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STUDIES IN STATISTICAL ECOLOGY

I. SPATIAL PATTERN

By J. G. SKELLAM

The Nature Conservancy, London

1. Introduction

1·0. In the world of organic nature there seems to exist an uneasy balance between the factors which increase randomness and those that oppose it.

This is particularly true of the distribution in space of animals and plants. The broad outlines of the pattern are determined by the main structural features of the physical environment. But even under constant conditions neither uniformity nor complete randomness prevail.

On the one hand the reproduction of organisms and the interactions between them tend to develop a closely knit pattern; whilst on the other, locomotory movements and dispersive processes bring about an ever-increasing randomness. An ecological complex of interacting species is a dynamical system, which may not only display a regular seasonal rhythm, but also appears liable by reason of its intrinsic nature to undergo oscillations (Volterra, 1931) or cyclical changes (Watt, 1947), all of which are liable to be disturbed in an irregular manner by apparently unpredictable fluctuations in weather conditions or by the spasmodic arrival of additional components to the system from outside.

In order to study the community quantitatively or to assess the densities and abundances of living organisms in their habitats, ecologists have found it profitable to sample the space in which the organisms occur, and to record the composition of each sample. In this first paper we are concerned mainly with the distribution of the number of individuals per sample, for which the term census distribution is proposed. The illustrations given are drawn from observations on plant species for which the most convenient method of sampling is the marking out of quadrats on the ground. Clearly census distributions are discrete and can only be applied to species which consist of individuals or clearly defined aerial shoots each of which can be regarded for the purpose as an individual.

Census distributions are important for two reasons. First, they provide estimates of the density of the individuals in the region sampled together with information relating to the reliability of the estimates. Secondly, they contribute to our understanding of certain aspects of the pattern or arrangement of the individuals in space.

It is unfortunate, however, that the use of probability generating functions should not have featured more prominently in the literature on these and related topics, for by means of them the subject under consideration can be given greater unity and understanding. Many statistical results already deduced with much labour by the pioneers of quantitative ecology can be derived immediately by this method, and the way opened for further generalization and development.

2. NOTATION

2·1. $G(z) = \sum_r p_r z^r$ is a probability generating function. So are $g(z)$ and $\gamma(z)$.

$\phi(t) = G(e^t) = \Sigma\mu'_r t^r/r!$ is an ordinary moment generating function.

$\Phi(u) = G(1+u) = \Sigma\mu_{(r)} u^r/r!$ is a factorial moment generating function.

$\psi(t) = \log\phi(t) = \Sigma\kappa_r t^r/r!$ is an ordinary cumulant generating function.

$\Psi(u) = \log\Phi(u) = \Sigma\kappa_{(r)} u^r/r!$ is a factorial cumulant generating function.

3. PATTERN AND PROCESS

3·1. It is universally realized by ecologists that the frequency distribution of the number of individuals of a particular species per quadrat is the natural outcome of the spatial arrangement of those individuals. If, for example, a number of points are distributed over an area in accordance with some scheme of laws (which may or may not involve notions of probability) it is possible, assuming sufficient mathematical knowledge, to deduce the probability distribution of the number of individuals per quadrat laid down at random.

But though the passage from cause to effect involves no special logical problem, the reverse process does. Unfortunately, we cannot with any certainty arrive at an understanding of the spatial arrangement of the points from a knowledge of the frequency distribution alone. One purpose of the present paper is to enumerate some of the more important probability distributions to be expected on certain reasonable physical models. It will be seen in a number of cases that two fundamentally distinct models may give rise to the same probability distribution, and in consequence no statistical analysis whatsoever can discriminate between them.

Fundamentally the limitations are inherent in the method itself. If further advances are to be made, the method must be extended and developed so as to incorporate additional information of a somewhat different kind. Such can be gained, for example, by employing quadrats of different sizes, by studying the relationships between the numbers in nearby squares, and the distances between individuals and their nearest neighbours.

If it is at all obvious from general observation that the arrangement of individual plants approximates to some simple model, then it may be possible to give a physical meaning to the parameters of the corresponding probability distribution. But if nothing is known *a priori* concerning the spatial pattern, the parameters have only descriptive value in a somewhat remote sense, and no great purpose is at present served in estimating them.

For the same reason I reject the use in this connexion of the Gram Charlier Type B series and the other series developments of § 3·17, at the same time recognizing their value in other ways (§ 3·18).

3·2. Consider a wide expanse of exposed open ground of a uniform character such as would be provided by the muddy bed of a recently drained shallow lake, and consider the disposition of the independently dispersed wind-borne seeds of one of the species which will colonize the area. That the number occurring in a quadrat square marked on the surface is a Poisson variate is seen from the fact that there are many such seeds each with an extremely small chance of falling into the quadrat. This result was pointed out in analogous circumstances by Student (1907) in connexion with haemacytometer counts, and has been used by

Blackman (1935) and more recently by Barnes & Stanbury (1951). The distribution of the number of seeds per quadrat then has p.g.f.

$$G(z) = e^{\lambda(z-1)}. \tag{1}$$

The probability distribution of the total number of seeds falling into an area is Poissonian even if the process takes place irregularly over a long period, for then

$$G(z) = \prod_j e^{\lambda_j(z-1)} = \exp\{\Lambda(z-1)\},$$

where $\Lambda = \Sigma\lambda_j$. Alternatively,

$$G(z) = \exp\left\{\int_0^T (z-1)\,\lambda(t)\,dt\right\} = \exp\{\Lambda(z-1)\}, \tag{2}$$

where $\lambda(t)$ is a rate, and $\Lambda = \int_0^T \lambda(t)\,dt$.

3·3. Suppose now that the probability that a seed germinates is p and that they are not sufficiently packed together to interact at this stage. The distribution of the resulting seedling will, by a well-known theorem (Watson, 1889; Fisher, 1922; Haldane, 1927) have p.g.f.

$$G(pz+q) = e^{\lambda(pz+q-1)} = e^{\lambda p(z-1)}.$$

Clearly then, as long as the fates of the individuals remain independent of one another, the Poisson form persists, and the survivors continue to be distributed at random.

Though adverse conditions have profound effects on population numbers they do not appear to affect the functional form of the more important distributions which we shall consider.

