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Author(s): C. B. Williams
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THE STATISTICAL OUTLOOK IN RELATION TO ECOLOGY

By C. B. WILLIAMS, Sc.D.

Rothamsted Experimental Station, Harpenden, Herts

(BEING THE PRESIDENTIAL ADDRESS READ TO THE BRITISH ECOLOGICAL SOCIETY ON 6 JANUARY 1953)

(*With eight Figures in the Text*)

In the past hundred years the old and somewhat anecdotal Field Natural History has changed into the science of ecology largely by increased knowledge, increased accuracy of observations, and increased use of measurement. Whenever measurements are concerned there is always the possibility of using mathematical techniques.

Mathematics is only a form of condensed logic, and just as there are two kinds of logical reasoning, 'deduction' from the general law to the special case, and 'induction' from the special case to the general law; so there are two types of mathematical reasoning, formal mathematics in which arguments are from the general to the particular or from one generalization to another, and statistical mathematics in which the problem is to infer a general law from a small number of special cases.

For example, if there was a general law that robins laid five eggs in every nest, then one would know that ten nests in a particular wood would contain fifty eggs. This would be by deduction and the result would be absolutely correct or 'true' (provided of course that the law is true). However, biological research seldom works this way. If, for example, we found fifty eggs in ten robins' nests in a particular wood, to say that the average was five per nest in the particular group of nests adds nothing to our understanding—but to infer that because these ten nests contain an average (arithmetical) of five eggs then other nests in the same wood might also be expected to average five—or, still wider, to suggest from the data that 'robins' laid on an average five eggs would be inferential reasoning and subject to the criteria of statistical mathematics.

It is perhaps worth noting at this stage that to say that the ten nests had an average of five eggs is not even a summary of the available knowledge, as it is normally impossible to obtain the total number of eggs in all ten nests without knowing the number in each. For example, in theory at least, the nests might contain:

0, 0, 0, 0, 0, 0, 0, 0, 0, and 50 at one extreme
or 5, 5, 5, 5, 5, 5, 5, 5, 5, and 5 at the other.

Both give an arithmetic mean of 5 exactly, but the inference from one set of data is very different from the inference from the other.

Deduction and conclusions from formal mathematics are absolute. Inferences and conclusions from statistical methods are never proved; they only become more and more likely to be true as the amount of available data increases. And there is no doubt that in biology it is the inferential process which is the basis of all progress. Laws can only be discovered from a smaller or larger number of special cases, and all such laws may break down by failing to fit some new observation.

Let us turn for a moment to the effect of this outlook on the technique of field experiments, which is a fundamental part of ecology. When I was at the University about forty years ago it was almost an axiom of experimentation that the problem should be simplified as far as possible. If, for example, an Agricultural Station wished to test deep ploughing versus shallow ploughing; early planting versus late planting; variety A against variety A^1; and manure B against manure B^1, it was considered necessary to carry out four separate experiments; and further (owing to the lack of recognition of the need for measurement of variation) there was little or no reduplication. The result of such a policy was a set of clear-cut results, presumed to be accurate, in which it was demonstrated that (within the limits of the experiment) this treatment was better than that, or this was no better than that.

With the advent of the statistical outlook, chiefly between 1920 and 1930, Fisher and his school showed that more information, and more accurate information, could be obtained in less time with less work, first by reduplication to enable small errors to be estimated; and secondly, by combining several simple experiments into one more complicated, whereby not only the primary results, but also many interactions, might be measured. It will be seen, for example, that no experiment of the earlier type would show if early planting was better with variety A, and late planting better with variety A^1. This information, however, can be readily extracted from the more complicated type of experiment by statistical analysis.

There is, however, one great advantage of the older type of experiment at an Experimental Station like Rothamsted—it is easy to demonstrate to visitors! Once we used to say 'Here we have an experiment to show the effect of A against A^1. You can see the difference in the height of crop showing obviously that A^1 is better.' But to-day it is different: we have to say 'This plot is exactly the same height as that. It is a quite simple result of the first plot having treatments A^1, B, C^1, D, and the second having treatments A, B^1, C, D^1.' The visitors go away somewhat confused.

About twenty years ago I joined the staff at Rothamsted, and, after a discussion with the Director, Sir John Russell, it was agreed that I should work on the effect of weather conditions on insect activity and populations. I feel sure that had I embarked on this problem twenty years previously I would have first built a controlled-temperature controlled-humidity room, I would have chosen one particular species of insect, perhaps one sex only, all individuals of the same age and parentage, and of course with a food supply which could be standardized in quality and quantity. Then very carefully one climatic factor or another would have been varied and the effect noted.

