
A table of contents for *Journal of the Transactions of the Victoria Institute* can be found here:

https://biblicalstudies.org.uk/articles_jtvi-01.php

JOURNAL OF

THE TRANSACTIONS

OF

The Victoria Institute

OR

Philosophical Society of Great Britain

VOL. LXXIII

1941

LONDON:

PUBLISHED BY

THE INSTITUTE, 1, CENTRAL BUILDINGS, WESTMINSTER, W.C.1

840TH ORDINARY GENERAL MEETING.

HELD IN COMMITTEE ROOM 19, LIVINGSTONE HOUSE, BROADWAY, S.W.1, ON MONDAY, MARCH 17TH, 1941, AT 6.0 P.M.

DOUGLAS DEWAR, ESQ., B.A., F.Z.S., IN THE CHAIR.

The Minutes of the previous meeting were read, confirmed and signed.

The CHAIRMAN then called on Mr. B. D. W. Morley, F.Z.S., F.R.E.S., to read his Paper entitled "Biology in Figures. A Study in Mathematical Biology."

The Meeting was then thrown open to discussion in which the following took part: Dr. F. T. Farmer, Mr. W. E. Leslie and Mr. Douglas Dewar.

A written communication was received from Dr. W. T. Marshall.

BIOLOGY IN FIGURES.
A STUDY IN MATHEMATICAL BIOLOGY.

By B. D. W. MORLEY, F.Z.S., F.R.E.S., ETC.

NEARLY two thousand years ago Empedocles began to develop the equivalent of the modern Atomic theory, by means of pure reasoning unsupported by known facts. This was followed up by Lucippus, the real author of the Greek Atomic theory which Democrates put forward with all the glorious reasoning of the old Greek philosophers.

The amazing correlation between the modern Atomic theory and that of the Greek philosophers points out what could be done to aid the biologist if reasoning governed by established laws was to be applied to the immense number of facts which the biologist accumulates, without being able either to correlate them one to another, or to proceed to further researches without an enormous waste of time and labour in following unfruitful lines of investigation.

Pure mathematical biology fulfills this function.

Before proceeding to the discussion of pure mathematical biology, however, I intend to deal, at some length, with the manner in which mathematics has become more and more essential and widely used in everyday biology. That is, I am now going to deal with mathematical biology in the widest sense of the term.

Mathematics in Everyday Biology.

Everyone is familiar with the plain straightforward biological statistics such as those concerning birth and mortality rates. Most people are familiar also with the fact that the chances of

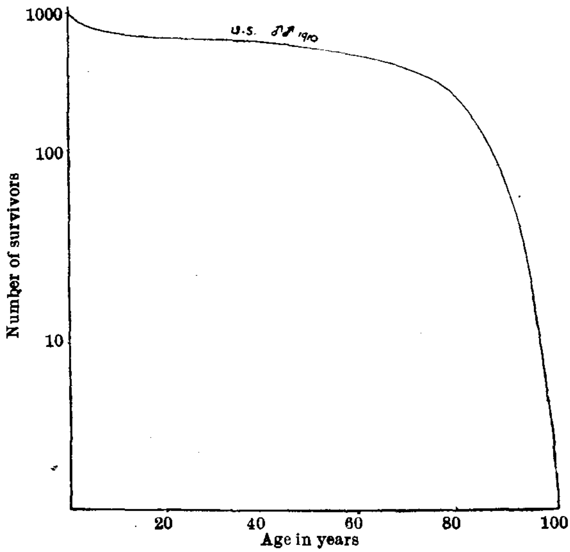

Fig. 1.—(*After Lotka.*)

survival decrease with increasing age. Statistical biology can, however, take the matter further. Take, for example, the survival curves of males in the United States of America for the year 1910 and plot them on a logarithmetic scale (Fig. 1). The resultant curve will give the "Force of Mortality" in man throughout his life. From this curve it will be seen that the Force of Mortality is very great during the first three or four years of life and then gradually decreases until the age of twelve or thirteen years is reached, finally increasing again continuously until death is achieved.

If similar life curves be plotted for the rotifer *Proales decipiens* and for a fruit fly *Drosophila* (Fig. 2), and the length of life be brought to a common base an interesting comparison can be made.

Actually, in making this comparison, it is simplest to omit the first twelve years of life in man from the curve, thus ridding

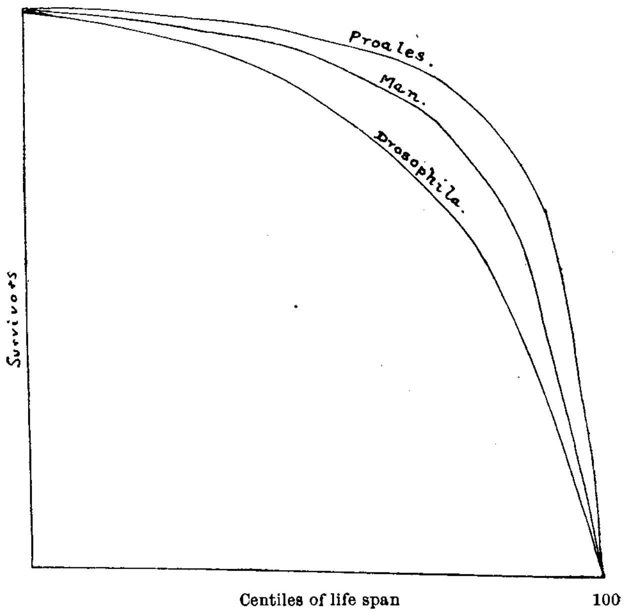

FIG. 2.—(*After Lotka and Pearl.*)

it of its inflexion. It will be seen that the curves planned on this basis are extraordinarily alike, that of man being intermediate between those of *Proales* and *Drosophila.*

