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Some Simple Quantitative Relationships in Ecology, with particular reference to Birds.

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Some Simple Quantitative Relationships in Ecology, with particular reference to Birds.*

By D. G. TUCKER, Ph.D.

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1. Introduction.

It is perhaps not generally realised, especially by the amateur, how useful statistical methods can be to the ecologist in determining the simple quantitative relationships which should be a fundamental part of his work. The majority of naturalists, it is true, are not greatly interested in numerical studies; behaviour of animals or the rare occurrence of certain species are to them more fascinating. But the ecologist, whose object is to unravel the complex interrelationships between the various types, species, etc., of organisms and their environments has a task so immense and with such complicated ramifications that he cannot afford to ignore the methods of quantitative study.

It is, of course, commonly said that figures can be made to prove anything; that a statistician is one who, starting from unjustifiable assumptions, reaches a foregone conclusion; and it will undoubtedly be said by some that the conclusions reached in this paper are obvious, and would have been reached more quickly by commonsense. There is generally a grain of truth in such sayings, but only a grain! Ill-informed statistical work can certainly suggest the most absurd things, and it is imperative that in any scientific work only methods which are well-tried or supported by enough field data should be used. It is necessary to test every result, and often it is possible to state the exact degree of certainty with which a certain result is put forward. Correct methods of statistical analysis generally mean a large amount of mathematical and computing work, but it is hoped that the present paper will show how worth-while this is.

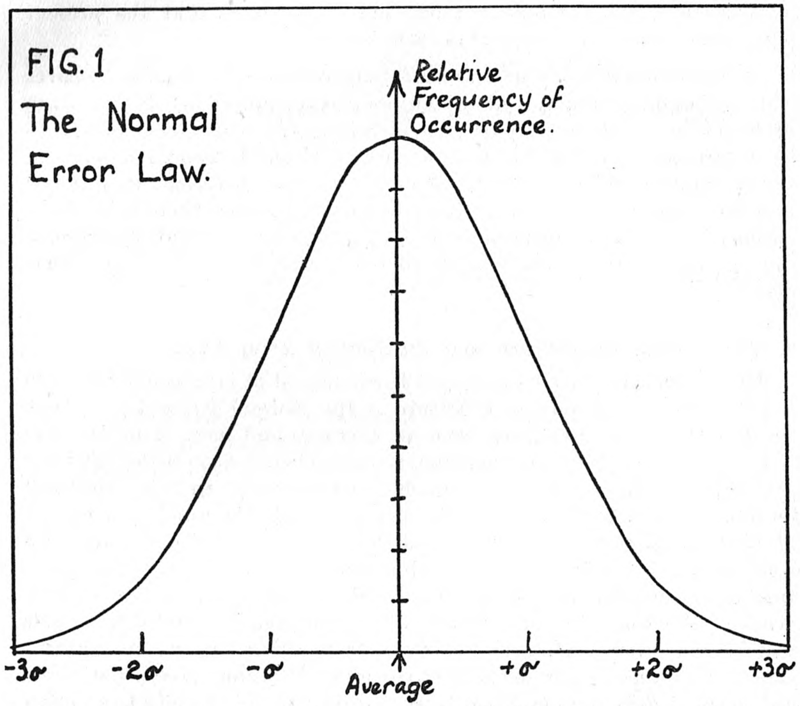
In the limited scope of one short paper it is not possible to cover many different methods, and the author has confined himself to certain processes in which he is particularly interested, and which appear to be of greatest interest to the ecologist. Even if readers find themselves uninterested in the mathematical processes involved, it is hoped that this paper will at least stimulate them to record their field observations in numerical form, and to plan their observational and recording methods so that those who do like statistical analysis can use their results.

*Based on a paper read and discussed before the Ecological Section on February 5, 1946.

