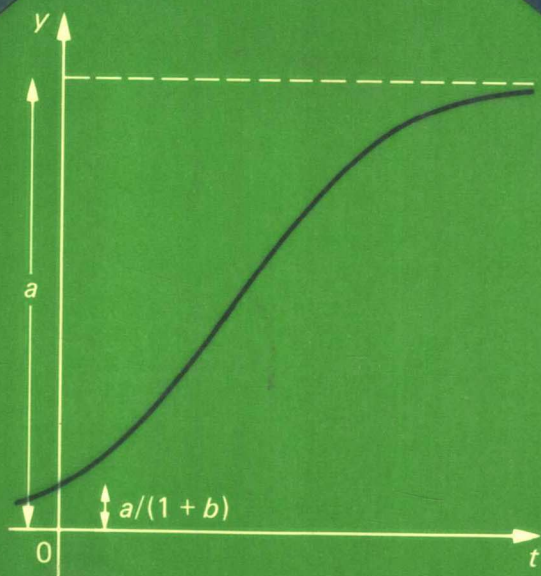# A Biologist's Mathematics

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CONTEMPORARY BIOLOGY

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CONTEMPORARY BIOLOGY

Spectacular progress in biological research in recent years has led to many changes in the form and content of the biological curriculum. Advances in molecular biology and comparative studies in many fields have emphasised the importance of the unity of life as well as its diversity. This series of student texts has been designed against this background.

Preface

Mathematical methodology, in the widest sense, now pervades many aspects
of biology; but most biology students are not mathematically minded.
This state of affairs is often a headache to teachers of biological sciences
in institutions of higher education, and there is no easy way out of the
dilemma.

The most widely used mathematical techniques in biology are the
statistical methods of analysis of experiments and surveys. These methods
have been taught to most postgraduate students of biology for many years,
and more recently to undergraduates. However, modern biology requires
more of its students than the ability to analyze designed experiments and
surveys. The development of any science proceeds from the largely
qualitative to the largely quantitative; physics, for example, made the
transition about two to three centuries ago, whereas biology is making the
transition now.

For this reason an increasing number of biological science schemes of
study in universities, colleges, and polytechnics include courses in mathe-
matical ideas and methods, and the main object of this book is to provide
a text for such courses. However, rather more is included here than would
be deemed to constitute a basic course in mathematics for biologists; the
opportunity has been taken to present a wide range of mathematical topics
to enable the more advanced student to understand most biological sub-
jects which are treated mathematically. It must be emphasized, however,
that the book is primarily meant for first and second year undergraduate
courses or equivalent, in keeping with the general aim of books in this
series. The path of such students through the book is made clear by means
of a plan for a basic scheme of study (page xii) and directions at relevant
places in the text. The topics selected for this basic scheme correspond

closely with the course given to all first year students of biological sciences here at Aberystwyth.

After an introductory chapter on the role of mathematics in biology, the book considers the fundamental properties of numbers, indices, and logarithms, in Chapter 2. Chapter 3 is also a foundation chapter, dealing with the basis of the geometrical interpretation of many aspects of mathematics relevant to the biologist. A full multi-dimensional approach is adopted; and the topics of location in space, the measurement of distances between points, and linear functions and their geometric representation are covered, examples being given of the biological use of each topic. Chapter 4 then considers non-linear functions and their curves, but in two dimensions only, and also contains a section on some general properties of curves to serve as an introduction to the following chapters on calculus.

The next four chapters deal with the calculus. Chapter 5 describes principles and methods of the differential calculus, while Chapter 6 is concerned with physical interpretation and usage. Chapters 7 and 8 deal with the two aspects of integration: the former chapter introduces the indefinite integral and methods of integration, while the latter deals with the definite integral. Some relatively major portions of these two chapters are best avoided by the beginner, and these are indicated in the text.

