

# THE COMMONNESS, AND RARITY, OF SPECIES

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## SECTION I. GENERAL

The purpose of this paper is to deduce, from a number of examples and from theoretical considerations, some plausible general law as to how abundance or commonness is distributed among species. Experimentally, this could be done by making a complete *census* of every species, but, with rare exceptions, this procedure is quite impractical. We therefore attempt to deduce the "universe" from a sample.

Commonness, as understood by ecologists, has several rather different meanings: we are here concerned with (1) the total number of living individuals of a given species, which might be called its global abundance, (2) the total number of individuals living at any instant on a given area, such as on an acre or a square mile, which might be called its local abundance, (3) the ratio which the number of individuals of one species bears to that of another species, i.e., its relative abundance, and (4) the number of individuals observed, for example, the number of a moth species counted in a sample from a light trap, its "observed," "apparent," or "sample" abundance. There will not usually be any difficulty in deciding which phase of the subject is under discussion at any time. The Raunkiaer "Index of Frequency" is a measure of ubiquity rather than of commonness as above defined: its relation to our other concepts is discussed later.

As a rule, we are interested in a sample only in so far as it throws light upon the "universe" that is being sampled. The sample will be a sufficiently accurate replica of the universe provided (1) it is a perfectly "random" sample, and (2) no species is represented in the sample by less than 20 or 30 individuals.

In most ecological work condition (2)

will never obtain, and much of the present paper will center on this difficulty. Condition (1) will not usually obtain in the broadest sense, and needs a moment's consideration.

A geologist sampling an ore-body, whose boundaries have been delimited accurately by previous exploration, has a known "universe" and merely needs information on composition. His universe is permanent. But in ecological work, the "universe" changes rapidly. The moths flying tonight are not those that flew a month ago, or will fly a month hence. Those flying this year are a vastly different association from those that flew last year in the same area. The same thing is true of rodent populations, of birds, and of plants. We are dealing with a fleeting and fluctuating assemblage, a "universe" continually expanding, contracting, and changing in composition. Thus it is important to recognize at the outset that, for the purposes of our present investigation, the "universe" from which the sample is drawn is that universe declared to us by the sample itself, and not our preconceived notion of what the universe ought to be.

Further, it is important to recognize that the randomness we seek is merely randomness *with respect to commonness or rarity*. A light trap is satisfactory in this respect and samples its own universe appropriately. It is definitely *selective* in respect of phototropism, but it is *random* in respect of commonness, i.e., it does not care which of two moths, equally phototropic, it catches, though one may be a great rarity and the other of a very common species. On the other hand, an entomologist, or even an intelligent boy, with a net, is not a satisfactory collector, for he will go after the rarity. For this reason we have to reject Corbet's ('41)

collection of Malayan butterflies, as not being a *random* sample.

*Previous discussions.* In the early years of the present century an extensive literature accumulated in connection with Raunkiaer's Law of Frequency. This was apparently intended as an index of commonness or rarity, more particularly in plant associations but not necessarily confined thereto, and, subject to some assumptions, it is a measure of commonness or rarity. The method of expressing the results, though it appears simple, is in reality very inconvenient, and gives no direct clue to the nature of the universe being sampled.

An analysis of Raunkiaer's findings must be postponed, in the present paper, until after we have established the relationship between sample and universe.

More recently Williams ('43) and his collaborators have taken up the subject from a different point of view.

Williams was struck by the fact that in a "random" collection of butterflies or moths there were usually great numbers of species represented by a single specimen (hereinafter called "singletons"), a much less number of species represented by two specimens ("doubletons") and still fewer species represented by three, four, and so on. He noticed further than if  $N$  be the number of species represented by singletons, the number represented by doubletons was  $N/2$ , the number represented by three was  $N/3$  and so on.

Hence in the collection, if the observation were valid indefinitely, we should have a series

$$N \left( 1 + \frac{1}{2} + \frac{1}{3} + \frac{1}{4} + \frac{1}{5} + \dots \right)$$

as the number of species represented by

1    2    3    4    5    ...

specimens.

This is a harmonic series, and it has the grave theoretical disadvantage that the sum of its terms is infinite, calling for an infinite number of *species* in the collection. As if that were not bad enough, the number of *specimens* is of the order of infinity to the second power.

Williams, aware of these difficulties, apparently sought the help of Fisher ('43) who introduced an arbitrary modifying term into the series, so that it was no longer strictly harmonic, and both species and specimens were reduced to finite numbers. The degree of agreement thereby produced may be judged from the group of papers by Corbet, Williams and Fisher ('43). Even on the collections on which it was tested it does not work too well, and Corbet, in an earlier paper ('41), was aware that as collecting continued, it would represent the facts increasingly poorly.

*Method of graphing.* It has often been a matter of comment by ecologists that one or two species are extraordinarily abundant at a particular time and place: all others seem rare in comparison. Thus in Seamans' moths of Alberta, discussed later, out of a total of 303,251 specimens, 91,502 belonged to a single species; while in Dr. King's moths of Saskatchewan, 38 species accounted for 77,260 specimens, and 237 more accounted for only 9,850 additional individuals.

Under these circumstances it would be logical, merely as a matter of convenience, to try plotting commonness (number of individuals per species) on a logarithmic base. But there is a more cogent basis for so doing. Commonness is a *relative* matter. One species, we say, is twice as common as another, and a natural series of groups representing commonness would run:

Species group	A	B	C	D	E	F	G	H	I	J	etc.
Approximate specimens observed of that species	1	2	4	8	16	32	64	128	256	512	etc.

These groups are a sequence of *octaves* of frequency. It is the most natural grouping possible, but our ultimate justification for adopting it is not its naturalness, but the fact that it works. It is a geometric, or logarithmic series, and this paper produces evidence that commonness of species appears to be a simple Gaussian curve on a geometric base (i.e. "lognormal" curve). The intervals of an octave turn out to be a convenient size of interval, as well as the most readily grasped ones.\*

*Boundaries of the octaves.* An octave is simply an interval of two-to-one. On the piano it may be from C to C' or G to G': similarly in our ecological studies, it is the interval 4-to-8 or 6-to-12. We might choose the numbers 1, 2, 4, 8, etc., as the mid-points of our octaves, but it is more convenient to choose them as the end-points, or boundaries between octaves. Thus denoting the octave 1 to 2 as A, and so on, we have octave D comprising the interval whose boundaries are 8 and 16.

Thus if a given species is represented by 9, 10, 11, 12, 13, 14 or 15 specimens, it clearly falls in octave D. All species falling in octave D may be thought of as having roughly the same degree of commonness, in comparison with those falling for instance in octave J, which are represented by from 513 to 1023 specimens.

If a species is represented by 8 specimens, octave D is credited with half a species, and octave C is credited with the other half. Similarly a species with 16 specimens is credited half to D and half to E. Octave B is comprised of all species having 3 specimens in the sample, plus half the species having 2 and half the species having 4. Octave A is composed of half the species represented by singletons, and half those represented by dou-

bletons. Half the singletons have to be assigned to octaves below A, which we designate by Greek letters and discuss later.

*Procedure.* We obtain a sample (say a catch of moths in a light trap), and make a complete tally of the relevant material (e.g., macrolepidoptera, noctuids, all lepidoptera, or all insects), determining the "representation" (number of individuals) of each species. This assigns the species to its appropriate octave of frequency. We count the number of species in each octave. This is the ordinate of our curve, and the abscissa is a scale of octaves of increasing commonness.

The experimental points thus obtained might, as the reader will doubtless observe, be "graduated" quite well as a Poisson distribution. Indeed, it is possible that that might be the most formal approach, and in the long run the most accurate. However, experience shows that an ordinary Gaussian curve (the "normal curve of errors"  $y = e^{-(ax^2)}$ ) is very satisfactory also, provided the curve is "decapitated" at the veil line as discussed later. The use of this curve has special advantages. Singleton ('44) has worked out a method of fitting a decapitated Gaussian curve in accordance with the principle of Maximum Likelihood: this method was used by Dr. J. L. Glathart (of the Preston Laboratories) to graduate many of the curves we have used. Others are graduated by a graphical method of our own. Both give comparable results, and the methods, for lack of space, will not be discussed in the present paper.

#### *Relation between Williams' harmonic series and the octave plot*

If Williams' unmodified law were true, viz. that if there are N species represented by one specimen each, there will be  $N/2$  represented by two specimens, and so on, we could calculate how many species would fall in each of our octaves. It comes out as follows:

\* The above procedure is equivalent to taking the ordinary logarithms of the number of specimens per species and grouping the species into the groups whose logarithms extend over an interval of 0.3010 i.e., such groups as 0-0.3010, 0.3010-0.6021, 0.6021-0.9031, etc.

Octave	Number of species in that octave
A (1-2)	0.7500 $N$
B (2-4)	0.7083 $N$
C (4-8)	0.6971 $N$
D (8-16)	0.6941 $N$
E (16-32)	0.6934 $N$
F (32-64)	0.6932 $N$
G (64-128)	0.6932 $N$

All subsequent octaves have approximately  $0.6931 N$ , where  $0.6931 = \log_e 2$ . Except for the first two octaves, the number of species in each octave would be constant to within one per cent. The data are graphed in figure 1.

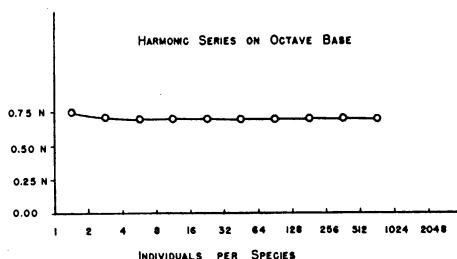


FIG. 1. The harmonic series on an octave base. If the commonness of species followed the (unmodified) Williams' law, then the number of species in each octave would be essentially constant.

Experimental evidence shows that this state of affairs is far from the truth. Theoretical considerations also require its categorical rejection. There are an infinite number of octaves to the right, and if they were all equally filled with species, there would be an infinite number of them, and excessively common species would be as numerous as very moderately common ones, which we know is not the case. Therefore the curve must descend to the right. Williams himself recognizes this, and this is the basis of Fisher's modification of the Harmonic Series Law, which modification produces a descent to the right.

But as will appear later, the real curve also descends to the left. It is a humped curve. This requires a totally different approach.

We are now ready to consider the experimental evidence.

## SECTION II. EXAMPLES

We have one or two examples of bird-counts that meet our essential requirements, and four or five of moths in light traps. Most counts do not meet our requirements, but some throw light on the central problem and seem to extend our findings to other biological universes.

### I. Saunders ('36). *The birds of Quaker Run Valley, western New York State*

Saunders attempted a complete census of the breeding birds on a tract of 16,967 acres. His main reliance was upon a count of singing males, aided by a few auxiliary methods.

Table I-A below is the number of breeding pairs of each species, from commonest to rarest, in the order in which Saunders reported them, but with the names of the species omitted.

Table I-B condenses this information ready for graphing, and the plot is given in Fig. 2.\*

The total number of species here reported is 80, but Saunders states:

"At the present date 141 species of birds are known to occur in Allegany Park and its vicinity during the months of July and August. Of these birds, 27 occur as fall migrants or late summer wanderers. Thirteen breed outside the park itself, but evidently in the near vicinity. Eleven more breed in the park but not, so far as is known, in the Quaker Run Valley. The remaining 90 occur in their breeding season and undoubtedly breed or have bred in the Quaker Run Valley in the past 12 years. Of these 90 species, 11 are irregular in their occurrence and have not been found every year. The remaining 79 are regular breeders and, judging by past experience, can be expected to breed in the area every year."