The result would have been a very exact estimation of the effect of each factor within the very narrow limits of the experiment—accurate but extremely difficult to apply to the infinitely more complex conditions of the normal life of insects—information of considerable value, but not of the type I was seeking.

Instead, therefore, of this approach by simplification I attacked the problem from the other end. If we have a sampling system that will give a measure of the relative numbers of insects flying at different times, let 'Nature' ring the changes in weather conditions, and then see if the results can be analysed. So we designed a light trap and caught insects each night for two periods of four years, almost three thousand nights, with a total of nearly one and a half million insects captured and counted.

On the first night Nature presented us with temperature A, humidity B, wind C, rain

D, moonlight *E*, etc., etc., and on the next night a new complex, and so on. Given enough nights, and accurate simultaneous measurements of both the catch and of the physical factors, we hoped that it might be possible to analyse or extract the most likely effect of each of the factors, even if these factors are themselves closely correlated.

On the whole the method has worked, and we were able, for example, after even so short a time as a month, to calculate the effect of changes in minimum temperature in the form that, other things being equal, a rise of minimum temperature of about 4·5° F. (2·5° C.) from one night to the next doubles the number of insects caught.

Further study of the catches night by night over the eight years enabled us to separate the effect of weather conditions at the moment on the activity of the insects, and of weather conditions in previous months on the population level; and it then became possible to calculate the regression, or effect per unit change, of such factors as the rainfall and temperature in any three consecutive months on the population in the fourth month. It was found, for example, that high temperature in winter produced a distinct increase in the insect population a month or two later—but in the summer the effect was to reduce the population. High rainfall, on the contrary, produced a definite increase in population in summer and autumn, but little or no effect in winter and spring. Finally, it was possible to estimate or forecast population changes from a known series of weather conditions, and to compare them with actual changes in the field.

Fig. 1 shows the departures from normal for the time of the year of the insect population at Harpenden as observed from the light-trap catches and as calculated from our formulae for the two periods of four years 1933–7 and 1947–51 during which our trap was working continuously; and the close resemblance can easily be seen.

Sometimes, however, the method of letting Nature ring the changes breaks down. For example, in mid-September 1933 (the first year of trapping) there was a night of heavy fog, unusual for so early in the year, on which twenty-two specimens of a particular moth were captured in the trap, as compared with only four others in the whole of the first four years. Was this an effect of the fog? We are still waiting for a repetition of the unusual combination of factors to test this hypothesis. On the other hand, I don't see how the fog problem could have been solved, or even discovered, in the laboratory.

The approach to biological problems from the simplified end and from the complex end are both necessary, and perhaps like engineers tunnelling through a mountain from both sides research workers may some day meet in the middle and shake hands. But in the recent past there is little doubt in my mind that the complex field approach has been neglected. It is slow and full of unforeseen difficulties and disappointments, but it must be tried, however hard and however slow. I have spent much of my time in the last twenty years keeping my staff from disappearing into constant-temperature rooms!

The statistical approach to a problem is usually based on the conception of 'population' and 'samples'. The population is something about which you wish to know certain properties. The sample is a portion which is available for examination. From the properties of the sample you try to infer the properties of the population. Your inference will be more accurate the larger the sample it is possible to deal with. If your total sample can be broken up into a number of subsamples it is possible to measure the error of your conclusions—and from that can be estimated the likelihood that they are based on real differences and not accidental variations inherent in all forms of sampling.

