APPLICATION OF THE $\overset{*}{m}$-m METHOD TO THE ANALYSIS OF SPATIAL PATTERNS BY CHANGING THE QUADRAT SIZE[1]

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INTRODUCTION

In previous papers (IWAO, 1968; IWAO and KUNO, 1971), a comprehensive method for analyzing the aggregation patterns in biological populations has been developed on the basis of the relation of mean crowding ($\overset{*}{m}$) to mean density (m); for a given quadrat size, the relation of $\overset{*}{m}$ on m in a series of populations having common properties can widely be fitted by a linear regression, $\overset{*}{m} = \alpha + \beta m$. Here, α indicates whether a single individual or a positive or negative association of individuals is the basic component of the distribution, and β suggests how such basic components distribute themselves over the space.

It is well known, however, that statistical characteristics of the distribution of a given population may often be different when the size of the quadrat used is different. The purpose of the present paper is first to examine some basic $\overset{*}{m}$-m relationships that are expected when quadrat size changes successively in a single population as well as in a series of populations having common properties, and secondly to develop a method for detecting the spatial structure of biological populations on the basis of these relationships. Similar lines of research have been attempted by GREIG-SMITH (1952) and MORISITA (1959); the former proposed a method for detecting the approximate area occupied by a clump[2] (refer to as *clump area*, in distinction from *clump size*, the number of individuals per clump) by using the mean-square-versus-quadrat-size relation in a grid of contiguous quadrats, and the latter devised a means of detecting not only clump area but also the spatial pattern of individuals within clumps (*intra-clump distribution*) by use of his I_δ-index. Both the methods, however, do not provide any information on the distribution pattern of clumps themselves, which is often more desirable to know by ecologists than the clump area.

Although the $\overset{*}{m}$-m method is intimately related with I_δ, the $\overset{*}{m}$-m relation with successive changes of quadrat size in a single population (*unit-size relation*) may suggest some additional information such as the distribution pattern of clumps, at least in some cases. Moreover, if the distribution maps for several populations of

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[1] Contributions from JIBP-PT, No. 151.

[2] 'Clump' is used as a general term which includes not only aggregate of individuals related to innate properties of the species ('colony') but also any concentration of individuals in response to environmental heterogeneity.

the species under study are available, we can get the $\overset{*}{m}$-m relation between popu-
lations for each of successive quadrat sizes (*series relation*) as well. The more
detailed picture of the spatial structure of the species is thus obtainable by the
combined use of both the unit-size and the series relations of $\overset{*}{m}$ on m.

THEORETICAL CONSIDERATIONS

Random Distributions

When individuals are distributed purely at random over the whole area (assumed
infinite), we have a Poisson distribution at any size of the quadrat unit:

$$\overset{*}{m}_u = m_u, \tag{1}$$

where u stands for the relative size of quadrat, i. e., the ratio of a given quadrat
size to the quadrat size taken as a standard ($u=1$). Namely, the $\overset{*}{m}$-on-m regression
with changing u passes through the origin ($\alpha'=0$) with the slope of unity ($\beta'=1$)[1],
as in the series relation for randomly distributed populations.

If the area is finite, however, the binomial distribution would be expected and
the relation is being

$$\overset{*}{m}_u = m_u - 1/N_u = um_1 - u/N_1 \tag{2}$$

or

$$\overset{*}{m}_u = (1-1/T)m_u, \tag{2'}$$

where N_u is the total number of quadrats of size u contained in the population and
$T=m_u N_u$ the total number of individuals. The regression of $\overset{*}{m}_u$ on m_u, therefore,
passes through the origin but its slope would become somewhat smaller than unity
$(\beta'=1-1/T)$, if the total number of individuals in the population is not large. It
should be noted that in a series of randomly distributed populations over the finite
space, the series $\overset{*}{m}$-m relation for a fixed quadrat size has the intercept of $-1/N_u$
and the slope of unity, which is different from the unit-size relation in a single
population.

Since usually T is not so small in our cases, the following discussion will be
confined to the infinite population.