In the graph (fig. 2) the curve drawn is a Gaussian curve, with its mode (crest) at  $i = 30$  specimens (breeding pairs) per species, that is, near the end of the 16-32 octave: the general equation of such a curve is

$$n = n_0 e^{-(aR)^2},$$

\* The Veil Line shown in this and other graphs will be discussed later.

## Birds of Quaker Run Valley

TABLE I-A. Values of  $i$  (specimens per species)

1670	1656	1196	868	723	723	675	506	477	389	367
324	311	310	288	282	280	270	220	188	181	179
161	160	158	152	138	111	109	91	90	88	79
60	57	56	50	46	46	43	43	35	34	33
32	32	30	28	28	26	24	23	22	17	15
14	12	10	10	10	10	8	8	7	6	
6	5	5	4	4	4	3	3	3	3	
2	1	1	?	?	?	?	?	?	?	
?	?	?								

TABLE I-B. Values of  $n$  (species per octave)

Octave	<1	1 to 2	2 to 4	4 to 8	8 to 16	16 to 32	32 to 64	64 to 128	128 to 256	256 to 512	512 to 1024	1024 to 2048
Species per octave	>1	1½	6½	8	9	9	12	6	9	11	4	3

where  $n_0$  is the number of species in the modal octave,  $n$  is the number in an octave distant  $R$  octaves from the mode, and  $a$  is a constant to be calculated from the experimental evidence.

In this particular case

$$n = 10e^{-(0.194R)^2}.$$

The curve theoretically extends to infinity, asymptotic to the  $x$ -axis, both to left and right. The area "under" the curve (between curve and  $x$ -axis) from minus infinity to plus infinity, is theoretically the *universe being sampled*, i.e. the total number of species theoretically available for observation.

$$N = \int_{-\infty}^{+\infty} n dR = n_0 \sqrt{\pi}/a,$$

where  $\pi = 3.1416$  and  $\sqrt{\pi} = 1.77$ . Putting  $n_0 = 10$  and  $a = 0.194$  we get  $N = 91$ , which agrees very closely with Saunders' own estimate (quoted above) of what it is.

## II. Preston and Norris ('47). Breeding birds of the Frith (Preston Laboratory Grounds)

From table II of the paper by these authors, we may obtain data of the total pairs of breeding birds, and the total number of "expected" nests (remembering that some species make more nests than one, even if successful with the first, and most species make a second nest if the first is unsuccessful). The count for the combined years 1944 and 1945 gives:

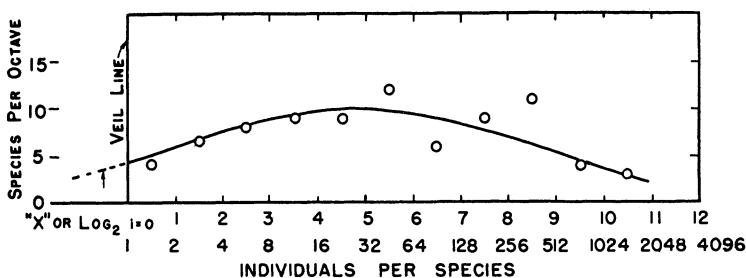


FIG. 2. Saunders' breeding birds. The octaves are definitely not equally filled, and the curve looks as if it is humped up in the middle.

Octave <i>i</i>	— <1	A 1-2	B 2-4	C 4-8	D 8-16	E 16-32	F 32-64	G 64-128	H 128-256	I 256-512
Species ( <i>n</i> ) Nests	>3½	5	6½	10	7	5	4	4	2	0
Species ( <i>n</i> ) Bird-Pairs	>5	6	7	11½	8½	4	7	1	0	0

TABLE II. Values of *n* (species per octave)

Octave	<1	1 to 2	2 to 4	4 to 8	8 to 16	16 to 32	32 to 64	64 to 128	128 to 256	256 to 512	512 to 1024	1024 to 2048	2048 to 4096	4096 to 8192	8192 to 16384
Species per octave	>19	37	42	49½	45½	42	28½	26½	30	14	9	2	0	2	2

These results are not graphed, as only a few hundred bird-pairs and nests were involved, and statistically this is hardly sufficient. So far as the data go, however, they support a humped distribution with its crest in octave C, both for birds and for nests.

### III. Dirks ('37). Moths in a light trap at Orono, Maine

Dirks operated a light trap over a period of four years (1931-34). Exclusive of microlepidoptera he caught 56,131 specimens. These he classified as to species and sex, and gives three tabulations: total moths, female moths, gravid female moths. Since most females were gravid, the third tabulation closely resembles the second and will not concern us here.

Condensing his tabulation for total moths produces table II.

This is graphed in figure 3. The first number (for the octave less than 1) is indicated by an upward pointing arrow, meaning that the true number for this range is above the tip of the arrow, a point to which we shall return later. The other points are plotted as circles. The smoothed curve drawn through the points appears to have its crest at about 7 or 8 specimens per species. The left-hand end of the curve is, of course, quite incomplete. It represents the rarer species which were absent from the catch. The general shape of the curve, however, appears clear enough, and we may assume that it is approximately a "normal" probability curve with its mode at, or very near, 8 specimens per species.

The equation of the curve is  $n = 48e^{-(0.207R)^2}$ , and on this basis the total number of species in the universe being

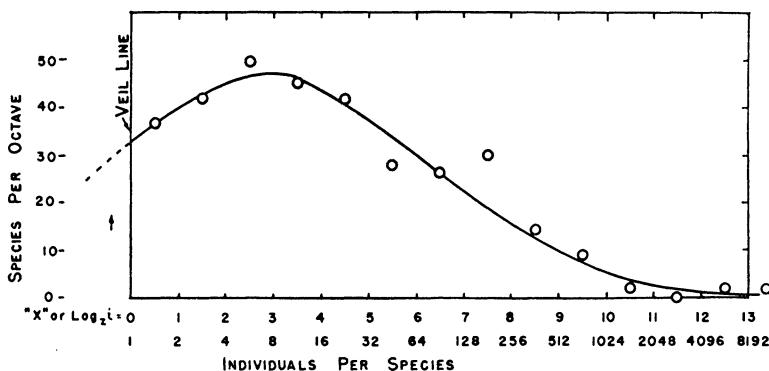


FIG. 3. Dirks' moths of Orono, Maine. The octaves are not equally filled; the curve is humped; we see the right-hand tail, but the left-hand one is hidden behind a veil.

sampled is

$$48 \sqrt{\pi}/(0.207) = 410 \text{ species}$$

approximately.

Dirks actually obtained 349 species, so his sample represents about 85% of the species that were theoretically available at Orono, during the four years in question, for trapping by means of such a light trap as he used.

#### IV. Dirks ('37). Female moths in a light trap at Orono, Maine

The condensed statement of results follows:

TABLE III. Values of  $n$  (species per octave)

Octave	<1	1 to 2	2 to 4	4 to 8	8 to 16	16 to 32	32 to 64	64 to 128	128 to 256	256 to 512	512 to 1024	1024 to 2048	2048 to 4096	4096 to 8192
Species per octave	>27½	42	39½	27½	28	23	19½	9	4	4	0	0	1	1

This is graphed in figure 4, whose mode is at or near  $1\frac{1}{2}$  specimens per species, and equation is

$$n = 42e^{-(0.205R)^2}.$$

On this basis, the available universe comprised 363 species, of which 226 were represented in the sample, in the form of 12,799 individuals. Females in Dirks' sample were only 22.8% of the total, which probably means, not that they were rarer in the outer world, but that they were travelling less than the males. Dirks obtained a sample of 85% of the "total" species (410) in the total universe, but only 62% of the females ( $226/363 = 62\%$ ) which constituted a smaller universe (363 species as against 410).

#### V. Williams ('43). Moths in a light trap at Rothamsted, England

The condensed tabulation is:

TABLE IV. Values of  $n$  (species per octave)

Octave	<1	1 to 2	2 to 4	4 to 8	8 to 16	16 to 32	32 to 64	64 to 128	128 to 256	256 to 512	512 to 1024	1024 to 2048	2048 to 4096
Species per octave	>17½	23	27½	36	27½	33	31	13½	19	5	6	0	1

The corresponding graph is given in figure 5. Its mode is at about 8 specimens per species and its equation is

$$n = 35e^{-(0.227R)^2}.$$

The total population being sampled is  $N = 35 \sqrt{\pi}/(0.227) = 273$  species. Williams actually trapped, in the four years covered by his report, 240 species, involving 15,609 specimens (macrolepidoptera).

Williams comments that the total Hertfordshire fauna (of this type of lepidoptera) amounts to 461 species, and tries to figure how long it would take to catch

examples of all of them. But if our present theory is valid, the "universe" he was sampling was not the whole Hertfordshire fauna, but a local population comprising about 60% of the Hertfordshire total. This may be compared with the experience of Dirks, who was sampling not the fauna of Maine, but a local population near Orono.

#### VI. King (unpublished). Moths in a light trap at Saskatoon, Saskatchewan

This is a collection of macrolepidoptera, numbering 87,110 individuals, 277 species, caught in Dr. King's "Trap A," over a period of 22 years, from 1923 to 1944 inclusive.

The data are graphed in figure 6, and the curve, calculated by Singleton's method, has its mode at 4 specimens per species and the equation

$$n = 33.0e^{-(0.152R)^2}.$$

TABLE IV. Values of  $n$  (species per octave)

Octave	<1	1 to 2	2 to 4	4 to 8	8 to 16	16 to 32	32 to 64	64 to 128	128 to 256	256 to 512	512 to 1024	1024 to 2048	2048 to 4096
Species per octave	>17½	23	27½	36	27½	33	31	13½	19	5	6	0	1

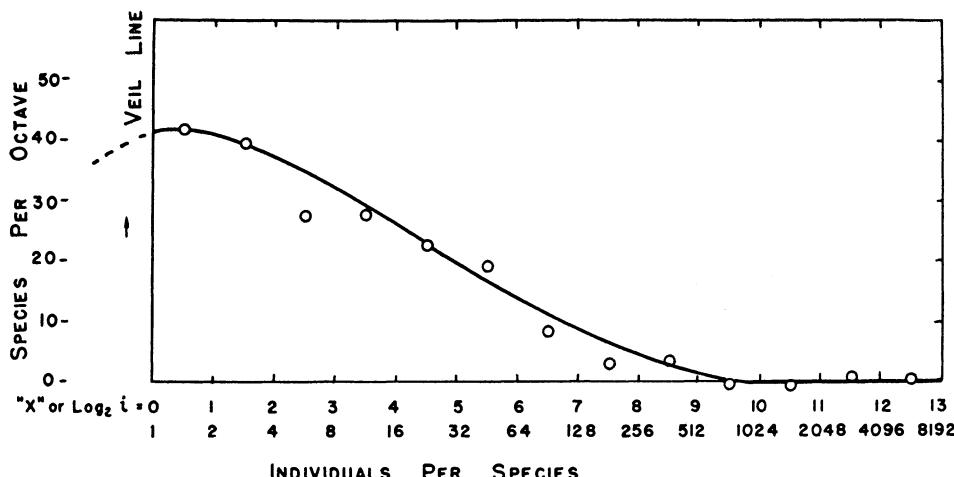


FIG. 4. Dirks' female moths. The hump seems to be very close to the veil. In Sweadner's moths of Wyoming (not illustrated), the veil has moved to the right of the hump, and all we see is the descending side.

The "universe" accordingly comprises 384 species, and since Dr. King caught 277, his trapping is seemingly 72% complete.

It may seem strange that after 22 years the collection should be so incomplete, when 4 years of trapping at other places yield values over 80%. But it must be remembered that what is being sampled during the 22 years is a 22-year universe, not a 4-year universe, and that the moths available for trapping, in Saskatoon at any rate, vary enormously from year to

year. This will be dealt with, briefly, in the later discussion.