Hitherto, the principal type of mathematical function used is the polynomial, although other kinds of function of potential interest to the biologist are introduced in Chapter 4. Exponential and related functions, which are of outstanding importance to biologist and mathematician alike, are described in Chapter 10. Although so important, they are introduced relatively late in the book for three reasons. Firstly, their mathematical properties are not as straightforward as are those of polynomials, and it seems better to use the mathematically simple polynomial functions to illustrate the principles and methods of the calculus. Secondly, students often have difficulty in assimilating the concept of the number e, but the difficulty is minimised if one can discuss e^x as a function whose gradient is always equal to the function itself. Thirdly, it is convenient to define e by means of the exponential series. Accordingly, the preceding chapter, Chapter 9, deals with mathematical series in their own right, as well as serving as a prelude to the exponential series in Chapter 10. The last main section of Chapter 9, which is meant for the more advanced reader, demonstrates how many types of mathematical function can be defined and evaluated by means of infinite series.

Chapter 11 has been excluded from the basic course, not because of great mathematical difficulty, but because the subject matter is specific to plant science. It is included in the book because the material illustrates so well an example of the biological relevance of the calculus. The whole of Chapter 12, on trigonometric functions is considered to be for the more

advanced and specialized students, but the earlier parts of Chapter 13 on differential equations should be regarded as part of a basic course in biological mathematics.

Anyone using this as a textbook may thus follow it through in its natural order. There is one possible exception to this. Chapter 14 can be read at any stage, since very little of it depends on material presented earlier in the book, and some of the ideas basic to the chapter now appear in school mathematics syllabuses. It has not been included in the recommended 'first course' because it will be needed at different times in biology courses at different institutions, depending on the applications envisaged.

Mention of applications highlights a particular and ever-present difficulty in teaching mathematics to biologists. Since, for the majority of such students, mathematics is not in itself an interesting subject they are very concerned to see the biological relevance of every mathematical topic discussed. Good biological examples involving *simple* mathematics are very scarce. Biological phenomena are so complex that problems which are not so oversimplified as to be far-fetched require either complicated mathematics, or the application of techniques of probability and statistics. Biological examples are presented whenever possible, but there are sizable portions of the book which are purely on mathematics without any reference to biology. This is inevitable when developing a theme. For example, the convergence of a series and the idea of a limit have hardly any biological connotations, but these ideas lead on to the differential calculus which does have considerable relevance in the life sciences.

Some exercises are provided at the end of each chapter. On the whole, these are to give practice in the methods presented in the chapter, but, where appropriate, exercises involving direct biological situations are presented. Those exercises marked with an * relate to sections of the text which are not included in the basic scheme of study.

Finally, it should be stated that the level of mathematical knowledge assumed of the reader is that of GCE 'O' level, or equivalent, but where possible, topics are developed from first principles.

I should like to express my appreciation to Professor J. Gareth Morris for his constant encouragement at all stages, and for his critical evaluation of the section on the growth of a microbial culture. Dr. Geoffrey M. Clarke read the entire manuscript, corrected my errors, and made a number of other valuable comments and suggestions for which I am very grateful. Any remaining mistakes and obscurities are my own responsibility. Finally, I should like to thank the staff of Edward Arnold for their friendly assistance throughout, and for the excellent clarity of the final production.

Llanrhystyd, Aberystwyth   D.R.C.
1976.

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I

Why Mathematics in Biology?

Probably the most significant event that occurred during the rise of man to
pre-eminence, from being merely 'another animal', was the development
and use of language. At first, language was only spoken, but it did enable
relatively large quantities of information to be communicated from one
individual to another. More than that, language also provided a means for
controlling and monitoring thought itself. The important point is that
language provides concepts which can be manipulated independently of
the objects to which they refer, and later it becomes possible to think
logically without reference to any particular objects at all. Hence, during
the history of man, abstract thought became feasible, and from this
beginning arose philosophy.

If we had to select an area of application of language that has been
outstandingly successful, we should undoubtedly choose the expression of
human emotion. The evidence for this is clear when one considers the
achievements of oratory and literature. However, when it comes to con-
veying scientific information, ordinary language is less successful. This is
because it is almost impossible to convey precise meaning, since most
words in a language have more than one meaning, even if these meanings
differ only marginally. Again, because of these various shades of meaning,
a particular word means a slightly different thing to different people. This
is fine for the literary use of a language where part of the onus for inter-
pretation lies with the reader or listener, but it is not so good for scientific
use, where data and hypotheses must be presented with complete
unambiguity.