2. The Normal Distribution and the Normal Error Law.

One of the most useful and most fundamental of laws connected with the distribution of things in Nature is the Normal Error Law. It is the law of chance variations from an average, and most of us are prepared to accept the statement that random chance is probably the biggest influence in Nature. As our chief consideration in this paper will be numbers of species, we can take as an example the number of species of birds in a certain type of woodland. Provided the habitats are similar in every other way, including size, we can see that the variation in the number of species from wood to wood must be due to pure chance. We shall find an average number of species, and most woods will have a number of species fairly close to this average. As we consider larger and larger deviations from this average, so we find fewer and fewer woods having these larger deviations. This effect is shown graphically in Fig. 1. The vertical scale represents the frequency of occurrence of numbers of species shown on the horizontal scale. The graph is symmetrical about the average. This relationship is called the Normal Error Law, and the distribution of numbers of species is called the Normal Distribution. It can be shown mathematically (1) that the curve is defined by the " standard deviation " (σ), which is the square root of the sum of the squares of all the individual deviations from the average value. The number of woods in which the deviation from average is less than σ is two-thirds of the total number. Similarly, the proportion of woods in which the deviation is less than 2σ is just slightly over 95 per cent.—i.e. in only 5 per cent. of cases is the deviation from average greater than twice the standard deviation. A deviation of 3σ is only exceeded three times in a thousand, and of 4σ only once in more than 10,000 times. The accuracy of any observations on this basis evidently depends on there being a very large number of woods to consider.

The real use of this law is that it enables us to test any observation in relation to the background of knowledge. As a simple, but very important, illustration, consider some observations made by the author in Highams Park, Essex, during December 1945 and January 1946. On each visit made to this well-defined area of Epping Forest, the number



of birds of each species seen was recorded.* The visits were all of approximately the same duration and the exploration of the area, if not thorough, was always consistent. As a rule the visits had to be made at week-ends, when at least 100 humans and about 20 dogs visited the Park each hour. The results obtained for seven such visits were as follows:—

Number of species seen:	9, 12, 11, 10, 9, 11, 12.
Total no. of birds seen:	55, 84, 48, 49, 41, 96, 75.

However, on one occasion it was possible to visit the Park on a weekday when not a single human being was to be seen. The result this time was 16 species and 75 individuals.

On the face of it, one would say that there were obviously more species to be seen when there were no human beings or dogs about. But there was only one occasion to judge on; it may have been pure chance. Admitting this, the statistician would proceed to determine the probability that it *was* only pure chance.

Now, since on the week-end visits, all circumstances were reasonably consistent, it is safe to assume that the number of species and number

*No account was taken of house-sparrows; they were far too numerous to count, and obviously domiciled in the nearby residential area rather than in the Park.

of birds vary from occasion to occasion only through the workings of chance. We see that the average number of species was 10.6, and the largest deviation only 1.6. Applying the normal error law to the deviations from average, we find the sum of the squares of the deviations to be 9.72, the average square to be 1.39, and the square root of this to be 1.18. In a case like this where the number of observations is small, we should apply (1) a correction factor $\sqrt{N/(N-1)}$ (N is the number of observations being considered) to this square root in order to obtain the standard deviation, σ. This gives us $\sigma = 1.27$.

The odd visit when no people were about gave 16 species. This is a deviation of 5.4 from the previous average. This deviation is over four times the standard deviation, and the Normal Error Law gives us the result that this could only happen by pure chance once in over 10,000 times. This probability of chance occurrence is so small that we can neglect it. Consequently we can state that in the absence of human visitation the number of species of birds to be seen in Highams Park is significantly higher than when many people are about. *We know now the exact significance of this conclusion.*

It is worthy of mention that other visits at quiet times confirm this result, as can be seen from the author's report on Highams Park in the Epping Forest Survey (*post*, p. 109).

As regards the total number of birds seen on each visit, similar reasoning shows that the number of birds seen on the quiet visit would occur by chance about once in three times anyway, so that there is no significance in the figure on this particular occasion.