Since we have Dr. King's data year by year, it is quite possible to make up subsamples and plot the results year by year or quadrennium by quadrennium. The curves retain their general shape, though the height at the mode tends to fall to about 24 species per octave instead of the 33 species per octave in the 22-year aggregate. This alone, of course, shows a likelihood that we are dealing with a vastly more extensive universe if we trap

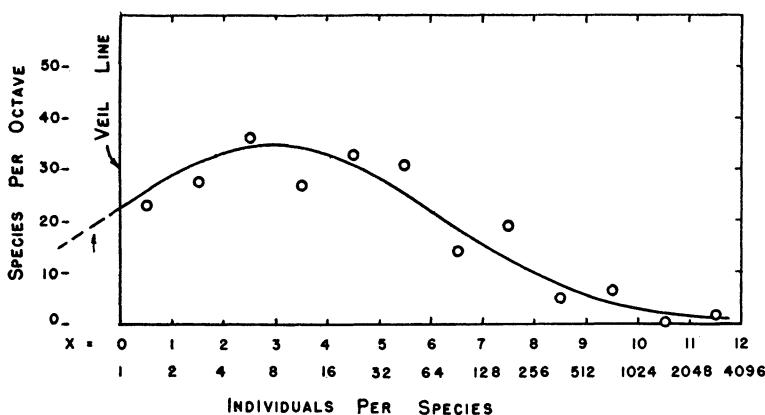


FIG. 5. Williams' moths. This resembles figure 3.

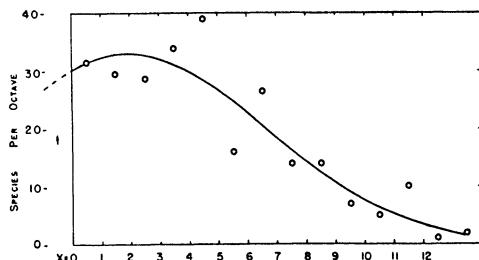


FIG. 6. King's moths of Saskatoon.

for a longer period—at any rate at Saskatoon.

#### VII. Seamans (*unpublished*). Moths in a light trap at Lethbridge, Alberta

Seamans' records cover the period 1921–43 inclusive, with the exception of the year 1938, when the collections were damaged by mice before they could be catalogued. The number of specimens is 303,251; of species, 291. This is the most extensive collection at present available to me in a completely counted condition.

The graph is given in figure 7: its mode is at about 32 specimens per species, and its equation

$$n = 30.0e^{-(0.160R)^2}.$$

The theoretical universe is accordingly 332 species and the collection is about 88% complete.

With the Lethbridge data, as with those of Saskatoon, it is possible to make up samples for individual years, or for quadrennia. For individual years the modal octave tends to hold about 20 species per octave: for quadrennia it averages about

25: for the 22 years, about 30, but the general shape is very similar. The graphs are accordingly not reproduced here.

These few examples show what the experimental plottings look like, and the degree of fit between the Gaussian curve and the data. In all these examples we have a sample with more than half the universe represented, i.e., the crest of the curve is in sight. Fragmentary collections are available where the crest has not been reached, and probably Raunkiaer's collections (discussed later) were of this type.

With the aid of these actual examples,\* thus very briefly presented, we now pass to a discussion of the general principles, the veil line, the relation between sample and universe, and some deductions about the nature of biological universes in general.

### SECTION III. DISCUSSION

#### *The veil line*

If the universe contains species so rare that the sample, if perfectly proportioned to that universe, should theoretically contain only a fraction of a specimen, it is most likely that the species will be unrepresented in the collection. It cannot be represented by less than one whole specimen, and by definition this would be

\* Hinton ('40) gives data on a collection of adult Mexican water-beetles, and some others. This graduates very well as a decapitated Gaussian curve. The internal evidence suggests it was a random collection, but since Hinton gives no comment on that point, discussion is omitted in the present paper.

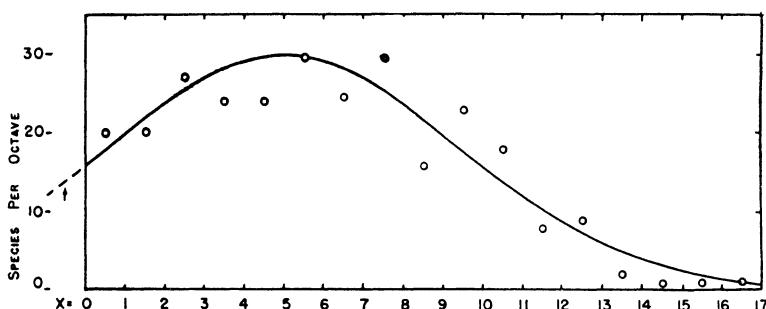


FIG. 7. Seaman's moths of Lethbridge.

over-representation. Some species indeed will achieve this over-representation, just as some species which "ought" to be represented by 1, 2, 3 or even more specimens, may fail of representation. But on the average, those relatively uncommon species whose theoretical representation is appreciably less than one specimen, will be missing from the sample. These species may themselves be of very different degrees of rarity; some "ought" to be represented perhaps by half a specimen, others by 1/20 or 1/200 of a specimen. In other words, they belong to different octaves, but these octaves are all "missing" in the sample.

There is therefore a veil line at the left end of octave A, at a representation of one specimen. The sample indicates clearly what the universe is like to the right of the veil, but we have to infer what it is like to the left of it.

Now doubling the size of the sample, other things being equal, doubles the number of individuals of each of the commoner species, in the sample. This is equivalent to moving every species one octave to the right, which in turn is equivalent to withdrawing one more octave from under the veil. The process can be repeated until the whole universe, in effect, is exposed. Thus the graph of the universe is identical with the graph of the sample, except that it is not decapitated by a veil line. The graph in fact behaves as if it were drawn complete upon a movable card, and the card slipped with its left-hand end under a veil. Continued sampling, if the universe remains constant, merely withdraws the card progressively from under that veil.

If this last statement is true, it is a very valuable property of our method of representing our results. It will be obvious to all, that it is quite accurately true for those species which, in the sample, are represented by at least a score or two of specimens. These species will be present in the sample in virtually the exact proportion in which they are present in the universe. It will not be obvious that it

will be true of those species whose representation in the sample is small, so that, by the laws of small samples, they have a good chance of being substantially over- or under-represented.

The next page or two, on the Relation between Sample and Universe, show that though any one of the less common species may very well get into the wrong octave, the probability is that every octave has very nearly the correct number of species. This is what we graph, and therefore our graph is not appreciably affected by the interchange of species among the octaves close to the veil line.

In other words, the "shape" of our universe is constant. If however we want to know the exact status of a specified species in that universe, we cannot be sure of it until the sample contains a dozen or two specimens.

#### *Relation of sample to "universe"*

Consider any universe, Gaussian or otherwise, made up of at least several hundred species, and fix attention on any one species, say a melanic, which is not one of the very common ones. Then the numbers of individuals of this species must be less than one in a thousand compared with the non-melanics. Suppose for the moment that it is one in ten thousand.

If we catch, at random, a single specimen from our universe, we have one chance in ten thousand that it is a melanic; and if we make a catch of 10,000 specimens, "perfect representation" would call for one melanic in the collection.

If we now released the specimens unharmed back into the universe, so as not to deplete it, we could make many random collections of 10,000 specimens, and when we tallied up the number of samples (collections) that showed zero, one, two, etc., melanics, we should find they conform to the several terms of the Poisson Series,

$$e^{-1} \left( 1 + \frac{1}{1!} + \frac{1}{2!} + \frac{1}{3!} + \dots \right)$$

probability for

0	1	2	3	...
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melanics.

Similarly if perfect representation calls for exactly two melanics in the collection, which would be the case if we collected 20,000 specimens all told, then the probability of our finding zero, one, two, three . . . specimens is given by the terms of the Poisson series

$$e^{-2} \left( 1 + \frac{2}{1!} + \frac{2^2}{2!} + \frac{2^3}{3!} + \text{etc.} \right).$$

More generally if perfect representation calls for " $p$ "\* melanics in the collection, our series is

$$e^{-p} \left( 1 + p + \frac{p^2}{2!} + \frac{p^3}{3!} + \frac{p^4}{4!} + \dots \right).$$

The terms of this series are easily calculated if  $p$  is small or fractional, but it is tedious if  $p$  is large, as the series then diverges at first and converges thereafter very slowly. Fortunately we do not need to use very high values of  $p$ .

What is true for melanics is of course true for any other sort of moth or species which is present to the same extent as the melanic. Thus if a hundred different species are present in identical proportions, and the sampling is carried to the point where we might expect exactly 3 specimens of each, we can tell how many of these species are in fact likely to be represented by 3 specimens, or by any other number.

Next let us suppose that, in the universe, the species in any octave of frequency are all concentrated at the midpoints of the octaves, so that if one species is present to the extent of 6 M where M is some large number—a million say—then there are a number of other species also present to the extent of 6 M, but none to the extent of 4 M, 5 M, 7 M, or 8 M. Similarly the species of the octave

\* " $p$ ," as used here, stands for "perfect representation," or "average expectation," more often denoted perhaps by  $c$ . It must not be confused with " $p$  for probability" in the classical binomial  $(p+q)^n$ .

2 M–4 M are all concentrated at 3 M; \* and so on.

Then we can so conduct our collecting that any species occurring in the universe ought to be present, with perfect sampling, to the extent of 3, 6, 12, 24, 48, 96, . . . individuals and not to the extent of any intermediate figure. Similarly the rarer species, if perfectly sampled, would contain fractions of specimens, and would be represented by  $1\frac{1}{2}$ ,  $\frac{3}{4}$ ,  $\frac{3}{8}$ ,  $\frac{3}{16}$ , . . . specimens.

Now in real collections, a species has to be represented by an integral number, or be absent; and the perfect sampling has to be replaced by the most probable sampling given by the Poisson series we have just been discussing. And what is true of fractional examples is equally true of the "perfect" integral numbers. A species that ought to be represented by exactly 3 specimens will, five times out of a hundred, have zero representation, and about one time in a thousand it will have as many as ten specimens to its credit. Otherwise expressed, if there are one thousand species (in a universe containing many thousands of species) which are entitled with *perfect* sampling to a representation of three individuals, then with *random* sampling fifty of these thousand species might very likely be unrepresented, while one species might well be present to the tune of ten specimens.

Perfect sampling can be accomplished only by a conscious agent: random sampling is what happens in the absence of conscious selection.

The whole story may now be reduced to a tabulation (table V).

In this table, the left-hand column gives the midpoints of 12 octaves, six behind the veil line and six out in the open. For instance  $p = 3$  represents the (arithmetical) midpoint of the octave 2–4. Suppose a given species is present in the

\* There may be some argument that the midpoint of the octave should be  $2\sqrt{2}$  M rather than 3 M, the geometric rather than the arithmetic mean: but the final numerical results will be nearly the same either way.

"universe" to such an extent that a perfect sample would contain exactly three specimens, that is, let the sampling be continued just long enough to justify an expectation of exactly three specimens of this species; then let us return the specimens unharmed to the universe and repeat our sampling many times. Then 12.5% of these many samples would

show the species falling in the range 0-1, 18.7% in the octave 1-2, 42% in its own octave 2-4, and so on.

The second column from the left represents all the times in which we should expect zero representations, and half the times we should expect singletons.

The third column represents half the singletons and half the doubletons.