Mathematical curves are very necessary in biology, since they demonstrate most clearly the inter-relation between different types of data. To take an example from my work on Ants.* It appeared to me that there was probably some

* "The Kinetics of Ants and the practical uses of such a study." VIIth Int. Cong. Ent., Berlin, 1938.

relation between the length of leg of an ant and its speed and I therefore measured both the length of leg and the speed of a number of different species of ants. Now to procure any value from the data obtained it is obviously necessary to measure also the total body length of the ants concerned and express the length of their legs in proportion to the length of their bodies, at the same time bringing, by simple mathematics, these proportions to a common base.

Next another difficulty was encountered in that the speed of an ant is known to increase or decrease, corresponding to the increase and decrease in temperature of its surroundings. The actual proportions are a fifteen-fold increase for every thirty degrees centigrade rise in temperature. The temperature, therefore, must also be calculated to a common proportional mean.

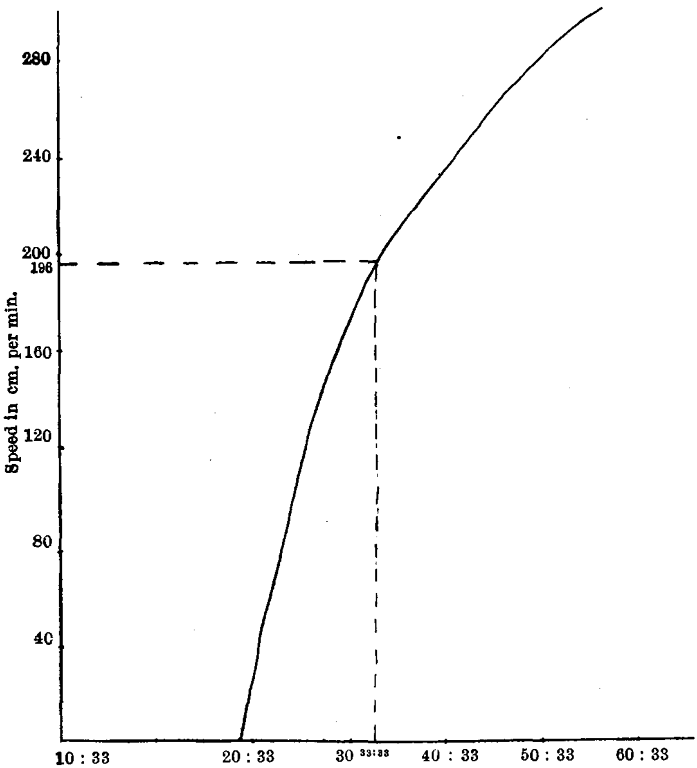

Fig. 3.—*Length of leg when length of body brought to common number* **33.**

It is now possible to plot the graph correlating the speed of an ant to its length of leg and a nice curve (Fig. 3) is obtained which fully demonstrates the interdependance of the two phenomena.

Now without mathematics such a conclusion could never have been reached.

I have shown above how mathematics may be useful to the biologist in helping him to make accurate comparisons, where comparison would be impossible without the aid of mathematics. Also how the correlation between biologically apparently isolated factors and a known result may be brought to form a logical series of interlinked factors leading to a result that can be accurately forecast by means of mathematics. The use of mathematics to forecast biological results is both extremely important and, if the data supplied to the mathematician be correct and complete, extremely accurate.

To return for a moment to the population of the United States, Kostitzin has shown that by using the logistic law

$$p = \frac{197{,}273{,}000}{1 + e^{-\cdot 03134\,(t - 1913\cdot 25)}}$$

the population of the United States can be forecast with amazing accuracy, as the following table demonstrates.

Year.	Observed Population.	Calculated Population.	Year.	Observed Population.	Calculated Population.
	millions	millions		millions	millions
1790	3·9	3·9	1870	38·7	39·4
1800	5·3	5·3	1880	50·3	50·2
1810	7·2	7·2	1890 ...	63·1	62·8
1820	9·6	9·8	1900	76·1	76·9
1830	12·9	13·1	1910	92·3	92·0
1840	17·1	17·5	1920	106·5	109·4
1850	23·2	23·2	1930	123·2	123·9
1860	31·5	30·4			

That this is so is the more amazing, for, as Kostitzin says* :—"Since 1790 the United States have waged five major wars, conquered new territory, colonised vast spaces, developed a formidable industrial organisation, and have received and absorbed a mass of emigrants from all parts of the world."

* Kostitzin. "Mathematical Biology." London, 1939.

Similar work by Verhulst on the populations of France and Belgium has shown almost, if not quite, equal agreement between the calculated and observed populations.