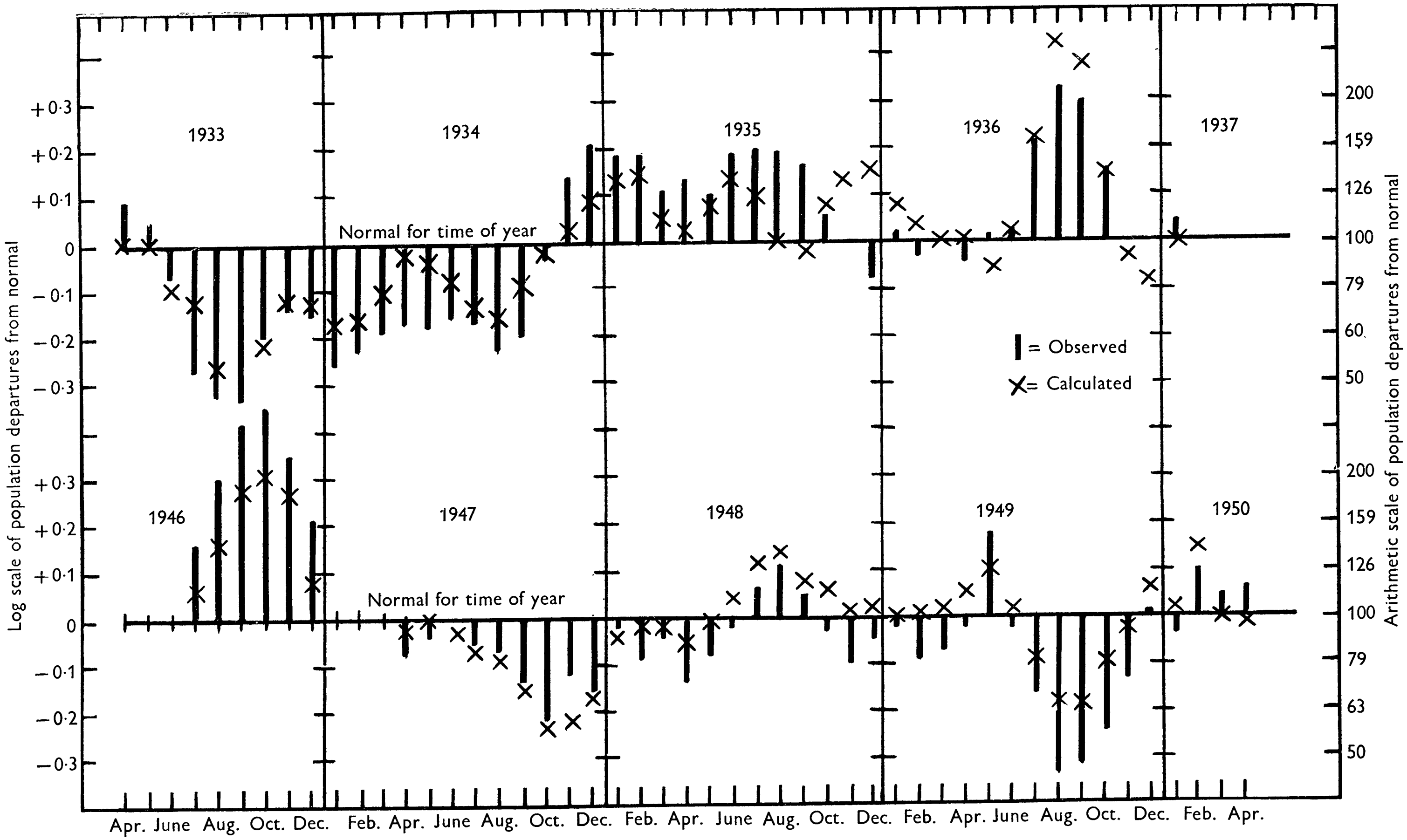

Fig. 1. Monthly observed and calculated changes in nocturnal insect populations at Rothamsted over two periods of four years, expressed as logarithmic departures from the normal for the time of the year. The histogram shows changes observed from catches in a light trap each night—and the crosses (×) are values calculated from formulae dependent on the rainfall and temperature departure of each of the three preceding months.

Not merely, however, is it necessary to measure the extent of variation in your sample, but also its form; which leads to the study of frequency distributions of properties of successive samples. The most usually recognized form is the 'normal' curve—where variations are arithmetically symmetrical about the arithmetic mean. But in many biological problems variation is not arithmetic but geometric; and in such cases arithmetic means and measures of variation based on the arithmetic scale are misleading. It is easy to see, for example, that if catches in an insect trap on the different nights of a week were:

1, 53, 105, 157, 209, 261, 313,

or instead of this: 1, 3, 9, 27, 81, 243, 729,

one's conclusions would be very different for the two cases. Both have a total of 1093 for the week's catch, but in the first the nights differ arithmetically and the correct inference is arithmetic variation about an arithmetic mean of 156, i.e. $156 \pm k$. In the second case, although the arithmetic mean is still 156, the proper conclusion is that they are varying geometrically round a geometric mean of 27, that is to say, $27 \div$ or $\times k$; or simpler if put in mathematical terminology as $\log 27 \pm \log k$.