3. The Logarithmic Series for Relating the Number of Species to the Number of Individuals (or to the Area).

3.1. *Description.*

We have seen how the Normal Error Law enables us to examine data of one type, e.g. the distribution of numbers of species *or* numbers of individuals. In dealing with bird populations, however, as with many other branches of natural history, we are interested even more in the relation between the number of species and the number of individuals. It is only fairly recently that this matter has been satisfactorily explored theoretically, and the mathematical relations which follow are due to R. A. Fisher (2). The application of this theory to ecological problems has been discussed from several points of view by C. B. Williams (3). Although particularly concerned with insect populations, to which the theory is shown to apply with considerable accuracy, he also discusses its application to botanical and other zoological problems, including classification as well as population. Birds, however, are hardly discussed at all, presumably due to the lack of published data.

In a homogeneous population of plants or animals, the number of species which can be expected to be each represented by precisely n individuals is shown by Fisher to be

$$\frac{\alpha}{n} x^n \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

where α is a factor called "Index of Diversity" by Williams, and x is a number less than unity. If in such a population, or in a sample of it, the total number of species is S and the total number of individuals is N, then the following relations apply:—

$$S = -\alpha \log_e (1-x) \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (2)$$

$$N = \frac{\alpha x}{1-x} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (3)$$

$$S = \alpha \log_e \left(1 + \frac{N}{\alpha}\right) \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (4)$$

The Index of Diversity indicates the extent to which the population is divided into species; a high value means that the population is very diverse. For a given population the value is independent of the size of sample taken, but if it is calculated from the values of S and N in a very small sample, it is obviously less accurate. Since, then, the value of α is independent of how large a sample is observed, it is a fundamental characteristic of the population, and as such is of great ecological value in giving us something by which different populations may be compared.

In order to apply this useful method to the analysis of any particular type of population, it is first important to establish the fact that the basic relation giving the number of species represented by a certain number of individuals really is that quoted earlier; in other words, the number of species represented by 1, 2, 3 ...... etc., individuals must agree with the logarithmic series

$$\alpha x, \quad \frac{\alpha x^2}{2}, \quad \frac{\alpha x^3}{3}, \quad \ldots\ldots\ldots\ldots \quad \frac{\alpha x^n}{n}, \quad \text{etc.}$$

Since the original theoretical work is based on certain assumptions, it must not be regarded as a natural law until tested against reliable observations.

We will proceed to establish this law for a particular bird population for which data is available, namely, that of the Society's Survey Area at Limpsfield Common, Surrey (5). The general procedure is to consider the number of species S, and the number of individuals N, for any sample; then by the use of the chart given in Fig. 2, the corresponding value of α is easily obtained with enough accuracy for most purposes. Greater accuracy can be obtained by using the method and special tables given by Fisher (2). From the relation $N = \alpha x/(1-x)$, x is easily calculated. The theoretical values for the logarithmic series above are then readily calculated, and these are tested against the observed figures.

3.2. *The Limpsfield Common Censuses.*

Two comprehensive winter censuses of the bird population of Limpsfield Common were made in December 1938 (5a) and December 1939 (5b) respectively by a team of members of the Society. From the published