The application of mathematics to population increase is not, of course, confined to man, but in lower animals, more especially in the invertebrates, the problem is complicated by the greater importance of the inter-relationships between predators, parasites and prey.

Genetics is undoubtably the branch of biology in which mathematics has gained the greatest foothold, indeed there can almost be said to be two kinds of geneticists, the entirely mathematical and theoretical geneticists and the experimental or practical geneticists.

[As this paper is intended to make survey of the various ways in which mathematics has entered and has been accepted as essential to the various branches of biology, space cannot be wasted in explaining the fundamentals of the various branches of biology concerned. A knowledge of the bases of genetics, etc., is therefore assumed in the following pages.]

Mathematics in Genetics.

A simple and basic example of mathematics in genetics is the chromosome map (*see* Fig. 4). To take an actual example,* two *Drosophila* are crossed :—scute and cross-veinless $\times$ echinus.

$F_1 \dfrac{+ \; ec \; +}{sc \; + \; cv}$ and in the F_2 give :—

$$\begin{array}{llll}
\left\{\begin{array}{lll} + & ec & + \\ sc & + & cv \end{array}\right. & \ldots\ldots & \left.\begin{array}{r} 810 \\ 828 \end{array}\right\} & \\
\left\{\begin{array}{lll} sc & ec & + \\ + & + & cv \end{array}\right. & \ldots\ldots & \left.\begin{array}{r} 88 \\ 62 \end{array}\right\} & 7 \cdot 6\% \left(i.e., \dfrac{150}{1{,}980}\right) \\
\left\{\begin{array}{lll} + & ec & cv \\ sc & + & + \end{array}\right. & \ldots\ldots & \left.\begin{array}{r} 103 \\ 89 \end{array}\right\} & 9 \cdot 7\% \left(i.e., \dfrac{192}{1{,}980}\right) \\
\left\{\begin{array}{lll} + & + & + \\ sc & ec & cv \end{array}\right. & \ldots\ldots & \left.\begin{array}{r} 0 \\ 0 \end{array}\right\} & \\
\text{Total} & \ldots & 1{,}980 &
\end{array}$$

[$sc =$ scute ; $ec =$ echinus ; $cv =$ cross-veined ; $+ =$ normal.]

Now these figures show that it is only possible to get echinus and scute if there are two crossovers simultaneously, since the

* Waddington.

percentage would be about 50 if only one crossover were necessary.* Therefore echinus must be placed between scute and cross-veinless and their distances apart determined by the percentage of times *sc* and *ec* and *ec* and *cv* appear together. The crossover frequency is, of course, determined by observation, but as can be seen, the length of the map in genetic units can be calculated from this, while the actual plotting of the genes on the map is largely mathematical. Very simple mathematics, such as everyone can understand, can be of great use in considering problems of inheritance.

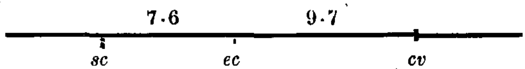

FIG. 4A.

The inheritance of the nest-odour of ants, coupled as it must be, since it is sex-linked being inherited through the X chromosome, with the sex determining mechanism is extremely difficult to understand. Yet the use of simple mathematics clarifies the problem immensely.

In ants the ♂ ♂ are usually unfertilised (*see* Fig. 5), though if two Y chromosomes come together (a very unusual event) a super ♂ is formed. It is not yet certain whether the difference between the ☿ ☿ and the true fully developed ♀ ♀ is genetical or merely a matter of feeding, but it would seem probable that the XX ants are the fully developed ♀ ♀ and the XY ants the ☿ ☿ (*see* Fig. 5).† Now the problem to be considered is the inheritance

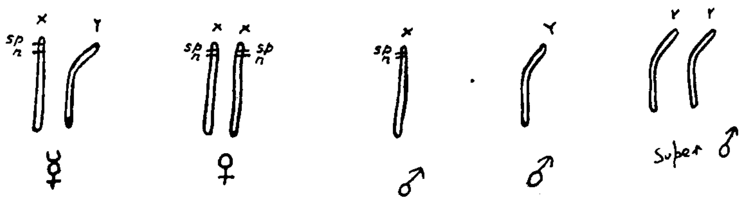

FIG. 5.—*Sex chromosomes of ants.* (*Diagrammatic.*)

* A chiasma (crossover) frequency of 1·0 means that in an average two out of four chromosomes have one crossover, *i.e.*, crossing over takes place in 50 per cent. of the cases between two points situated at opposite ends of a chromosome. From this it will be seen that a bivalent having a crossover frequency of 1·0 has a length of 50 genetic units.

† If this method of sex-determination is correct the haploidy of the X and Y ♂ ♂ cannot be due to lack of fertilisation but must be due to reduction division after fertilisation. Otherwise there could not possibly be any Y ♂ ♂. It seems certain there is a genetic, or at any rate a prenatal difference between ☿ and ♀ and it is difficult to imagine this without XY ☿ and XX ♀.

and spread of any particular nest odour, call it z, throughout an area inhabited by a certain species of ant.

[Actually both the species odour and the nest odour are inherited on the X chromosome (the reason for coming to this conclusion cannot be gone into here), the nest odour being provided by a gene differentiating the species odour.]

