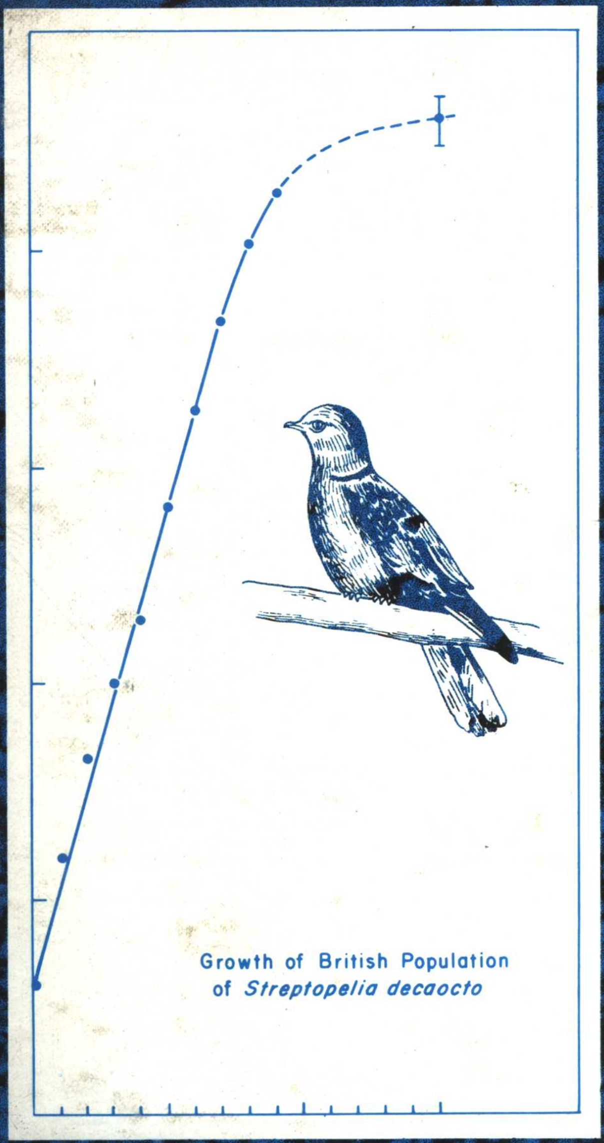


# An Introduction to Population Ecology

G. Evelyn Hutchinson

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# Preface

THIS book is ultimately derived from a course of lectures that I gave for many years under the title Ecological Principles. Though primarily addressed to first year graduate students and senior undergraduates whose main interests were biological, the course was open to, and sometimes taken by, students from other disciplines, not all in the natural sciences.

After I had given the lectures to so diversified an audience, they seemed to turn into a written version that would appeal not only to beginners in ecology but also to an occasional historian, economist, or sociologist, and even more to those biologists in other areas of the science who may have wondered what the people who talked unceasingly about populations were trying to say.

It is impossible to write about population ecology without using some mathematics. In spite of the appearance of a few pages, the amount employed here is pared down to a minimum. All that one really needs to follow the argument is a memory of the simplest parts of high school algebra, a knowledge that $dN/dt$ means the rate of change of $N$ (here the size of the population, with time denoted by $t$), and enough faith to take a few results from linear algebra on trust. It also helps to have an idea of what integration is; this is explained in a very simpleminded way in an appendix, which was handed out to the class, with the title *Ratiocinator infantium*. Once over the early pages of the initial chapter, most of the mathematics can be skipped at first reading without losing the ultimate biological content of the work.

The subject matter of the book is developed along classical lines. This may appear old-fashioned to those who would prefer a more stochastic treatment or who put most of their trust in computer simulation. The approach, however, seems to have been appreciated by a surprisingly large number of people who have become distinguished ecologists. I cannot help thinking that what I have found interesting and useful may also interest and help others.

Even with the obvious restrictions that are imposed on the field, it is impossible, in a book intended as an introduction, to discuss everything that might appear related to the themes that are developed. For those who want more, there are now a number of compendious works. I would particularly recommend:

R. E. Ricklefs, *Ecology*. Newton, Mass.: Chiron Press, 1973, x, 861 pp.

R. Margalef, *Ecología*. Barcelona: Ediciones Omega, S.A., 1974, xv, 951 pp.

F. Schwerdtfeger, *Ökologie der Tiere*. Hamburg and Berlin: Paul Parey; vol. 1: *Autökologie*, 1963, 461 pp.; vol. 2: *Demökologie*, 1968, 448 pp.; vol. 3: *Synökologie* 1975, 449 pp.

Anyone seriously interested will need to be familiar with:

C. S. Elton, *Animal Ecology*: London. Sidgwick and Jackson, 1927, xvii, 207 pp., a short, quite unmathematical but deeply fundamental book, which has improved with reading over half a century. I would also suggest:

L. B. Slobodkin, *Growth and Regulation of Animal Populations*. New York: Holt, Rinehart, and Winston, 1961, viii, 184 pp.

Both these books, being small, are particularly recommended for desert-island reading.

I would also note, as a close relative of what I have written, though its title may not indicate this:

Alison Jolly, *The Evolution of Primate Behavior*. New York: Macmillan, 1972, xiii, 397 pp.

The best places to get an idea of what is being done at the moment are, of course, the recent numbers of journals such as *Ecology*, *Evolution*, and *The American Naturalist*. Two books, moreover, give a very up-to-date picture:

M. L. Cody and J. M. Diamond, editors, *Ecology and Evolution of Communities*. Cambridge, Mass.: Belknap Press of Harvard University Press, 1975, xiv, 545 pp.

R. M. May, editor, *Theoretical Ecology, Principles and Applications*. Philadelphia and Toronto: W. B. Saunders, 1976, viii, 317 pp.

I am deeply aware of the help of a great variety of friends. That birds figure largely in any work devoted to animal ecology is partly due to most species being diurnal and possessing color vision, but also to the genius of two of the outstanding investigators of the subject, David Lack (1910–73) and Robert Helmer MacArthur (1930–72), whose close friendship I enjoyed and whose memories I cherish. Many other students of birds have helped me. I particularly would acknowledge, with great affection, the influence of S. Dillon Ripley which extends far beyond the conventional limits of ornithology.

Every student who asked questions or contributed to the discussions that followed the lectures probably added something to the book. I thank them all.