A still more subtle cause of trouble is when, by bad planning or by necessity, the only samples available are not a random selection of the population, thus resulting in a biased error. An example of this, though qualitative rather than quantitative, came into our work on insect migration. For many years we had to depend for our evidence (i.e. our samples) largely on 'random' records of mass movements of insects, published at various times in various countries by many different obervers, few of whom ever saw a second movement. We collected together these records from all sources and used them to study the problem of whether or not certain insects regularly moved in one direction at one season and in a reverse direction at another season; if, in fact, insects migrated like birds. A biased error in the observations then came to light. We found that in the few established cases of a return flight the migrations were large (and so conspicuous) in one direction, and thin (and so inconspicuous) in the reverse flight. As conspicuous flights are more likely to be recorded by the general public than inconspicuous ones, the information available tended to obscure the frequent occurrence of small reverse flights, and it was not until more continuous observations were taken by trained observers that the evidence became reliable.

A particularly interesting form of distribution is when all the errors are in one direction. This is found, for example, in the study of phenology when a number of observers are recording the first appearance of a bird in a particular district. It is not possible to see the bird before it arrives, but it is possible to miss seeing it for several days after the arrival. Thus the actual day of arrival of the bird that we are trying to determine is not near the average of the observations but is at, or previous to, the earliest of the records. There is even another complexity in this problem, as a bird such as the cuckoo, which is easily recognized by sound, is less easily overlooked than a bird, such as the swallow, which has to be seen to be recorded. Thus the error of lateness in observations on the swallow is likely to be greater than in the case of the cuckoo. Fig. 2 shows a number of years' records of first appearance of these two species, and since the observed difference is about five days, with the cuckoo later, the true difference is likely to be greater than this.

The relation between sample and population is not always simple. A sample is not merely a small-scale reproduction of the population, just as a population is more than a collection of individuals. For example, if a population consisted of a large number of species all equally abundant, then in any random sample of individuals the species would not be equally abundant—in fact, the number of species represented by 0, 1, 2, 3, etc., individuals would form a Poisson series. Thus, if we find such a Poisson series in a random sample the biological problem is not to explain the Poisson distribution but to explain the *equality* of abundance of the species making up the population.

As a matter of fact we do *not* find, in any mixed wild population of animals or plants, an equal abundance of the different species that make up the complex. Always some species are common and some are rare; and the study of the mathematical forms of distribution of relative abundance has been particularly interesting.

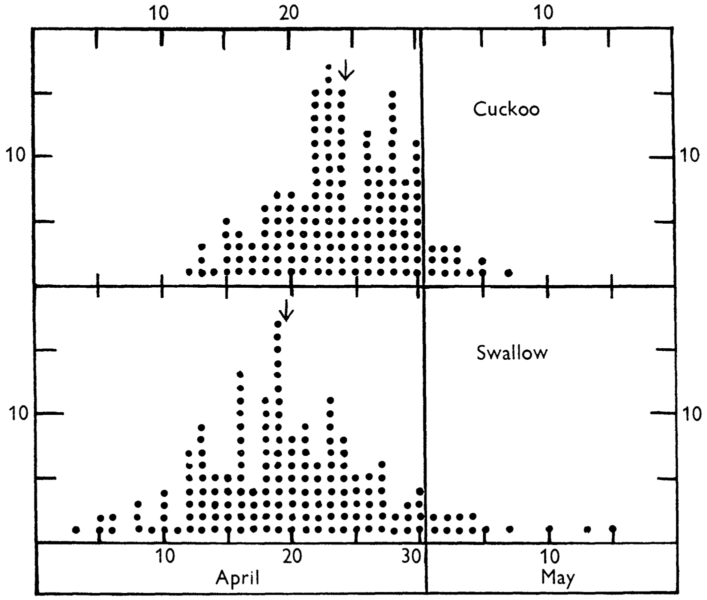

Fig. 2. Data of first observation each year of the swallow and the cuckoo from the Marsham records taken at Hevingham, Norfolk, nearly every year from 1736 to the present time. The average date for the swallow is earlier than the cuckoo, and the variability greater.

As an example we may take the case of a random sample of moths caught in a light trap at Rothamsted during four successive years. Altogether there were 15,609 individuals representing 240 species. Of these nearly eighty species, or one-third of the total, are very rare, each represented by four individuals or less in the four years trapping; while at the other end only twelve of the commonest species accounted for more than half the total number of individuals caught.

Fig. 3 shows that there was a mathematical order in the relative number of species with 1, 2, 3, 4, etc., individuals in the sample, and from this we infer that there must have been some related order in the population that we were sampling. The statistical problem is to find a mathematical series which will provide a close fit to these, and many other similar observations; and then, using any such series as a working hypothesis, to see what we can deduce from it and what further observations and experiments it suggests as desirable. Fig. 3, in addition to the observed data, shows a calculation using the 'logarithmic series' as a basis, which gives a close fit; but more recent studies suggest that the 'log-normal' distribution may provide an even closer approximation, particularly when we are dealing with larger samples.