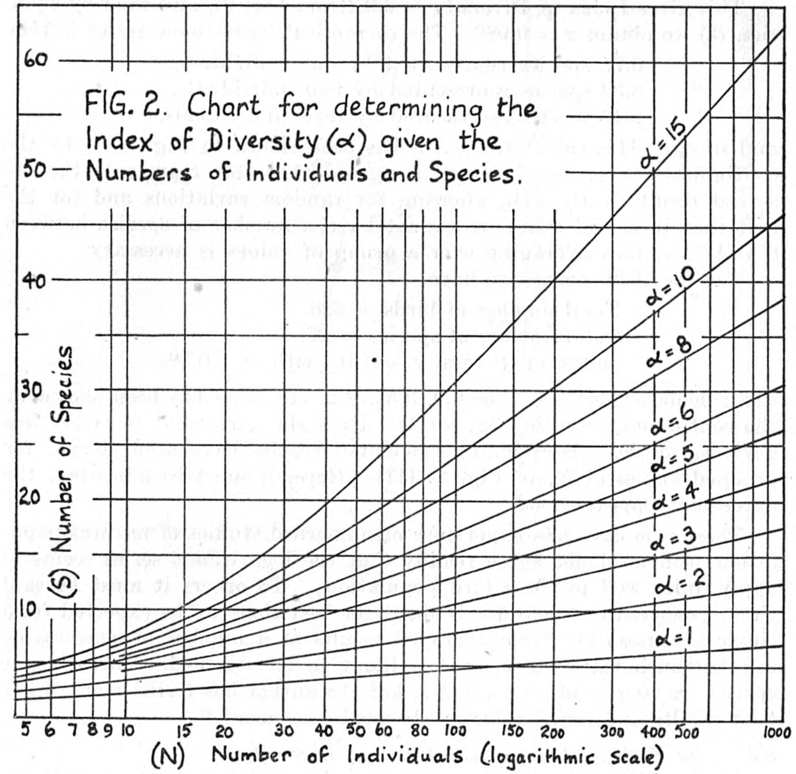


FIG. 2. Chart for determining the Index of Diversity (α) given the Numbers of Individuals and Species.

results it is easy to tabulate the number of species, each represented by a certain number of individuals. This relationship is shown in graphical form for each census by the vertical lines terminated in dots in Fig. 3. It is quite evident that there are more species represented by only a few individuals than by many individuals, which agrees with the general nature of the logarithmic series. The observed results form somewhat irregular relationships, however, which is only to be expected from single counts, owing to the random variations always to be found in Nature. To emphasize the essential consistency of the results, therefore, the 1939 figures have been re-arranged in Fig. 3 (III) in groups; all species represented by 1-5 individuals have been lumped together in the first group, and so on. It will be seen that the irregularities are considerably reduced by this process, and the real nature of the relationship is made clearer.

For the 1938 census, we have

Total number of birds (N) = 385
Total number of species (S) = 28

This gives Index of Diversity = 6.9 (from Fig. 2), and then by equation (3) we obtain $x = 0.982$. The theoretical logarithmic series is then

6.77 species represented by one individual,
3.32 species represented by two individuals,
2.17 species represented by three individuals,

and so on. This calculated series has been shown in Fig. 3 (I) by the continuous curve, and it must be agreed that this represents the observed results fairly well, allowing for random variations and for the fact that in a real count we cannot have a number of species between 0 and 1, so that averaging over a group of values is necessary.

For the 1939 census, we have

Total number of birds = 328.
Total number of species = 27.
Index of Diversity = 7.0, with $x = 0.98$.

The calculated series is thus 6.9, 3.35, 2.2, etc., and has been shown by the continuous curve in Fig. 3 (II). Here the agreement is rather less obvious, so the corresponding calculated results have been shown, for grouped values of N, in Fig. 3 (III). Here, it must be admitted, the agreement appears good.

Those who have had experience of numerical studies of natural populations will no doubt agree readily that the logarithmic series seems to apply quite well to these bird populations. To others it must be said that agreement of this order is about the best that can be expected from single censuses; but from averaged results of a number of censuses or counts, much better agreement is likely to be obtained. There is not space here to give other examples, but the author has tested many other field results and found consistently good agreement.*

3.3. *The Ecological Use of the Index of Diversity.*

Having shown that the logarithmic series applies to bird populations, we can proceed to determine what useful application of the Index of Diversity (which depends on the logarithmic series being true) can be made in ecological work.

The main use is likely to be to compare the diversity of bird populations in different habitats. It is always difficult to make comparisons between the population of one habitat and that of another; there are so many factors to consider. The index of diversity is a single number representing an inherent property of a particular population, *quite irrespective of the size of the habitat and the density of the population.* Moreover, it is not necessary to make a census to determine it; a few short sample counts will be enough to determine it approximately. Thus the index of diversity can be used for obtaining quick and compact comparisons.