The debt to my colleagues at Yale University is great; individual enumeration would be invidious as the number of people to be thanked is so great that some would be accidentally omitted. Four institutions in the university have, however, meant so much to me and my work that I want to mention them specifically. I first take this opportunity to express my deep appreciation, over more than the past three decades, to the fellowship of Saybrook College in Yale University. The historical and other ancillary material used here owes a great deal to friendships formed in that institution where Basil Duke Henning, Master of the College for many years, and his wife Alison created a tradition which I know their successors, Elisha and Elizabeth Atkins, will continue, of the loving exchange of learning, which is the greatest value that a university can afford. Of the present fellows I would particularly thank Richard S. Miller who has read the book in manuscript, Phoebe Ellsworth who helped in the hunt for the elusive Roswell Johnson, the reluctant inventor of the ecological niche, and who encouraged my belief that what I have written can be read by really literate social scientists, and Marjorie Garber who unwittingly led me, by a beautiful if circuitous path, to the final lines of the book. Second, the collections of the Peabody Museum were always available to provide classroom demonstrations of organisms mentioned in lectures. No one can have profited from this more than I did. At a time when such institutions do not take a very high place in the priorities of university administrators, I would emphasize the importance of a natural history museum with a really extensive collection in giving substance to names and ideas that might otherwise become rather meaningless abstractions. I would specifically like to thank Charles Remington for perennial help relating to insects and Eleanor Stickney for her kindness in the bird room. Third, the Kline Science Library and its staff, ever willing to help satisfy the most impossible requests and indeed often able to do so, demand my admiration as well as my gratitude. Last, the Beinecke Rare Book and Manuscript Library proved to contain a remarkable number of books and pamphlets bearing on the history of ideas about population. It is also a delightful place in which to work.

Both Eric L. Charnov of the University of Utah and Robert H. Whittaker of Cornell University have read the book in manuscript. I am deeply indebted to them for many suggestions.

I thank Messrs. Faber and Faber for permission to publish the frontispiece and the Guildhall Museum, London, for figures 3, 4, and 5. I am extremely grateful to Maxine

Watson for figures 66, 67, and 104 based on material now in press in her own papers, and James Porter for figure 134. Pamela Parker and Rudi Strickler both made available manuscripts of papers now in press. William B. Keller made the transcription of the epitaph on the memorial to Malthus in Bath Abbey. Mary M. Poulson helped in innumerable ways. For assistance in the final stages of prepaning the manuscript, I thank Anna Aschenbach. For the excellence of the typescript derived from a refractory longhand manuscript I thank Beverley Dooling and Alice Pickett, and I am specially grateful to Virginia Simon for the loving care lavished on the illustrations. At the Yale University Press, Lottie M. Newman has been a superb copyeditor and Jane Isay, as a perfect godmother, has watched over the growth of the book from its earliest infancy.

My gratitude to my wife increased daily as each new page was written.

G. E. H.

New Haven, Connecticut

All Hallow's Eve 1976

# *Contents*

Chapter One

# *M. Verhulst*

IN this first chapter we will look at some of the ways in which we can construct mathematical models of populations. For this purpose we shall need, in addition to the ordinary postulates of mathematics which we may assume to be satisfactory for our purposes, at least two additional biological postulates. These appear to follow from everyday experience, though the first of them was not generally believed of all organisms until the nineteenth century, while a glance at a newspaper often suggests that many people behave as if the second postulate were false.

*The postulate of parenthood*

This states that every living organism has arisen from at least one parent of like kind to itself; it is often called the principle of abiogenesis and expressed epigrammatically as *omne vivum ex vivo*. For anyone who believes in the initial terrestrial origin of life, the postulate is not universally valid; but since under present conditions spontaneous generation has never been observed, we can take it as true enough to use in our investigation of contemporary populations.

The use of this postulate limits our investigation to living beings, trees but not the telegraph poles that can be made from them, people but not the cars that they drive. The stochastic dynamics of destruction or death can be applied to sets of both nonliving and living objects, but the equivalent dynamics of birth only to living populations.

*The postulate of an upper limit*

The second postulate is that in a finite space there is an upper limit to the number of finite beings that can in some way occupy or utilize the space under consideration. This may be merely a geometrical limitation as in some sessile animals like barnacles; in such a case it is deducible from mathematics. Much more often it is due to the objects requiring a supply of energy at a certain rate to maintain their stability; obviously the space cannot contain more of such objects than utilize the energy input into the space. Comparable limits may be set by the rate of supply of nutrient materials such as water, carbon dioxide, phosphorus, nitrogen, or soluble iron. In the case of animals, more complicated situations, involving limitation by a food supply that itself depends on the rate of supply of radiation, water, or nutrients, are of course frequent. More subtle limitations, notably involving territoriality, are common among the more complex invertebrates and the vertebrates. Some of these types of limitations will be discussed in greater detail in later chapters.

*Convention of continuity*

In addition to the biological postulates of parenthood and of an upper limit, it is convenient for mathematical reasons initally to adopt the convention that the variation of a population of size $N$ behaves as if $N$ were a continuous variable, capable of taking any value, integral or fractional, between the possible lower and upper limits of the population. This permits the use of the infinitesimal calculus. The convention, though strictly untrue, is harmless when we are dealing with a sufficiently large population of organisms not having definite breeding, or dying, seasons, in which reproduction occurs at random among all members of the appropriate age class, and death occurs according to some statistically defined pattern not varying with time. When definite breeding seasons occur, or when mortality is much greater at some times of year than at others, finite difference equations have to be used. At first this seems an inelegant and inflexible approach, but as will later be apparent, it can lead to some remarkable results.

*The logistic equation of Pierre-François Verhulst*

The initial approach to an equation of population growth, ultimately due to Pierre-François Verhulst, of whom more hereafter, will be that of Lotka, as developed in his remarkable book *The Elements of Physical Biology*.[1] This book was written to provide for biology, or at least parts of biology, a basis comparable to that given by theoretical physics to experimental physics. Lotka probably knew a smaller proportion of the relevant biology of his time than a theoretical physicist usually knows of experimental physics. This gives parts of his book a curiously naïve character. In spite of this limitation it is a great work, one of the foundation stones of contemporary ecology.

Lotka generalizes the behavior of a population in the following equation:

$$\frac{dN}{dt} = f(N). \qquad (1.1)$$

This merely tells us that the rate at which the number of individuals, $N$, in the population changes with time depends in some way on the number present. This sounds very reasonable, but it could be untrue, in a sexually reproducing species, for all $N > 2$. Suppose a species with a restricted breeding season and the property that any individual that starts to breed inhibits chemically or behaviorally the breeding of all other individuals, except its own mate, in a small localized population. This could mean that only one pair could breed at a time and consequently the rate of growth of the population would be independent of $N$. Cases where a single dominant male inhibits the breeding activity of many other males are well known, so the discovery of a case of this sort is not quite out of the question; small populations of babblers of the genus *Turdoides* can indeed behave in this way.[2] This example at least indicates that we may not always find $f(N)$ to be a very simple function.