Not only can species be grouped in a frequency distribution according to the number of individuals in each, but genera also can similarly be grouped according to the number of species, families with different numbers of genera, and so on. Fig. 4 shows the tabulation of 805 species of Mantidae (Prying Mantis of the Orthoptera) classified by Kirby in 1910 into 208 genera; together with a logarithmic series with the same number of units and groups. The very close fit is at least suggestive that this or some similar mathematical law may be of use in interpreting the relationship.

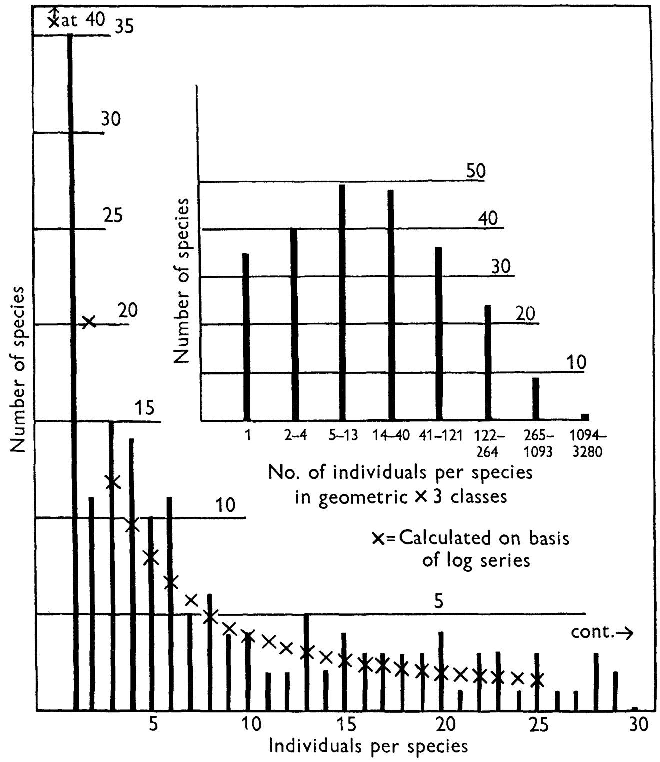

Fig. 3. Numbers of species of Macrolepidoptera with different number of individuals, from captures made in a light trap at Rothamsted during the four years 1933 to 1936—giving a total of 15,609 individuals belonging to 240 species: together with a series of calculated values for the same number of individuals and species based on the logarithmic series: the same data is also shown classified in × 3 geometric classes.

Even more extraordinary is that the distribution of parasites on hosts shows a similar order, and may possibly be represented by similar mathematical laws. Fig. 5 shows the frequency distribution of the number of human heads with 1, 2, 3, 4 lice in a sample containing 7442 lice on 461 heads (original data from P. A. Buxton). Records for fleas on rats, and for mites on rats, also show the same general type of frequency distribution.

An interesting idea which has developed from this statistical approach to ecology is the conception of 'diversity' as a measurable property of a mixed population. Supposing one went into a natural forest in a cool temperate area and, with one's eyes shut, touched first one tree at random, and then a second. The chances are quite high that both trees might belong to the same species, because the make-up or pattern of the forest is undiversified. If, however, the same test was carried out in a tropical forest it might be necessary to select a dozen or more pairs before both belonged to the same species. Here the population is diversified—for the same number of individuals we have many more species. The number of pairs of individuals that have to be selected from any population so as to include, on an average, one conspecific pair is a measure of the specific diversity of the population being sampled.

