's attacks, there were enough other problems with the simple logistic curve to put Pearl's oft-cited "plain facts of experience" under fire. These had to do with the procedure of curve-fitting in general. Cambridge zoologist James Gray (1929) demonstrated how easily the same set of observations could fit two different sigmoidal curves, and therefore left no way of choosing between them on the basis of fit. Lancelot Hogben (1931), quoting Gray's remarks, pointed out that the logistic curve, by its lack of uniqueness, lost all claim to being a universal biological law of population. Sewall Wright (1926) seized on the same issue. Any flexible mathematical formula resulting in a sigmoid shape could be made to fit the data. An obvious alternative was the Gompertz curve, an asymmetrical sigmoid curve proposed by Benjamin Gompertz in 1825 and subsequently used in several growth studies. For population growth, the differential equation of the Gompertz curve is written (Smith, 1952):

$$\frac{dN}{dt} = rN \log_e \left(\frac{K}{N}\right) \qquad (5)$$

Pearl did not answer these criticisms himself, but suggested to a student, Charles P. Winsor, that he should compare the alternatives. Winsor's study showed that both logistic and Gompertz curves had similar properties for the empirical representation of growth, neither one having a substantial advantage over the other (Winsor, 1932a). He noted, however, that the differential form of the logistic curve could be more readily deduced by mathematical reasoning than the Gompertz equation, a feature which later contributed to the ultimate acceptance by many persons of the logistic curve. P. B. Medawar (1940) eventually demonstrated how the Gompertz curve might be derived as a description of the growth rate in the chicken's heart, but it is less easy to see how this argument could be adapted to a population. F. E. Smith (1952) pointed out a more serious problem to the general validity of the Gompertz curve. Because it sets no limit to the rate of increase, the constants in the equation can only be interpreted biologically between about one-third saturation and full saturation.

Apart from the problem of curve-fitting, the logistic had very definite advantages over any other curve: it was mathematically simpler and easier to interpret in a biological context. But it was not Pearl who demonstrated these advantages. In fact, he avoided analysing the assumptions that were at the basis of the logistic curve, and preferred to write the equation, not in the differential form where the relation between the assumptions and the mathematical expression could be clearly seen, but in the more complicated integral form. Part of the reason was his interest in forecasting human populations: for this purpose, the S-curve was most useful, and it is reasonable that he would have written the integral equation corresponding to that curve. But his reluctance to write the differential form, even in the *Drosophila* experiments, was a reflection of a general lack of analysis of the equation itself. For Pearl, it was enough to demonstrate that it fitted the data and appeared to have an underlying biological mechanism in the effect of density on fertility.

Ironically, Pearl's stubborn faith in his curve as a law of growth seems to have been the cause of his failure to express it in a biologically meaningful manner. By sticking to the integral equation, he was unable to strengthen the theory with an analysis of the constants in the equation. But the invention persisted because other people, not committed to Pearl's naive notion of scientific law, were able to understand the role of the logistic curve as a tool of research. This understanding was based on a willingness to treat the logistic equation, not as a lawlike statement of a population's actual growth, but as a logical argument which expressed how a population might grow if certain initial conditions were met.

In this respect the logistic equation resembles the Hardy-Weinberg law in population genetics, which establishes the constancy of gene and genotype frequencies in a randomly breeding population. The Hardy-Weinberg statement is derived from a number of assumptions that greatly simplify the behavior of real populations, but by looking at how a population departs from the law, one gets a more realistic idea of the actual mechanisms underlying evolutionary processes (Emlen, 1977, pp. 2–3). Similarly, the logistic curve cannot be tested by comparison with observations, as one would test a scientific hypothesis, for it is neither a law nor a hypothesis, but a logical argument based on a variety of assumptions. By looking at deviations from the logistic curve, however, one can refine these assumptions to gain a more accurate understanding of how a population behaves. The logistic equation can therefore be useful as a tool of research even though it is not a realistic description of growth.

Pearl certainly did not understand this use of his equation, nor did most of his critics. The vehement tone in which the whole debate was conducted, while it helped to publicize the equation, also impeded the use of the equation in a more insightful manner. The positive steps in this direction were left to more dispassionate observers who, although involved with Pearl in some way, managed to remain aloof from the thundering style of both Pearl and his critics. Pearl still had an important role to play as a publicist of his curve, however, for his activities gave the logistic curve a visibility that encouraged exploration and development of the theory.