TABLE V. *Probabilities of representation (expressed as percentages), when "perfect" representation is  $p$  specimens*

(Specimens) actual ( $m$ )	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Perfect ( $p$ ) representation	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
3/128	97.6	2.4															
3/64	95.4	4.5	0.1														
3/32	91.1	8.5	0.4														
3/16	83.0	15.5	1.4	0.1													
3/8	68.7	26.1	4.8	0.4													
3/4	47.3	35.5	13.3	3.3	0.6												
1½	22.3	33.4	25.1	12.5	4.7	1.4	0.4	0.1									
3	5.0	15.0	22.4	22.4	16.8	10.0	5.0	2.1									
6	0.2	1.5	4.5	8.9	13.4	16.2	16.2	13.9	10.4	6.9	4.1	2.2	1.1	0.5	0.2	0.1	5.5
12					0.5	1.3	2.5	4.3	6.5	8.7	10.5	11.5	11.5	10.7	9.0	7.2	
24											0.1	0.3		0.5	0.9	1.5	2.2

This table gives the percentage probability that a species will be represented, in the sample, by exactly 0, 1, 2, 3, ... individuals, if its frequency or commonness in the universe (Gaussian or any other) would lead us to expect in the sample an exact representation of " $p$ " specimens. We are interested, however, in knowing something a little less ambitious than this, viz., not the probability of a particular number of specimens, but the probability of the species falling in its proper octave of the sample, or in any other octave. The table can therefore be condensed into a shorter one, covering the first four octaves of the sample. This is done below in table VI.

TABLE VI. *Probabilities of representation in each octave when "perfect" representation would be " $p$ " specimens*

Being a condensation of the previous table (V)  
(Probabilities expressed as percentages)

$p$	Octaves						Veil Line
	Below 1	1-2	2-4	4-8	8-16	16-32	
3/128	98.8	1.2					
3/64	97.6	2.3	0.1				
3/32	95.3	4.5	0.2				
3/16	90.7	8.5	0.8				
3/8	81.7	15.5	2.8				
3/4	65.0	24.4	10.3	0.3			
1½	39.0	29.3	27.4	4.2			
3	12.5	18.7	42.0	25.9	0.8		
6	0.9	3.0	17.8	58.2	20.3		
12			0.2	11.6	75.1	3.1	
24				4.4			
		107.4	101.6	100.2	100.6		

The fourth represents half the times we should expect doubletons, all the times we should expect three specimens, and half the times we should expect four specimens.

This is in accord with our previous methods of figuring things.

The broken horizontal line is the veil line. A species theoretically represented by  $\frac{3}{4}$  of a specimen should be absent. A species theoretically represented by  $1\frac{1}{2}$  specimens should be represented by at least one.

The sloping interrupted line indicates the percentage probability with which a species should fall in its "own" octave. A species which in a "perfect" sample would have to be represented by  $1\frac{1}{2}$  specimens has less than a 30% chance to be represented in its own octave, while a species theoretically represented by 12 specimens has better than a 75% chance to fall in its own octave.

We thus have (in the table) substantially exact information about the composition of the first four visible octaves of the sample (1-2, 2-4, 4-8, 8-16). Beyond this point the calculations become very tedious and the table has not been computed. But it is easy to see that in the next octave (16-32) it is most probable that well over 90% of all species that should fall in it, *do* fall in it, and that from this point forward (32-64), and onwards, practically every species falls in its own octave, and no octave derives any adventitious support. Therefore it is the first four octaves that are important. Beyond this point the sample is a faithful replica of the "universe," whatever the distribution of commonness and rarity in that universe may be, so long as it is a reasonably smooth continuous sort of function.

We may therefore proceed to calculate what our samples should theoretically be, for two kinds of "universe." The first universe is the one in which all octaves are equally filled, the kind that results from the harmonic series of Professor Fisher and Dr. Williams. The second

universe is the Gaussian one, with the coefficient "a" in the exponent set equal to 0.20.

#### *Harmonic series: octaves in universe equally filled*

This is very easily dealt with. All we have to do is to add up the columns (except the first two) in table VI, as is done at the foot of that table. It will be seen that (allowing for small errors of calculation) all columns add up to just about 100% except the first, where there seems to be about 7% excess. That is, in this column, if we had a right to expect 14 species we should most likely get 15. This error is not very serious, and we might very well say that there are no errors beyond this point. Thus for this sort of universe, the sample is a very faithful replica.

#### *Gaussian universe*

The calculations here are more tedious, and have to be made for several cases; the veil line in the sample may coincide with the crest of the curve in the universe, or it may be at any point on the ascending or descending slopes. If we consider the universe as fixed, we can bring the veil line to any point we wish by continuing our collecting. Ultimately we collect the whole universe, and then the sample coincides with the universe, and is obviously a complete Gaussian curve if we postulate that the universe also is. We are more interested in the cases where the sample's veil line is within a few octaves of the crest of the "universe."

Let the number of species falling in each octave of the universe be assumed to be

$$n = 100e^{-(0.20R)^2},$$

where  $R$ , as before, is the number of octaves to left or right of the crest of the curve.

In most of the "universes" we have encountered in practice there is a tendency for "a" to be somewhere near 0.20, so it is logical—since we must use some speci-

TABLE VII. *Distribution of species in the Gaussian universe*

$R =$	0	$\pm 1$	$\pm 2$	$\pm 3$	$\pm 4$	$\pm 5$	$\pm 6$	$\pm 7$	$\pm 8$	$\pm 9$	$\pm 10$	$\pm 11$	$\pm 12$
$n =$	100	96.1	85.2	69.8	52.7	36.8	23.7	14.1	7.7	3.9	1.8	0.8	0.3

fic value for our calculations—to use this figure. The assumption that the modal octave will have 100 species is of course entirely arbitrary, but if it has some other number, it will merely result in all our figures being multiplied by a constant, both in the universe and in the sample, and will not affect our ultimate result in any way.

Let us now take three cases as follows: (1) with the veil line placed so that the first "exposed" octave in the sample is the modal octave of the universe, (2) with the veil line four octaves to the left of the above position, and (3) with the veil line four octaves to the right of the first position.

Applying table VII to table VI, we see, in Case (1), that the modal octave ought to be made up of 29.3% of the 100 species that "belong" there, plus (24.4 + 18.7)% of the 96.1 species that theoretically belong in the immediately adjoining octaves, plus smaller contributions from more distant octaves of the universe. After completing the calculations for all the octaves, and for all three cases, we reach the following conclusions:

proximate the veil-line position of Case (1) rather than the others, it appears likely that even in the other octaves the errors will not usually exceed a few per cent. In figures 8A, 8B, 8C and 8D, we show the (species) curve for the postulated universe, and for the three samples of Cases (1), (2) and (3), respectively. In b, c, and d, the solid line is the most probable sample curve, and the broken line the corresponding curve for the universe.

This method of computing the curves is an approximation only, and the postulate that the sample curve is essentially a decapitated version of the universe curve is likewise only an approximation; but it seems that it is sufficiently close for our present purposes.

#### Raunkiaer's law

Some twenty years ago there was some discussion of Raunkiaer's law in the pages of ECOLOGY, (Kenoyer, '27; Gleason, '29; Romell, '30) and a much more extensive literature elsewhere. This law concerns itself with the question whether a given species occurs, or does not occur.

Sample octave	1-2	2-4	4-8	8-16	Specimens/Species
<i>Case (1)</i>					
Most probable representation in sample "Perfect" representation	96 100	96 96.1	87.2 85.2	— —	Number of species in the octave Number of species in the octave
<i>Case (2)</i>					
Most probable representation "Perfect" representation	45.5 52.7	64.0 69.8	81.5 85.2	94.7 96.1	Number of species in the octave Number of species in the octave
<i>Case (3)</i>					
Most probable representation "Perfect" representation	69.3 52.7	44.4 36.8	27.3 23.7	16.0 14.1	Number of species in the octave Number of species in the octave

In all cases, though there are errors in the first two or three octaves, representation becomes close to perfect beyond this point: and since most samples tend to ap-

Twenty-five test areas of equal size are examined, which areas may be a square meter in size, or one-tenth of a square meter, or of some other size. The only

question involved is whether species  $S_1$  (say) is present in all quadrats, or only in some, and if so in how many. It does not concern itself (in its original form)

with the question whether it is represented by thousands of specimens or only one.

The species  $S_1$ ,  $S_2$ , etc., are then clas-

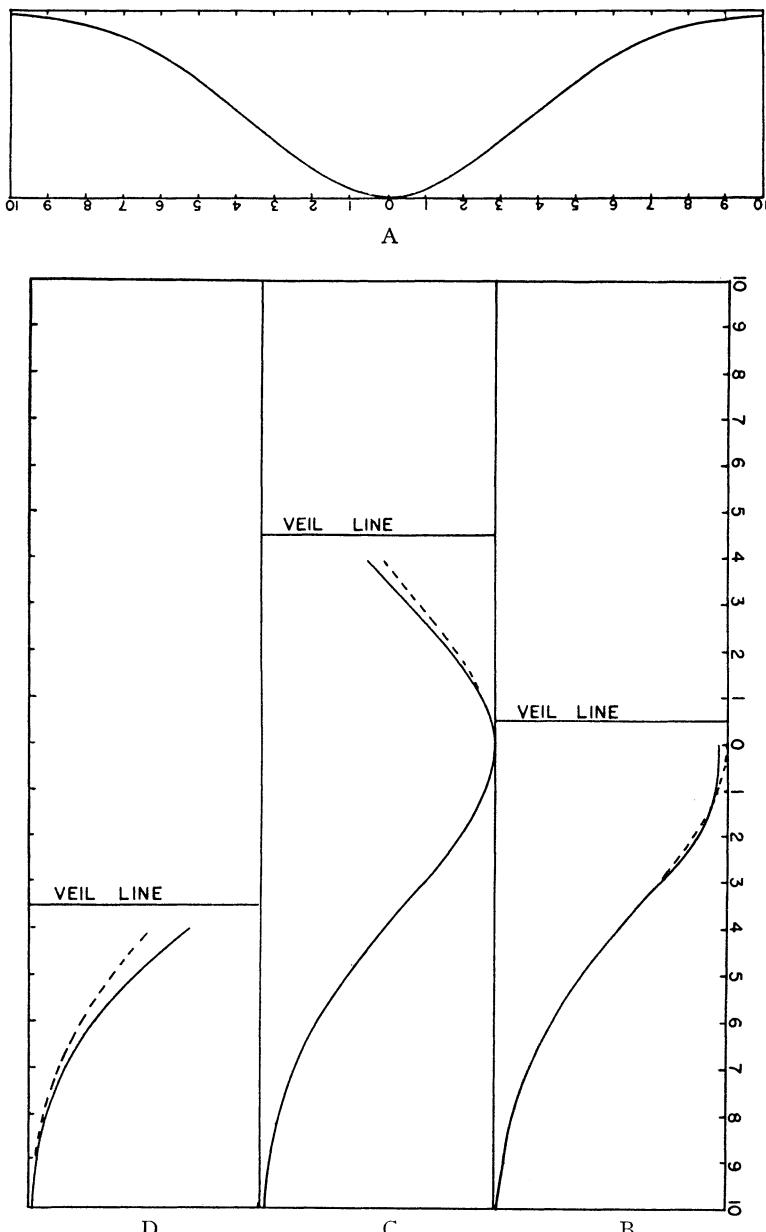


FIG. 8. A: a typical Gaussian curve. B, C and D, approximate relation of sample (solid line) to universe (broken line) with different degrees of decapitation (i.e., different sizes of sample). The samples follow the universe curve fairly closely.

sified into groups: Group A is represented in from 1 to 5 of the quadrats, B in 6 to 10, C in 11 to 15, D in 16 to 20, E in 21 to 25. Raunkiaer found that if the quadrat size were appropriately chosen, then group A was the largest, B less, C less still, but E tended to be larger than D. This sway-backed curve is usually described as "having two peaks."

It will be observed that what is directly measured is not commonness as understood in the present paper, where we are concerned with the numerical representation of a species in the sample or in the universe from which the sample is drawn; what Raunkiaer is concerned with is a measurement of *ubiquity*.