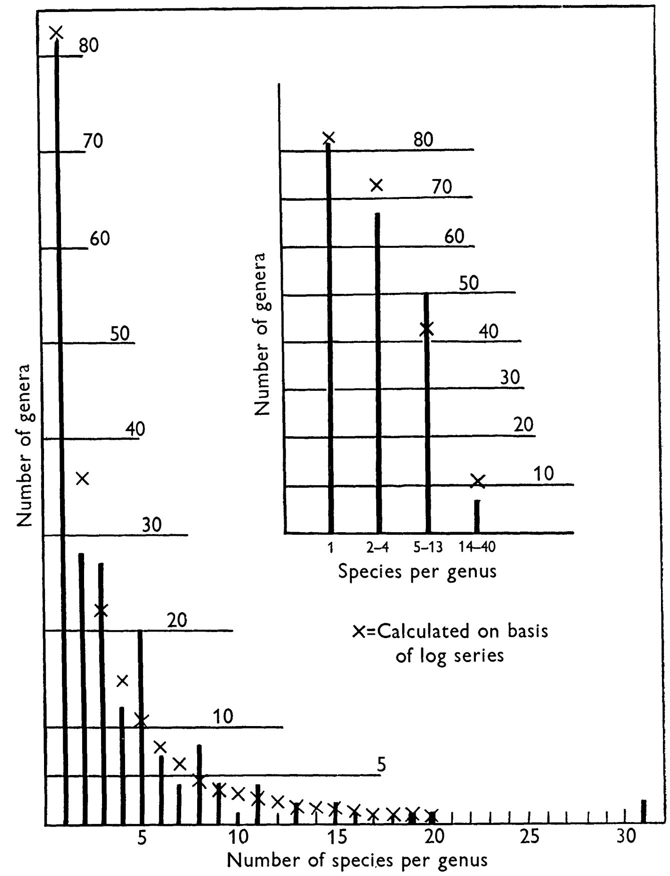

Fig. 4. The number of genera with different numbers of species in the classification of 805 species of the insect family Mantidae into 209 genera, made by W. F. Kirkby (1910); together with values calculated on the assumption of logarithmic series for the same number of species and genera. The same data is also shown classified in × 3 geometric classes.

This conception of diversity as a measureable character arose out of some of our work on the frequency distributions in species when arranged in a logarithmic series; but it has been expressed in the simplest form by Simpson (*Nature, Lond.*, **163**, 688, 1949) as follows:

If a population contains N units it is possible to select different pairs in $N(N-1)/2$ different ways.

If within the population there is a group with n units it is possible to select within it $n(n-1)/2$ pairs. For all the groups within the population the possible number of pairs belonging to the same group is thus $\Sigma n(n-1)/2$.

Thus it follows that the number of pairs that must be selected on an average to contain one pair of the same group is $\frac{N(N-1)}{\Sigma n(n-1)}$; which is the diversity of the population.

There are other methods of calculating the diversity if we know the pattern of the distribution of species with different frequencies, and from one of these I have shown that the 'diversity' in samples of adult Macrolepidoptera caught in a light trap at Rothamsted is low (about 3) in April, rises to a peak of about 26 in July and falls again to about 5 in the October (see Fig. 6). The seasonal change from cold to warm and back to cold is thus producing a similar effect to the change from temperate to tropical and back to temperate regions.

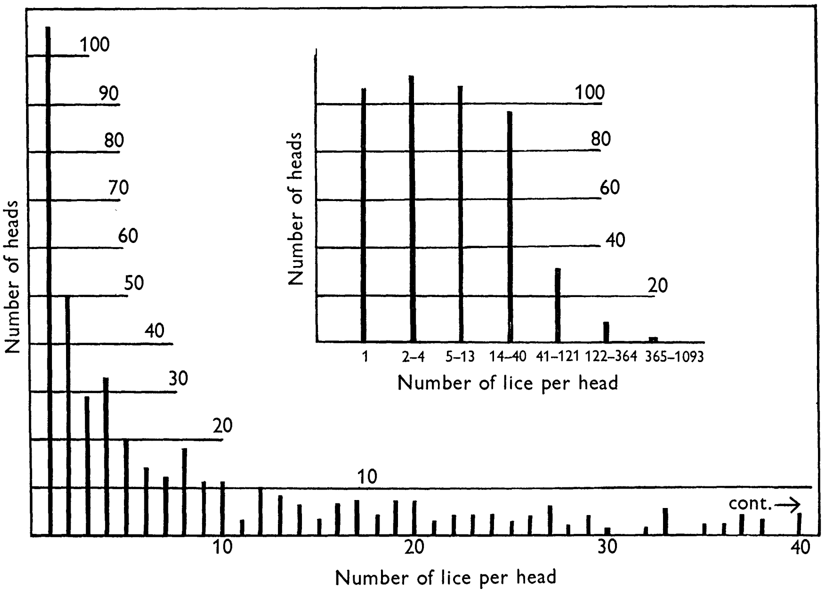

Fig. 5. Numbers of heads of men with different numbers of lice per head, from data obtained from an Indian jail by Dr P. A. Buxton. The same data is also shown in × 3 geometric classes.