Uniform (Regular) Distributions

If every quadrat has the same probability being occupied by an individual but
the capacity of quadrat is limited, we have the positive binomial distribution. The
relation is shown by

$$\overset{*}{m} = m - m/k',$$

where k' is the maximum number of individuals possible in a quadrat (IWAO, 1968).
This pattern may be expected when each individual occupies an exclusive space

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[1] Since the $\overset{*}{m}$-on-m regression in the unit-size relation is not necessarily identical with
that in the series relation, the symbols α' and β' is generally used to describe the inter-
cept and the slope of the regression in the former if $\overset{*}{m}_u$ is linearly related with m_u.

due to territorial behaviour or competition for space. Let assume as a standard the small-sized quadrat into which just one territory area could contain (i.e., $k'_1 = 1$), then $\overset{*}{m}_u = 0$ for the quadrat size equal to, or smaller than, this. With increasing the quadrat size, both m_u and k'_u increase at the same rate, and hence m_u/k'_u remains constant and equals m_1. This means that the $\overset{*}{m}_u$-m_u relation is linear with the intercept of $-m_1$ and the slope of unity. In other words $(\overset{*}{m}_u + m_1)/m_u$, instead of $\overset{*}{m}_u/m_u$, equals unity in this case. Thus the relation is expressed by

$$\overset{*}{m}_u = m_u - m_u/k'_u = m_u - m_1. \tag{3}$$

The completely uniform distribution can be considered as a special case where $m_1 = 1.0$. Thus the intercept α' will change between 0 and -1 according to the level of density, m_1. When k'_u is infinitively large, the distribution converges to the Poisson.

For a fixed quadrat size, the $\overset{*}{m}$-m relation for a set of populations conforming the positive binomial distribution with a common k' is also linear but it passes through the origin and has the slope of $1 - 1/k'$ (IWAO, 1968). With increase of quadrat size, therefore, the slope β of the series relation will increase towards unity.

The uniform pattern can be defined without any assumption on the capacity of quadrat. Biologically this may happen when the negative contagion process through repulsive interaction among individuals takes place as observed in egg deposition of the azuki bean weevil, *Callosobruchus chinensis* (IWAO and KUNO, 1971). In such a case, there may be a particular quadrat size corresponding to the basic habitat unit characteristic of the species on which repulsive interaction can operate. For larger quadrat sizes, therefore, the distribution pattern may often be clumped. Similarly, we can imagine various kinds of non-random arrangements of territories over the space, resulting in the change of distribution from uniform to aggregated pattern with increasing the quadrat size.

It might be possible to assume the pattern whose unit-size $\overset{*}{m}$-m relation can be fitted by a linear regression with a slope lower than unity, but biological process generating such a pattern is not easily conceivable.

Aggregated Distributions of Independent Individuals

Aggregated patterns arise from various kinds of processes, and in many cases the unit-size $\overset{*}{m}$-m relation would not be linear. There are, however, some cases where a linear relation holds at least for a certain range of quadrat sizes.

IWAO and KUNO (1971) have shown that if a certain number of individuals are randomly removed from the population having an arbitrary distribution, m and $\overset{*}{m}$ should decrease at the same rate. The reverse process can be considered as adding of individuals with the same rule of spatial disposition. It is possible to assume the cases where the change of quadrat size is equivalent to the random removal of individuals from quadrats of a given size or its reverse process.

A simple case is the heterogeneous Poisson mixture. Assume that the whole

area be divided into patches of different densities, in each of which individuals are distributed at random. Then the following relation can be derived for the range of quadrat sizes that are sufficiently smaller than the area of a patch (MORISITA, 1959; PIELOU, 1968):

$$\overset{*}{m}_u = \frac{\Sigma \pi_j m_{u(j)}}{m_u{}^2} \cdot m_u, \tag{4}$$

where π_j means the proportion of the area of the jth patch to the total area, $m_{u(j)}$ the mean density per quadrat of size u in the jth patch, and $m_u = \Sigma \pi_j m_{u(j)}$. Since m_u and $m_{u(j)}$ change at the same rate with changing quadrat size, $\Sigma \pi_j m_{u(j)}/m_u{}^2$ $(=\overset{*}{m}_u/m_u)$ remains constant and takes a value of greater than unity (i. e., $\alpha'=0$, $\beta'>1$). The simplest case falling in this category is the random distribution of individuals in a part of the whole area.

When the quadrat size becomes larger than the area of a patch, the above relation does not hold, and the regression will be governed by the configuration of patches over the space.

If there are several populations conforming the above relation but differing in the level of mean density, the series $\overset{*}{m}$-m relation falls onto the same regression line. Generally speaking, however, the unit-size relation and the series relation are not necessarily identical with each other in the aggregated patterns.