A long time, perhaps many thousands of years, after the rise of lan-
guage, a new kind of medium for transferring information from one
individual to another was evolving. This was at the time when the first of

the ancient civilisations — Egypt and Sumer — were flourishing. These civilizations, besides being the architects and builders of large buildings and other monuments, also developed a calendar. Such achievements required precision: precision in measurement, precision in the subsequent manipulation of measurement, and precision in the transmission of such data to other people. All this could be achieved through another kind of language — the language of mathematics.

The mathematical language is just the opposite to ordinary language in that its elements are precise and unambiguous, or at least should be. Every quantity and symbol used can be accurately defined in terms of earlier quantities and symbols already defined. Thus, mathematics is built up on precision and fact, whereas ordinary languages are, to some extent, based on the variability and imprecision of human feelings and emotions.

THE DEVELOPMENT OF A SCIENCE

The study of any science, viewed historically, consists of two main phases. First it is studied almost exclusively from a qualitative point of view; but after an initial period, quantitative methods come to be used increasingly. One of the main reasons for this type of development, from the qualitative to the quantitative, is that a science begins as an observational study, progresses to an experimental, and finally to a theoretical study. At first, phenomena are observed as they occur in nature; later scientific work consists of performing experiments, drawing inferences from the results, and then trying to formulate general laws. By their nature, some sciences have to make the jump from observation to theory without the intervening benefits of experimentation. Astronomy is an obvious example here, and it is remarkable that observational and theoretical astronomy have proceeded side by side for several millennia.

At the present time, physics is the science which is pre-eminent in the use of mathematics. Many physical phenomena are rather less complex than are those of other sciences, and the subject has progressed through the stages of observation and experiment, and has emerged as a theoretical science. This is not to say that observation and experiment are not still carried out in physics; the main point is that physics has reached the stage in which there exists a substantial body of theory, mathematical in nature, which has its origins in observation and experiment. In physics at the present time, the experimental and theoretical sides of the subject are of equal importance.

The phenomena of chemistry are often more complex than those of physics, and this subject has not progressed quite as far as physics on the

theoretical side. Although there have been spectacular advances in theoretical chemistry in recent years, chemistry as a whole is still, at present, somewhat more of an experimental science than is physics.

In biology, the situation is very different. Firstly, biological phenomena are highly complex; secondly, there is almost unlimited scope for pure observation of biological phenomena. Hence it is mainly only in the present century that biology has become an experimental science, whereas experimental work in the physical sciences has been undertaken for several hundred years. As a result, it is only now that 'theoretical biology' is tentatively emerging.

From the above remarks, it would seem that mathematical theory is the ultimate aim in a scientific discipline. This is true; not for its own sake, but because in the last resort the phenomena of nature can only be explained in the precise terms of mathematics. Consider this example from physics.

Observation: a stick immersed in water at an angle to the surface (other than a right-angle) so that part of the stick is out of the water and part submerged; the stick appears bent at the surface of the water.

Experiment: a vessel of water is set up on the laboratory bench, and rays of light are traced through the water for various angles of the incident beam; it is found that at an air—water surface (assume that the vessel is made of very thin glass) the ratio of the sine of the angle of the light beam on the air side of the surface to the sine of the angle of the beam on the water side of the surface is constant, and this constant ratio is called the refractive index.

Theoretical deductions: this experimental result can be used in conjunction with facts gleaned from experiments on other phenomena of light, such as reflection, diffraction, interference, to establish knowledge on the nature of light. For instance, it has been found that the velocity of light in a dense medium is less than in a sparse one. This latter experimental finding coupled with the result of the refraction experiment can be analysed mathematically to show that light travels in a wave form.

For this particular example, there is an obvious relationship between observation, experiment, and theoretical deduction. Such examples can be multiplied many fold. In chemistry, we observe a particular reaction, and we experiment to find out the exact conditions under which the reaction occurs. When we then enquire why this particular reaction occurs and not some other, it is necessary to look to the concepts of physical and theoretical chemistry, both of which are founded on mathematics.

Whether or not all biological phenomena can be explained by the physical sciences, or that ultimately it is found that the property of life is 'something extra', it is already quite evident that the manifestations of 'life' can be explained in terms of the physical sciences, particularly

chemistry. Since the physical sciences are based on mathematics, so also, indirectly, are the biological sciences.