To go back to equation (1.1), it at first looks trite and uninteresting. Since, however, from Taylor's Theorem it may be expanded as a power series, we may write

$$\frac{dN}{dt} = a + bN + cN^2 + dN^3 + . \qquad (1.2)$$

This looks more interesting than equation (1.1). From our postulate of parenthood, if $N = 0$, $dN/dt = 0$, so $a = 0$, and we may write

$$\frac{dN}{dt} = bN + cN^2 + dN^3 + . \qquad (1.3)$$

Since we are looking for a suitable equation we may regard (1.3) as a set of equations in which the coefficients have any rational value including zero. We then invoke the principle of parsimony or simplicity, often called Ockham's razor, after the fourteenth-century English Franciscan friar William of Ockham,[3] which tells us that it is vain to do by more what can be done by less. In this case we begin by considering just one term, $bN$,

1. A. J. Lotka, *Elements of Physical Biology*. Baltimore, Williams and Wilkins, 1925, xxx, 460 pp. Reprinted in 1956 as *Elements of Mathematical Biology*. New York, Dover.

2. For the reproduction of babblers see A. J. Gaston, Brood parasitism by the pied crested cuckoo *Clamator jacobinus*. *J. Anim. Ecol.*, 45:331–48, 1976.

3. William of Ockham, Ockam, or Occam, was born at Ockham in Surrey, England, late in the thirteenth century. He studied at Merton College, Oxford, which at that time was a center of scientific thought. At some time while at Oxford he became a Franciscan. He taught in the university until 1323. His later life was largely taken up in controversy with Pope John

before going on to $cN \cdot N$ or two or more combinations of terms. Our first attempt gives

$$\frac{dN}{dt} = bN \qquad (1.4)$$

or

$$N = e^{bt}$$

which is what Malthus, and indeed his predecessors, thought in principle, and correctly, about the inherent growth of populations, but which here must be rejected since there is no upper bound. This is true of all equations using just one term of the expansion.

In equation (1.4), $b$, which represents the unrestricted rate of increase per individual, birthrate minus death rate, in the kind of ideal population that we are considering, is often called the Malthusian parameter.

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XXII and his successors, at first over the concept of evangelical poverty and later on the question as to whether the Emperor could depose the Pope. After captivity at Avignon, from which he escaped, he spent the later years of his life in Munich, under the protection of Ludwig IV of Bavaria. He died late in the 1340s, probably as an excommunicated heretic; he was buried in the Franciscan Church in Munich, which was pulled down early in the last century.

The famous passage *quia frustra fit per plura quod potest fieri per pauciora*, "because it is vain to do by more what can be done by fewer," occurs casually, almost as if it were a universally accepted opinion, as may well have been the case, in a demonstration that substance itself is quantity, *ipsamet substantia est tunc quantitas*, in the *Tractatus quam gloriosus de sacramento altaris, et in primis de puncti, lineae, superficiei, corporis, quantitatis, qualitatis et substantiae distinctione venerabilis Inceptoris Guilhelmi Ockham Anglici* ... (The very celebrated tract on the sacrament of the altar and particularly on the distinction of the point, line, surface, solid, quantity, quality, and substance, of the venerable Inceptor William Ockham the Englishman ...). An inceptor was someone who had not yet achieved a higher degree; on a copy of his lost tombstone he appears as doctor. The book, apparently based on lectures given at Oxford, seeks to establish a foundation theory of a geometrical kind as the basis for the exposition of the doctrine of transubstantiation in the Holy Eucharist. The *De Sacramento Altaris* is an extremely difficult book for anyone not fully familiar with the language of medieval philosophy. The most accessible edition, which, however, seems at times not to meet the most exacting standards of modern scholarship, is one edited by T. Bruce Birch (Burlington, Iowa, Lutheran Literary Board, 1930, xlvii, 576 pp.). This edition provides, opposite the Latin, a literal English translation which lovingly preserves all the obscurities of the original; the passage quoted may be found on on p. 104 (Latin), p. 105 (English).

Ockham had an important influence on Luther and has been hailed as the forerunner of many later philosophers from Locke to Bertrand Russell. Modern writers have discussed the simplicity postulate in a variety of ways. The approaches used by Harold Jeffreys in *Scientific Inference* (Cambridge University Press, 1931, 1937) are of particular scientific interest.

Jeffreys argued more or less as follows. Given any set of data the total number of laws that can explain the data is infinite. Jeffreys restricts his treatment to quantitative laws, expressible as differential equations that can be rationalized to have integral exponents and coefficients. There is a denumerable infinity of such laws. If we consider any set of data, the sum of the prior probabilities of all the laws must be unity, unless we assume that full explanation of the data is forever impossible. The probabilities cannot be infinitely small, and evidently also cannot be finite and equal. Jeffreys supposes that they are finite and unequal and form a convergent series summing to unity. The differential equations representing different laws can each be given a number by summing the order, degree, and a term representing the numerical coefficients. In the kind of equation that we use in biology, in which the coefficients such as $r$ or $K$ can have any of a wide range of values, representing boundary conditions of a sort, it is probably best to use just the irreducible number of such terms. Thus

$\frac{dN}{dt} = bN$ would have a complexity of 3.

$\frac{dN}{dt} = bN - cN^2$ would have a complexity of 5.

$$\frac{dN}{dt} = bN - cN^2 + dN^3$$

would have a complexity of 7.

Jeffreys rejects the idea that simple laws are initially chosen for their convenience, because this mode of choice would give no confidence that the law would be correct if a value of $N$ previously untested was considered in the equation. He therefore maintains that the simple law is in some sense actually more likely to be true than any randomly chosen law of greater complexity. This view leads to certain difficulties, though it does describe the attitude of the investigator trying one of a hitherto unknown body of laws. This aspect of simplicity does not seem to have been much considered in recent years. Most readers will probably feel that whatever other reasons we may have for adopting Ockham's razor, it does give the best entry into further complexities. As Lagrange said, "Seek simplicity but distrust it."

In later discussions we shall use $r$ rather than $b$ for the Malthusian parameter or unrestricted rate of increase, since $r$ has been so widely used that it has become part of compound nouns, notably $r$-selection. For the present, while we are constructing our equation, $b$ will be retained.