For suppose that the individuals of a species are exposed independently to the risk of extermination with probability $q = 1-p$, and we take samples of the space in which they live. Instead of the distribution $G(z)$ we obtain $G(pz+q)$. Consequently whenever $G(z)$ has the form $F(a_0+a_1z)$ that functional form is unchanged. This property of functional invariance under random selection is possessed by all the elementary discrete distributions.

3·4. For the Poisson distribution

$$\begin{aligned} \kappa_r &= \lambda \quad (\text{all } r), \\ \kappa_{(r)} &= 0 \quad (r>1), \\ &= \lambda \quad (r=1). \end{aligned}$$

The ratio $\mu_2/\mu_1' = 1+\kappa_{(2)}/\kappa_{(1)}$ has been used by Clapham (1936) and other botanists as a standard for the comparison of census distributions. In the case of the Poisson distribution this ratio $= 1$, and the individual plants were then regarded as being located at random. The plants were said to be over-dispersed when the ratio was greater than unity and under-dispersed when it was less than unity. The quantity $\sum_{j=1}^{n}(x_j-\bar{x})^2/(\bar{x}[n-1])$ was used as an estimator of μ_2/μ_1'. Here $\bar{x}$ denotes $\sum_{j=1}^{n} x_j/n$.

The statistic $\sum_{j=1}^{n}(x_j-\bar{x})^2/\bar{x}$, as originally suggested by Fisher (1925), is commonly used to test the significance of the departure of an observed set of values $(x_1, x_2, \ldots, x_n)$ from the Poisson form. This statistic (the index of dispersion) is treated as a χ^2 variate with $n-1$

degrees of freedom. It is not defined for $\bar{x}=0$, but as Haldane (1939, p. 350) has shown within the conditional set of samples for which $\bar{x}$ is constant, the variance is

$$2(n-1)\{1-1/(n\bar{x})\}.$$

A discussion of the adequacy of the χ^2 approximation when the expectation, λ, is small is given by Lancaster (1952) elsewhere in this issue.

The problem for small λ has been taken up by Fisher (1950) where further refinements and modifications are discussed.

It might be noted that there are serious objections to the unqualified acceptance of Clapham's ratio as an index of non-randomness for it is not in general independent of the size of quadrat employed (cf. §§ 3·7 and 3·14; see also Evans, 1952).

3·5*a*. A more direct and profitable approach to the problem of spatial non-randomness is to study the distribution of the distance between an individual and its nearest neighbour, and to compare the observed distribution with that which could be expected on the assumption of randomness.

If the density of the particles $= \lambda/\pi$, the number occurring in any circle of area A has a Poisson distribution with parameter $A\lambda/\pi$. Now take any particle at random as centre and construct circles with radii r_1 and r_2, where $r_1 < r_2$. The probability that no particle occurs inside the inner circle is $e^{-\lambda r_1^2}$. The probability that at least one point occurs in the annulus is $1-e^{-\lambda(r_2^2-r_1^2)}$. The probability that the nearest point lies in the annulus is then $\exp\{-\lambda r_1^2\}[1-\exp\{-\lambda(r_2+r_1)(r_2-r_1)\}]$. The probability that the distance of the nearest point lies in an element dr at a distance r is obtained by allowing $r_2 \to r_1 = r$. Hence

$$dF(r) = e^{-\lambda r^2}\, 2\lambda r\, dr.$$

Alternatively $z = \lambda r^2$ has the exponential distribution

$$f(z) = e^{-z} \quad (0 \leqslant z < \infty).$$

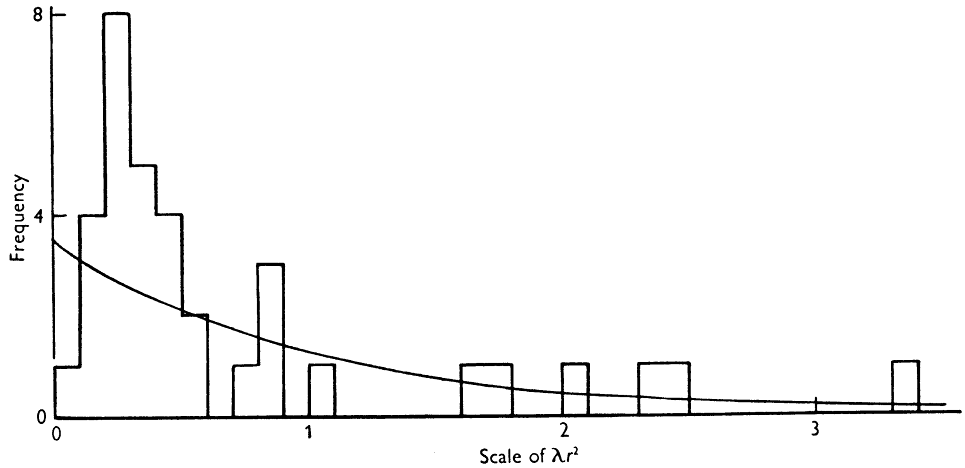
It follows that if r_j $(j = 1, 2, \ldots, n)$ are a set of independent values, the statistic $2\lambda \sum_{j=1}^{n} r_j^2$ is distributed as χ^2 with $2n$ degrees of freedom.

3·5*b*. As an illustration consider the following data referring to *Plantago major* L. in an area 2×8 metres marked out because of the apparent uniformity of the vegetation in and around it. The area was divided into 10 strips, each 20 cm. wide, and every 10th individual encountered in traversing every 2nd strip was chosen as a centre. In this way 35 centres were chosen from a total of 723 plants in the area. In some cases, of course, the nearest neighbours lay just outside the area.

The distance from the centre of one plant to that of its nearest neighbour rarely exceeded 10 cm., and was determined with sufficient accuracy by means of a ruler.

The frequency distribution of λr^2 is shown in the figure and compared with the theoretical exponential distribution. It is immediately apparent that there are few very small values of the variate due possibly to competition between nearby individuals; but there is aggregation nevertheless. For in this example the statistic $\chi^2 \equiv 2\lambda\Sigma r^2 = 47$ for 70 degrees of freedom, giving $P(\chi^2 \leqslant 47) < 0{\cdot}02$, so that the mean of the observed distribution is significantly less than that expected on the null hypothesis of randomness. The reason for this aggregation may well be that offspring tend to remain associated together in the neighbourhood of their parent.