Gleason is quoted by Kenoyer as having called attention in 1920 to the relation existing between the actual number of individuals of the species, and the frequency index (Raunkiaer group) thereof.

But though there is a reasonable presumption that a ubiquitous species is a commoner one than a more local species, there is no *necessary* connection between the two things. We might have two species, buttercups and daisies. One buttercup occurring in each of 25 quadrats will rank the species as of a very high frequency; 25,000 daisies on a single quadrat, but missing from the other 24, will rank it as of a low frequency. Unsociable insects like the praying mantis, which on account of its cannibalism can be found only in a well-scattered arrangement, may be ranked as "frequent" but a colonial species like the bald-faced hornet, or an ant, might be infrequent, though at the nest there might be many thousands of individuals.

However, subject to biological factors of this sort, it still remains true that on the average there will be a definite relation between commonness and ubiquity, and it is easy to pass from the one to the other.

The Raunkiaer Index of Frequency is a measure of the probability that the species will occur (i.e., be represented by one or more specimens) in any one sam-

ple quadrat. Thus if the species occurs in 6 quadrats out of the 25, i.e., in 24% of them, the probability of its occurring in any one quadrat chosen at random is 0.24.

In a Raunkiaer quadrat or its equivalent, there may be one or more species to which the Poisson distribution laws do not apply. The condition for applicability is that there must be room in the quadrat for several times as many individuals as actually occur: this room will be non-existent if the species is already tightly packed in a dense stand, or if the individual bulks so large that it occupies a substantial part of a quadrat: it will also be non-existent for territorially-minded birds, and the like, where biological or ecological factors negate the possibility. The proof of the pudding, however, is in the eating, and experiment shows that normally such species, in a Raunkiaer test, are few or absent, and that therefore we can apply the Poisson distribution series with a sufficiently high degree of accuracy to all species.

In a Raunkiaer analysis, the great majority of species must be *absent* from one or more quadrats out of twenty-five, and in a random set of samples this implies that the *average* number of specimens of any one species in a *single* quadrat will rarely be as high as five.

Thus if  $p$  be the "average expectation" or "perfect representation," the series

$$e^{-p} \left( 1 + p + \frac{p^2}{2!} + \frac{p^3}{3!} + \text{etc.} \right)$$

gives the probability that the species will be represented by

0    1    2    3

specimens in any one quadrat.

We are concerned now only with the first term, representation by zero specimens. The probability that the species is completely unrepresented in a sample (quadrat) chosen at random is simply  $e^{-p}$ . Therefore the probability that it is *not* unrepresented is  $(1 - e^{-p})$ .

This is true whatever the shape or character of the universe may be.

TABLE VIII

Veil Line  
↓

Arbitrary name of octave	$\zeta$	$\epsilon$	$\delta$	$\gamma$	$\beta'$	$\alpha$	A	B	C	etc.
Perfect representation $p$	3/128	3/64	3/32	3/16	3/8	3/4	1½	3	6	etc.
Probability that species is not unrepresented (%)	2.4	4.6	8.9	17.0	31.3	52.7	77.7	95.0	99.8	etc.
Raunkiaer index of frequency	A	A	A	A	B	C	D	E	E	etc.

Now the values of  $e^{-p}$  are given in table V above, or rather the values there given are  $100 e^{-p}$ . Hence the values of  $100(1 - e^{-p})$  are immediately obtainable for a series of values of perfect proportionality  $p$ . This gives us table VIII above.

The boundaries between the Raunkiaer groups A, B, etc., are incorrectly given in some treatises: the correct values, given in percentages, are A, 2–22%; B, 22–42%; C, 42–62%; D, 62–82%; E, 82–100%. It is obvious that with 25 quadrats, a species cannot occur in  $5\frac{1}{2}$  of

them: it may occur in either 5 or 6; if in 5 (= 20%), it falls in group A; if in 6 (= 24%), it falls in group B. If its calculated chance of being present in a single quadrat is 22%, then it is equally likely to be in A or B, so the boundary between groups is at 22%. Similarly, if its chances are 2%, it is equally likely to be represented in one solitary quadrat, or to be totally unrepresented in all.

In order to find the boundaries between groups a little more accurately, we graph the data of table VIII in figure 9. Here the circles are the calculated points,

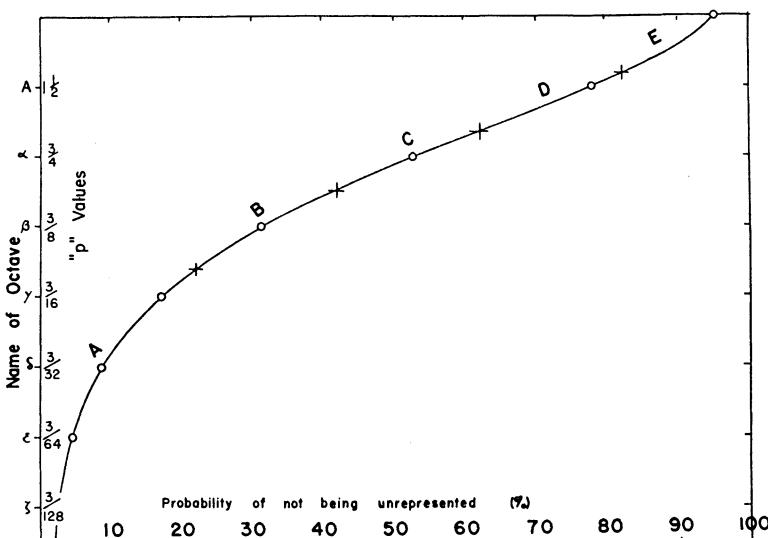


FIG. 9. Raunkiaer's frequency groups, A, B, C, D and E, in terms of octave ratings. The boundaries between groups are at 2, 22, 42, 62, 82%, as measured on the abscissa. The corresponding octave ratings are given by the ordinates. A horizontal line half way between  $\alpha$  and A is the veil line, which cuts Raunkiaer's group D. It follows that Raunkiaer's groups are concerned for the most part with samples so small that most species in the universe are behind the veil line of the sample.

and the crosses mark the boundaries of the Raunkiaer groups. In terms of octaves, the groups are made up as follows:

The total number of species, 674.2, is of course based on the assumption that in the universe the modal octave contains

TABLE IX

< A (missing species)	All octaves to left of $\zeta$ (zeta).
A	$\zeta, \epsilon, \delta$ , and about 90% of $\gamma$ .
B	$\beta$ and about 10% of $\gamma$ .
C	About 85% of $\alpha$ .
D	About 15% of $\alpha$ and 70% of A.
E	About 30% of A and all octaves to right of A.

So far the argument has been perfectly general. We have assumed nothing whatever about the "universe" from which the sample is drawn. Any universe whatever can be plotted on a logarithmic or octave base, and our discussion so far is pure mathematics. Now it becomes necessary to assume either that the octaves are all equally filled, or that they are not. The first assumption produces a universe with an infinite number of species, and of specimens: a finite universe demands unequally filled octaves. Let us therefore test the possibility that our Gaussian universe, on a logarithmic base, is the real one, and see if it agrees with the Raunkiaer findings.

Table VII above gives the ordinates of a Gaussian curve, i.e., the relative number of species in each octave if the universe is Gaussian, with an " $a$ " value of 0.20 typical of our work with moths and birds.

Put the veil line just to the left of octave + 4, i.e., between + 3 and + 4.

Then category A contains the following number of species:

$$\begin{array}{rcl}
 85.2 + 96.1 + 100.0 + (0.9)(96.1) & = & 368.0 \\
 B(0.1)(96.1) + 85.2 & = & 94.8 \\
 C(0.85)(69.8) & = & 59.2 \\
 D(0.15)(69.8) + (0.70)(52.7) & = & 47.3 \\
 E(0.30)(52.7) + 89.1 \text{ (all to right)} & = & 104.9 \\
 \hline
 \text{Total} & & 674.2
 \end{array}$$

TABLE X

Raunkiaer group.....	A	B	C	D	E
Kenoyer's values (experimental)	53%	14%	9%	8%	16%
Our values (theoretical)	54.6	14.1	8.8	7.0	15.6

from infusions of hay. Thus the logical assumption is that these "universes" also are Gaussian.

Gleason ('29) and Romell ('30) both have excellent criticisms of the Raunkiaer law, but their perplexities seem to be removed by the present demonstration of the connection between sample and universe. Thus Gleason's concluding sentence reads: "Raunkiaer's Law is merely the expression of the fact that in any association there are more species with few individuals than with many; that the law is most apparent when quadrats are chosen of the most serviceable size to show Frequency, and that it is obscured or lost if the quadrats are either too large or too small."

This comes within an ace of correctly summarizing the situation, and yet is quite wrong. It should read, "In any association there are just as many very rare species as there are very common ones, but species of moderate abundance are vastly more numerous than either. In a *small sample* however, there will be

more species with few individuals than with many, because those with many are the excessively common ones, and these species are few."

Romell likewise comments trenchantly ('30, p. 593): "It follows that statistics made with different sizes of sample areas cannot be compared, because there is no safe way of correcting the results for another size of analyzing area." (The italics are his.) Figure 10 is a chart permitting the transition, from one sample size to another, that Romell desires. On the assumption that the universe is logarithmically Gaussian with the exponent  $a = 0.20$ , we can calculate what the sample will be like for any position of the veil line with respect to the vertex of the Gaussian curve. This sample can then be expressed in terms of Raunkiaer groupings. Figure 10 represents the end result of the calculations.

Our chart consists of four sigmoid lines ascending from lower left to upper right. These lines mark out five domains, one each for the A, B, C, D, and E groups.

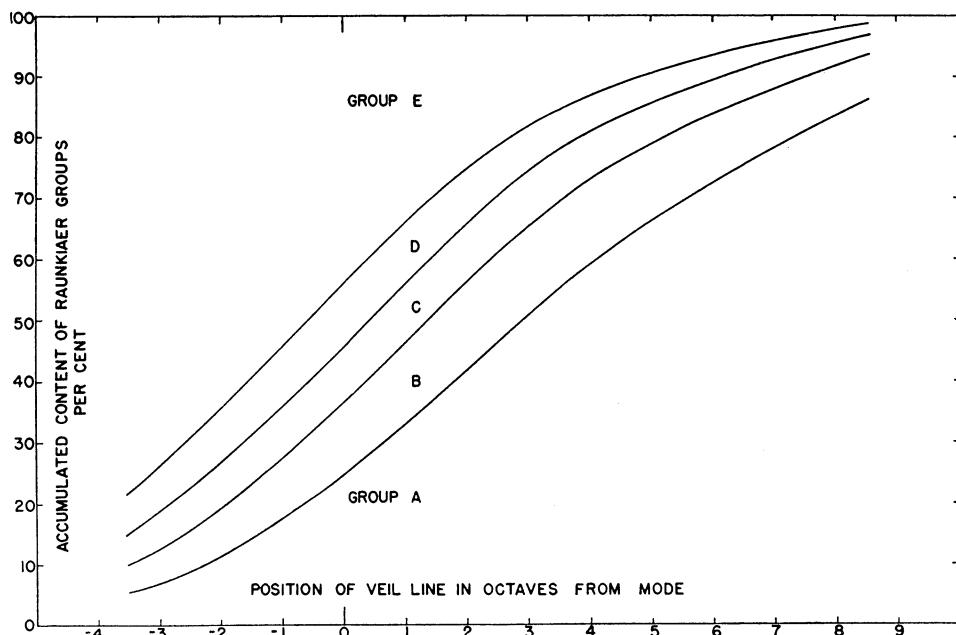


FIG. 10. Distribution of species among Raunkiaer groups and its variation with size of sample, assuming that the universe is logarithmically Gaussian.