Still following William of Ockham, we now try the two simplest terms together, taking

$$\frac{dN}{dt} = bN + cN^2 \qquad (1.5)$$

which after a moment's thought, writing $c = -b/K$, becomes

$$\frac{dN}{dt} = bN\frac{(K-N)}{K}$$

or as we shall now write

$$\frac{dN}{dt} = rN\frac{(K-N)}{K} \qquad (1.6)$$

which expresses, in the simplest possible way, the growth of a population increasing in a biological manner to an upper asymptote $K$, continuously and without catastrophes. The population increases at a rate determined by $N$, the number of individuals present, their maximum rate of increase $r$, and the proportion of the potential asymptotic population $K$ which is still unrealized. The term $(K - N)/K$ giving this proportion would today be called negative feedback, but there is nothing in the equation to suggest how the feedback works.

The rate of increase rises slowly to a maximum as $N$ reaches $K/2$, and then falls asymptotically to zero as $N$ approaches $K$. Integration gives

$$N = \frac{K}{1 + e^{-rt}} \qquad (1.7)$$

time ($t'$) being now measured backward and forward, from the time of the maximum value of $dN/dt$, when $N = K/2$.

Graphically the integral curve of a growing population is sigmoid, at first rising slowly but increasingly fast from any arbitrarily small starting population, inflecting when $N = K/2$ and then ever more slowly approaching the asymptote $K$ (figure 1).

Experience has shown that most people prefer to think about the differential equation but to draw the integral graph. With regard to the latter it should be noted that if we artificially set $N > K$, the feedback term becomes negative, the population falling asymptotically to $K$, as indicated in the upper branch in figure 1. Richard Levins[4] pointed out that if in the usual form of the equation,

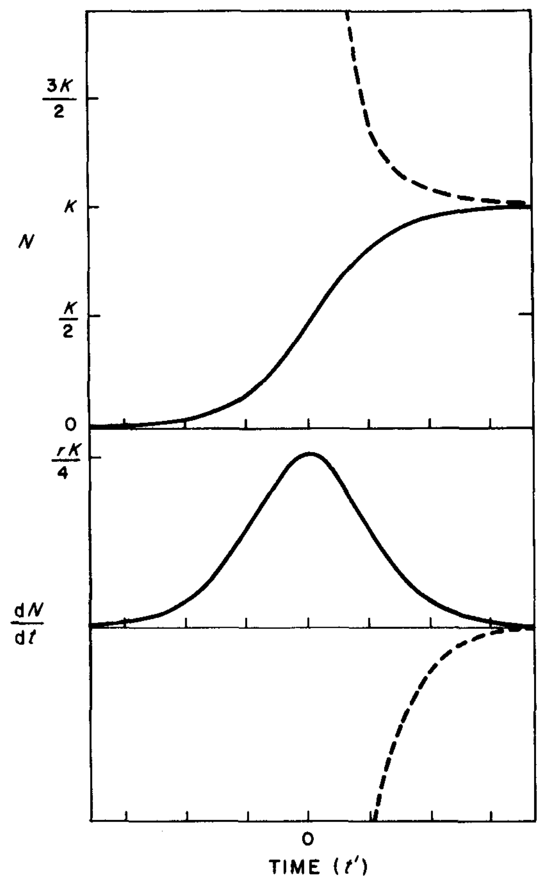


FIGURE 1. Solid line, upper panel: population increasing according to Verhulst's logistic; lower panel: rate of increase of such a population with a maximum corresponding to the inflection point in the upper curve, at $t' = 0$. Broken line, upper panel: hypothetical population declining from infinity at $t' = 0$ according to the logistic; lower panel, rate of such decline (in part after Lotka and after Pearl and Reed).

4. Richard Levins in an informal ecology seminar entitled "Some things that don't work," May 27, 1971, Osborn Memorial Laboratories, Yale University.

$r$, which is ordinarily regarded as an inherent birthrate (**b**) minus an inherent death rate (**d**), be negative, setting $N > K$ leads to an impossible result, for $dN/dt$ is positive and increases indefinitely with $N$. An additional biological postulate is clearly required to imply that $r \geq 0$, so avoiding negative populations as well as impossible values of the rate of increase in a dying overcrowded world.

The very explicit presentation of Lotka's approach to the logistic, far more elementary and more detailed than his own, has been given to exhibit quite clearly what is behind most of the theoretical reasoning that we shall use. The argument is not axiomatic, there are plenty of places where it can go wrong. Williams[5] has pointed out that a much more rigorous derivation is possible. This involves several postulates as to the uniformity of the environment in space and time and the uniform distribution of organisms in it; these postulates, which express what one tries to achieve in a properly constructed experiment, are described by Williams as *instrumental*. It also involves two postulates of a biological, or as Williams calls it an *anacalyptic*, kind: that the properties of all organisms are the same at any time, and that the properties of a single organism are invariant with time. Like the convention of continuity, these postulates are strictly untrue; but in many circumstances the divergence from truth, within a genetically uniform population, is unimportant. If one adds the further anacalyptic postulate that all organisms with respect to their impact on the environment or on each other are identical through time, density cannot alter the reproductive rate and we can derive the exponential growth equation. If instead one postulates that growth rate declines linearly with increasing density, one gets the logistic. In the treatment based on Lotka, stopping at the second term to give an upper bound is in fact equivalent to the postulate of an inverse linear dependence of growth rate on density.

*A historical digression*

While it was convenient to present the logistic equation in Lotka's way, so making clear what it is about, it is also interesting to see how the ideas on which it is based came into being, particularly as their history is rather curious.

Scientific demography may be said to have begun in 1662, with the publication of John Graunt's *Natural and Political Observations mentioned in a following index and made upon the Bills of Mortality.*[6] Graunt was mainly a collector and classifier of facts, which he obtained initially by tabulating the Weekly Bills of Mortality that were published, from the early sixteenth century onward, recording the deaths in the City of London, in the first instance as an early warning of the incidence of plague. Christenings were also reported, at least from the later years of the sixteenth century, and in the next century indications of causes of death other than plague were given. The reports were submitted to each Parish Clerk by two searchers, honest and discrete matrons sworn truly to search the body of every person dying in the parish; no great level of competence in pathology, even by seventeenth-century standards, can be expected (figures 2, 3). In addition to the

5. F. M. Williams, Mathematics of microbial populations, with emphasis on open systems. *Trans. Conn. Acad. Arts Sci.*, 44:397–426, 1972.