THE LOGISTIC CURVE REVIVED

The analysis of the constant r was carried farthest by Alfred James Lotka, whom Pearl had invited to his laboratory in 1922 to write his book, *Elements of Physical Biology* (1925a). Lotka had been developing the ideas which became incorporated into this book since 1901, largely in his spare time, and he was only too glad to have Pearl's encouragement, along with a small but adequate fellowship, to enable him to complete the project. His contributions to the logistic theory began with his realization, in the course of writing this book, how neatly the logistic curve fitted into his general discussion of the "kinetics of evolving systems." This was a phrase borrowed from physical chemistry and used by Lotka to refer to problems related to the exchanges of matter among the components of a system, and the velocities with which those changes took place. Population growth was one example which fitted this category.

Lotka had been interested in population growth for several years without, however, using a sigmoid curve, despite the fact that he was acquainted with T. B. Robertson's articles at least as early as 1910 (Lotka, 1910). One of his early articles (Lotka, 1907) dealt separately with examples in which growth was exponential and where the population was stationary, but he did not then combine the two into a single equation including both a rapid increase and an equilibrium phase. In subsequent papers written prior to his book, he assumed that growth was basically exponential. In fact, he seems to have interpreted Robertson's term "autocatalytic" in the correct, strict sense as referring only to the accelerating phase of growth, although in his book his usage of the term is less precise and apparently refers to the whole S-curve.

Contact with Pearl at first failed to excite his interest in the logistic curve. His opinion changed dramatically in the summer of 1923, when he discovered that it offered a solution to one of his problems in population theory. His derivation of the curve, with numerous examples from the studies of Pearl and others, made up one chapter of his *Elements of Physical Biology* (pp. 64–76). The derivation itself was straightforward. Lotka first expressed the rate of growth as a general function of the existing population and equated the function with zero, because he was interested in the values at which the population remained stable:

$$\frac{dN}{dt} = f(N) = 0 \qquad (6)$$

He then expanded the function by Taylor's theorem (while omitting the first absolute term of the series so that dN/dt would vanish with N):

$$\frac{dN}{dt} = aN + bN^2 + cN^3 + \ldots \quad (7)$$

Assuming that the expression describing population growth had at least two roots, or two values of N at which $dN/dt = 0$, Lotka terminated the expansion at the simplest expression satisfying this condition:

$$\frac{dN}{dt} = aN + bN^2 \quad (8)$$

By solving the expression he obtained the logistic equation.

Reviewing the various applications of the logistic equation, Lotka remained unimpressed by Robertson's autocatalytic hypothesis and instead suggested that the reason individuals followed the same growth curve as populations was that they consisted basically of "populations" of cells. He proposed the term "autocatakinetic," borrowed from German chemist Wolfgang Ostwald, to replace "autocatalytic" as a description of this type of growth because it carried no implication of the underlying mechanisms of growth (1925a, p. 76).

Like Pearl, Lotka referred to the logistic equation as a "law" of growth. Pearl, however, considered his curve to be a law that was universally valid, whereas Lotka understood law to mean an empirical relation between events, having no apparent connection to principles of a more general nature. He perceived (Lotka, 1925b) that an empirical law of this kind imposed limits in two ways. First, because the fundamental principles underlying the curve were unknown, the exact form of the equation had to be determined anew for each example. Second, it was not possible to extrapolate much beyond the observed range of events, because unknown factors might come into play outside this range and cause departures from the "law."

Yet an expression of this sort could still be useful as an entry into further analysis, as Lotka explained (1925b): "An empirical formula is therefore not so much the solution of a problem as the challenge to such solution. It is a point of interrogation, an animated question mark." These comments were delivered in 1925 at a meeting in New York devoted to the problem of forecasting populations, a meeting at which Reed and Pearl also spoke. Lotka's remarks, later made more forcefully by less sympathetic critics, appear to have had little direct impact on Pearl, however. No doubt he was content to let Lotka pursue the logistic curve along his own lines, but was not competent to follow him along this mathematical path.