Insufficient work has been done so far on this subject to enable concrete examples to be given; but the following table gives some provisional values of the index of diversity for birds for typical or average habitats of certain broad types in England.

*A number of other examples were included in the paper as read to the Society.

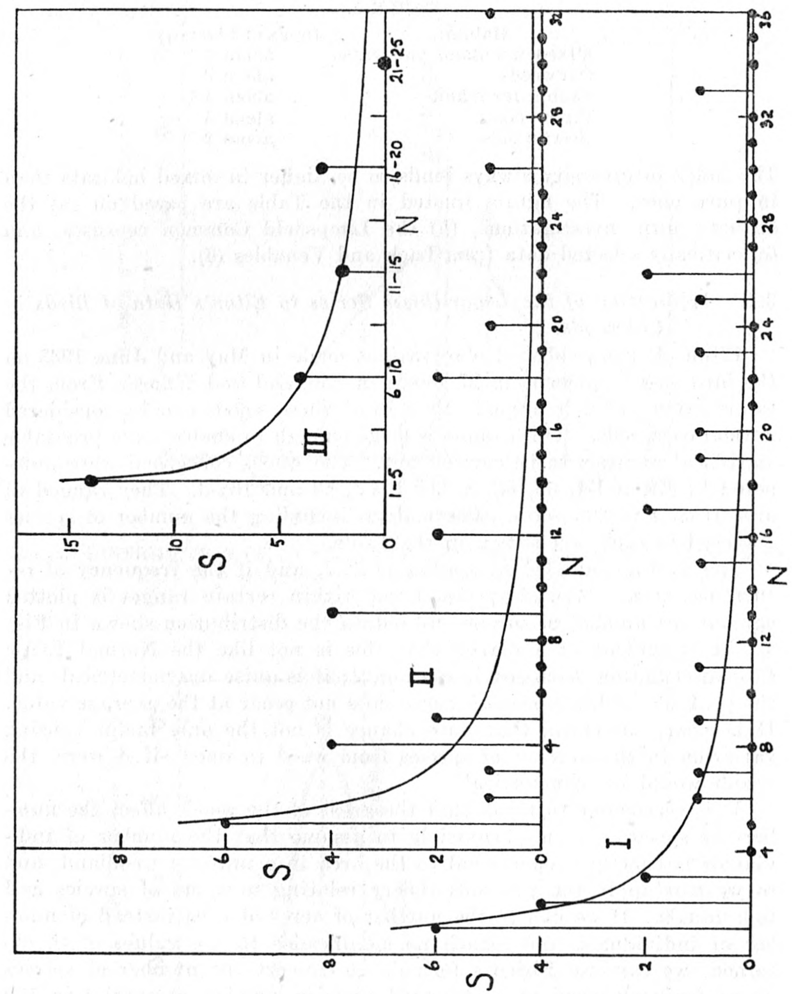


Fig. 3. RELATION BETWEEN NUMBER OF SPECIES (S) AND NUMBER OF INDIVIDUAL BIRDS (N) AT LIMPSFIELD COMMON.

I—1938, Winter Census.
II—1939, Winter Census.
III—1939 (as II) but N grouped into blocks of 5.
Continuous curves calculated.
Dots are observed values.

TABLE I.

Habitat.	Index of Diversity.
Mixed woodland and grass	about 7
Oakwoods	about 6
Arable farmland	about 4-5
Pinewoods	about 4
Beechwoods	about 3

The index of diversity always tends to be higher in mixed habitats than in pure ones. The figures quoted in the Table are based on (a) the author's own investigations, (b) the Limpsfield Common censuses, and (c) critically selected data from Lack and Venables (6).

3.4. *Application of the Logarithmic Series to Elton's Data of Birds in Oakwoods.*

Elton (4) has published observations made in May and June 1933 on the bird species present in 27 woods in England and Wales. From the information given it appears that 16 of these woods can be considered normal oakwoods. This sample is large enough to enable some profitable statistical analysis to be carried out. The woods concerned were numbered by Elton 1-4, 5b, 6a, 8, 9a, 10a-c, 13 and 16a-d. They ranged in area from 1 to 200 acres. Particulars, including the number of species observed in each, are shown in the Table.