Mosaic patterns will be further discussed later (see p. 102).

Colonial Distributions

If the basic component of the distribution is not a single individual but a group of individuals, we have a colonial distribution. If the colony is so compact that it hardly cuts through even by the edges of the quadrats of the smallest size possible, the $\overset{*}{m}$-m relation is simply different in the point that the regression has the intercept of a positive value corresponding to $\overset{*}{m}_c$, the mean crowding for the frequency distribution of the number of individuals per colony. The slope of the regression is determined by the distribution pattern of colonies over the space. The relation can be shown by

$$\overset{*}{m}_u = \overset{*}{m}_c + \frac{\overset{*}{m}_{bu}}{m_{bu}} m_u, \tag{5}$$

where m_{bu} and $\overset{*}{m}_{bu}$ are mean density and mean crowding of the number of basic components (colonies) per quadrat of size u (IWAO and KUNO, 1971). Distributions composed of single individuals can be regarded as special cases of the above expression where $\overset{*}{m}_c=0$. If $\overset{*}{m}_{bu}/m_{bu}$ remains constant over the range of u as in the afore-mentioned distributions of single individuals, a linear regression of $\overset{*}{m}_u$ on m_u will be expected.

The equation (5), however, can not be applied if the distribution of colonies is more uniform than random. For the positive binomial distribution of colonies, the relation is being

$$\overset{*}{m}_u = (\overset{*}{m}_c - \frac{m_{bu}}{k'_{bu}} m_c) + m_u \quad \text{(for } k'_{bu} \geq 1), \tag{6}$$

where k'_{bu} is the maximum number of colonies a quadrat of size u could contain, and m_c the mean number of individuals per colony. If such colonies that are composed of equal number of individuals are distributed uniformly, m_{bu}/k'_{bu} equals unity and hence eq. (6) becomes $\overset{*}{m}_u = -1 + m_u$, which shows the completely uniform distribution.

Since usually the colony occupies an appreciable area, however, the chance of cutting a colony through quadrat edges would not be negligible, especially when the quadrat is small in size. Within the range that the size of quadrat is considerably smaller than the area occupied by colony, the unit-size $\overset{*}{m}\text{-}m$ relation is determined by the spatial arrangement of individuals within the colonies as well as the proportion of the total area occupied by colonies to the whole area. If the intra-colony distribution is random, the relation is similar to that given by eq. (4). Some forms of aggregated pattern within the colonies (e. g., presence of density gradient from centre to periphery in the dispersal range) may also be similar. In these cases, the regression would be linear with $\alpha' = 0$ and $\beta' > 1$. If the intra-colony distribution is more or less uniform (positive binomial), the regression is also linear but has a negative value of α' $(0 > \alpha' \geq -1)$.

On the other hand, when the quadrat size becomes sufficiently large as compared with the colony area, the unit-size $\overset{*}{m}\text{-}m$ relation similar to the distribution of compact colonies would be expected, provided that the probability that any quadrat lies across the boundary of a colony is negligibly small.

A simple case is illustrated by the double Poisson distribution known as Neyman type A. NEYMAN (1939) first derived this distribution on the assumption that the egg masses of an insect are distributed at random and the larvae emerged from each egg mass disperse randomly within a definite area Γ_u (defined by the number of quadrat units). In this case, we have

$$\overset{*}{m}_u = m_c/\Gamma_u + m_c m_{bu} = (1 + \frac{1}{m_{bu}\Gamma_u}) \, m_u, \tag{7}$$

where m_c is the number of surviving larvae from an egg mass. Since Γ_u is defined by the number of quadrat units, $m_u\Gamma_u$ remains constant over the range of quadrat sizes that are sufficiently smaller than the absolute range of dispersal of a larval colony. Namely, the $\overset{*}{m}_u\text{-on-}m_u$ regression passes through the origin with the slope of $(1 + \frac{1}{m_{bu}\Gamma_u})$. When the quadrat size exceeds the absolute range of dispersal, Γ_u takes the value of unity and no further change occurs. It is apparent that the regression for this range has the intercept of m_c and the slope of unity.