Lotka developed his ideas around an analysis of r while employed as a statistician at the Metropolitan Life Insurance Company, from 1925 on. Before "interrogating" the logistic equation, he reworked it to express the rate of increase per head (dN/Ndt) as a function of N:

$$\frac{dN}{Ndt} = r_0\left(1 - \frac{N}{K}\right) \quad (9)$$

where r_0 was now the maximum or "incipient" rate of increase, the same as r in equation 2. Lotka interpreted the term $r_0\frac{N}{K}$ as representing a complex of factors contributing to the decrease in the rate of growth; as such, it was sensitive to changes in economic and social conditions and was therefore difficult to analyze. The upper limit K was therefore of economic character primarily, but it also had a biological component in that, for every value of K, there would correspond a definite lower limit of fertility which would ensure that the population remained stable at that level.

The parameter r_0, on the other hand, was amenable to more detailed analysis. In 1925, Lotka coauthored with Louis I. Dublin (Dublin and Lotka, 1925) an article "On the True Rate of Natural Increase," in which they showed that the conventional method of measuring the rate of increase as birth-rate minus death-rate could be misleading, as a result of the effects of age distribution on these measures. They described a method of obtaining a true measure of the natural rate of increase, given a certain age schedule of fecundity and mortality in the population. As a sequel to this study, Lotka (1927) probed the meaning of the "incipient" rate of increase in the logistic equation.

With the American population as his test case, he calculated the maximum fertility of women in the late eighteenth century, when the rate of growth was close to the maximum. Expressing the fertility in terms of the average interval between births, he found that in the most fertile age group the interval was 13¼ months. Therefore the biological significance of r_0, the maximum rate of increase, was that it was determined by the reproductive capability of the species; in this case, the necessity in humans of allowing just over a year between successive births. Later, Lotka fleshed out his study by a thorough analysis of the demographic characteristics of a population growing according to the logistic curve. A short talk on the subject was given to the American Statistical Association in 1931, and was followed by a more detailed version presented to the International Union for the Scientific Investigation of Population Problems. The longer version was published both in the *Proceedings* of the meeting (Lotka, 1932a) and in Pearl's journal, *Human Biology* (1931). A comparison of the theoretical characteristics with those actually observed in the U.S. population showed close coincidence, and thus offered confirmation that the population was in fact growing logistically, at least up to 1930.

Lotka always maintained a conservative attitude towards the logistic equation, regarding it as an approximation to actual trends. His analysis was aimed simply at discovering how much could be said about a population, given the reasonable assumption of logistic growth. But Pearl's work also attracted attention from biologists who were interested in exploring the logistic curve from a different perspective, that of the experimentalist. Why they should have chosen the logistic rather than a different curve is partly owing to the relative simplicity of the equation, but not entirely: the logistic was also a highly "visible" curve as a result of the way Pearl was promoting it. Pearl's ability to weather the growing storm of criticism in the late twenties with apparent impunity, at least until the Harvard scandal of 1929, owed a good deal to his unique position at the Johns Hopkins University, which combined financial comfort with complete intellectual freedom. His position gave him the ability to attract people sympathetic to his approach: the result was that, along with the mounting criticisms of the logistic curve, a parallel body of work was accumulating in which the potential of the logistic curve was explored in a more positive manner.

From 1925 to 1930, Pearl was the director of the Institute for Biological Research, created at Johns Hopkins with a grant from the Rockefeller Foundation, essentially in order to allow Pearl to pursue his research with complete freedom. The Institute's program was a direct extension of the work Pearl had begun in the Department of Biometry and Vital Statistics, where he had tried to integrate statistical and experimental methods as applied to problems of general biology. This methodological emphasis was a blend of the two approaches pursued separately by his former teachers, Karl Pearson and Herbert Spencer Jennings, respectively. Projects were divided into two categories. Under the heading of "human biology" were statistical studies on health, longevity, population growth, and human genetics. The second heading of "general biology" encompassed the same broad range of topics, but consisted of experimental studies on lower organisms. One of the objectives was to show how an experimental attack on such problems might shed light on human biology. Fruit-flies (*Drosophila*) were the main subjects, but investigations involving other invertebrates and plant seedlings were also included. As part of the Institute's activities, Pearl founded two journals, *The Quarterly Review of Biology* in 1926 and *Human Biology* in 1929.