If, of course, all we want is the general shape of the distribution of λr^2, it is not necessary for the observations to be independent, and the simplest procedure is then to draw samples from every strip, and if there is a shortage of material to use if necessary every plant in the delimited area as a centre.



3·6. There is an alternative derivation of the elementary result of § 3·2 which has a bearing on a more fundamental issue.

Imagine the area to be divided into a large number of small cells each of which is potentially capable of supporting one plant of a given species, and suppose that the chances that circumstances will actually permit a cell to support one such plant are extremely small. If the fates of the cells are independent and if in a quadrat the number of such cells is large and the conditions are similar for all quadrats, the number of plants per quadrat will vary in accordance with the Poisson law.

Observe that this conclusion follows whatever the pattern of cells might be—no matter how regular their arrangement.

The principle which emerges here is that if the elements of a uniformly dense population are exposed independently to a serious risk of extermination, the resulting census distribution will be Poissonian for large quadrats, whatever the original pattern may have been.

This phenomenon is well illustrated by the sedge *Carex arenaria* L. on sand-dunes. In the early stages of colonization, its rhizomes grow out in almost straight lines, and aerial shoots arise at almost constant intervals. The pattern is essentially that given by a number of intersecting 'dotted' lines of finite length (see Weaver & Clements, 1938, Fig. 78). At a later stage, a marked competition develops, and other species invade the area. Vegetative reproduction comes to an end, and the aerial shoots one by one disappear. For a time the original pattern may still be discerned, though not indefinitely, and towards the end the few survivors seem scattered and to all appearances at random.

There can be little doubt that this process plays a not unimportant part in maintaining that disorderliness which is such a striking feature of the plant carpet. If $G_0(z)$ is the initial distribution and $G_1(z)$ the new, and p is the probability of individual survival

$$\left.\begin{aligned} G_1(z) &= G_0(pz+q), \\ \Phi_1(u) &= \Phi_0(pu), \\ \text{and the new } \kappa_{(r)} &= p^r \times \text{old}\,\kappa_{(r)}. \end{aligned}\right\} \qquad (4)$$

Accompanying this reduction of the cumulants is a change in the form of the distribution, which becomes markedly J-shaped. In practice it is almost impossible to distinguish between samples from such a distribution and those arising from a Poisson distribution with the same low mean.

3·7. Some insight into the interpretation of the coefficient $\kappa_{(2)}/\kappa_{(1)} = \mu_2/\mu_1' - 1$ is gained by considering the effect of clustering. Suppose for illustration that the randomly distributed seedlings of some particular species give rise by vegetative multiplication to clusters of upright shoots, and for the purpose of the present argument let us suppose that the clusters are so compact in relation to the size of the quadrat that only a negligible proportion are cut through by its boundary. If $g(z)$ is the p.g.f. of the distribution of the number of shoots in a cluster, the p.g.f. of the number of shoots per quadrat will be

$$\exp\{\lambda(g(z)-1)\}.$$

The f.c.g.f. is then
$$\lambda\{\mu_{(1)}u+\mu_{(2)}u^2/2!+\ldots\},$$

where $\mu_{(r)}$ refer to the distribution of shoots per cluster. The coefficient $c_2 = \kappa_{(2)}/\kappa_{(1)}$ for the compound distribution equals $\mu_{(2)}/\mu_{(1)}$ and is independent of λ, the average number of clusters per quadrat. The only information it conveys is about the clusters themselves.

Clearly $c_2 = 0$ if and only if $g(z)$ is linear, that is, if the clusters do not contain more than one individual.

3·8. In the majority of species of plant and animal the number of potential offspring per parent is quite large and the chances of individual survival very small. Provided that the offspring develop independently of one another and that the *expected* number per family does not fluctuate widely among families, it is reasonable to assume that the actual number of offspring in a family has a Poisson distribution. Even when the premises do not strictly hold, this is a very convenient simplifying assumption, which I believe to be justified at this early stage of development of analytical biology.

3·9. The simplest compound distribution of the type considered in § 3·7 is in my opinion the Neyman Type A. It arises by putting $g(z) = e^{m(z-1)}$, a step which can be justified in the circumstances such as those discussed in § 3·8. Its p.g.f. is then

$$\exp\{\lambda(e^{m(z-1)}-1)\} \tag{5}$$

and
$$\kappa_{(r)} = \lambda m^r.$$

The distribution has been applied to plant quadrat work (Archibald, 1948; Barnes & Stanbury, 1951), and to the quadrat sampling of insect larvae (Beall, 1940), where the larvae arise from batches of eggs laid at random and are presumed not to spread very far from their starting point.

3·10. In the model we have just considered, the parent plants disappear on giving rise to the next generation. If, however, they were to persist it would be necessary to write $g(z) = z\,e^{m(z-1)}$ as the g.f. of the number of individuals in a cluster.

We then obtain the compound distribution

$$G(z) = \exp\{\lambda(z\,e^{m(z-1)}-1)\}, \tag{6}$$

derived otherwise by Thomas (1949). The necessary conditions might well hold in the second year of colonization of open ground (Barnes & Stanbury, 1951). The distribution is not genuinely applicable if the clusters are not compact, or if the process extends to later generations, so that its usefulness is limited. The distribution is sometimes unfortunately called the double Poisson, a term which could more appropriately be given to Neyman's Type A distribution, and has been regarded by Archibald (1950) as the simplest of the contagious distributions. One reason why Thomas's distribution sometimes gives slightly better graduations than the ordinary Neyman Type A is, I think, because in the latter $g(z) = e^{m(z-1)}$ fails to reflect the effects of the competition which so often occurs within a compact aggregate of individuals with similar requirements. Now in a case of this sort it can be shown that the classical binomial distribution is more appropriate than the Poisson. We then have

$$G(z) = \exp\{\lambda[(pz+q)^n - 1]\}. \tag{7}$$

The graduation of Miss Archibald's data on *Carex flacca* Schreb. by this function (with $n = 3$; $p = 0{\cdot}295416$; $\lambda = 1{\cdot}59323$) is shown in Table 1, col. iv, and compared with the excellent graduation (col. iii) already given by Miss Archibald using the Thomas series.