There are three kinds of ♂ ♂ (Fig. 5), one of which possesses the gene for the nest odour.

Now let a be the number of X chromosome ♂ ♂ in a colony. Then a is the number of Y chromosome ♂ ♂ in the same colony.

The number of YY chromosome ♂ ♂ is very small and is probably in the region of a^{-a}, but since this may not be always accurate, let their number be $a^{-a'}$.

Then let c be the number by which the ♂ ♂ exceed the ♀ ♀.

Then $2\,a + a^{-a'}$ is the number of ♂ ♂ in the colony

$2\,a + a^{-a'} - c$,, ,, ,, ,, ♀ ♀ ,, ,, ,,

Then $a + a^{-a'}$ is the number of ♂ ♂ with Y chromosomes and a the number with X chromosomes.

Now there are more ♂ ♂ than ♀ ♀ and though a ♀ may copulate with several ♂ ♂ only one will count in considering the nest odour; further a ♀ may be copulated by only Y ♂ ♂. This latter feature has already been expressed by dividing by two, but the former feature may be brought in as follows:—

$$\left(\frac{a}{c} + \frac{2\,a + a^{-a'} - c}{2}\right)d.$$

Where the latter is the number of ♀ ♀ produced by the colony and their chances of being fertilised by an X male; and d is the coefficient of mortality of ♀ ♀ before colony foundation after copulation.

Then because the ♀ or ♂ copulated or effecting copulation may have a gene of a different nest odour :

$$\left(\frac{a}{2\,c} + \frac{2\,a + a^{-a'} - c}{4}\right)d - e$$

where e is the number of ♂ ♂ and ♀ ♀ fertilised in the nest. Now if the data worked on, namely that the nest odour of ants is inherited on the X chromosome, be correct, then two conclusions can be drawn from the above expression which gives the spread of the nest odour z from one colony in one year. The first is that although the ♀ may be copulated by several ♂ ♂ only two count, one with X chromosomes and one with Y chromosomes. Secondly, the ♂ ♂ always copulate with ♀ ♀ of a different colony, unless forced to copulate with one of their own colony by the workers (this sometimes occurs when the colony is in danger of dying out, or else to bring about the formation of interlinked polycalic colonies as in *Formica execta, L*). It seems highly probable that both these conclusions are correct, though it would be extremely difficult to verify the first one. e may, of course, be nought.

$$\left\{\left[\left(\frac{a}{2\,c}+\frac{2\,a+a^{-a'}-c}{4}\right)d-e\right]^2\right\}\left\{\frac{\text{Average fertility of } ♀\,♀}{\text{Fertility of } ♀ \text{ or } ♀\,♀ \text{ of first nest.}}\right\}$$

would represent the number of nests at the end of the next year from a genetic point of view, though actually some of the nests of the year before would have been destroyed by enemies, climate or accident; which would have to be taken into account to get a really accurate result. Further d and e are variables. Indeed it would be a very difficult world for us if all ants squared the number of their colonies each year, but it does demonstrate what might and sometimes does occur under ideal conditions or when the balance of predators, parasites and prey is disturbed and d and e are nil, or very small.

In a rather different sphere of genetics, that of breeding for a special character, simple mathematics is also useful.

Suppose, for example, in a cross between two animals or plants, a dominant is the character wanted. Then for breeding purposes only dominants would be selected. In the F_1 the progeny would be 3 dominants to 1 recessive. The recessives would be discarded and breeding continued with the dominants. On account of the segregation of the recessives by heterozygotes the proportion of dominants would only rise slowly.

$$\begin{array}{llll}
P_1 & \mathrm{X}x \times \mathrm{X}x & & \\
F_1 & \mathrm{XX} \quad \mathrm{X}x & xx & \tfrac{3}{4}\text{ dom.} \\
 & \quad\ \downarrow & \text{discard} & \\
 & \mathrm{X} \quad \mathrm{X} \text{ and } x & & \\
 & \quad\ \downarrow & & \\
 & (2\,\mathrm{X}+x)^2 & & \\
 & \quad\ \downarrow & & \\
 & 4\,\mathrm{XX} \quad 4\,\mathrm{X}x & xx & \tfrac{8}{9}\text{ dom.} \\
 & \quad\ \downarrow & \text{discard} & \\
 & (3\,\mathrm{X}+x)^2 & & \\
 & \quad\ \downarrow & & \\
 & 9\,\mathrm{XX}+6\,\mathrm{X}x & +\,xx & \tfrac{15}{16}\text{ dom.} \\
 & \quad\ \downarrow & & \\
 & \quad \text{etc.} & &
\end{array}$$

Thus the number of generations it will take to get an almost, if not quite, true breeding stock for the dominant character X by means of selection can be estimated. Such estimation is of great use to breeders.

Having shown how simple and statistical mathematics is of use to the biologist in a variety of ways in interpreting statistics, correlating data and foretelling the results of such important processes as increase in population, etc., I now intend to conclude this survey by touching very briefly on what might be termed pure mathematical biology.

Pure Mathematical Biology.