In summary, experimental results are usually in a quantitative form, even in biology, and therefore sound theoretical deductions can normally only be made by mathematical analysis. This is why, ultimately, mathematics is indispensable to any science; and so any scientist, whatever his or her speciality, should have an adequate knowledge of mathematics.

BIOLOGY, MATHEMATICS, AND STATISTICS

The mathematical model

From the penultimate paragraph of the previous section, one might infer that the utility of mathematics to the biologist is indirect, arising only after experimental results have been interpreted by the concepts of physical science. This, however, is not so. Mathematics is applied directly to the results of biological observation and experiment in a similar manner to the physical sciences but, because of the complexity of the phenomena, its application is much more difficult.

In the present state of biological knowledge, it is impossible to apply a rigorous mathematical analysis to a biological system, such as may be applied, for example, to an electric circuit. What is done, however, is to construct a **mathematical model** of the phenomenon in which we are interested. Certain **assumptions** about the system have first to be made, and put into mathematical form. These assumptions are based on current knowledge obtained from previous observations and experiments. Next, appropriate **mathematical methods** are applied to the assumptions to achieve an end result which **simulates** the system under study. The simulated result can then be compared with what actually happens. If agreement between the theoretical result and the observed happening is good, then we gain further insight into the process under study; and moreover, we can use the model for predictive purposes. In any science, an ultimate aim is **prediction**. For instance, in an electrical circuit we can predict how the current will change for a given change of resistance, using the mathematical description of the circuit. In a biological system that has been 'described' mathematically by means of a model, predictions of what will happen under certain changes of conditions can also be made. If the results of using the model do not agree with actuality, then one or more of our basic assumptions must be wrong (assuming the absence of mathematical errors!), and so, in a negative sense, our knowledge is still increased. An example of the construction of a very simple mathematical model is given in Chapter 6.

Statistics in biology

There is yet another complication to the would-be user of quantitative methods in biology, and that is **variability**. The phenomenon of variability is not confined to biology, but arises whenever experimental work is undertaken. Even in the physical sciences, repetitions of a single experiment will give slightly different results, e.g. measurement of the refractive index of a substance, or the location of an end point in volumetric analysis. This kind of variability, which is called **experimental variability** or **experimental error**, arises solely because a human being attempts to measure something; the something does not change, but the reactions of the human being during the conduct of the experiment do change.

Experimental variability also occurs in biology, but here it is considerably augmented by the variability inherent in biological material. If we measure the refractive index of a block of glass very carefully, we are safe in asserting that our result *is* the refractive index of this kind of glass, under the conditions of the experiment. On the other hand, if we measure the increase in height of a sunflower plant over one day, we certainly cannot say that this is the growth rate of sunflower plants in general, even under the same experimental conditions. The same plant may have a noticeably different growth rate at an earlier or later stage in its growth; and even if we take two plants which germinated from the same source of seed at the same time, they will almost certainly show different growth rates at any instant, aside from experimental error. So to be able to make any sort of general statement about the growth rate of sunflower plants of a given age and under defined conditions, we have to measure several plants and take an average. This immediately raises the question as to how reliable our result is, and this cannot be answered without employing a branch of mathematics known as **statistics**.

Even when no experiment is involved and one is only trying to summarize observations usefully and build a model from them, a simple mathematical approach may not be very satisfactory because of the variability of biological material. A good illustration is afforded by Example 10.3 on page 186. Read the general description of the situation through, note that a mathematical expression is used to describe the situation, and then carefully read the questions asked, each one of which obviously requires a single numerical answer. Now, without worrying about how the answers were obtained, read the last sentence of each of the three sections, and note that each answer is a precise figure. Bearing in mind that a 'cohort' in this context is a natural stand of similar-aged plants, it is quite obvious that these precise answers are only statements of likely results around which actual results will deviate to a greater or lesser extent. One immediately asks, 'How much deviation can be expected?'. The **deterministic** mathematical model that has been erected to describe the situation

in this example cannot answer such a question. If, however, the same model had been set up, but with an added feature — a **probability** structure — then we should be in a position to answer questions like the above. The mathematical model would now be a **stochastic** model; it is much more realistic, and more complex.