The average number of species is 22.7, and if the frequency of occurrence of numbers of species lying within certain ranges is plotted against the number of species, we obtain the distribution shown in Fig. 4. It is evident at a glance that this is not like the Normal Error Law distribution discussed in Section 2; it is quite unsymmetrical, and the peak of the likely smooth curve does not occur at the average value. It is clear, therefore, that pure chance is not the only factor causing variation in the number of species from wood to wood—if it were, the graph would be symmetrical.

It is reasonable to think that the areas of the woods affect the numbers of species. It is permissible to assume that the number of individuals is exactly proportional to the area in a uniform woodland, and so we can apply the previous theory relating numbers of species and individuals. If we call N the number of acres of area instead of number of individuals, and attach no significance to the values of α obtained, we can use Fisher's formula to convert the number of species given for each wood to a standard basis of number of species in 100 acres. This has been done: the corrected numbers of species are shown in the last column of the Table, and the frequency distribution (or frequency of occurrence of certain groups of values) is shown in Fig. 5. It will be seen that this distribution is reasonably symmetrical. If we try to fit this to a Normal Distribution, we calculate that the standard deviation of the figures is 12.4, on an average number of species of 31.8 in 100 acres of woodland. This Normal Error Law distribution is plotted as a dotted curve in Fig. 5, and it will be seen that the agreement with observed (and corrected) values is good, considering that the observed frequencies must be whole numbers and, in view of the small sample,

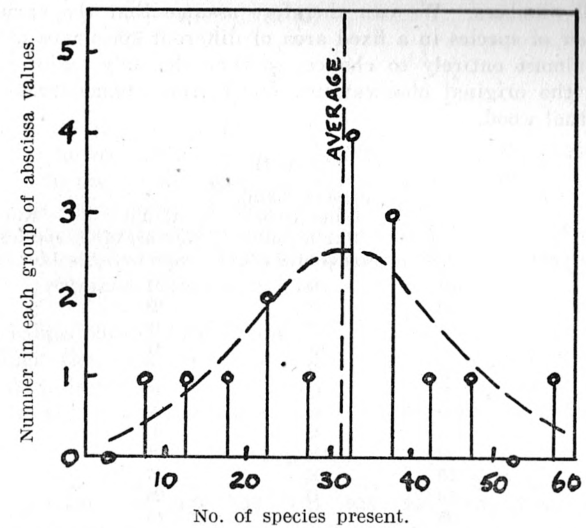


Fig. 4. DISTRIBUTION OF NUMBERS OF SPECIES AS OBSERVED. (The curve is a likely smooth curve through points.)

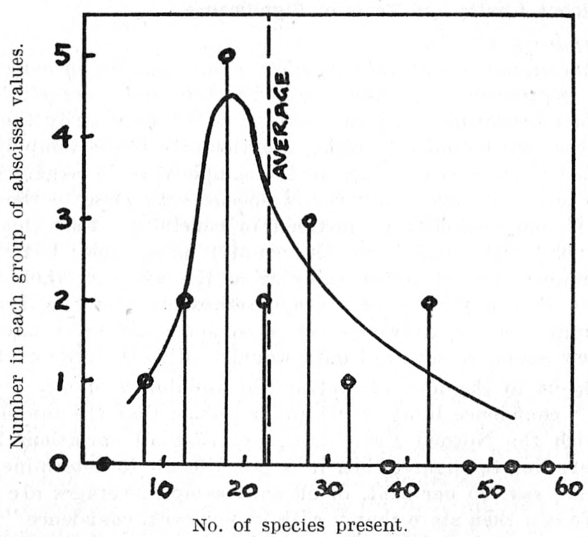


Fig. 5. DISTRIBUTION OF NUMBERS OF SPECIES AFTER CORRECTION TO A STANDARD 100 ACRES. (The dotted curve is the Normal Error Law corresponding to the mean of 31.8 and standard deviation 12.4.)

also small numbers. We can therefore assume that the variations in the number of species in a fixed area of different specimens of oakwood are due almost entirely to chance, so that the only major factor influencing the original observations, apart from chance, was the area of the actual wood.