Similarly, using data from the Challenger Expedition on the number of individuals and species dredged at different depths in the sea it can be shown (Fig. 6) that the specific diversity in benthic marine animals decreases with depth.

Just as specific diversity is based on the relative number of species with different numbers of individuals making up a population, so we can calculate a generic diversity from the number of genera with different numbers of species. This will be a measure of the number of pairs of species that one will have to select from the population to get on an average one congeneric pair.

If a *random* sample of species is taken from a population the generic diversity should be the same in the sample as in the population. Therefore if we compare the generic diversity in a group of animals or plants over a larger area with that of a smaller area within the larger, any difference between the two represents a natural non-random selection of species in respect to their generic relations. For example, if the diversity of the smaller

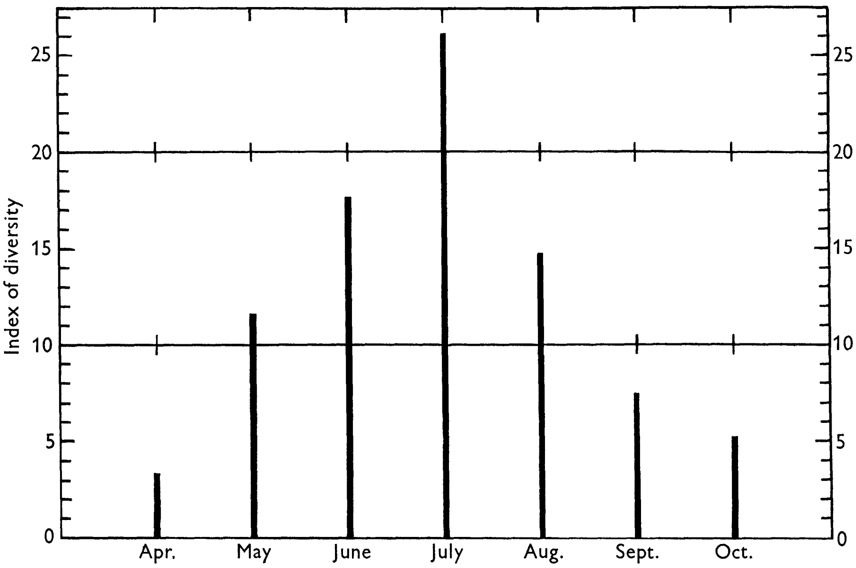

Fig. 6. Changes in diversity in the population of adult nocturnal Macrolepidoptera during the summer months at Rothamsted, calculated from samples obtained by means of light traps over a period of six years.

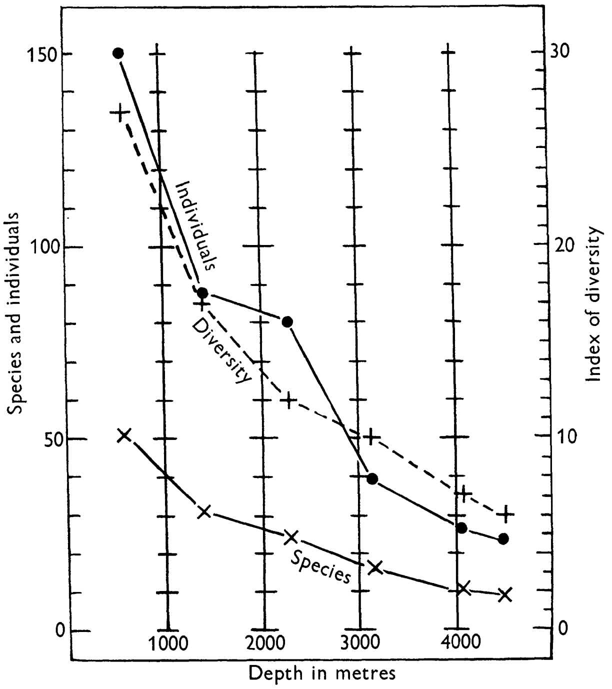

Fig. 7. Numbers of Benthic animals dredged during the voyage of the *Challenger*, showing the average number of individuals and species found at different depths together with the diversity calculated at the same depths. The results show a steady fall of specific diversity with depth.

area is greater than the larger, then there has been a natural selection against congeneric species, while if it is smaller there has been a natural selection in favour of congeneric species. This has given a statistical method of approach to the vexed question of intrageneric competition.