TABLE XI

Group.....	A	B	C	D	E of Raunkiaer
Skead (observed)	75.4	13.1	5	5	1.6 per cent
"Theoretical," from chart	75.2	10.6	5.1	3.5	5.5 per cent

The vertical intercept between any two lines represents the percentage of species falling in one of the groups B, C, or D. On any ordinate the intercept between the lowest sigmoid and the base line represents the percentage falling in group A, and the intercept between the highest sigmoid and the ceiling line represents the percentage falling in group E.

The chart is one hundred units high. To use it, take any experimental Raunkiaer grouping, and, on the edge of a piece of paper of this same height, mark off the accumulated percentages, in sequence, A, B, C, D, and E. Move this strip of paper, with its ends in register with base and ceiling lines, from left to right till the best fit is obtained with the sigmoid lines. We have then located our sample with respect to its "universe": i.e., we have located our veil line.

Skead ('47), for instance, gives a Frequency-Grouping for birds observed over a period of a year on a small area of the Bushveld. This departs widely from Kenoyer's example, but apparently only because it was so small a sample, containing only 61 species out of the many hundred that might conceivably be observed over a much longer period. When these are separated into five groups, they average only 12 to a group, which is not enough for good statistical work. But taking the veil line at  $6\frac{1}{2}$  octaves to the right of the mode, we get table XI, below.

The fit is fair. It cannot be expected to be much better, for Skead's group E contains only a single species, and no group but A is large enough for good statistical work. The fit in group C is accordingly accidental, as are the slight discrepancies in the others. All that we can say is that Skead's results are not inconsistent with the hypothesis that they are drawn from

a universe of the same general shape as all our other examples.

More generally, we may note the agreement of the chart with the basic conclusions of the Raunkiaer investigations. The four curves mark out a relatively narrow belt across the field, so that groups A and E together always greatly exceed B, C, and D combined. Group C is usually comparable in size with D; group B is usually greater than either; A is usually much greater than B, and E is usually greater than D, normally considerably greater (except for very small samples).

These seem to be the experimental conclusions as reported in the literature: they are immediately deducible from the chart.

The available evidence apparently does suggest that a great many biological "universes" have the logarithmically-Gaussian form, with a coefficient "a" not far from 0.20. If birds in a valley, moths in a trap, plants in a quadrat, insects in a sweep net, and micro-organisms in a suspension of hay do in fact all agree in this, it would seem that some very general law must lie behind it all.

#### *Williams' law of collection enrichment*

Williams, referring to his moths and other insects, observes: "Doubling the number of insects caught, (and hence the time of trapping) at any level, except for very small samples, always adds about 30 species to the total."

Now we have seen that doubling the sample simply means adding one more octave that was previously veiled; and so long as Williams was working over the intervals  $\frac{1}{8}$  year, 1 year, 4 years, he would be working near the crest of the curve, where one octave contains (in his

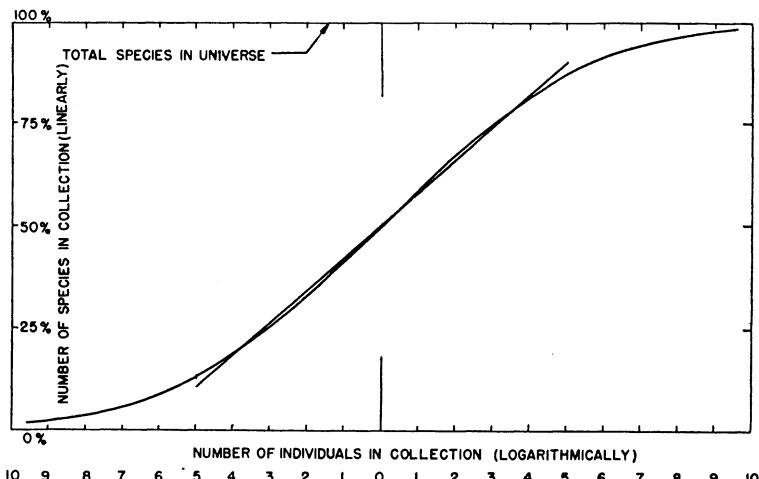


FIG. 11. Curve of collection enrichment in an unchanging universe. This "sigmoid" curve is simply the integral of the Gaussian curve. It indicates that over a wide range, doubling the size of the sample, or doubling the time of collecting, tends to add a constant increment of species to the collection (Williams' law). A compromise line as drawn sufficiently replaces the curve itself over about 8 octaves, a much longer interval than Williams tested. (But the Williams' law remains true in spite of the fact that the universe is not unchanging.)

case) about 30 species, and he would be covering about 5 octaves.

If the universe remained constant during the trapping, it is easy to show that Williams' law must necessarily be very nearly true over a range of several octaves. It is perhaps most easily seen from the integral curve. For the collection at any time consists of

$$y = n_0 \int_R^{+\infty} e^{-(aR)^2} dR \text{ species.}$$

This integral ( $y$ ) plotted against  $R$  is a sigmoid curve which can be approximated very closely by a straight line over several octaves near the point of inflection.

Figure 11 shows such a curve, using a value for " $a$ " of 0.16, close to the Saskatoon and Lethbridge figures rather than Williams' value ( $a = 0.227$ ), for reasons that will appear later. The octave intervals are marked and it is clear that a straight line is a good approximation over 6 or 8 of the central octaves.

The surprising thing, in practice, is that Williams' law holds so well in a universe so rapidly and radically changing as the real biological universes are.

#### *The changing "universe"*

That ecological assemblages are continually changing is well understood. There is the slow business of plant "successions"; there is the remarkable build-up and subsequent crash of many mammal populations (Elton, '42); and there is the obvious fact, in a temperate region, that the moths flying tonight are not the same species that flew a month ago. Yet we might expect that the *annual* catches of moths in a given light trap would be fairly constant. This is not the case.

Dr. King tells me that the environment around his Saskatoon trap did not change in any obvious manner during 22 years, and that the trap and its efficiency did not change in any material way. Yet the catch varied considerably both in number of species and of individuals caught (fig. 12).

Even when the species remain fairly constant as to *number*, as they did over the last decade, they do not remain the same species from year to year. Species come and go from year to year to a surprising extent. Out of 277 species observed, only 38 were present every year. Table XII below shows how inconstant the fauna was.

Seamans' moths of Lethbridge confirm the picture. Figure 13 graphically summarizes the annual catches both as to number of species and as to number of individuals. As at Saskatoon the fauna seems to have become on the whole more

diversified ("richer") with the passing years.

As regards the constancy of the trap itself, Mr. Seamans has this to say:

"The trap is identical, has remained in the identical spot and, except for a period of one week in 1923, has been lighted with a 60-watt clear-glass incandescent bulb. During that one week we used a 100-watt bulb and caught an entirely different series of moths, while those which normally came to the light were found roosting on the trees 15 feet away, indicating that they were susceptible to variations in light intensity. At the end of the week we switched back to our ordinary globe and have used it ever since."

"The trap is on the corner of the laboratory

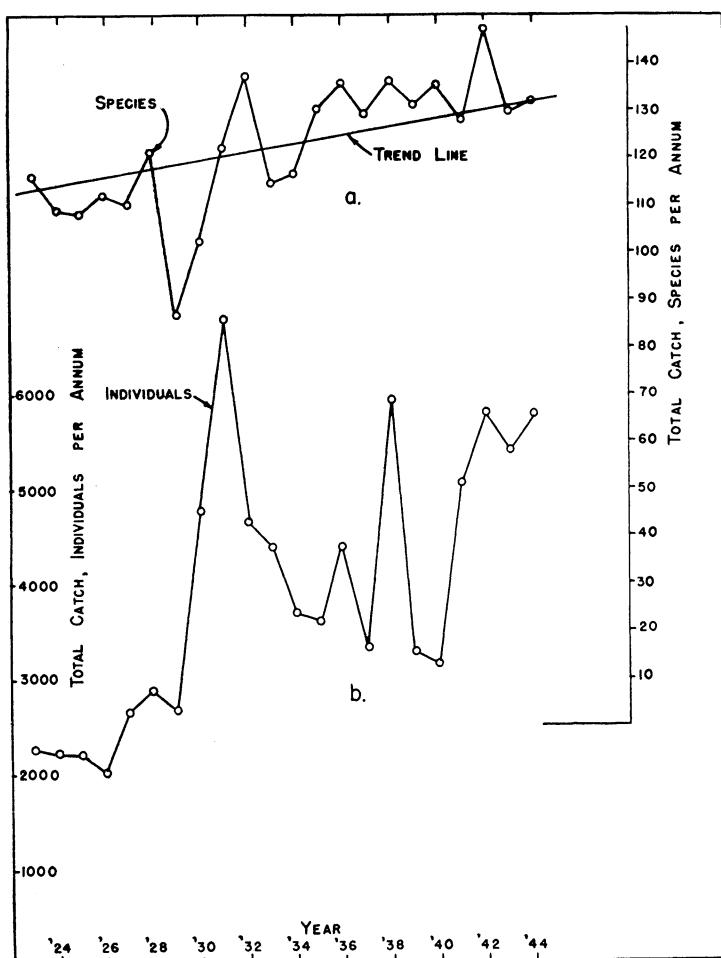


FIG. 12. Fluctuation in numbers of species and numbers of individuals in the Saskatoon trap.

TABLE XII. *Constancy of the Saskatoon fauna*

Present for $N$ years out of 22	$N$	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Number, $S$ , of species thus present	$S$	49	29	9	16	8	10	12	6	11	8	11	15	3	6	6	11	8	1	7	7	6	38

TABLE XIII. *Constancy of the Lethbridge fauna*

Present for $N$ years out of 22	$N$	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Number, $S$ , of species thus present	$S$	45	21	19	13	12	10	8	9	9	17	11	5	7	7	7	6	8	15	16	16	15	15

building, which is located on the Dominion Experimental Station grounds. The only crop changes are the normal changes which are made in rotations on irrigation plots, but none of these plots is any nearer than 70 feet from the trap.

"We have tried to maintain this trap in identical conditions in order that our yearly records may be comparable in anticipating outbreaks of the various cutworms which occur in this part of the country."

Out of the 291 species that were observed during the period, only 15 were observed in every year. This indicates how inconstant the fauna is, but the tabulation below illustrates the matter somewhat more completely.

#### *The changing universe and Williams' law*

We have seen that in a fixed universe, doubling the sample moves the curve one octave to the right, but does not change the height of the crest, or the dis-

persion (value of "a"). If the universe changes, it is not difficult to show that the most probable result is to increase the height of the mode, to withdraw the curve less than one octave to the right, and perhaps to leave the dispersion but little changed. These in fact are the results we also find in practice, as mentioned previously in connection with the Saskatoon and Lethbridge annual and quadrennial curves.