One of the largest projects during the first two years was the experimental study of populations, especially of *Drosophila*. Pearl (1927) reviewed this work in *The Quarterly Review of Biology*, but apart from that review, nothing appeared in print on the subject until 1932, when he laid out the results of his work on the influence of density on fertility in populations growing according to the logistic curve. Pearl also used the logistic curve to describe the growth of individual plant seedlings, as part of a separate series of studies on growth and senescence in individuals. As far as population studies went, however, there were relatively few publications of an original nature. Nevertheless, the Institute was a hive of activity with respect to the logistic curve, and those who had contributed to the work in Pearl's laboratory later published a few articles of their own on the logistic equation. While these papers did not contribute to the extension of the theory, they did serve to establish examples of its use in the literature.

Charles Winsor left his job as engineer for the New England Telephone and Telegraph Company in 1927 to join the Institute's staff, and later at Pearl's request he contributed to the mathematical discussions of the logistic curve (Winsor, 1932a, b). Of Pearl's closest associates, Winsor most clearly understood the use of equations such as the logistic curve as tools of research. At the Cold Spring Harbor Symposium on Quantitative Biology in 1934, he argued eloquently for the use of mathematical analysis in population biology, commenting in passing on the logistic curve: "I do not wish to imply that I consider the logistic as the 'true' equation of population growth. Under some sets of conditions it does undoubtedly give a good approximation to the facts. Under other conditions it fails more or less completely. I should be much more interested in an account of why it succeeded or failed than I am in a dispute as to whether it does succeed" (Winsor, 1934).

Other Institute workers publicized the logistic curve in different ways. Biometrician John Rice Miner (1933) wrote on the historical aspects of Verhulst's work. The director of the Imperial Fisheries Institute of Tokyo, Arata Terao, was in Pearl's laboratory from the fall of 1926 to February, 1928, during which time he was involved in the *Drosophila* project. It was Terao's research which showed that the decline in the growth rate of the fly populations with density was the result of an actual reduction in egg-laying, rather than of higher egg or larval mortality, results which Pearl incorporated into his 1932 paper. Terao himself published a series of short articles along similar lines, using populations of the water-flea, *Daphnia*, whose growth he described by a logistic curve (Terao and Tanaka, 1928).

Perhaps the most important visitor to Pearl's Institute was the Russian biologist Vladimir W. Alpatov, privat-docent at the University of Moscow. Alpatov actively publicized the logistic curve on Pearl's behalf, but a more permanent contribution to Pearl's reputation was achieved indirectly, through Alpatov's influence on his own student, Georgii Frantsevich Gause. Alpatov had become interested in biometry through his work on geographical distribution and variation in insects, and applied for a fellowship from the International Education Board of the Rockefeller Foundation in order to study the subject with Pearl in Baltimore. Arriving in America in the summer of 1927, he spent the first three months at Cornell, where he continued his studies on the honey bee, before going to Baltimore in the fall. Once in Pearl's laboratory, he quickly became engaged in the ongoing *Drosophila* work. Alpatov's (1929) own project was on larval growth, where he tried to show, although not with complete success, that the stages of growth between molts could be represented by logistic curves.

A renewal of the Rockefeller fellowship enabled Alpatov to stay in America until August, 1929. During this year he pursued *Drosophila* studies on the influence of temperature and starvation on the physical constitution of the flies. He returned to Russia much impressed by the way science was carried out in America, and by Pearl himself. The enthusiasm for experimental biology that Pearl had generated in Alpatov was in turn passed on to Alpatov's bright young student, G. F. Gause, with notable results.

While Alpatov was in America, Gause was engaged in ecological research on animal abundance in relation to habitat. He spent the summers of 1928 and 1929 gathering data on the distribution of grasshoppers in the Northern Caucasus, and published the first year's results in *Ecology* (1930). When he heard of Pearl's work from Alpatov, he grasped the relevance of the experimental method to his own studies on the correlation between population and environment. In the field it was only possible to correlate abundance with the whole microclimatic complex. Under the simpler conditions of the laboratory, Gause felt, it would be possible to determine accurately how a specific ecological factor influenced population size. After a preliminary exploration using data from other published sources, he expanded his ideas on the basis of his own investigations and sent an article to Pearl, who published it in *The Quarterly Review of Biology* (Gause, 1932). At the same time, Gause and Alpatov (1931) jointly wrote a review article on the logistic curve, which explained the theory and cited various applications of the curve. The article, published in German and in Russian, was intended primarily to publicize the logistic curve in these countries.