TABLE II.

Wood (Elton's Number).	Area (Acres).	Preserved and Quiet (Q) or Public and Frequented (F).	Actual Number of Species.	Number of species corrected for 100 acres.
1	108	Q	41	40
2	102	F	28	28
3	40	F	13	15
4	30	F	17	22
5b	20	F	7	9
6a	2	Q	16	32
8	200	Q	26	23
9a	4	Q	20	34
10a	86	F	31	32
10b	100	F	17	17
10c	30	Q	25	33
13	35	Q	44	57
16a	4	Q	21	36
16b	1	Q	15	37
16c	1	—	17	44
16d	3	F	26	50
Average	...	... ...	... ... 22.7	31.8

4. Confidence Limits and Tests of Significance.

4.1. *Confidence Limits.*

In determining the average number of bird species in oakwoods, for example, as previously discussed, we had to take the average of a sample number of observations, and the average is not necessarily the same as the true average for *all* oakwoods. Particularly if the sample is small, the possible error in the average of the sample may be large. If all the oakwoods observed gave a number of species very close to the average, then we should obviously be justified in concluding that this average was probably fairly reliable for the country as a whole; but if the observed numbers varied considerably from the average, then we could hardly say that the observed average represented very accurately the true average, because oakwoods varied so much among themselves that only a very extensive series of data would lead to the true average.

This leads to the idea of stating the reliability of any average in terms of "confidence limits." If we can show that the sample is consistent with the Normal Error Law, i.e. that all variations from the average are due to chance, then it is not difficult to determine between what limits, say, 95 per cent. of all such sample averages are likely to come. We can then state that "with 95 per cent. confidence" the true average lies somewhere between A and B, where A and B are the limits just determined. This process is more fully explained in other works (1c). The formula used is

$$\bar{X} = \bar{x} \pm \frac{s}{\sqrt{N-1}}\, t \quad \ldots\ldots\ldots\ldots (5)$$

where $\bar{X}$ is the true average,

$\bar{x}$ is the average of the sample,

s is the root-mean-square of the deviations of the various items in the sample from the average of the sample.

N is the number of items in the sample.

t is a quantity dependent on N and on the degree of confidence desired. For various confidences and N values it can be obtained from tables (1c).

The two values obtained by taking the + or − sign are the limits between which the true average will lie with the degree of confidence stated. Any degree can be used, but it is usual to take 95 per cent. For 95 per cent. confidence, the values of t are related to N thus

TABLE III.

N	2	3	4	5	6	7	8	9	10	15	20	30
t	12.71	4.30	3.18	2.78	2.57	2.45	2.37	2.31	2.26	2.145	2.093	2.045

This can be applied to Elton's data on birds in oakwoods after the correction for area has been made, because then, as shown earlier, the distribution of the numbers of species does follow the Normal Error Law. Taking the figures shown in Table II, we find that the average number of species, $\bar{x}$, in 100 acres is 31.8, and the root-mean-square deviation, s, is 12.4. As there are 16 woods considered, $N=16$, and for 95 per cent. confidence limits, we see that $t=2.13$. Thus, from the formula, the true average of all oakwoods, $\bar{X}$, is 31.8 ± 6.8; or we can say, with 95 per cent. confidence, the true average lies between 25 and 38.6. These limits obviously apply only to the period (May and June 1933) when the observations were made, and to the region (the southern part of England and Wales) covered by the sample observations. It will be seen that these limits are rather wide ones, and that the data, which looked so promising, are really inadequate to give us a firm value for the true average. This is an example of how a statistical analysis can show up the weakness of data.