#### *Lethbridge and Saskatoon data and the Williams' law*

The pronounced "trends" towards enrichment in the annual count of specimens at both the above places have to be eliminated before we can do much towards testing the Williams' law. This elimination can be done by an artifice. Let us assume that at some time or other the fauna will show a trend towards im-

TABLE XIV. *Lethbridge collection enrichment with trend eliminated  
(new species appearing each year after first)*

Forwards 1921-43 (102)	42	27	4	2	9	13	11	10	7	3	1	6	10	4	7	5	2	5	12	7	2
Backwards 1943-21 (155)	31	32	10	2	7	9	3	8	6	1	4	2	3	1	4	2	0	1	5	2	3
Trendless (257)	73	59	14	4	16	22	14	18	13	4	5	8	13	5	11	7	2	6	17	9	5

TABLE XV. *Saskatoon collection enrichment with trend eliminated*

Forwards 1923-44 (116)	22	11	8	10	11	1	4	9	11	6	9	7	7	11	7	4	6	1	8	2	2
Backwards 1944-23 (132)	29	33	10	11	13	10	5	9	3	6	2	4	1	0	1	1	0	2	1	1	3
Trendless (248)	51	44	18	21	24	11	9	18	14	12	11	11	8	11	8	5	6	3	9	3	5

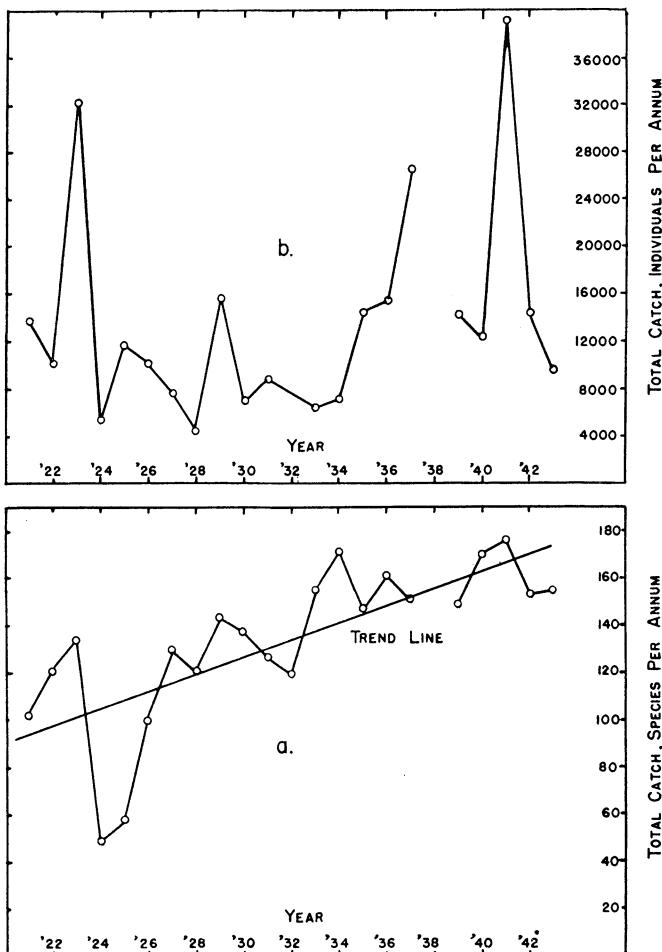


FIG. 13. Fluctuation in numbers of individuals and numbers of species in the Lethbridge trap.

poverishment exactly equal to its present trend towards enrichment. Then we might collect a set of data exactly like the present one, with the years reversed. That is, we could pretend that 1943 was really 1921, 1942 was really 1922 and so on. Adding the two sets together, we should obtain a series from which "trend" has been eliminated.

We can analyze such a series to see how many new forms appear each year in a trendless world. This is the same thing as finding how many species appear each year, for the *first* time, in the real series,

and how many appear each year, for the *last* time in the real series. This gives us two sets of data, the first of which we write "forwards" and the second "in reverse." It is most easily understood by carrying out the process as is done below. In the Lethbridge case, the year 1938 is missing, so the series is "telescoped" in order not to leave a gap.

The Williams' law says that doubling the period of observation always adds a constant increment of "new" species. We may test the law somewhat crudely as follows:

TABLE XVI. "New" species resulting from doubling the period of observation

End of year	1	2	4	8	16
Increment at Lethbridge	(257)	73	73	56	77
Increment at Saskatoon	(248)	51	62	65	93

It would seem that the law is by no means a bad approximation.

A more accurate method of testing the law involves putting it into a slightly different form, which might read: "The number of species in the collection increases as the logarithm of the time of collecting."

This may be expressed mathematically in either of two forms, which are equivalent:

$$N - N_1 = (N_{10} - N_1) \log_{10} t$$

or

$$N = N_1 + \frac{\Delta N}{\log_{10} 2} \log_{10} t \\ = N_1 + (3.3\Delta N) \log_{10} t.$$

Here  $N$  is the number in the collection after  $t$  years;  $N_1$  is the number at the

end of the first year;  $N_{10}$  the number after 10 years of collecting, and  $\Delta N$  is the constant number or increment which Williams says is added as a result of doubling the collection.

More briefly, what Williams says is that if we plot the number of specimens in the collection on a natural scale, as ordinate, against the logarithm of the time of collecting as abscissa, we shall get a straight line. Inasmuch as the Canadian data are much more extensive than those from which Williams deduced his law, we tabulate below the status of the Lethbridge and Saskatoon collections, year by year, corrected for trend. (Note: The number of species reported is finally twice the total collection of species, since we add the inverted sequence to the observed sequence, and do not halve the result to strike an average).

The results are plotted in figure 14, and it seems that they do bear out Dr. Williams' beliefs. Straight lines may be drawn fairly closely approximating the results, and what is more, the two straight

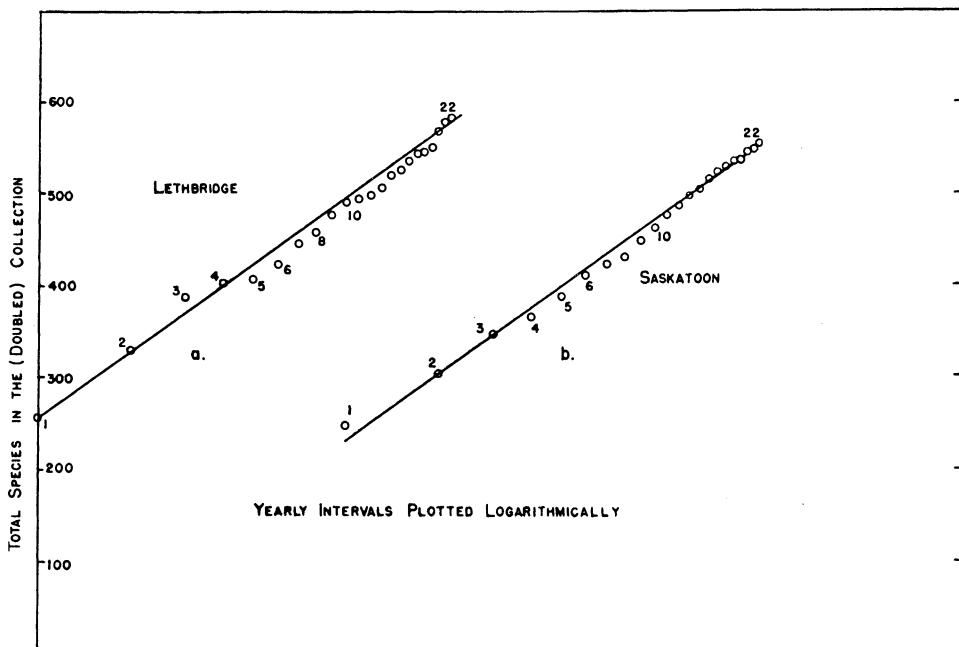


FIG. 14. Lethbridge and Saskatoon data on collection enrichment.

lines have the same slope. The number of species added by doubling the period of observation is in each case approximately 72. This is the value in each of two collections of comparable richness, having approximately 250 species in the first (composite) year. In the actual collections, which would have about 125 species in the first (or average) year, the increment  $\Delta N$  to be expected from doubling the period of trapping is about 36 species, in the absence of trend. This is about 30% of an average year's catch.

TABLE XVII. *Rate at which collections (of species) grow at Lethbridge and Saskatoon (composite collections, corrected for trend)*

Years from start	Species (Lethbridge)	Species (Saskatoon)	Years	Lethbridge	Saskatoon
1	257	248	12	499	481
2	330	299	13	507	492
3	389	343	14	520	500
4	403	361	15	525	511
5	407	382	16	536	519
6	423	406	17	543	524
7	445	417	18	545	530
8	459	426	19	551	533
9	477	444	20	568	542
10	490	458	21	577	545
11	494	470	22	582	550

Williams' own statement is, "Doubling the number of insects caught (and hence the time of trapping) at any level, except for very small samples, always adds about 30 species to the total." His average annual catch (for four years) was 176 species. The question of "trend" is not dealt with in his report, and probably could not be usefully treated of, even if suspected. But it seems that his new species,  $\Delta N$ , amount to about 17% of an average annual catch of species, instead of the 30% found at the Canadian stations.

#### Certain special "universes"

The universes we have been considering are mostly universes of taxonomic groups, since these are the only ones on which we appear to have adequate data. However if the correspondence between the Raunkiaer results and our present ones is accepted, then the older data on

Raunkiaer groups may be considered as adding ecological assemblages to our universes, and hinting that they are Gaussian and with values of " $a$ " not very different from those of taxonomic universes.

The universe of a light trap is not comprised in a definite area. Some species, weak fliers, like many of the geometrids, will presumably be collected only from close quarters, while strong flying noctuids or sphinges may have come from miles away—in England, for instance, they will often have come from beyond the English Channel or North Sea. The universe involved is a product of the actual commonness of the moths as we imagine an omniscient being might count them, multiplied by a factor representing relative phototropism of the various species, multiplied again by a factor representing power-of-flight, and perhaps other factors, as indicated by Seamans.

However, it will probably be conceded that the universes, whatever they are, are humped distributions approximating to a Gaussian curve on a geometric series as a base.

We should perhaps like some further evidence that the left-hand end of the curve, which is so inaccessible experimentally, actually does become asymptotic to the same axis as the right-hand end. This can only be done by a consideration of the universes themselves.

#### *The Nearctic avifauna*

As one such "universe" we might take the breeding birds of the Nearctic, which comprises, approximately, that part of the North American continent, and adjacent islands, north of the Rio Grande and the Straits of Florida. Its area is about 8.5 million square miles or  $5.5 \times 10^9$  acres. Peterson ('40) estimated that there may be  $5 \times 10^9$  individual birds in the continental U.S.A., so a figure of  $10^{10}$  for the whole Nearctic, or roughly one pair per acre, may not be unreasonable. According to the American Ornithologists' Union Check-list, these individuals are distributed among 641

species, of which 35 are essentially Neotropical species whose breeding range extends slightly north of the Rio Grande. This leaves us with 606 species which may fairly be called Nearctic ones.

Now  $10^{10} = 2^{33}$  approximately. Thus no species can have as many as  $2^{33}$  individuals; and since no species can have less than one individual, the whole fauna must be comprised within less than 33 octaves, probably within 30 octaves as a maximum. In fact, since the total of all species is estimated at about  $5 \times 10^9$  pairs, and the commonest species will not have one-fifth of all the individuals, the range of commonness will not extend over so much as from 1 to  $10^9$  pairs.

Let us divide this range into three equal parts (i.e., equal logarithmically, on our basis of plotting), viz. 1 to  $10^3$ ,  $10^3$  to  $10^6$ , and  $10^6$  to  $10^9$  pairs.

Species falling in the range 1 to  $10^3$  or

perhaps in the range 1 to  $10^4$ , the first ten or twelve octaves or therabouts, appear to number about fifty-five, according to a conscientious study of the A. O. U. Check-list by a competent ornithologist friend. These are the rare species. The very common species, whose numbers exceed  $10^6$  pairs, or possibly  $10^7$ , may number about sixty. Therefore the species of an intermediate level of commonness, from  $10^3$  to  $10^6$  or possibly  $10^7$  pairs, number about 490 and are thus in a great majority.