In the meantime, Alpatov was trying to find a way for Gause to study with Pearl in America, but it was especially difficult for Gause to get the same fellowship as Alpatov, owing to the heavy competition from other Russian candidates and to Gause's youth, for when he began work in this area in the winter of 1929–30, he was barely nineteen years of age. Thinking that the publication of a book in America might enhance his chances for the fellowship, Gause proposed to Pearl a work based on his latest population research. Pearl responded favorably, and Gause sent him the manuscripts for translation. After some delay on Pearl's part, they were ready for publication in 1934. Although Gause still failed to get the Rockefeller grant, his small book, called *The Struggle for Existence*, eventually became a landmark in the history of experimental population research.

In *The Quarterly Review of Biology* article, which preceded the book, Gause explained the connection between his field work and his recent experimental studies and reported the results of his second year's work on grasshoppers as well as the laboratory investigations. He originally began with studies on some *Drosophila* populations that Alpatov had brought back with him from Pearl's laboratory, studies testing the influence of temperature on population growth. His concern was with the variability of the upper limit of population, in other words with K in the logistic equation. Fitting the populations to logistics, he found that the asymptotic values varied according to temperature. These results confirmed Arata Terao's work on the water-flea and supported his own field observations on species abundance in grasshoppers. Fruitflies, however, were not very satisfactory experimental subjects. There were too many technical problems involved in measuring population densities and in breeding the flies. For his next series of experiments, therefore, he chose yeast populations, which had already been studied by the American biologist Oscar W. Richards.

Richards had been working on yeast since 1923, while a graduate student, and had published a series of articles in 1928 on the conditions influencing the growth of these populations (Richards, 1928a, b). His goal was partly to test a general assumption behind T. B. Robertson's work, that the nature of the reactions underlying growth could be determined by a mathematical analysis of the growth curve. He found, however, that the upper portion of the sigmoid curve reflected only the retarding effect of accumulated wastes. By holding the environment constant, the growth rate could be kept at an accelerating pace (1928b). Growth was therefore not governed by the chemical processes which Robertson had hypothesized on the basis of an S-shaped curve. This meant that any attempt to specify the nature of the growth process by analysing the S-curve could not be successful. Richards (1932) expanded his investigations into a Ph.D. thesis, and found that in all cases his results showed that the situation was considerably more complicated than that revealed by any growth equation. He concluded, with great caution, that any such formulas should be avoided until the processes underlying growth were better understood.

Gause built his work on Richards' findings, but he did not adopt the conclusion that the logistic curve should be rejected because it did not tell the whole story. "We must not be afraid of the simplicity of the logistic curve for the population of unicellular organisms and criticize it from this point of view," he wrote. "At the present stage of our knowledge it is just sufficient for the rational construction of a theory of the struggle for existence, and the secondary accompanying circumstances investigators will discover in their later work" (1934, p. 43). He readily acknowledged that the logistic curve did not reflect the complexity of growth, and was therefore only an approximation, but he felt this fact should not prevent analysis of those cases where the logistic equation did appear to describe the course of a population.

In his book, Gause attempted to quantify the Darwinian idea of the struggle for existence. The concept was interpreted in this case as a problem of the interactions between species in mixed growing groups of individuals, where the "struggle" could be measured simply in terms of the growth or decline of the various populations. This approach owed a great deal to the mathematical work of the Italian physicist Vito Volterra. The starting point of any such study was an examination of growth in homogeneous groups of individuals living under conditions of limited resources, where a "struggle" would be expected to occur. The logistic curve, which described this situation, was therefore the entry-point into the analysis of the struggle for existence. "We may say that the Verhulst-Pearl logistic curve expresses quantitatively and very simply the struggle for existence which takes place between in-individuals of a homogeneous group" (1934, p. 42).