4.2. *Tests of Significance.*

A problem of common occurrence in ecological work is concerned with whether or not there is any significant difference between two sets of results obtained from different samples. For example, in Elton's data on birds in oakwoods the description of the woods is complete enough to enable us to label 7 of them as frequented by the public and 8 as unfrequented. Thus we can divide the data into two; one sample of 7 represents frequented woods and the other sample of 8 represents unfrequented woods. The numbers of species (corrected to the 100-acre standard) in the two samples are as follows:—

Frequented:—28, 15, 22, 9, 32, 17, 50. Average 24.7.
Unfrequented:—40, 32, 23, 34, 33, 57, 36, 37. Average 36.5.

On the face of things it appears that when the woods are frequented the number of species is very considerably reduced. But one unfrequented wood has fewer species than the average for the frequented woods, and one frequented wood has more species than the average for the unfrequented woods. This should sound a note of warning, even on common-sense reasoning.

If we apply confidence limits to these averages, as described before, we find that, with 95 per cent. confidence, the average for all frequented woods lies between 12.1 and 37.3, and the average for all unfrequented woods lies between 28.5 and 44.5. These ranges overlap. So the problem is: with what confidence can we state that public access reduces the number of species? Here we must use what is termed " a test of significance " of the difference between the averages. The actual test used is called the " Two-mean t test " (1b). It is really the reverse of the confidence-limit calculation; this time we do not state the probability factor, but instead wish to determine it.

Calculate first

$$t = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\left(\frac{N_1+N_2}{N_1+N_2-2}\right)\left(\frac{N_1s_1^2+N_2s_2^2}{N_1N_2}\right)}} \quad \ldots\ldots\ldots\ldots\ldots\ldots \ (6)$$

where the symbols mean the same as before, except that subscripts 1 and 2 are used to distinguish the values for the two samples. There is no need to calculate s_1 and s_2, however, in this case; $N_1s_1^2$ and $N_2s_2^2$ are merely the sum of the squares of the deviations in each sample.

The value of t thus determined has a probability value associated with it, depending on the value of N, where we now take $N=N_1+N_2-1$. This probability (which is the probability that the difference between averages is due only to pure chance), can be determined from tables (1c), or by means of a special chart (1b). If we only wish to know whether the probability is greater or less than 5 per cent. (which corresponds to 95 per cent. confidence), then we can use Table III. If the t value calculated is less than the value given for the correct value of N, then the difference between the means is probably due only to chance, but if it is greater then the difference is " significant."

Returning to the example of frequented and unfrequented oakwoods, we have

$\bar{x}_1=24.7$	$\bar{x}_2=36.5$	
$N_1=7$	$N_2=8$	$N=14$
$N_1s_1^2=1111$	$N_2s_2^2=652$	

This gives $t=1.96$. (We can ignore the fact that the formula gives this a minus sign.)

Referring to Table III, we see that this value is below that corresponding to 5 per cent. probability. So, in spite of the large difference between averages, the result might be due to chance! The exact value of the probability corresponding to $t=1.96$ is $7\frac{1}{2}$ per cent. We can state the result thus:—With $92\frac{1}{2}$ per cent. confidence the number of species is reduced when the wood is frequented.

5. Conclusions.

An attempt has been made to show the usefulness of some simple statistical processes in analysing ecological data, and the examples taken have all referred to bird populations. The main object of the mathematical approach is to ensure that only the right conclusions are drawn from a particular set of data; and if in many cases the results obtained seem perhaps a little too obvious to justify the amount of mathematical work used in the analysis, then the reader must be careful to appreciate that this may be because (a) simple examples were chosen, or (b) what seems obvious after analysis is not always obvious before. It is only too easy to make wrong conclusions from data by relying on what seems obvious—a fact well known by politicians and advertisers—and the application of the normal-error law, confidence limits and tests of significance is intended to mitigate or even eliminate this danger.

A brief account of a new technique—the logarithmic series and the index of diversity—has been given as it is thought that this has considerable possibilities in amateur ecological work, especially in ornithology, where the mobility of the populations makes complicated comparisons unreliable.

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