Pure mathematical biology may be said to be the application of mathematical reasoning to biological data expressed in mathematical terms. There has always been some repugnance among biologists to reasoning about figures. They admit that figures (*e.g.*, statistics and correlating graphs) have a right of entry into biology and are invaluable in facilitating and foretelling results and in correlating data, as shown above ; but when it comes to using mathematical reasoning as distinct from simple mathematical calculation, their backs go up. Mathematical reasoning frightens and startles many biologists because they are used to verifying every step. In ordinary reasoning this can be done, but in mathematical reasoning the steps are taken too quickly for this to be so, also the results often appear (and often are) arbitary or untrue. One of the reasons for this is the distortion caused by sacrificing a number of factors or details for simplification purposes, which errors or omissions very soon get multiplied many fold and cause arbitrary or untrue results.

The chief workers on this branch of biology have been Lotka, Volterra, Teissier and Kostitzin, though Haldane should also be mentioned on account of his work on Natural Selection.

It should be mentioned that the fundamental ideas such as the variables and co-efficients of the equations, which I don't intend to go into in detail in this paper, are founded on the results of long statistical elaboration. Though the logical, or reasoning, apparatus is purely analytical.

The equations nearly all belong to the type of differential or integro-differential equations of the first order. This field of the study being opened up by Lotka and Volterra.

Numerical results are not always reached, but qualitative results, the only ones capable of verification, owing to the heterogeneousness of the biological data, are obtained.

In order to illustrate the working of mathematical biology I am going to set out below a simple and classical example, worked out by Kostitzin, as being easy to understand.

The Nitrogen Cycle.

The nitrogen in the atmosphere is assimilated by living organisms with the help of microbes in the soil. It is also liberated in certain processes of decomposition. For the purpose of this study and to simplify the equations it is assumed that the micro-organisms which are capable of fixing atmospheric nitrogen live in symbiosis with plants.

Now in considering this problem there are six variables to be taken into account :—

(1) The total weight of free atmospheric oxygen.
(2) The total weight of carbon dioxide in the atmosphere and ocean.
(3) The total weight of free nitrogen.
(4) The total weight of nitrogen, carbon dioxide and oxygen in animals.
(5) The total weight of nitrogen, carbon dioxide and oxygen in plants.
(6) The total weight of nitrogen, carbon dioxide and oxygen in the earth's crust.

Let these be represented by x, y, z, u, v and s respectively. Then the relation between these variables may be expressed by either Fig. 6 or by the following differential equations :—

(1) $x^1 = - \alpha_{14}u + (\alpha_{51} - \alpha_{15})v.$
(2) $y^1 = \alpha_{42}u - (\alpha_{25} - \alpha_{52})v.$
(3) $z^1 = - \alpha_{35}v - \varepsilon.$
(4) $u^1 = - (\alpha_{42} + \alpha_{46} - \alpha_{14})\, u + \beta uv.$
(5) $v^1 = (\alpha_{15} - \alpha_{51} + \alpha_{25} - \alpha_{52} + \alpha_{35} - \alpha_{56})\, v - \beta uv.$
(6) $s^1 = \alpha_{35}\, u + (\alpha_{45} - \alpha_{65})\, v + \varepsilon.$

Equation (1) shows that O_2 is consumed by the respiration of animals $- \alpha_{14}u$, and of plants $- \alpha_{15}v$ and that is liberated in the process of assimilation by plants $+ \alpha_{51}v$.

Equation (2) shows that the atmosphere receives the CO_2 evolved by animals $+ \alpha_{42}u$ and by plants $+ \alpha_{52}v$ in the process of respiration and decomposition of living matter, and that plants assimilate $CO_2 - \alpha_{25}v$.

Equation (3) deals with the assimilation of nitrogen by the earth's crust and by plants, $- \varepsilon$ and $- \alpha_{35}v$, respectively.

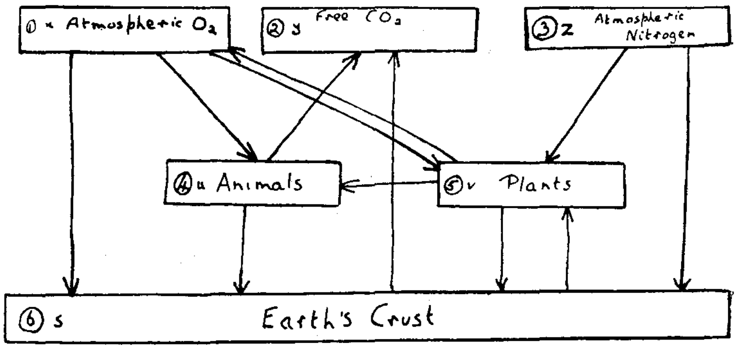

FIG. 6.—(*After Kostitzin.*)

Equation (4) concerns the amount animals add to or extract from the atmosphere $+ \alpha_{14}u$ and $- \alpha_{42}u$. $- \alpha_{46}u$ represents the fertilisation of the soil by the products of animal metabolism and βuv shows that animals live at the expense of plants and that the process is regulated by the encounter between predators and victims.

The remaining equations can be similarly explained.

The point to remember is that each term represents an arrow in the diagram (Fig. 6).

Now suppose that if plants were absent, the balance of animal life will diminish ; an obvious fact.