Table 1

Plants per quadrat	Observed frequency	(iii)	(iv)
0	181	174·31	177·45
1	118	130·72	124·38
2	97	92·14	95·75
3	54	53·31	54·03
4	32	27·01	27·37
5	9	12·50	12·55
6	5	3·45	5·22
7	9 { 3	10 { 2·16	8·5 { 2·1
8	1		

3·11. If the number of individuals in a cluster has the Pascal or negative binomial distribution $g(z) = (1-\tau)^k(1-\tau z)^{-k}$, a very reasonable possibility, we obtain as the g.f. of the number of individuals per quadrat the expression

$$G(z) = \exp\left\{\lambda\left[\left(\frac{1-\tau}{1-\tau z}\right)^k - 1\right]\right\}. \tag{8}$$

I propose to call this the generalized Polya-Aeppli distribution. The special case where $k = 1$, so that $g(z)$ is geometric, is given in Polya (1930) in another connexion, and its properties are mentioned by Anscombe (1950). This case, with $g(z)$ geometric, applies as a close approximation where the clusters have arisen by branching stochastic processes analogous to those considered by D. G. Kendall (1948) and others in continuous time.

3·12. If in the previous example k is very small,

$$\frac{g(z)-1}{k} \simeq \log\left(\frac{1-\tau}{1-\tau z}\right).$$

The g.f. of the distribution is then the Pascal distribution

$$G(z) = (1-\tau)^{k\lambda}(1-\tau z)^{-k\lambda}. \tag{9}$$

This result is clearly equivalent to Quenouille's theorem (1949), originally given in connexion with the distribution of the number of bacteria per Petri dish on the assumption that the number of colonies had a Poisson distribution and the number of bacteria per colony a logarithmic one.

3·13. As an illustration of the dangers to be faced in interpreting the parameters of a frequency distribution in terms of the biological situation, it may be noted that

$$\exp\{\lambda[g(z)-1]\} = \exp\{\Lambda[\gamma(z)-1]\}$$

if

$$\gamma(z) = \frac{a+g(z)}{a+1} \quad \text{and} \quad \Lambda = \lambda(a+1),$$

where a is arbitrary. Hence, even if this kind of model is appropriate, the frequency data tell us nothing of the term independent of z in $g(z)$. It is advisable to fix this arbitrarily as zero unless other information is available, and to interpret λ as the density of actual rather than potential clusters.

3·14*a*. Unlike the previous examples, we now consider the case where the aggregates are not compact and the quadrat small in comparison.

Consider a large two-dimensional area $(-n \leqslant x \leqslant n;\ -n \leqslant y \leqslant n)$ and a number $(4n^2c/\pi)$ of centres of aggregation (x_j, y_j) scattered at random through the region. Thus c is the average number of centres in a circle of unit radius. At first for simplicity it is supposed that all clusters contain M potential individuals, and the co-ordinates of the individuals belonging to the jth cluster are distributed as a random sample from the bivariate normal population

$$dP = \pi^{-1}\exp\{-(x-x_j)^2-(y-y_j)^2\}\,dx\,dy.$$

This is the familiar distribution of shots round a bull's eye.

In this way the unit of distance is taken as the root-mean-square deviation from the centre of the population. For the present we place a quadrat at the origin. Its size is πh^2, where h is much less than unity. Later we shall allow n to tend to infinity, so that it will be immaterial whether the quadrat is at the origin or not. Since the quadrat is quite small the probability distribution of the number of individuals falling into it from the jth cluster will be given by

$$g(z) = \exp\{\lambda_j(z-1)\},$$

where

$$\lambda_j = q\exp\{-x_j^2-y_j^2\} \quad \text{and} \quad q = Mh^2v,$$

v being the probability of individual survival. The contributions from all clusters may be compounded by multiplying their generating functions. The resultant distribution is then

$$G(z) = \prod_j \exp\{\lambda_j(z-1)\}.$$

The distribution so far is based on a particular disposition of the centres (x_j, y_j). We shall require $G_n(z)$ the mean value of $G(z)$ for all possible arrangements of the centres. Since $G(z)$ is the product of independent distributions it follows that

$$G_n(z) = [\mathscr{E}\{e^{\lambda_j(z-1)}\}]^{4n^2c/\pi} = [1+\mathscr{E}\{e^{\lambda_j(z-1)}-1\}]^{4n^2c/\pi}.$$

The f.m.g.f. of this distribution is

$$\Phi_n(u) = \left[1+\frac{1}{4n^2}\int_{-n}^{n}\int_{-n}^{n}(e^{uq\exp\{-x^2-y^2\}}-1)\,dx\,dy\right]^{4n^2c/\pi}$$

By the polar transformation $x = r\cos\alpha$, $y = r\sin\alpha$, the double integral may be written

$$\int_0^{2\pi} d\alpha \int_0^{n\theta} (e^{uq\exp\{-r^2\}}-1)\,r\,dr,$$

where $1 < \theta < \sqrt{2}$ for the integrand does not change sign. It follows that

$$\Phi(u) \equiv \lim_{n\to\infty} \Phi_n(u) = \exp\left\{c\int_0^\infty (e^{uq\exp\{-r^2\}}-1)\,2r\,dr\right\}.$$

Hence
$$\Psi(u) = c\int_0^q (e^{ut}-1)\frac{dt}{t} = c\sum_{j=1}^{\infty} q^j u^j/(j\,.\,j!). \tag{10}$$

The coefficient of $u^j/j!$ is the jth factorial cumulant

$$\kappa_{(j)} = cq^j/j!.$$

The following relations may then be deduced:

$$\kappa_{(1)} = cq, \quad \text{as is otherwise obvious,} \tag{11}$$

$$\kappa_{(2)}/\kappa_{(1)} = \tfrac{1}{2}q, \tag{12}$$

$$2\kappa_{(2)}/\kappa_{(1)}^2 = 1/c. \tag{13}$$

The criterion
$$\kappa_{(3)}\kappa_{(1)}/\kappa_{(2)}^2 = \tfrac{4}{3}.$$

3·14*b*. It should be noted that $c_2 = \kappa_{(2)}/\kappa_{(1)}$ increases with the number in a cluster, as in the distributions referred to in §§ 3·7–3·12. The present case is different, however, in that c_2 necessarily increases with quadrat size—a phenomenon which is well known to statistical ecologists. The following data on *Plantago major* L. were obtained in the same locality using two quadrat sizes, one twice the other.