In the distributions comprising loose colonies, the value of α for the series $\overset{*}{m}\text{-}m$ relation will increase until the quadrat size exceeds the area of colony but the value of β remains to be the same, if the distribution of colonies and the intra-colony distribution follow random or aggregated pattern having a constant $\overset{*}{m}_u/m_u$ ratio

(Fig. 1, A). If, however, the spatial distribution of individuals within colonies is random but the colony distribution follows either positive binomial or complete uniform, β would equal zero until quadrat size exceeds colony area and then it gradually approaches unity as quadrat size increases (Fig. 1, B). Also, if the intra-colony distribution is uniform but the colony distribution is random, the regression for quadrat sizes smaller than colony area would be divided into two parts with $\beta = 0$ and $\beta = 1$, provided that individuals have no territories. If a linear regression
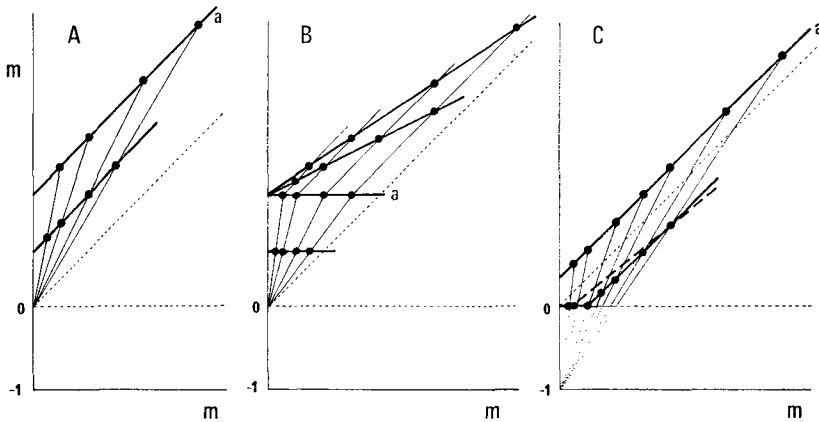

Fig. 1. Expected changes in the series $\overset{*}{m}$-m relationships with changing the quadrat size in loose-colony models.

A: Distribution of colonies and intra-colony distribution of individuals are random; B: Distribution of colonies is uniform and intra-colony distribution is random; C: Distribution of colonies is random and intra-colony distribution is uniform.

The mean colony size is assumed to be constant over the range of mean densities. Thin lines connected points indicate the unit-size relations for respective populations of differing mean density. Heavy lines show the series relations for different quadrat sizes. The regression for the quadrat size equivalent to the colony area indicates by symbol a. The heavy broken line in figure C shows a linear regression line fitted to the bending pattern in the true relation.

is incorrectly fitted to such a case, its slope β becomes smaller than the slope corresponding to the distribution pattern of colonies. (If individuals have territories of a fixed size, obviously $\beta = 0$ for the quadrat size equivalent to, or smaller than, the territory size.) For the quadrat size larger than colony area, β will rightly reflect the distribution pattern of colonies (Fig. 1, C).

Mosaic Patterns

Although a simple case of mosaic pattern is briefly mentioned earlier (p. 99), the more general expression will be given below.

Let assume that the general area be divided into several subareas differing in mean densities and/or distribution patterns of individuals. The mean crowding for

quadrat size u is then shown by

$$\overset{*}{m}_u = \frac{\Sigma \pi_j m_{u(j)} \overset{*}{m}_{u(j)}}{m_u}, \tag{8}$$

where π_j is the proportion of jth subarea to the whole area, $m_{u(j)}$ and $\overset{*}{m}_{u(j)}$ the mean density and mean corwing per quadrat of size u in the jth subarea, and $m_u = \Sigma \pi_j m_{u(j)}$. If the unit-size $\overset{*}{m}$-m relation in each subarea can be fitted by a linear regression:

$$\overset{*}{m}_{u(j)} = \alpha'_{(j)} + \beta'_{(j)} m_{u(j)},$$

$\overset{*}{m}_u$ is written as

$$\overset{*}{m}_u = \frac{\Sigma \pi_j \alpha'_{(j)} m_{u(j)}}{m_u} + \frac{\Sigma \pi_j \beta'_{(j)} m_u{}^2{}_{(j)}}{m_u{}^2} m_u, \tag{9}$$

provided that quadrat size u is small relative to the size of any subarea. Since $m_{u(j)}$ and m_u change at the same rate with changing quadrat size, $\Sigma \pi_j \beta'_{(j)} m_u{}^2{}_{(j)}/m_u{}^2$ as well as $\Sigma \pi_j \alpha'_{(j)} m_{u(j)}/m_u$ remain constant and so the $\overset{*}{m}_u$-on-m_u regression is linear.