This will give :—

$$\lambda = \alpha_{42} + \alpha_{46} - \alpha_{14} > 0$$

and similarly :—

$$\mu = \alpha_{15} - \alpha_{51} - \alpha_{52} + \alpha_{35} - \alpha_{56} > 0.$$

In this case the variable z is always decreasing and equations (4) and (5) have periodic solutions.

Add the equations for the atmospheric gases (1) and (2).

Then :—

$$x^1 + y^1 + z^1 = u(\alpha_{42} - \alpha_{14}) - (\alpha_{15} - \alpha_{51} + \alpha_{25} - \alpha_{52} + \alpha_{35})v - \varepsilon.$$

Integrating this equation for t from t to $t + \omega$ and the average rate of disappearance of the atmosphere is given :—

$$\frac{x(t+\omega) + y(t+\omega) + z(t+\omega) - x(t) - y(t) - z(t)}{\omega} = - \frac{\lambda\alpha_{56} + \mu\alpha_{46}}{\beta} - \varepsilon < 0.$$

This shows that the atmosphere and the nitrogen in it are gradually disappearing though at a very slow rate.*

In Conclusion.

Though this paper is written by one who is no expert on the subject, I hope enough has been said to show the value to biologists of a study of mathematics. There seems little doubt that, in future, mathematics will be as important to the biologist as to the physicist. *It is to be hoped, therefore, that our universities will recognise this and will insist on students of biology possessing a sufficient knowledge of mathematics and its application to their problems to enable them to make full use of the great new field of research opened up.*

* It is calculated from this that the atmospheric nitrogen will last about another 2,000,000,000 years.

Discussion.

The Chairman (Douglas Dewar, Esq.) said : Mr. Wragge Morley's paper is most interesting. With much of it I agree, but I do not agree that the use of mathematics to forecast biological results is extremely important. It is often dangerous. I am not impressed by Kostitzin's forecasts of the growth of the population of the U.S.A., a young and expanding nation. I should, however, be much impressed if given a formula whereby the fluctuations of the population of the United Provinces of Agra and Oudh could have been foretold, as I worked as an official for many years in those provinces. Here are the census figures in millions : 1881, 44·1 ; 1891, 46·9 ; 1901, 47·7 ; 1911, 46·8 ; 1921, 45·4 ; 1931, 45·4. Is it possible accurately to forecast the figures for 1941 and 1951 ?

As regards Mr. Morley's curve relating to the speed of ants. Am I right in thinking that it purports to enable anyone to know the exact speed of any species of ant, given the length of its leg and of its body ? Thus, will the speed of any kind of any of which the ratio is 33 : 33 be 196 cm. per minute ? If so, I hope that Mr. Morley will give details showing the number of species measured by him.

In my view, mathematics are invaluable to the biologist, provided they are used with caution, and not to make wild forecasts.

I agree that biologists are often averse to reasoning about figures. I think there are two main reasons for this—one legitimate and the other not. The legitimate reason is that mathematical results are misleading unless based on complete and accurate data, and in the present state of biology such data are rarely available. Take, for example, Kostitzin's calculation that in about 2,000 million years atmospheric nitrogen will have disappeared. Now, two of the data on which this estimate is based cannot be ascertained with anything approaching accuracy, viz., the amount of N, CO_2 and O in plants and animals. The estimate of 2,000 million years cannot, therefore, be taken seriously. Moreover, it is based on the assumption that during this immense period there will be no adventitious addition or subtraction of N. from the atmosphere. A classic example of the mistake of applying mathematics to incorrect data is the calculation by Lord Kelvin of the age of the earth on the assumption that its sources of heat are limited to its original heat, and that derived from the sun. The illegitimate reason why biologists are repugnant to reasoning about figures is that to most of them the doctrine of evolution is a creed, and such reasoning often shows that the doctrine is false. This theory must stand or fall by the testimony of the fossils. Admittedly none of the requisite fossils have been found linking the phylas and classes, and connecting such peculiar forms as whales, bats and turtles to their supposed generalised ancestors. This means either that the theory is untrue or that the geological record and our knowledge of it are extremely imperfect. Now, there are data available which, if collected and dealt with mathematically, enable us to ascertain whether or not the record is fragmentary. Incredible though it seems, the late Mr. Levett-Yeats and I seem to be the only people who have collected such data, which are scattered about in hundreds of scientific journals, *i.e.*, the only persons to make any attempt to ascertain the extent to which animals and plants are fossilised.

Among the data we collected are (1) the number of genera of mammals now living in the world ; (2) the number of these of which fossils have been found. Clearly, if fossils have been found of every genus, the fossil record of mammals is complete. If fossils of only ten per cent. have been found, our knowledge of the record is imperfect ; so, probably, is the record itself. Here are the actual figures : of the 215 genera of bats, fossils of 17·67 per cent. have been found ; of the 408 genera of land mammals, fossils of 57·6 per cent. ; and of the 41 genera of marine mammals, fossils of 70·73 per cent. have been found. These percentages represent the degree of the completeness, not of the fossil record, but of our knowledge of it. This is shown by taking the data for land mammals by continents. The percentages of genera of which fossils have been found are : Australia, 45·85 ; Africa, 49·65 ; Asia, 70·15 ; South America, 72·09 ; North America, 90·14 ; Europe, 100.