In plants it is not usually possible to count the numbers of 'individuals' in a sample, and as a result the technique of analysing plant populations has developed along the line of recording the presence or absence of a species in a number of small samples of fixed area—known as quadrats. Making only the assumption, generally accepted by botanists, that, at least over a fair range of sample size, the number of species present is proportional to the logarithm of the number of quadrats (that is to say, if you *multiply* your area by a constant factor you *add* a constant number of species), it is possible to show that the form of frequency distribution of species occurring in increasing proportions of the quadrats is dependent on:

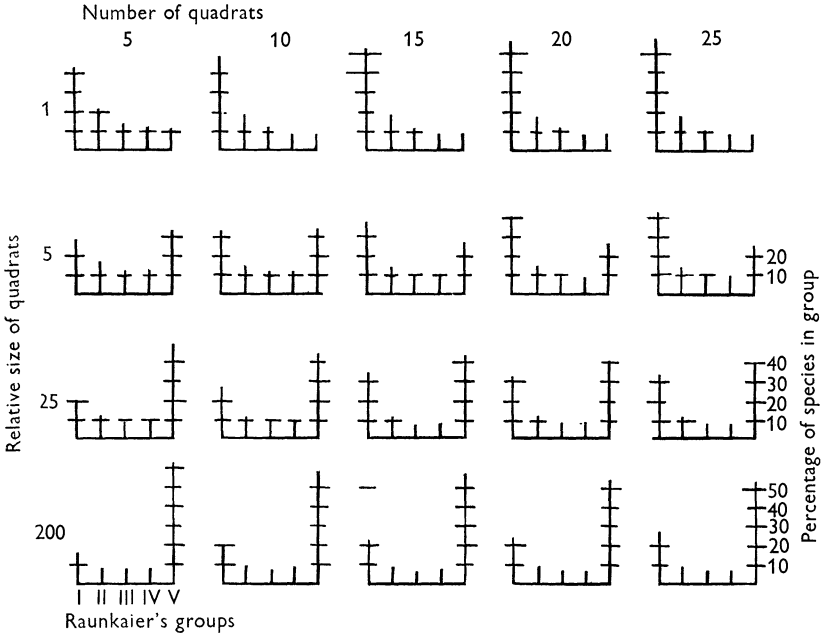

Fig. 8. Calculated changes in the relative proportion of plant species in a single association which may occur in Raunkaier's five percentages groups (0–20, 20–40, 40–60, 60–80 and 80–100%) of quadrats in plant sampling, when the number of quadrats or the size of the quadrats is altered. Any type of distribution from the J to the U, and to the reversed J can be obtained, showing that such differences may be the result of technique and nothing to do with the structure of the population.

(1) The size of the quadrat.
(2) The number of quadrats.
(3) The diversity of the population.

Since the first two are matters of convenience only, and can be changed at will, the only biological factor involved is the diversity of the population.

Fig. 8 shows the theoretical differences in the distribution of species occurring in 1–20, 21–40, 41–60, 61–80 and in 81–100% of the quadrats (Raunkaier's grouping) when the size and number of the quadrats are varied.

One more example of a rather different type might conclude this survey. In our studies of insect migration we found that the well-known migrant, the Painted Lady butterfly (*Pyrameis cardui* L.), had been recorded as abundant in western Europe in 27 years out of the 74 years 1865–1938; and in the U.S.A. and Canada in 20 years during the same period. Table 1 shows the number of years that it was simultaneously recorded as abundant or scarce in both continents, together with the calculated frequencies on the basis of no correlation. It will be seen that there is an excess of observed simultaneous abundance and simultaneous rarity, and a deficit of the two cross-combinations, suggesting immediately that the species tends to be abundant, or to be rare, simultaneously on both sides of the Atlantic. A statistical test of significance shows that such results are likely to be produced by chance less than once in 100 repetitions and so may be considered to be real. Since the immigrant butterflies come into western Europe from North Africa and the immigrants into North America come from Mexico it will be seen that we have a statistically sound basis for considering that some at least of the causes of abundance of migrants must be acting simultaneously in areas separated by over 100° of longitude—or about 6000 miles.

Table 1

		Abundant in Europe		Not abundant in Europe		
		Obs.	Cal.	Obs.	Cal.	Total
Abundant in America	Obs.	13		7		20
	Cal.		7·6		12·4	
Not abundant in America	Obs.	14		40		50
	Cal.		19·4		34·6	
Total		27		47		Total 74 years

Perhaps I may conclude by saying that the application of statistical methods to biological subjects is still in its infancy—and no doubt as many mistakes will be made by this as by any other approach. But let us go ahead, for: 'He who never makes a mistake never makes anything.'

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