Gause interpreted the logistic curve in terms of the basic postulate that a population was prevented from realizing its full potential for increase because of environmental pressures. He then connected this simple idea to two concepts developed in a different context by the American ecologist Royal N. Chapman (1928). Working on laboratory populations of flour beetles, Chapman had envisaged their growth as being analogous to Ohm's law, which stated that the current at any point over a given time depended upon the potential difference in the conductor and the resistance offered to the current by the conductor. In the same way, Chapman thought, the density of a population depended upon its "biotic potential," or maximum capability for growth, and the "environmental resistance" which acted to inhibit growth. Gause showed how the concepts of biotic potential and environmental resistance could be related more meaningfully to the differential equation of the logistic curve (1934, p. 35):

$$\frac{dN}{dt} = rN\left(\frac{K - N}{K}\right) \tag{10}$$

Chapman's "biotic potential" was represented by the product rN, while the degree of realization of this potential was given by $(K - N)/K$, which in turn depended upon the environmental resistance. Gause considered the actual measure of environmental resistance to be $1 - (K - N)/K$. Unlike Chapman, he did not resort to the analogy with Ohm's law, which was entirely inappropriate in any case, but instead thought of the enclosed "microcosm" as having a certain number of available places, which the individuals filled as the population grew. The environmental resistance was a measure of the number of vacant places left to be filled. Having given Chapman's ideas quantitative meaning by connecting them to the logistic equation, Gause proceeded to analyse how environmental resistance limited the biotic potential of a population. He recognized that the logistic equation by itself was only an empirical expression; but, he argued, if the environmental resistance, calculated separately by physiological means, could be shown to coincide with the value predicted by the logistic curve, then this would constitute proof that the logistic equation did in fact express the mechanism of growth in a limited environment. His experiments on yeast were designed to prove this suposition.

Gause took it for granted that the logistic curve was an accurate description of growth in a single population. He then considered a mixed population of two species of yeast, where the growth of each species would be affected by the other species. This interaction could be expressed as follows:

$$\frac{dN_1}{dt} = r_1N_1\,\frac{K_1 - (N_1 + \alpha N_2)}{K_1} \tag{11a}$$

$$\frac{dN_2}{dt} = r_2N_2\,\frac{K_2 - (N_2 + \beta N_1)}{K_2} \tag{11b}$$

where N_1 and N_2 represented the numbers of species 1 and species 2, respectively. These equations, as Gause showed, coincided with equations used by Volterra (1926), equations that were, as Lotka (1932b) later pointed out, a simple expansion of the logistic curve. Volterra (1938, 1939) himself eventually contributed two articles on the logistic curve for Pearl's *Human Biology*. The coefficients α and β expressed the struggle for existence between the two competing species: α represented the intensity of the influence of species 2 on species 1, β the intensity of the influence of species 1 on species 2. The values r_1, r_2, K_1, K_2 could be calculated directly from the logistic equations describing the growth of the species by themselves. The values for N_1 and N_2 could likewise be calculated directly from the equations describing their growth in the mixed population. Inserting these values into the equations, Gause solved for α and β and arrived at numerical estimates for these two coefficients.

The next problem was to determine the coefficients independently, from a study of environmental factors. Richards' work had shown that the accumulation of toxic wastes was responsible for the decrease of growth: choosing alcohol as the most likely toxic factor in the case of yeasts, Gause calculated α and β on the basis of the comparative alcohol production of the two species. In the case of anaerobic cultures, he found only a rough agreement of the two sets of calculations. This result he interpreted as indicating that the interaction was complicated further by other toxic wastes in the medium. But for aerobic cultures, he found a closer agreement between the coefficients calculated empirically (from the logistic curves) and experimentally. These results indicated that, under aerobic conditions, both species were limited chiefly by the accumulation of alcohol. More importantly, the coincidence of the independently calculated coefficient values seemed to prove that the logistic equation did have validity beyond that of simple description. "In this way," he wrote, "we have proved that the logistic equation actually expresses the mechanism of the growth of the number of unicellular organisms within a limited microcosm" (1934, p. 44).

Gause's results were not really as conclusive as he claimed. All he had actually shown was that in a mixed population, one species will inhibit the growth of another in a manner proportional to its production of toxic wastes. Although he did not demonstrate that the logistic was more valid than a different sigmoid curve, he did nevertheless show that it was an adequate, if approximate, description under the given conditions. His work also illustrated the mathematical advantages of the logistic curve, especially of the differential equation, which could be easily related to biological concepts and modified. This was essentially the conclusion reached by Willy Feller (1940) in a critical review of experimental attempts to verify the logistic equation. Moreover, Gause brought the logistic curve within the domain of ecology. He showed how it could be used as a starting point for a difficult problem, the analysis of competition experimentally. Although he was indebted to the theoretical work of Volterra, and to a lesser extent to Lotka, it was an important step to show how the theory might be translated to an experimental setting and related to broader ecological issues.