Both the mathematics of stochastic models, and of statistical methods for the analysis of experiments, are based upon the same theoretical subject — probability and statistics. It is a branch of applied mathematics in the broad sense, not in the narrow sense that the term 'applied mathematics' is often used to denote applications to physics. Therefore, probability theory and statistical science are based on mathematics, and a good knowledge of the subject is necessary for their study. In this book, we shall not deal with probability and statistics. Our concern will be with such topics in mathematics that are of a general nature, topics that have direct biological relevance, and also those that form a basis for the study of statistical science about which the modern biologist needs to know.

2

Numbers, Indices and Logarithms

Broadly, this chapter will be concerned with numbers and number systems. Numbers, including those defined by symbols (letters), are fundamental to mathematics, and so this chapter should be carefully read and understood even if you find that much of it is revision of material already familiar.

NUMBERS

Imagine a straight line, as in Fig. 2.1, extending indefinitely in each direction. The centre of this line will represent zero, and then at equal intervals on either side of the zero we may mark off points which represent the whole numbers: 1, 2, 3; −1, −2, −3, etc. By convention, positive numbers increase from zero to the right, and negative numbers increase from zero to the left. It is important to note that the symbols +∞ and −∞ do not represent numbers, however large. These symbols may be interpreted in different ways according to their context. Here, they mean that the line extends each way indefinitely.
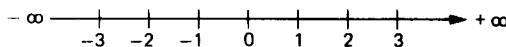

Fig. 2.1   The real number scale

Real numbers

Any number on the line defined above and shown in Fig. 2.1 is known as a **real number**; in other words, such numbers can be represented physically on a scale. Real numbers are sub-divided further, as follows.

Integer   An integer is a whole number, such as 3, 8, −45, 501.

Rational number   A rational number is one that can be expressed as the quotient (or ratio, hence the name) of two integers. Thus all whole numbers are rational, since each is the quotient of itself and 1. Also, many non-integers are rational, such as 1.5 (=3/2), 2.$\dot{3}$ (=7/3) and −1.$\dot{8}$ (= −51/27). A dot over a figure to the right-hand side of the decimal point indicates that that figure recurs indefinitely.

Irrational number   An irrational number is one that cannot be expressed as the quotient of two integers. Examples are $\sqrt{2}$, $\sqrt{7}$, and π. In general, a number which is neither a terminating nor a recurring decimal is an irrational number.

Thus, a real number may be either rational or irrational; and, if rational, may be either an integer or a fraction.

It may be wondered just why it is necessary to classify the real numbers in this way. The three types of real number that we have just considered would have evolved historically in the same way. The idea of number would have originated in the counting of objects, giving rise to integers. The simple arithmetic processes of addition, subtraction, and multiplication of integers always yield other integers. However, the division of one integer by another does not necessarily give a further integer; so, in order to give meaning to the arithmetic operation of division, another type of number besides the integer has to be visualized. This new kind of number is the rational number; and since whole numbers *can* result by dividing one integer by another, then rational numbers must include integers. When a rational number is a fraction, it either terminates (as in 3/2 = 1.5) or recurs (as in 7/3 = 2.$\dot{3}$). Recurrence is not necessarily confined to one figure: it may be a whole group of figures. Thus

$$6/7 = 0.85714285714285714$$

correct to 17 decimal places, so we can write 6/7 = 0.$\dot{8}5\dot{7}\dot{1}4\dot{2}$ since this group of figures recurs indefinitely. A rational number can be written down accurately either as a vulgar fraction or as a decimal; even 0.$\dot{8}5\dot{7}\dot{1}4\dot{2}$ is an accurate *representation* of 6/7.

Returning to the integers, squaring means multiplying an integer (or any number) by itself, e.g. 3 x 3 = 3^2 = 9. But the opposite process, taking a square root, may give a number which is not an integer, a terminating fraction, or a recurring fraction, i.e. it is not a rational number. To give meaning to the square root, another class of numbers must be designated — the irrational numbers. The main feature of these numbers is that they cannot be accurately written in fraction or decimal form. For instance, $\sqrt{2}$ = 1.414213562 to 9 decimal places; and π = 3.14159 correct to 5 decimal places, or we can write $\pi \triangleq 22/7$. The sign $\triangleq$ means 'approximately equal to' and it is used here to show that 22/7 *might* be used in