6. *Natural and Political Observations mentioned in a following index, and made upon the Bills of Mortality by John Graunt Citizen of London* ... London. Printed by Tho: Roycroft, for John Martin, James Allestry, and Tho: Dicas at the sign of the Bell in St. Paul's Churchyard. MDCLXII.

John Graunt (1620–74) was by trade a haberdasher; evidently a public-spirited man, and though a captain and later a major in the trained band, he was well known for his peaceable disposition. He was elected to the Royal Society as the result of a "Recommendation which the *King* himself was pleased to make, of the judicious Author of *The Observations on the Bills of Mortality*; In whose Election, it was so far from being a Prejudice, that he was a Shop keeper of *London*; that his Majesty gave this particular Charge to his Society, that if they found any more such Tradesmen, they should be sure to admit them all, without any more ado" (T. Sprat, *The History of the Royal Society*. London, 3rd ed., 1722, p. 67).

With regard to Graunt's calculation, the fact that we now would put the first human couple, however we defined them, at a point much further back in time, merely strengthens the argument.

London 9 From the 11 of February to the 18. 1661

| Parish | Bur. | Pl. | Parish | Bur. | Pl. | Parish | Bur. |
|---|---|---|---|---|---|---|---|
| St. Albans Woodstreet | 1 | | St. Gabriel Fenchurch | 1 | | St. Martins Iremongerla. | |
| St. Alhallowes Barking | 2 | | St. George Botolphlane | | | St. Martins Ludgate | |
| St. Alhallowes Breadstreet | 1 | | St. Gregories by St. Pauls | 4 | | St. Martins Orgars | 1 |
| St. Alhallowes Great | 2 | | St. Hellens | | | St. Martins Outwitch | |
| St. Alhallowes Honylane | | | St. James Dukes place | 1 | | St. Martins Vintrey | 1 |
| St. Alhallowes Lesse | | | St. James Garlickhithe | | | St. Matthew Fridaystreet | |
| St. Alhall. Lumbardstreet | | | St. John Baptist | 2 | | St. Maudlins Milkstreet | |
| St. Alhallowes Staning | | | St. John Evangelist | | | St. Maudlins Oldfishstr. | |
| St. Alhallowes the Wall | | | St. John Zachary | | | St. Michael Bassishaw | |
| St. Alphage | 4 | | St. Katharine Coleman | | | St. Michael Cornhill | 2 |
| St. Andrew Hubbard | 2 | | St. Katharine Creechurch | 2 | | St. Michael Crookedlane | 1 |
| St. Andrew Undershaft | 1 | | St. Lawrence Jewry | | | St. Michael Queenhithe | 1 |
| St. Andrew Wardrobe | 4 | | St. Lawrence Pountney | | | St. Michael Quern | 1 |
| St. Anne Aldersgate | | | St. Leonard Eastcheap | 1 | | St. Michael Royall | |
| St. Anne Black-Fryers | 2 | | St. Leonard Fosterlane | | | St. Michael Woodstreet | |
| St. Antholins Parish | | | St. Magnus Parish | 2 | | St. Mildred Breadstreet | 1 |
| St. Austins Parish | | | St. Margaret Lothbury | 2 | | St. Mildred Poultrey | |
| St. Bartholom. Exchange | | | St. Margaret Moses | 1 | | St. Nicholas Acons | 2 |
| St. Bennet Fynck | 1 | | St. Margaret Newfishst. | | | St. Nicholas Coleabby | 1 |
| St. Bennet Grace-Church | | | St. Margaret Pattons | | | St. Nicholas Olaves | |
| St. Bennet Paulswharfe | | | St. Mary Abchurch | 1 | | St. Olaves Hartstreet | 1 |
| St. Bennet Sherehog | | | St. Mary Aldermanbury | | | St. Olaves Jewry | 2 |
| St. Botolph Billingsgate | | | St. Mary Aldermary | 1 | | St. Olaves Silverstreet | |
| Christs Church | 2 | | St. Mary le Bow | | | St. Pancras Soperlane | 1 |
| St. Christophers | | | St. Mary Bothaw | | | St. Peters Cheap | |
| St. Clement Eastcheap | 1 | | St. Mary Colechurch | | | St. Peters Cornhil | |
| St. Dionis Backchurch | | | St. Mary Hill | 2 | | St. Peters Paulswharfe | 1 |
| St. Dunstans East | 2 | | St. Mary Mounthaw | | | St. Peters Poor | |
| St. Edmun. Lumbardstreet | | | St. Mary Summerset | | | St. Stephens Colemanstr. | 2 |
| St. Ethelbourgh | | | St. Mary Staynings | 1 | | St. Stephens Walbrook | 2 |
| St. Faiths | | | St. Mary Woolchurch | 1 | | St. Swithins | 2 |
| St. Fosters | 1 | | St. Mary Woolnoth | 1 | | St. Thomas Apostle | 4 |
| | | | | | | Trinity Parish | |

*Buried within the 97 Parishes within the Walls, of all Diseases* — 75 *Whereof, of the Plague* — 0

| | | | | | |
|---|---|---|---|---|---|
| St. Andrews Holborne | 11 | St. Botolph Aldgate | 13 | St. Saviours Southwark | 23 |
| St. Bartholomew Great | 1 | St. Botolph Bishopsgate | 9 | St. Sepulchers Parish | [illegible] |
| St. Bartholomew Lesse | | St. Dunstans West | 5 | St. Thomas Southwark | [illegible] |
| St. Brides Parish | 12 | St. George Southwark | 7 | Trinity Minories | [illegible] |
| Bridewel Precinct | | St. Giles Cripplegate | 22 | At the Pesthouse | |
| St. Botolph Aldersgate | 3 | St. Olaves Southwark | 11 | | |

*Buried in the 16. Parishes without the Walls, and at the Pesthouse* — 130 *Whereof, of the Plague* — 0

| | | | | | |
|---|---|---|---|---|---|
| St. Giles in the Fields | 22 | Lambeth Parish | 4 | St. Mary Islington | [illegible] |
| Hackney Parish | 2 | St. Leonard Shoreditch | 10 | St. Mary Whitechapel | 20 |
| St. James Clerkenwell | 6 | St. Magdalen Bermond. | 7 | Redriffe Parish | |
| St. Katharine Tower | 6 | St. Mary Newington | | Stepney Parish | 24 |

*Buried in the 12 out Parishes in Middlesex and Surrey* — 113 *Whereof, of the Plague* — 0

| | | | | | |
|---|---|---|---|---|---|
| St. Clement Danes | 18 | St. Martins in the Fields | 26 | St. Margaret Westminster | 16 |
| St. Paul Covent Garden | 4 | St. Mary Savoy | 1 | Whereof at the Pesthouse | 0 |

*Buried in the 5 Parishes in the City and Liberties of Westminster* — 65 *Whereof, of the Plague* —

FIGURE 2. Raw data for the demography of the seventeenth century: bill of mortality for the week 11–18 February, 1661 (o.s., i.e., 1662 n.s.), giving burials in all the parishes of London (Guildhall Museum Library, London, by kind permission).