Thus the percentage increases with the extent to which a continent has been explored geologically, and that is why the figures are highest for Europe and lowest for Australia. The figures for Europe indicate that in the course of its existence every genus of land mammal yields fossil remains. The low percentage for bats is largely due to the fact that, as they can fly, they, like birds, are less likely than ordinary mammals to meet with accidents of a kind likely to result in fossilisation of the victim. The figures demonstrate that in the case of land animals that cannot fly the fossil record is practically complete, and in the case of others nothing like so incomplete as evolutionists imagine. In other words, they are subversive of the evolution theory, and they are so unpalatable to transformists that the Zoological Society of London refused to publish the paper in which they are set forth ; the reason given for this refusal was : this kind of evidence leads to no valuable conclusion. Had our data shown that only a minute percentage of mammals had left fossil records, the data would have been deemed to lead to a very valuable conclusion ! These data have been briefly set forth in vol. 64 of the Transactions of this Institute.

Later I made a similar enquiry regarding the molluscs of the British Isles. The results are published in the *Landenberg Review* for 1938 : they are that of the 248 genera of British molluscs, fossils have been found of 178, or 70 per cent. In the case of bivalves the percentage is 100. The low grand total is due to the fact that many members of two families of univalves lack shells or other hard parts, and such are comparatively rarely fossilised. Of these two families, fossils of only 20 and 23 per cent. of the genera have been found. The above figures, then, indicate that the fossil record is nearly complete in the case of animals having skeletons or shells, and far from complete in the case of those lacking hard parts.

These conclusions can be checked by other data, such as the number of genera of mammals now living in any continent, and the number of genera, living and extinct, of which fossils have been found in that continent at any given point of geological time as evidenced by their known fossils. Such data for Europe and North America are set forth in the above-mentioned volume of the Victoria Institute *Transactions*. Both sets of data lead to the same conclusion.

The above percentages, being based on data consisting of accurate statistics, are accurate but not complete, because the data are incomplete. They are actual percentages, to which must be added an unknown quantity x. Thus they illustrate the limitations imposed on the mathematical calculations of the biologist. Although incomplete, these percentages suffice to overthrow the theory of evolution, at any rate in the form in which it is being taught in our universities and schools. The refusal to take notice of these percentages, which is retarding biological progress, is the result not of dislike of mathematical reasoning, but of prejudice. I therefore do not agree that universities should insist on biological students possessing a knowledge of mathematics. Such knowledge is of course useful, nay, indispensable, in some branches of biology ; but to make it compulsory on all biological students would choke off many who have neither taste nor aptitude for mathematics, but are deeply interested in the world of life. In my view ability to weigh evidence, lacking in so many biologists, is for the naturalist far more necessary than knowledge of mathematics.

In conclusion, I ask you to pass a hearty vote of thanks to Mr. Morley for his interesting paper.

Dr. F. T. Farmer said : The application of mathematics to biology is a branch of science which has only very recently come to the fore, yet one which has opened up new and important possibilities in the study of natural and living things. Much credit is due to Mr. Morley for tackling this out-of-the-way subject as he has done, and presenting us with a survey of the field which it embraces.

There are one or two points I should like to refer to. The first arises from his work on ants, and the relation he finds between the size of leg and the speed of their movement. Such an experiment is, I suppose, typical of scientific research : it takes a set of observations from Nature, and derives from them what may be called a natural law. In this case the law is represented by a curve drawn through the experimental points. But in every investigation of this type there is inevitably some spread of the experimental points on either side of the curve, and it is from this spread that the reliability of the law must be judged. For this reason I would have liked to see the points shown on the figure. The spread is not a sign of inaccuracy of the observers : their observations may be dead accurate ; but it is a sign of the entry of unknown factors. Thus, in the case of ants, the speed will not only be a function of size of leg and body—the relation sought for mathematically—but also of innumerable other factors such as nutrition, fright, health, rest, etc. These cannot be measured by our physical instruments, and it is precisely because of them that the type of analytical investigation Mr. Morley is discussing is so difficult. In physical science it is generally possible to eliminate these factors to a large extent, and, in consequence, well-established and exact laws have been derived, the reliability of which is confirmed by every further experiment made ; but in the less exact sciences, in biology in particular, these factors play a predominant part, and their influence must be taken into account. Mr. Morley has, presumably, done this in drawing his curves : it is implied in his statement that a " nice " curve is obtained ; but one would like to see just how " nice." Mr. Morley has stressed the need for a knowledge of mathematics among biologists. The greater need, to my mind, is a training in the technique of analysing empirical data, and extracting the significant from the random factors. It is here that the greatest skill is required, and the greatest mistakes have been made in the past.