It is clear therefore that our Nearctic universe is bell-shaped, with a high hump in the middle, and approximates to a logarithmically-Gaussian curve. At the left-hand end we approach the axis asymptotically with some octaves blank, or occupied by only a single species, such as the Ivory-Billed Woodpecker, with only one or two pairs surviving. The

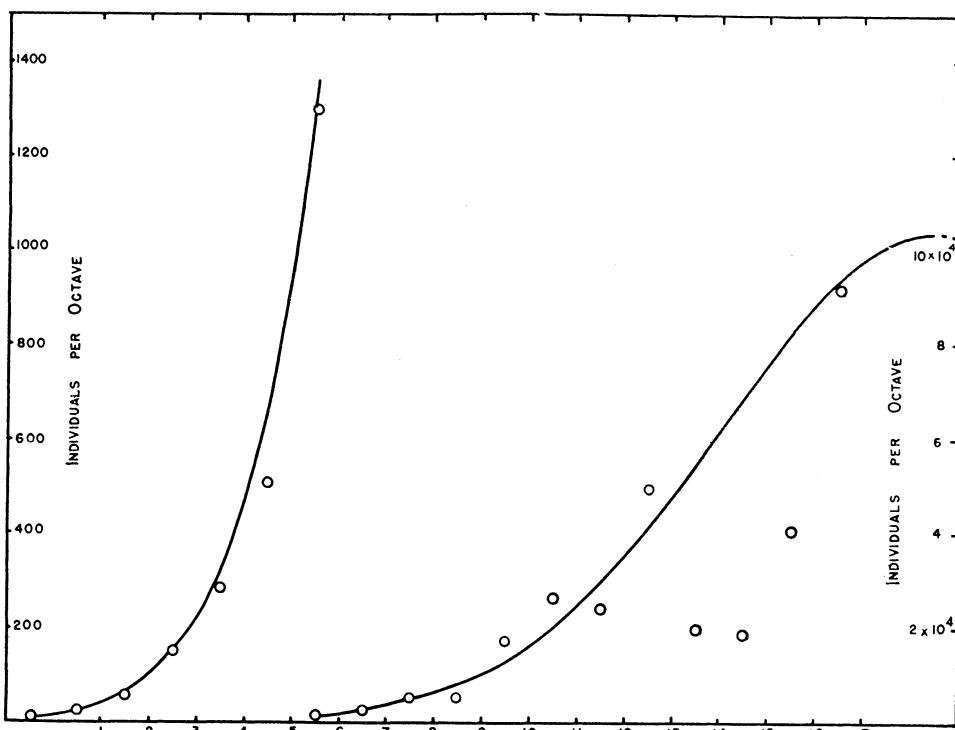


FIG. 15. "Individuals" curve for Lethbridge (1921-1943). The curve is a single curve, but the scale is changed at abscissa = 5.5. The curve is the left-hand half of a Gaussian curve.

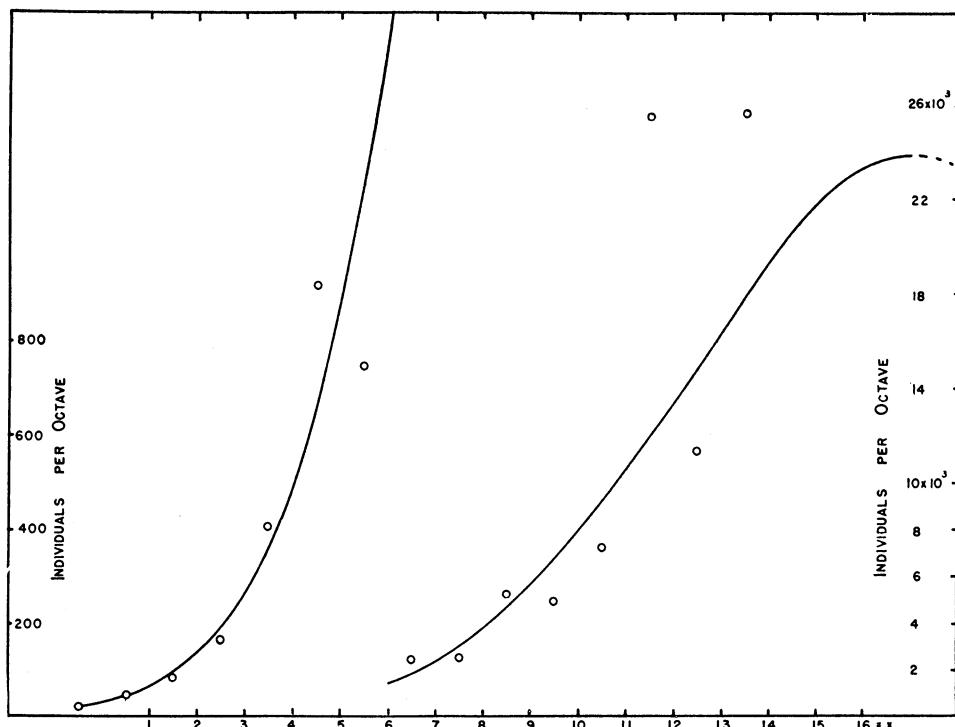


FIG. 16. "Individuals" curve for Saskatoon (1923-1944). The curve is a single curve, but the scale is changed at abscissa = 6.0.

first 10 or 12 octaves have only 55 species, or an average of 4 or 5 species per octave. The same thing is true of the last octaves to the right.

We do not know that the curve may not be "skew," but on the assumption that it is approximately symmetrical (Gaussian) we can compute its properties. The assumption is that the curve is of the form

$$n = n_0 e^{-(aR)^2},$$

the experimental information is: (1) that the total number of species

$$N = \sum n = \int_{-\infty}^{+\infty} n dR = 606 \text{ species},$$

and (2) that 490 species lie within the central third of the base line.

This results in an equation

$$n = 65e^{-(0.19R)^2},$$

where as usual  $n$  is the number of species per octave and  $R$  is the number of octaves to left or right of the modal octave, which should have about 65 species.

It may be noted that the dispersion constant "a" has a value of 0.19, which is very similar to the values we have obtained in many other instances.

Thus it seems likely that a study of a whole universe would bear out the evidence of our samples, that it is in fact a logarithmically-Gaussian universe.

#### *The "individuals" curve*

If the *species* that fall in a given octave are represented by

$$n = n_0 e^{-a^2(x-b)^2} = n_0 e^{-a^2R^2},$$

where  $n$  is the number of species in the  $x$ th octave from the *veil line*,  $n_0$  the number of species in the modal octave, which is distant " $b$ " octaves from the *veil line*, and " $a$ " is the dispersion coefficient, then

it is not difficult to show that the *individuals* falling in any given octave (that is, the total individuals representing all the species in that octave) are given by

$$q = n_0 2^b e^{(\ln 2/2a)^2} \cdot e^{-a^2[R - (\ln 2/2a^2)]^2}.$$

This also is a Gaussian curve with the same dispersion "*a*" as before, with a mode displaced to the right through a distance  $(\ln 2)/2a^2$  octaves, and with a height at the mode of

$$q_0 = n_0 2^b e^{(\ln 2)^2/4a^2}$$

individuals per octave.

Thus the curve can be derived directly from the "species" curves. The calculated "individuals" curves for Lethbridge and Saskatoon are given in figures 15 and 16, while figure 17 shows, for the Saskatoon data, the relative positions of the "species" and "individuals" curves.

The individuals curve thus derived,

however, though Gaussian, is only the left-hand half of a complete Gaussian curve. Experimental points stop at or near the crest of the curve. This is because the *species* curve, though graduated by a Gaussian which theoretically extends infinitely to the right, in practice stops finitely, for an octave cannot hold less than one whole species unless it holds none. If one of the blank octaves beyond the last observed point (which is usually one species in an octave) contained species, it would hold 2, 4, or more times as many individuals as the said last observed point. Thus we cannot, with the individuals curve, observe a declining number of individuals, and are limited to the ascending portion of the curve.

It follows that the distance between the modes of the species and individuals curves ( $= (\ln 2)/2a^2$  octaves) is approximately equal to the distance between the

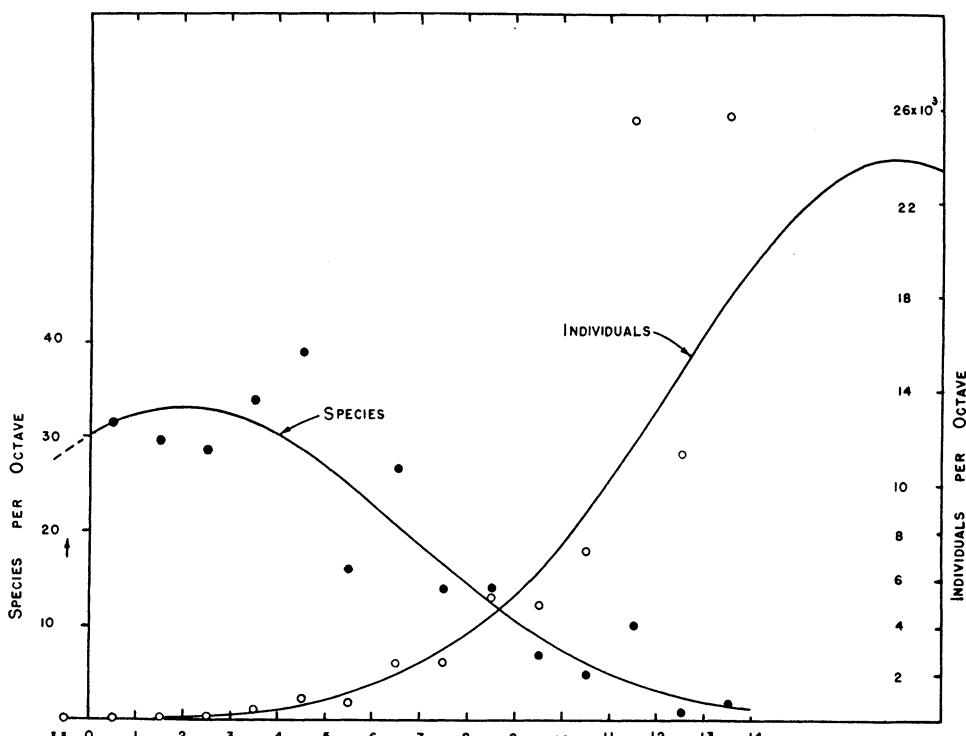


FIG. 17. "Species" and "individuals" curves for Saskatoon on the same base. The continuity of the "individuals" curve is made clear.

mode of the species curve and the observed last point on that curve.

The area under the individuals curve (assumed to be half a Gaussian curve) is

$$Q = \int_{-\infty}^0 q dR = \frac{n_0 \sqrt{\pi} \cdot 2^{b-1}}{a} e^{(\ln 2)^2 / 4a^2}$$

and represents the total number of individuals observed of all species.

Table XVIII gives a comparison of some of the  $Q$ -values thus calculated and the observed totals of individuals.

TABLE XVIII. *Total individuals*

Place	Period	Calc.	Obs.
Lethbridge	22 years	579,830	303,251
Saskatoon	22 years	139,310	87,110
Orono	4 years	27,126	56,131
Rothamsted	4 years	11,246	15,609
Quaker Run		30,940	14,353

The calculated values are of the same order of magnitude as the observed ones, sometimes greater, sometimes less: the "errors" in fact are + 48, + 38, - 107, - 40, + 54%, or an average - 1%, and are due essentially to variations in the number of individuals in the two or three commonest species.

#### Summary

Random samples of ecological or taxonomic assemblages indicate that the universes from which they are drawn have, at least approximately, the form of an ordinary Gaussian curve drawn upon a logarithmic base (a "lognormal" curve). The sample has the same general form as the universe, but is decapitated.

The exact relationship between sample and universe is explored, and the Raunkiaer Law of Frequency explained, as is Williams' Law of Collection Enrichment.

There is a remarkable tendency for the dispersion constant " $a$ " to be not far from 0.2 in a great variety of biological universes.

Various applications of the theory are made to rather inaccessible populations, such as the Nearctic avifauna in its entirety. The findings seem reasonable in all cases.

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