	Distribution (i)	Distribution (ii)	Ratio (i)/(ii) theory
No. of observations	400	200	
$\kappa_{(2)}/\kappa_{(1)}$	1·32	2·40	1:2
$\kappa_{(3)}/\kappa_{(2)}$	2·00	4·06	1:2
$\kappa_{(1)}\kappa_{(3)}/\kappa_{(2)}^2$	1·52	1·69	(i) = (ii) = 4/3

From the consistency shown in the above comparison a measure of support can be drawn for the hypothesis that the model discussed here is a reasonably adequate representation of the actual spatial pattern, and to my mind this support is of a kind different from but supplementary to that afforded by the fitting of frequency data alone (see Table 2, Graduation I).

3·14*c*. As in most compound distributions there is no simple formula for the general term of $G(z)$. In practice, however, we can obtain actual numerical graduations simply by expanding the g.f. in a systematic way. We require p_r the coefficient of z^r in $\exp\{\Psi(z-1)\}$. Since

$$\frac{\partial^r}{\partial z^r}\int_0^q (e^{(z-1)t}-1)\frac{dt}{t}\bigg|_{z=0} = \int_0^q t^{r-1}e^{-t}\,dt = \Gamma_q(r) \quad (r>0),$$

the coefficient of z^r in $\Psi(z-1)$ is $\quad a_r = c\Gamma_q(r)/r\Gamma(r)$.

In the notation employed in Pearson's actual table of the Incomplete Gamma Function,

$$a_r = \frac{c}{r} I\left(\frac{q}{\sqrt{r}}, r-1\right).$$

Alternatively
$$a_r = \frac{c}{r}e^{-q}\sum_{j=r}^{\infty} q^j/j!.$$

From this it is clear that a_r tend rapidly to zero as r increases.

We may now write
$$G(z) = e^{a_0} \prod_{r=1}^{\infty} \exp\{a_r z^z\},$$
where
$$a_0 = -\sum_{r=1}^{\infty} a_r, \quad \text{since} \quad G(1) = 1.$$

$G(z)$ is obtained as a power series by systematically multiplying exponential series. The computation is not formidable unless the variate extends to 15 or more. The simplest way of estimating the parameters is to substitute the sample values of $\kappa_{(1)}$ and $\kappa_{(2)}$ in relations (12) and (13) of § 3·14*a*. If q is small, there is good reason to think the procedure efficient for the estimation of the product cq for the distribution then approximates to the Poisson form.

In the numerical example which follows the estimates by moments are $q = 2{\cdot}63518$ and $c = 0{\cdot}323507$. Even so, the fit is quite good (Graduation I). The data relate to the distribution of the number of plants of *Plantago major* present in quadrats of area 100 sq.cm. laid down in grassland.

Table 2

Plants per quadrat	Observed frequency	Graduation I	Graduation II	Graduation III	Graduation IV
0	235	240·91	235·37	232·05	234·00
1	81	72·35	80·13	85·36	80·23
2	43	39·67	40·74	39·97	44·00
3	18	22·48	20·95	20·05	19·41
4	9	12·22	10·86	10·40	10·27
5	6	6·33	5·67	5·50	5·46
6	4	3·15	2·97	2·94	2·92
7	3	1·52	1·56	1·59	1·58
8	—	0·72		0·87	0·86
9	1	0·33		0·48	0·48
10	4 { —	2·85 { 0·15	3·3	3·73 { 0·26	3·71 { 0·26
11	—	0·07			
12	—	0·04			
13	—	0·02			
	400				

3·15. It is instructive to consider the distribution of the difference between the readings of two quadrats taken from the model studied in the previous paragraph.

(*a*) If the quadrats are laid down independently of one another, the difference between their readings has p.g.f. $G(z)\,G(z^{-1})$, so that the cumulant generating function is
$$\log G(e^t) + \log G(e^{-t}).$$
The odd order cumulants vanish. and those of even order are twice those of the distribution of a single reading. In particular,
$$\kappa_2 = 2cq(1+\tfrac{1}{2}q),$$
$$\kappa_4 = 2cq(1+\tfrac{7}{2}q+2q^2+\tfrac{1}{4}q^3).$$

(*b*) If a *small* quadrat is divided into two equal parts, pairs of readings can be taken simultaneously and compared. As in § 3·14*a*, consider the quadrats placed at the origin and the contributions made to them by the jth aggregate. The distribution of the difference between the two values has p.g.f.
$$\gamma(z) = \exp\left\{\lambda_j(z-1) + \lambda_j\left(\frac{1}{z}-1\right)\right\},$$
where
$$\lambda_j = q\exp\{-x_j^2 - y_j^2\}.$$

Proceeding exactly as in § 3·14a we find, after compounding the contributions from all aggregates and taking the mean value for all possible positions of the centres of aggregation, and proceeding to the limit, that the resulting generating function is

$$G(z) = \exp\left\{c\int_0^q \left(e^{w\left(z-2+\frac{1}{z}\right)}-1\right)\frac{dw}{w}\right\}.$$

The cumulant g.f. is then $$\Psi(t) = c\int_0^q (e^{2w(\cosh t-1)}-1)\frac{dw}{w},$$

giving

$$\kappa_{2n+1} = 0,$$
$$\kappa_2 = 2cq,$$
$$\kappa_4 = 2cq(1+3q),$$
$$\kappa_6 = 2cq(1+15q+20q^2).$$

If aggregation is negligible so that q is small, the distribution degenerates into the difference between two independent Poisson variates (Irwin, 1937; Skellam, 1946).