A somewhat different consideration arises in the analysis made of population increase in the United States. The author quotes an empirical expression which he shows gives remarkable agreement with the actual variation of population over a period of 140 years, in spite of various disturbing factors which he mentions. Now this expression is undoubtedly of value in throwing light on population trends; but is it correct to call it a method of prediction of population? The expression was derived to fit the existing data, which, indeed, it does very well, and there is reason to believe that it will give a reasonable approximation to future conditions; but it must be remembered that *any* set of experimental observations can be fitted by a mathematical function if this is made sufficiently elaborate, and that the *only* criterion by which the correctness of such a function for predicting future events can be judged is its *simplicity of form.* The expression given is not elaborate, but it is sufficiently complex to imply that its agreement with past data is partly the result of chance, and to this extent it must be unreliable as a means of forecasting future trends. It is accurate as far as the past is concerned, but we must not forget the underlying principle by which it must inevitably be less reliable when carried into the future.

The analysis of heredity given in the paper is interesting. To one who has not studied the subject in detail it is somewhat difficult to follow—perhaps unnecessarily so through a lack of any definition of the terms used. A very brief explanation of the meaning of the expressions and steps would have been a great help. This does not, however, detract from its value to those more familiar with the subject, and Mr. Morley has shown that mathematics is of great use in questions of selecting desired characteristics in any natural species. We hope he will continue to develop this important field of work.

Mr. W. E. LESLIE said: We now take the use of mathematics in physics for granted. The extension of the method to biology and psychology raises the question as to how far it can be carried. This is very important for the Christian view of God and the World.

It is possible to draw a straight line through any two points, or a triangle about any three points. We feel that this is necessary—it cannot but be. But when we contemplate the universe containing unnumbered thousands of millions of points, we have difficulty in believing that its order is something that cannot but be. It gives the impression of design.

Similarly in biology. The skeletons of certain lowly organisms seem to be determined by molecular forces. It seems natural that the length of leg of an ant should bear a relation to its speed. We are not surprised that the distribution of genes should conform to the laws of permutation and combination. But D'Arcy Thompson has called attention to a mathematical relation between the forms of certain organisms which it is difficult to regard as mechanical, or as functional adaptations. Imagine drawings of living forms on a sheet of rubber. The sheet can be stretched up and down or from side to side, or it can be moulded to a curved surface, and so on. This causes a change of shape of the drawings. In many, perhaps most, cases the resultant picture is a mere distortion of reality. But in a large number of cases Thompson has shown that it corresponds to an actual creature related to the first drawing. Is this not due to design, a beauty of mathematical relations that is not necessary ?

Written Communication.

Dr. W. T. Marshall wrote : As one who has applied mathematics to researches on inanimate things such as steel and concrete, I congratulate Mr. Morley on giving us this interesting paper on its application to much more lively things, such as ants.

Dr. Farmer gave in his remarks various criticisms and suggestions with which I am in complete agreement, and on my part I should like to make the following comments :—

(1) I feel the author should have given a little more thought to his audience. He assumed a knowledge of biology and higher mathematics much greater than most of us possessed, and I feel the paper would have been more enjoyable if certain parts had been omitted and others explained more fully : the paper gave one the impression of an attempt to cover a wide field in a very short time.

(2) With regard to the closing remarks on mathematics for biology students, it has to be remembered that the course covered for the degree at our universities is a very full one, and the addition of a further subject to the syllabus would in most cases be impossible

without making the course longer. Most biology students have a good grounding in elementary mathematics, and many have a working knowledge of the elements of the calculus: all that is really needed is a course of lectures on elementary probability, etc. Mr. Morley may be interested to know that such a course is included in the degree and diploma course for biology students at the Royal College of Science.

AUTHOR'S REPLY.

In answer to the Chairman's query as to whether it is possible to forecast accurately the population of the United Provinces of Agra and Oudh, I am afraid that much fuller information would be required than the mere census figures, and the expression, when obtained, would be of necessity more elaborate than that required in the case of the United States of America; and even that, as Dr. Farmer pointed out, is fairly elaborate.

The Chairman is right in thinking that the curve relating to the speed of ants applies to ants of all species, and that if the ratio of length of leg to length of body be 33 : 33, the speed will be within at least a 3 f. error of 196 cm. per minute, provided that the temperature be the normal average summer temperature. Any rise or fall above this temperature would have to be taken into consideration, since for the purpose of correlation the temperature has been brought to a common proportional mean.

The spread of the points in this curve is very little up to the region of 200 cm. per minute, but does become greater after that, although never very great. Full details concerning the method of calculating the figures from which the curve was plotted will be found in my paper on "The Kinetics of the *Formicidae*, and the practical uses of such a study," read at the Seventh International Congress of Entomology, the publication of the Transactions of which has been temporarily delayed by the war.

I agree with Dr. Farmer that the major need is for training in the technique of analysing empirical data, and in concluding my paper I stressed especially the need for training in the *application* of mathematics to biology.

While interested to learn from Dr. Marshall that a course of lectures on elementary probability is included in the degree and diploma course for biology students at the Royal College of Science, I cannot help feeling that rather more is needed than a grounding in elementary mathematics, a working knowledge of the calculus, and such a course of lectures. Certainly, however, the Royal College of Science must be congratulated in going so far when most universities have entirely disregarded the matter.

Finally, in answer to the Chairman's remarks on biological mathematics and the theory of evolution, I feel that I must point out the existence of Haldane's mathematical "proof" of the theory of evolution, although I am not prepared to discuss the rights or wrongs of its mathematics here.