## *The Di*[illegible] *and Caſualties this Week.*

| | | | |
|---|---|---|---|
| Abortive | 4 | Lethargy | 1 |
| Aged | 39 | Overlaid | 1 |
| Ague | 3 | Pluriſie | 2 |
| Bruſed | 1 | Quinſie | 3 |
| Burnt (an Infant) by accident at St. Alhallowes Great | 1 | Rickets | 7 |
| Cancer | 1 | Riſing of the Lights | 4 |
| Childbed | 4 | Rupture | 1 |
| Chriſomes | 15 | Scowring | 2 |
| Conſumption | 78 | Scurvy | 2 |
| Convulſion | 25 | Spleen | 1 |
| Diſtracted | 1 | Spotted feaver | 2 |
| Dropſie | 23 | Stilborn | 10 |
| Feaver | 37 | Stopping of the Stomach | 6 |
| Flox and Small-pox | 31 | Suddenly | 2 |
| Flux | 1 | Surfet | 4 |
| French-pox | 1 | Teeth | 29 |
| Gowt | 2 | Threw himſelf out of a window (being Diſtracted) at St. Clement Eaſtcheap | 1 |
| Griping in the guts | 20 | Thruſh | 1 |
| Jaundies | 4 | Tiſſick | 2 |
| Impoſtum | 2 | Ulcer | 1 |
| Infants | 14 | Winde | 2 |
| Kingſevill | 2 | | |

Born and Chriſtned { Males 109, Females 102, In all 211 } Buried { Males 194, Females 189, In all 383 } Plague 0

Increaſed in the Burials this week —— 34

Pariſhes Clear of the Plague —— 130 Pariſhes Infected —— 0

The Aſſiſe of Bread ſet forth by Order of the Lord Maior and Court of Aldermen,
A Penny Wheaten loaf [illegible] contain 5 Ounces and three half penny White loaves the like weight.

FIGURE 3. Verso of bill illustrated in figure 2, tabulating deaths by causes and giving a summary of baptisms and burials. No plague was recorded during this week (Guildhall Museum Library, London, by kind permission).

weekly bills, more convenient annual summaries were also prepared and published (figure 4).

Graunt also studied the records of birth and death, presumably from the parish register, in a country parish, identified by Hull as Romsey, near Southampton. Some of his results, notably those on the sex ratio at birth, will be noted later. Much of Graunt's work consisted of a study of the incidence of various causes of death. He made in addition a theoretical estimate of the rate of growth of the City of London, from the proportion of people of reproductive age and their supposed fertility. Though such a study was preliminary and unsatisfactory, it provided a starting point for further research. Graunt concluded that the population of London was doubling every 64 years, which compared favorably with an empirical estimate of doubling in 56 years. No adequate allowance, however, was made for immigration, which probably accounted for a great part of the empirical rate.

Graunt allowed himself to speculate that if the descendants of Adam and Eve, created according to Scaliger's chronology in 3948 B.C., had doubled every 64 years, they would have filled the world with "far more People, then are now in it" (p. 59). He did not give the number and might well have been terrified by it. In the period between 3948 B.C. and 1662 A.D., there would have been 87.7 doublings, giving a population of $2^{87.7}$ or about $10^{26}$, which is about a 100 million people on each square centimeter of habitable land. This example shows that Graunt was familiar with both the potential geometrical increase and some limitation imposed on that increase, but he paid no further attention to the general problem.

Sir Matthew Hale,[7] in a remarkable book posthumously published in 1677, seems to have been the first to use the expression "Geometrical Proportion" for the growth of a population from a single family. He was primarily interested in showing that the human population of the world was not an infinitely old one, living on an infinitely old earth, as some philosophers had maintained. This led him to an extensive study of pestilence, famine, wars, conflagrations, and floods as sporadic limitations to human populations. He rightly concluded that such factors were not enough to bring the population to "Equability," as he termed a stable state, though his empirical data were for the most part very inadequate. He used the Domesday Book to show that the population of Gloucester had increased in historic times, and believed the increase to be general. He gave no discussion of an upper bound. He did, however, believe that in animals, notably insects, various natural, if providential, calamities reduce the numbers to low levels intermittently, so maintaining usually appropriate populations, and producing a balance of nature. This idea was greatly developed by William Derham in his Boyle lectures published (probably in 1713) as *Physico-theology; or, a demonstration of the being and attributes of God from his works of creation.*[8]

Graunt's great friend, Sir William Petty, seems early to have been involved in the work on bills of mortality, continuing it after Graunt's death and extending it to a study of Dublin. Of a more speculative, though less accurate turn of mind than Graunt, Petty engaged in rather more extensive intellectual flights of imagination about the population of the world and its growth.

In *Another essay in Political arithmetick* of

7. Sir Matthew Hale, *The Primitive origination of mankind considered and examined according to the light of nature.* London. Printed by William Godbid, for William Shrowsbery at the sign of the Bible in Duke Lane, CIↃLXXVII.

Sir Matthew Hale (1609–76) was an eminent lawyer who became Chief Justice of the King's Bench in 1671. Though brought up as a strict puritan, he was a tentative evolutionist so far as the fauna of the New World was concerned. I have discussed this aspect of his work in: The influence of the New World on the study of natural history. Philadelphia Academy of Natural Sciences, Bicentennial Symposium (in press).

8. Rev. William Derham [1713(?)], *Physico-theology; or, a demonstration of the being and attributes of God, from his works of creation. Being the substance of sixteen sermons, preached in St. Mary-le-Bow Church, London; at the Honourable Mr. Boyle's lectures, in the years 1711 and 1712.*

# A generall Bill for this present yeere, ending the 16. of *December* 1641. according to the report made to the Kings most excellent Ma^tie.