(c) If the twin quadrats have their centres $2s$ units apart with the origin midway between them, the g.f. of the difference between their readings due solely to the jth aggregate is

$$G(z) = \exp\left\{\lambda_A(z-1)+\lambda_B\left(\frac{1}{z}-1\right)\right\},$$

where $$\lambda_A = q\exp\{-x_j^2-y_j^2-s^2+2s(x_j\cos\alpha+y_j\sin\alpha)\},$$
$$\lambda_B = q\exp\{-x_j^2-y_j^2-s^2-2s(x_j\cos\alpha+y_j\sin\alpha)\},$$

and $\alpha=$ the angle between the X-axis and the line joining the centres of the twin quadrats. Continuing exactly as before we obtain the cumulant generating function

$$\psi(t) = \frac{c}{\pi}\int_0^{2\pi}\int_0^\infty (\exp\{q(e^t-1)\,e^{-r^2-s^2+2sr\cos\gamma}+q(e^{-t}-1)\,e^{-r^2-s^2-2sr\cos\gamma}\}-1)\,r\,dr\,d\gamma.$$

By picking out the coefficient of $\frac{1}{2}t^2$ it will be seen that

$$\kappa_2 = \frac{c}{\pi}\int_0^{2\pi}\int_0^\infty (q\,e^{-r^2-s^2+2sr\cos\gamma}+q^2\,e^{-2r^2-2s^2}[e^{4sr\cos\gamma}-1])\,2r\,dr\,d\gamma.$$

Since $$\frac{1}{2\pi}\int_0^{2\pi} e^{2b\cos\gamma}\,d\gamma = I_0(2b) = \sum_{j=0}^{\infty} b^{2j}/(j!)^2,$$

where $I_0(x)$ is the modified Bessel function of the first kind, and since

$$\int_0^\infty e^{-R}\,I_0(2sR^{\frac{1}{2}})\,dR = \sum_{j=0}^{\infty}\frac{s^{2j}}{j!}\int_0^\infty e^{-R}\frac{R^j}{j!}\,dR = e^{s^2},$$

it follows that $$\kappa_2 = 2cq+cq^2(1-e^{-2s^2}). \tag{14}$$

When $s=0$, this result degenerates into that for adjacent quadrats, and, when $s\to\infty$, becomes that for independent quadrats.

Using twin quadrats with centres 10 cm. apart, the distribution of the difference between their readings was

Difference	−5	−4	−3	−2	−1	0	1	2	3	4	5	6	Total
Frequency	1	2	5	11	30	102	28	9	7	2	2	1	200

$m_2' = 2{\cdot}105$. The values of c and q have already been given as $c = 0{\cdot}3235$ and $q = 2{\cdot}635$. If these values are substituted into (14) it is found that $s = 0{\cdot}3$ approx., corresponding to a root-mean-square dispersion of about 17 cm.

Results of this kind are helpful in judging the adequacy of the basic model, for estimates of some particular aspect of the physical situation can always be compared with the direct evidence afforded to our senses; whilst sets of estimates obtained by varying the choice of quadrat size or distance between quadrats should be reasonably consistent among themselves.

3·16. From the theoretical standpoint, the distributions we have so far considered are rarely applicable to patterns which have arisen by processes operating over a large number of generations. We shall now suppose that a quadrat contains a number of annual plants, that one such plant will on the average give rise to η offspring within the quadrat and an unspecified number outside, and that an average of ϵ plants per quadrat originate from parents outside that quadrat. The reasonable simplifying assumption that the distribution of offspring is Poissonian leads to the equation

$$G(z) = e^{\epsilon(z-1)}\,G(e^{\eta(z-1)}) \tag{15}$$

as the condition for a stochastic equilibrium. This equation has been discussed by Haldane (1949) and Skellam (1948) in connexion with an analogous problem in evolutionary genetics. The equation may be written in the form

$$\Psi(u) = \epsilon u + \Psi\left(\eta u + \tfrac{1}{2}\eta^2 u^2 + \frac{1}{3!}\eta^3 u^3 \ldots\right),$$

whence

$$\kappa_{(1)} = \epsilon/(1-\eta),$$

$$\kappa_{(2)} = \epsilon\eta^2/(1-\eta)(1-\eta^2),$$

$$\kappa_{(3)} = \epsilon\eta^3(1+2\eta^2)/(1-\eta)(1-\eta^2)(1-\eta^3),$$

$$\kappa_{(1)}\kappa_{(3)}/\kappa_{(2)}^2 = (1+\eta^2)(1+\eta)/[\eta(1+\eta+\eta^2)] \simeq 2 \quad \text{if} \quad \eta \simeq 1.$$

The Pascal distribution is known to provide excellent approximations (Skellam, 1948) and to be exact for the corresponding problem in continuous time (D. G. Kendall, 1948).

3·17. If a discrete distribution ($x = 0, 1, 2, \ldots$) can be represented approximately by $f^*(x)$, then a closer approximation can be found in terms of $f^*(x)$ and its receding differences.

For if $f^*(x) = 0$ for $x < 0$ it is easily seen that

$$\sum_{x=0}^{\infty} (1+u)^x \nabla f^*(x) = -u \sum_{x=0}^{\infty} (1+u)^x f^*(x),$$

and by repetition that

$$\sum_{x=0}^{\infty} (1+u)^x (-\nabla)^r f^*(x) = u^r \sum_{x=0}^{\infty} (1+u)^x f^*(x).$$

If now $L(u)$ is a polynomial it follows that $f(x) = L(-\nabla) f^*(x)$ has f.m.g.f.

$$\Phi(u) = L(u)\,\Phi^*(u), \tag{16a}$$

where Φ^* refers to f^*.

If $$L(u) = \Sigma a_r u^r/r! = \exp \Sigma b_r u^r/r!$$

it follows that $$b_r = \kappa_{(r)} - \kappa^*_{(r)}. \tag{16b}$$

The well-known relations expressing a_r in terms of b_r are greatly simplified if the parameters of f^* are chosen so that the earlier $\kappa^*_{(r)} = \kappa_{(r)}$.

Owing to the very considerable sampling error of the higher $\kappa_{(r)}$ it is not advisable to estimate the coefficients of L by substituting sample values in (16*b*).

A more satisfactory procedure is to select a really suitable 'kernel' and to improve it by only one or two correction terms. If $\hat{f}(x)$ is the graduation at any stage, $E(x)$ the error and $aC(x)$ the next correction term to be applied, then the coefficient a may be determined by the formula

$$a = \Sigma QE/\Sigma QC,$$

where $Q = C/\hat{f}$, much in accordance with the principle of minimum χ^2.