This pioneering work on competition was elaborated in a far more rigorous, though initially unmathematical, experimental context by Thomas Park, who systematically studied competition in beetle populations (Park, Leslie, and Mertz, 1964). Park had spent four years, from 1933 to 1937, as a post-graduate student and later an instructor in Pearl's department, where he investigated population growth and the factors regulating it in *Tribolium confusum*, the same beetle Chapman had studied. In 1938 he discussed the role of population studies in general ecology as part of a conference on plant and animal communities held at Cold Spring Harbor (Park, 1939). Part of the paper was devoted to an overview of the logistic curve and to Gause's contributions to experimental biology, as well as a review of experiments on the influence of density on population interactions. Gause also contributed to the published discussion of Park's paper. In general, Park tried to show that statistical and experimental studies of populations could yield valuable insights for general ecological theory.

The substance of this paper was later incorporated into the section on population ecology that Park wrote for the 1949 reference book, *Principles of Animal Ecology* (Allee, Emerson, Park, Park, and Schmidt, 1949, chaps. 18–22). It was this book that probably did most to establish the legitimate place of the logistic curve in experimental population work. Reviewing the various applications of the logistic curve in both laboratory and field work, Park (pp. 304–305) was sympathetic to the criticisms that the logistic equation was not a law of growth and could not be used for predicting future populations. Nevertheless, he stressed its advantage as a demographic tool when used intelligently. The logistic curve, he felt, directed one's attention to general causative factors in population dynamics, and although it did not identify those factors specifically, it permitted them to be arithmetically evaluated and pointed the way for further study. In addition, he noted, it was well established by that time in the literature. At that time, Park was not using the logistic or the Volterra-Gause equations in his own work, but he was trying to establish population ecology as a distinct discipline within ecology, with particular emphasis on combined laboratory and field experimentation. His setting of an ecological context for the logistic equation was an important step in the definition of this discipline.

CONCLUSION

Although Raymond Pearl's invention survived partly through active promotion and partly through the fortuitous connection with people who were able to develop it properly, it would be a mistake to dismiss Pearl's own work on it as lacking significance. In some respects the same qualities of adventure and optimism that sometimes made his experimental methods faulty also contributed to his importance as an innovator in population biology. Not only was he the sole person to follow an experimental, demographic approach to animal populations in the 1920's and 1930's, but he was capable of generating enthusiasm for the potentialities of this approach among other biologists. For this reason he deserves a central place in the history of population ecology.

But Pearl was wrong to call his curve a law of population, as his critics made abundantly clear. His use of the word "law" implied that he considered it to be a generalization that was universally valid for the class of events which it described. The function of such laws is to allow some type of explanation, usually of a causal nature, to be made of specific events, and to provide a basis for prediction. Laws are generally deduced from facts obtained by observation and experiment, and their validity depends only on the validity of those facts, as opposed to their agreement with a theory or an a priori argument. Accordingly, any proposed lawlike statement, or hypothesis, should also be capable of being verified or falsified on the basis of observation. The logistic curve satisfied none of these requirements, and was therefore neither a law nor a hypothesis.

Although it needed to be pointed out clearly just why the logistic equation was not a law, this conclusion by itself was not very interesting. E. B. Wilson's massive outpourings in response to Pearl's lapses in reasoning did not, for all the ink spilled, advance understanding in any creative way much beyond Pearl's level of analysis. Nor was there any great need for such advance as long as the object of the enterprise was to describe and to forecast human population trends. It was only when the logistic curve was seen outside of the context established by Pearl and Wilson that its potential could be assessed dispassionately. That assessment depended on the frank admission that the logistic curve was a logical argument, based on a number of biological assumptions which might or might not be true. Its purpose, seen in this light, was not to describe growth precisely or to yield predictions, but to serve, in Lotka's felicitous phrase, as an "animated question mark." Lotka and Gause each treated the logistic curve as a logical argument in this sense, although with reference to very different problems. In Lotka's case, it was the demographic structure of a population; in Gause's, the ecological study of competition. Both persons clung to the term "law" to describe the curve, but it was clear that in practice neither considered the logistic to possess universality or predictability, as would be expected of a true scientific law.