By the Company of Parish Clearks of *London*, &c.

| Parish | Bur. | Pl. | Parish | Bur. | Pl. | Parish | Bur. | Pl. | Parish | Bur. | Pl. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ALbans Woodstreete | 52 | 13 | Christophers | 21 | 3 | Margaret Lothbury | 34 | 6 | Michael Bassishaw | 64 | 14 |
| Alhallowes Barking | 129 | 21 | Clements Eastcheape | 20 | | Margaret Moses | 15 | 1 | Michael Cornhill | [illegible] | [illegible] |
| Alhallowes Breadstreet | 28 | 1 | Dionis Back-church | 19 | | Margaret Newfishstr. | 33 | 3 | Michael Crookedlane | [illegible] | 1 |
| Alhallowes Great | 105 | 31 | Dunstans East | 119 | 16 | Margaret Pattons | 13 | | Michael Quenhithe | 54 | 7 |
| Alhallowes Honilane | 6 | | Edmunds Lumbardst. | 23 | 5 | Mary Abchurch | 27 | 3 | Michael Queene | 21 | [illegible] |
| Alhallowes Lesse | 58 | 2 | Ethelborough | 43 | 9 | Mary Aldermanbury | 44 | 2 | Michael Royall | 4[illegible] | [illegible] |
| Alhall. Lumbardstreet | 25 | 3 | Faiths | 40 | 2 | Mary Aldermary | 40 | 10 | Michael Woodstreet | 4[illegible] | |
| Alhallowes Staining | 74 | 23 | Fosters | 34 | 6 | Mary le Bow | 42 | | Mildred Breadstreet | 27 | 3 |
| Alhallowes the Wall | 70 | 13 | Gabriel Fen-church | 28 | 1 | Mary Bothaw | 16 | | Mildred Poultrey | 19 | |
| Alphage | 69 | 12 | George Botolphlane | 11 | 1 | Mary Colchurch | 6 | | Nicholas Acons | 13 | |
| Andrew Hubbard | 27 | 2 | Gregories by Pauls | 72 | 5 | Mary Hill | [illegible] | 2 | Nicholas Colesabby | 39 | 5 |
| Andrew Vndershaft | 45 | | Hellens | 38 | 3 | Mary Mounthaw | 19 | 2 | Nicholas Olaues | 22 | 1 |
| Andrew Wardrobe | 123 | 15 | Iames Dukes place | 58 | 11 | Mary Summerset | [illegible] | 10 | Olaues Hartstreet | 77 | 2 |
| Anne Aldersgate | 92 | 34 | Iames Garlickhithe | 54 | 5 | Mary Staynings | [illegible] | 13 | Olaues Iewry | 25 | 1 |
| Anne Blacke-Friers | 130 | 13 | Iohn Baptist | 50 | 4 | Mary Woolchurch | 26 | 5 | Olaues Siluerstreete | 5[illegible] | 9 |
| Antholins Parish | 23 | 1 | Iohn Euangelist | 7 | | Mary Woolnoth | [illegible] | 3 | Pancras Soperlane | 8 | |
| Austins Parish | 34 | 16 | Iohn Zacharie | 32 | 9 | Martins Iremonger. | 24 | | Peters Cheape | 2[illegible] | [illegible] |
| Barthol. Exchange | 34 | 2 | Katherine Coleman | 73 | 13 | Martins Ludgate | 79 | 9 | Peters Cornehill | 22 | 1 |
| Bennet Fynch | 26 | | Katherine Creechurch | 142 | 39 | Martins Orgars | 29 | 2 | Peters Pauls Wharfe | 22 | 3 |
| Bennet Grace-church | 18 | | Lawrence Iewry | 34 | 1 | Martins Outwitch | 22 | 2 | Peters Poore | 29 | [illegible] |
| Bennet Pauls Wharfe | 82 | 14 | Lawrence Pountney | 34 | 3 | Martins Vintrey | 72 | 8 | Steuens Colmanstreete | [illegible] | [illegible] |
| Bennet Sherehog | 11 | 1 | Leonard Eastcheap | 7 | | Matthew Fridaystreet | 10 | | Steuens Walbrooke | [illegible] | 1 |
| Botolph Bellingsgate | 41 | 2 | Leonard Fosterlane | 156 | 74 | Maudlins Milkstreet | 10 | | Swithin | [illegible] | 3 |
| Christs Church | 192 | 36 | Magnus Parish | 29 | 1 | Maudlins Oldfishstreet | 57 | 11 | Thomas Apostle | [illegible] | 6 |
| | | | | | | | | | Trinitie Parish | 35 | [illegible] |

*Buried in the 97 Parishes within the walls,* ——4268 *Whereof, of the Plague* ——643

| Parish | Bur. | Pl. | Parish | Bur. | Pl. | Parish | Bur. | Pl. | Parish | Bur. | Pl. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Andrew Holborne | 967 | 183 | Bridewell Precinct | 27 | 7 | Dunstans West | 348 | 36 | Sauiours Southwarke | 544 | 74 |
| Bartholmew Great | 146 | 17 | Botolph Aldersgate | 244 | 46 | Georges Southwarke | 441 | 22 | Sepulchres Parish | 1276 | 327 |
| Bartholmew Lesse | 35 | 7 | Botolph Algate | 802 | 78 | Giles Cripplegate | 1817 | 363 | Thomas Southwarke | 104 | 21 |
| Brides Parish | 599 | 180 | Botolph Bishopsgate | 619 | 67 | Olaues Southwarke | 1022 | 169 | Trinity Minories | 26 | 2 |
| | | | | | | | | | At the Pest-house | 109 | 96 |

*Buried in the 16 Parishes without the walls* ——9126 *Whereof, of the Plague* ——1697

| Parish | Bur. | Pl. | Parish | Bur. | Pl. | Parish | Bur. | Pl. |
|---|---|---|---|---|---|---|---|---|
| Clement Danes | 504 | 99 | Katherines Tower | 295 | 41 | Mary Whitechappel | 810 | 158 |
| Giles in the Fields | 961 | 118 | Leonards Shorditch | 483 | 45 | Magdalens Bermond. | 310 | 25 |
| Iames at Clarkenwel | 377 | 72 | Martins in the Fields | 1058 | 152 | Sauoy Parish | 103 | 17 |

*Buried in the nine out-Parishes, in Middlesex and Surrey.* —4901 *Whereof, of the Plague* —737

*The totall of the burials this yeere* — 18295
*Whereof, of the Plague* — 3067
*The totall of all the Christenings* — 10370