In Table 2, col. iv, is shown a graduation given by the Pascal distribution,

$$f^*(x) = (1-\theta)^k k(k+1)\dots(k+x-1)\,\theta^x/x!,$$

with $\theta = 0{\cdot}568517$ and $k = 0{\cdot}647015$. Both are estimated by means of the first two factorial cumulants of the observed distribution.

Col. v gives the graduation based on

$$f(x) = f^*(x) + 0{\cdot}0084\nabla^3 f^*(x).$$

Despite the remarkably close fitting (or over-fitting) achieved by series developments of this kind, I do not feel that such graduations contribute directly to the understanding of the biological issues involved.

3·18. If a census distribution has a Gram-Charlier development

$$f(x) = \left(1 + \sum_{r=2}^{\infty} a_r(-\nabla)^r/r!\right) e^{-\lambda}\lambda^x/x!$$

and if the individual organisms are subjected to a process of random selection as in § 3·6, it will be seen by writing pu for u in $\Phi(u)$, expressed as in (16*a*), that the new probability function

$$f_1(x) = \left(1 + \sum_{r=2}^{\infty} a_r(-p\nabla)^r/r!\right) e^{-\lambda p}(\lambda p)^x/x!. \tag{17}$$

If p becomes small it is clear that the *absolute* effect of the operator becomes negligible. It is of interest, however, that the values in the tail of the distribution though vanishingly small still remain abnormally disproportionate relative to those of the Poisson kernel, for the effect of the operation $\{p^r(-\nabla)^r\}(\lambda p)^x/x!$ relative to $(\lambda p)^x/x!$ as $p \to 0$ tends to $x^{(r)}/\lambda^r$, and this vanishes only when $x < r$.

This effect is illustrated numerically in Table 3. The initial p.f. was $f_0(x) = (1+\frac{1}{5}\nabla^2)\,e^{-1}/x!$. In col. ii is shown the distribution resulting from random selection with $p = \frac{1}{10}$ calculated by formula (17). The Poisson kernel is given in col. iii. The ratios between the corresponding values of the distribution and the kernel are given in col. iv, and the limiting values of those ratios in col. v.

In a sense, the vestigial remains of former non-randomness seem to be concentrated in the tail, where unfortunately in practice there are usually insufficient observations to permit the reconstruction of the archetype.

Table 3

(i)	(ii)	(iii)	(iv)	(v)
0	0·906647	0·904837	1·00	1·00
1	0·087046	0·090484	0·96	1·00
2	0·005981	0·004524	1·32	1·40
3	0·000314	0·000151	2·08	2·20
4	0·000012	0·000004	3·2	3·40

3·19. The species which are present in a region have varying abilities to tolerate the particular sets of conditions which exist locally. The slightest change in the vital coefficient in a dynamical system of interacting and competing species can have profound effects on the abundance and survival of the various components (Volterra, 1931; Skellam, 1951).

As a result, minute environmental differences are often reflected in a striking way in the composition of the flora and fauna. Even in small areas differences in the composition of the soil commonly occur sufficient to produce an irregular and perhaps ill-defined patchwork in the structure of the associated plant carpet.

This patchiness is particularly well marked in an unstable vegetation system, as, for example, where grassland gives way to heather moor, for the succession from one phase to the next does not proceed at the same rate everywhere. Stable climax vegetation has a more uniform texture, but even here we find a mosaic of variability determined by the disposition of the more dominant organisms.

Such heterogeneity is itself largely the outcome of apparently random events. Patches of shade plants may occur where a tree happens to have established itself, or nitrophilous species where animal excreta has enriched the soil. Irregular channels are eroded in uniform surfaces by the action of water and the sun cracks of drying mud have their own peculiar flora and fauna (see Weaver & Clements, 1938, Fig. 79).

3·20. In previous theorems we have considered a number of distributions arising from quadrat sampling under uniform conditions. Let $G(z, \theta)$ denote such a distribution. If now conditions vary in different parts of the region being sampled, so that the parameter θ has a distribution of its own, the resulting distribution will be

$$G(z) = \int_{-\infty}^{\infty} G(z, \theta)\, dF(\theta),$$

and similar expressions follow for ϕ and Φ.

The simplest case is that of the Poisson distribution with variable λ

$$\Phi(u) = \int_0^{\infty} e^{\lambda u}\, dF(\lambda).$$

Hence the factorial moments of the distribution are the power moments of the distribution of λ. Unbiased estimates of the moments of the unknown distribution of λ are therefore given by the sample values of the factorial moments of the census distribution.

(*a*) In the familiar case studied by Greenwood & Yule (1920) λ is a gamma variate. Hence

$$\Phi(u) = \int_0^{\infty} e^{\lambda u} e^{-p\lambda} \lambda^{k-1} p^k\, d\lambda/\Gamma(k)$$
$$= \left(1 - \frac{u}{p}\right)^{-k}, \qquad (18)$$

the f.m.g.f. of the Pascal distribution.

(*b*) If $\lambda = av$, a being constant, then $\Phi(u) = \phi(au)$, where ϕ is the m.g.f. of the distribution of v.

In particular, if v is approximately equivalent to a Poisson variate so that

$$\phi(t) = \exp\{m(e^t - 1)\},$$

we find that $\Phi(u) = \exp\{m(e^{au} - 1)\}$, the f.m.g.f. of Neyman's distribution of Type A.

(*c*) When the basic distribution is the Pascal

$$[\text{f.m.g.f.} = (1-\gamma u)^{-k}]$$

in which the parameter $k = av$ varies as in the previous example, we obtain

$$\Phi(u) = \sum_{v=0}^{\infty} (1-\gamma u)^{-av} e^{-m} m^v/v!$$
$$= \exp\{m[(1-\gamma u)^{-a} - 1]\}, \tag{19}$$

which is the f.m.g.f. of a generalized Polya-Aeppli distribution (3·11) with $\tau = \gamma/(1+\gamma)$.