Lotka's and Gause's analyses were in their different ways early illustrations of how simple logical arguments might be used as tools to interrogate nature. The purpose of this activity is essentially as a means of uncovering possibilities, as Hutchinson noted (1978, p. 239). The next step is to test whether these possibilities are in fact realized in nature: eventually one is led back to the original argument and to a modification of the basic assumptions to conform to the biological reality. On this basis, one builds up gradually a more detailed picture of the natural world. It was this perception, that logical arguments of this type could have a useful role in ecological analysis, that was the most important outcome of the logistic curve debate.

By the late 1940's, the logistic equation had become a working tool of population analysis in general and of competition studies in particular. Its acceptance was accompanied by a more cautious reappraisal of its limitations. A. C. Crombie (1945), following Gause, studied competition in granivorous beetles and stressed the need to pay careful attention to the truth of the assumptions behind the curve before making any biological deductions. L. C. Birch (1948, 1953), drawing on Lotka's work, with some mathematical aid from P. H. Leslie, investigated the biological significance of r, the intrinsic rate of increase. Later, Andrewartha and Birch (1954) included an extended discussion of several major assumptions of the logistic equation in their book on distribution and abundance. In a more positive vein, L. B. Slobodkin (1961) explored the usefulness of the logistic equation, while remaining mindful of its lack of reality.

Complementing the critical analyses of the assumptions, various modifications of the logistic curve were proposed in order to depict population fluctuations in nature more realistically. G. E. Hutchinson (1948) introduced a time lag into the equation, showing how this would produce oscillations in the curve. He also modified the competition equations by adding a cubic term (Hutchinson, 1947) to account for the possible influence of social coaction on the competitive ability of individuals. F. E. Smith (1963) devised a model, based on the logistic curve, in which population growth rate was related to density, measured as mass. His model contained an additional parameter, the replacement rate of mass per unit time in the saturation population. Park (Park, Leslie, and Mertz, 1964) eventually used a stochastic variant of the logistic equation, devised by P. H. Leslie.

Hutchinson (1978, pp. 32–38) has reviewed several variations on the logistic equation, such as the use of finite-difference and stochastic equations. Smith and Mead (1980) have compared the dynamics of deterministic, discrete-time models to a stochastic, discrete-time model of logistic growth. A discussion of the dynamical structure of nonlinear, discrete-time equations was given by May (1975), and along the same lines May and Oster (1976) showed how relatively simple deterministic models could give rise to apparently chaotic behavior. In a philosophical context, Wimsatt (1980) has recently discussed the work of May and others, with attention to the concept of randomness and the way models are used in scientific practice. A review of the different mathematical models that have been devised for populations is in May (1976) and Wangersky (1978).

Recently a great deal of work has been devoted to the effects on growth of random variation in parameters such as r and K (for example, Levins, 1969; Long, Duran, Jeffords, and Weldon, 1974; Nisbet and Gurney, 1976). The different approaches to environmental stochasticity have been catalogued by Roughgarden (1975), who himself investigated the effects of variance of the environmental carrying capacity. Other approaches include an examination of the topological dynamics of logistic forms with respect to the concepts of fitness and survival (Witten, 1978); a model that considers to some extent the dynamics of energy flow through the population (Timin and Collier, 1971); and a discussion of several models, including the logistic one, that takes into account the difference between closed and open systems (Williams, 1972). Ayala, Gilpin, and Ehrenfeld (1973) have examined ten alternative models of competition, eight of which include the Volterra-Gause equations as a special case. The use of models for competitive interactions is a complex problem, and has given rise to a voluminous literature, much of which has been reviewed and discussed recently by Hutchinson (1978).

The logistic curve continues to be used, criticized, and modified in population analysis. To the modern observer the prevalence of the logistic curve can appear puzzling and in need of explanation. F. M. Williams (1972) suggested that the reason might be psychological, resulting from the fact that the logistic equation can be derived in several ways, thereby apparently enhancing its scientific credibility as a robust model. Slobodkin (1980, p. 175) attributed its popularity to the influence of mathematicians who were more concerned with mathematical than biological criteria of validation. Both of these suggestions may have some validity, but it is clear that historical factors also played a part in securing a place for the logistic curve in population ecology. The history of the logistic curve is particularly fascinating because it shows how the acceptance of a model may depend on two very different conditions. One is the applicability of the model to a specific problem or research program. The other is the particular nature of the relationships between the scientists themselves.

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