## *The Diseases and Casualties this yeere.*

| | | | | | |
|---|---|---|---|---|---|
| Abortive & Stilborne | 511 | Executed | 8 | Mother | 4 |
| Aged and bed-rid | 793 | Falling sicknesse | 6 | Ouer-laid and starved at nurse | 29 |
| Ague and Feaver | 1434 | Fistula and Gangrene | 25 | Palsie | 29 |
| Appoplexie | 11 | Flocks and small Pox | 2483 | Plague | 3067 |
| Bleach and Swine pox | 6 | French Pox | 25 | Planet | 2 |
| Bleeding | 1 | Frighted | 1 | Plurisie | 36 |
| Bloody flux, scowring & flux | 512 | Gout | 7 | Purples and spotted Feaver | 204 |
| Burnt and scalded | 7 | Griefe | 18 | Quinsie and sore throate | 35 |
| Cancer and Wolfe | 17 | Hanged & made away themselves | 9 | Rickets | 80 |
| Canker Sore mouth & Thrush | 84 | Iaundies | 56 | Rising of the lights | 180 |
| Childbed | 228 | Iawfaloe | 6 | Rupture | 13 |
| Chrisomes and Infants | 1897 | Impostume | 117 | Scurvey | 33 |
| Cold, and Cough | 93 | Kild by severall accidents, | 62 | Sores, Issues Vlcers, broken and bruised limbs | 28 |
| Collicke and winde | 52 | Kings Evill | 49 | Stone & Strangury | 47 |
| Consumption and Tissicke | 2738 | Leprosie and Shingles | 3 | Stopping of the Stomacke | 31 |
| Convulsion and Crampe | 780 | Lethargy | 2 | Suddenly | 53 |
| Cut of the Stone | 3 | Livergrowne & Spleene | 96 | Surfet | 415 |
| Dead in streets, fields, &c. | 19 | Lunatique | 7 | Teeth and Wormes | 1217 |
| Dropsie, & Timpany | 499 | Meagroms | 26 | Vomiting | 9 |
| Drowned | 44 | Measles | 48 | | |

Christened: Males — 5292; Females — 5078; In all — 10370

Buried: Males — 9539; Females — 8756; In all. — 18295. Of the Plague — 3067

Increased in the Burials in the 122 Parishes and at the Pesthouse this yeere —— 5524

Increased of the Plague in the 122 Parishes and at the Pest-house this yeere —— 1617

| | Christned | Buried | Plague |
|---|---|---|---|
| S. Margret Westminst. | 582 | 1014 | 132 |
| S. Mary Islington | 60 | 133 | 17 |
| Lambeth | 132 | 270 | 46 |
| Stepney | 959 | 1382 | 110 |
| S. Mary Newington | 144 | 337 | 69 |
| Hackney | 55 | 79 | 1 |
| Redriffe | [illegible] | [illegible] | [illegible] |

*The totall of the Burials in these last [illegible] this yeere* — [illegible]
*Whereof of the Plague* — [illegible]
*The totall of the Christenings* — [illegible]

FIGURE 4. A general bill of mortality, for the year ending 16 December 1641, giving all the data for London in a year in which plague was the most prevalent cause of death.

1683,[9] Petty noted (p. 45) that few or no countries had a population density of more than 2 persons for 5 acres of land. He estimated that the inhabitable parts of the earth had an area of under 50 thousand million acres, or 50 billion acres in modern American parlance. In metric terms this would be under $2.10^8$ $km^2$, which figure is almost exactly twice the modern estimate of that part of the terrestrial land surface that is neither ice-covered nor desert. Petty's estimate of the total carrying capacity would thus be under 20 thousand million persons. He obtained a maximum rate of human increase by assuming that in any population of 600, there would be 180 "*Teeming* Females between 15 and 44" (p. 13), who ideally could bear a child every 2 years, thus giving 90 children per year. For sickness, spontaneous abortion, and natural barrenness he subtracts 15, and then another 15 to balance the expected death rate, thus obtaining a rate of increase of 60 or 10 percent per year. This he expresses as a doubling time of 10 years. Such instantaneous doubling times are used by Petty rather inaccurately over inappropriately long periods of time, blithely neglecting any consideration of the demographic equivalent of compound interest; the correct time would be just over 7 years.

In the City of London the actual rate of growth was estimated from the trend in the death rate, taken to be proportional to the population when comparison is made of sufficiently long intervals, in practice about 20 years. This approach indicated that between 1604 and 1682 a doubling of the population took place in about 40 years. This growth was largely attributable to immigration from the country. For the whole of England, study of the difference between recorded birthrates and recorded death rates led Petty to pitch on, if we may use his favorite expression for making an informed guess, doubling in 360 years, though he admits that some of the data could imply a much slower doubling, in 1,200 years. He points out that if the trends for London and for England as a whole continued unchanged, London would have absorbed practically the whole population of England, of 10,917,389 persons, in 1842, leaving but 198,509 employable in agriculture to feed the city. Actually he expected London to reach a maximum size of 5 million in 1800.

Petty clearly realized that under different circumstances the rates of increase would be different. Starting with the Deluge and the reestablishment of the human race from the 8 inhabitants of Noah's Ark, whom he supposed left that vessel in 2700 B.C., Petty concluded that it would take between 100 and 150 doublings to give the population of the world, which he put at 320,000,000, an alleged contemporary estimate the source of which seems not to have been identified. Actually if one starts with $2^3$, the figure should be about 25 doublings. Since his figures of 100 to 150 fell between the estimated maximum rate of doubling in 10 years and that for England of doubling in between 360 and 1,200 years, Petty concluded that the rate of reproduction fell off from the maximum that prevailed in immediate postdiluvian times to the low value characteristic of his own time. He published a tentative table to show this (figure 5), which he wisely left "to be Corrected by Historians, who know the bigness of *Ancient Cities*, *Armies*, and *Colonies* in the respective Ages of the World" (p. 24). He pointed out that to achieve a saturation population of 20 thousand million would take 6 doublings of his currently estimated 320,000,000, "And then, according to the Prediction of the Scriptures, there must be Wars and great Slaughter, &" (p. 17). It will be noted that in spite of sloppy arithmetic, a commitment to the historical accuracy of the Book of Genesis, and the unavailability of the infinitesimal calculus, Petty did get the idea of a declining rate of increase, though he gives

9. Sir William Petty, *Another essay in Political arithmetick concerning the growth of the city of London: with the measures, periods, causes, and consequences thereof.* London, Mark Pardoe, 1683. A second edition appeared in 1686 as *Multiplication of mankind with another essay in political arithmetick concerning the growth of the city of London.* London, Mark Pardoe.

Sir William Petty (1623–87), who made his reputation as a surveyor in Ireland, was a great friend of Graunt; there has been some argument as to what part Petty may have had in Graunt's work.