3·21*a*. As an illustration of the effect of heterogeneity on distributions arising from the use of small quadrats let us generalize the model of § 3·14 by taking c (the expected number of clusters in a unit circle) as a gamma variate

$$dP = \theta^{\omega} e^{-\theta c} c^{\omega-1} dc/\Gamma(\omega) \quad (0 \leqslant c < \infty),$$

with $\omega/\theta = \tilde{c}$ the mean value of c. For fixed c the f.m.g.f. is $e^{c\Omega}$, where $\Omega(u,q) = \sum_{j=1}^{\infty} u^j q^j/(j!j)$. The resulting generalization is then

$$\Phi(u) = \theta^{\omega} \int_0^{\infty} e^{-c[\theta-\Omega]} c^{\omega-1} dc/\Gamma(\omega)$$
$$= [1-\tilde{c}\Omega/\omega]^{-\omega}. \tag{20}$$

The factorial cumulants are $\kappa_{(1)} = \tilde{c}q$,

$$\kappa_{(2)} = \tilde{c}q^2\left(\frac{1}{2}+\frac{\tilde{c}}{\omega}\right),$$

$$\kappa_{(3)} = \tilde{c}q^3\left(\frac{1}{3}+\frac{3\tilde{c}}{2\omega}+\frac{2\tilde{c}^2}{\omega^2}\right),$$

and

$$\kappa_{(1)}\kappa_{(3)}/\kappa_{(2)}^2 = (4\theta^2+18\theta+24)/(3\theta^2+12\theta+12)$$

takes values in the range $\frac{4}{3}$ to 2. At one extreme the distribution is identical with that of § 3·14, and at the other with the Pascal distribution. By reason of the expansion of $\Omega(z-1,q)$ already considered (§ 3·14*c*), the p.g.f. of the distribution may be written in the form

$$G(z) = \left[\frac{1-\sum_{r=1}^{\infty} b_r}{1-\sum_{r=1}^{\infty} b_r z^r}\right]^{\omega}, \tag{21}$$

where the coefficients are obtained either by employing tables of the Incomplete Gamma Function or alternatively by

$$b_r = s_r \Big/ \left(\frac{\omega e^q}{\tilde{c}} - \sum_{j=i}^{\infty} s_j\right),$$

where

$$s_r = \frac{1}{r}\sum_{k=r}^{\infty} \frac{q^k}{k!}.$$

3·21*b*. Graduated values may be obtained if required by the systematic expansion of $G(z)$. Since the b's are small the powers of b soon vanish, and of course no coefficient of z^x in $\Sigma b_r z^r$ is needed for $x >$ maximum variate value required.

There is a useful independent check on the probability that $x = 0$, for

$$G(0) = \left[1 - \frac{\tilde{c}}{\omega}\Omega(-1, q)\right]^{-\omega}$$

and
$$\Omega(-1, q) = \int_0^q (e^{-t} - 1)\frac{dt}{t} = -[C + \log q - \mathrm{Ei}(-q)], \tag{22}$$

where C is Euler's constant and $-\mathrm{Ei}(-z)$ is the exponential integral $\int_z^\infty e^{-t}\,dt/t$ which has been tabulated.

Rough estimates of the parameters are readily obtained, using the sample values of the first three factorial cumulants as population cumulants. In practice I have found it preferable to modify them so as to satisfy the first two factorial cumulants and the observed frequency at $x = 0$, for if quadrat size is small (as it has been assumed to be) this class is by far the greatest and its weight considerable.

For any given trial value of q we can find in succession

(i) $\tilde{c} = \kappa_{(1)}/q$, (ii) $\tilde{c}/\omega = \kappa_{(2)}/(q\kappa_{(1)}) - \frac{1}{2}$,
(iii) ω from (i) and (ii), (iv) $\Omega(-1, q)$ by 22, (v) $G(0)$.

As an illustration, the following trials were made during the graduation of the *Plantago* data given earlier:

	By moments	1st trial	2nd trial	3rd trial
q	1·5717	1·5	1·0	0·6
$NG(0)$	238·9	238·7	237·1	235·37

The fitted values with $q = 0{\cdot}6$ are shown as Graduation II in Table 2.

3·22. In the case of contagious distributions an additional complication arises when the individuals of the same species differ in their reproductive potential. When these differences are an expression of genetic variability within the species they are displayed under constant environmental conditions.

As an illustration consider the effect of such variation on the model of § 3·9, where the resulting distribution is Neyman Type A. The distribution of the number of individuals per cluster will now be

$$g(z) = \int_0^\infty \exp\{m(z-1)\}\,dF(m).$$

Under the hypothesis that m has a Gamma distribution (compare § 3·20), the distribution of the number of individuals per quadrat, which is $G(z) = \exp\{\lambda(g(z) - 1)\}$, will be seen to be the general Polya-Aeppli (§ 3·11).

As a further example, suppose that in the model of § 3·14a, $q = Mh^2v$ has distribution function $F(q)$ and m.g.f. $\phi(t)$.

We then have

$$\Phi(u) = \exp\left\{\frac{c}{\pi}\int_0^\infty \int_0^{2\pi} \int_0^\infty [\exp\{uq\,e^{-r^2}\} - 1]\,r\,dr\,d\alpha\,dF(q)\right\},$$

$$\Psi(u) = c\int_0^\infty \int_0^1 [\exp\{uqt\} - 1]\frac{dt}{t}\,dF(q)$$

$$= c\int_0^1 [\phi(ut) - 1]\frac{dt}{t} = c\sum_{r=1}^\infty \frac{\mu_r''}{r}\frac{u^r}{r!},$$

where the μ'' refer to the distribution of q.

In the special case where q has an exponential distribution,

$$\phi(t) = \chi/(\chi-t),$$

$$\Psi(u) \doteq c\int_0^1 \frac{u\,dt}{\chi-ut} = -c\log\left[1-\frac{u}{\chi}\right],$$

and $\Phi(u) = \left[1-\dfrac{u}{\chi}\right]^{-c}$ the f.m.g.f. of the resulting Pascal distribution.

4. Summary and Conclusions

1. A number of distributions arising in quadrat sampling are considered in relation to the underlying pattern of organisms.

2. It is most noticeable that the same distribution may arise from several quite distinct models.

3. Satisfactory graduations of frequency data are usually possible on a wide variety of alternative hypotheses.

4. Whether a given model is appropriate must be determined in the light of additional evidence of a different kind. A few ways are briefly suggested as to how this problem might be approached.

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