If the individuals are randomly distributed in each subarea, the first term of eq. (9) equals zero and $\beta'_{(j)} = 1$ for all j, and hence the equation becomes identical with eq. (4). If only two subareas are contained and all the individuals are distributed in the first of them, then the slope becomes $\frac{1}{\pi_1} \beta'_{(1)}$, which means that the slope becomes steeper in inverse proportion with the relative size of the subarea occupied by individuals.

Since mosaic patterns may usually be related with the spatial heterogeneity of habitat conditions, it is difficult to suppose more or less general patterns after the quadrat size exceeds the area of respective patches. In anyway, the regression would be bending around the quadrat size equivalent to the area of the smallest patch. The relation for the random combination of quadrats (see below) may be considered as a very simple model where the mosaic is comprising the subareas of equal size that are arranged independently and randomly from each other and the quadrats never lie across the boundaries between subareas.

Random Combination of Quadrats

Let the mean density and the variance of the numbers of individuals among the quadrats of an arbitrary size be m and σ^2 respectively. Then the sum of h quadrats randomly chosen from the population contained total N quadrats would be distributed with the mean hm and the variance $\frac{N-h}{N-1} h\sigma^2$. Then we have

$$\overset{*}{m}_h = hm + \frac{N-h}{N-1} (\overset{*}{m} + 1 - m) - 1$$

$$= \frac{N}{N-1} (\overset{*}{m} + 1 - m) - 1 + \left[1 - \frac{1}{m} \frac{1}{(N-1)} (\overset{*}{m} + 1 - m)\right] hm.$$

If $N \gg h$, the above equation is reduced to

$$\overset{*}{m}_h = (\overset{*}{m} - m) + hm \qquad \text{(for } h \geq 1\text{)}, \tag{10}$$

which means that the $\overset{*}{m}$-on-m regression for variable h has the intercept of $(\overset{*}{m}-m)$ and the slope of unity in the infinite population. (The ratio $\overset{*}{m}_h/hm$ equals MORISITA's $I^*_{\delta s}$. See MORISITA, 1971). Strictly speaking, the relation is applied to the repeated random sampling of h quadrats from the population. But, since the probability of choosing the same quadrat more than once is very small in the infinite population, eq. (10) would be appropriate as the expected relation when there is no spatial correlation among small quadrats comprising the larger units. When the distribution pattern in the initial quadrat size is specified, we can get the unit-size $\overset{*}{m}$-m relations for various forms of random distributions of the basic components mentioned before: $(\overset{*}{m}-m)$ equals zero in the Poisson (eq. 1), $-m/k'$ in the positive binomial (eq. 3, including the completely uniform distribution where $-m/k'=-1$), and $\overset{*}{m}_c$ and $(\overset{*}{m}_c-m/k'_b)$ respectively in the Poisson and the positive binomial distributions of compact colonies (eqs. 5 and 6). If there is a positive or negative correlation between the numbers of individuals in the adjacent quadrats, the slope of the regression with variable h will be larger or smaller than unity. Thus the relation shown by eq. (10) would be useful as a criterion to detect the spatial correlation among quadrats.

Supposing that there are several populations whose series $\overset{*}{m}$-m relation for the initial quadrat size can be shown by

$$\overset{*}{m}=\alpha+\beta m,$$

the relation will be changed to

$$\overset{*}{m}_h=\alpha+(\frac{\beta-1}{h}+1)\ hm \tag{11}$$

after h quadrats are combined randomly to form a larger quadrat unit. Namely, α does not change but β approaches unity if $\beta\neq1$ initially.

As mentioned before, eq. (10) may be regarded as a simplified model of the mosaic pattern when the quadrat sizes are larger than the size of subarea. Then, from eqs. (9) and (10), we can imagine that the unit-size $\overset{*}{m}$-m relation over a wide range of quadrat sizes will be more or less similar to that for loose-colony distribution if the mosaic is composed of similarly shaped subareas.

Pattern Indices

From the above considerations, it may be concluded that if there is some colonial or clumpy structure, the $\overset{*}{m}$-on-m regression obtained by successive changes of quadrat sizes would have a turning point around the quadrat size approximately equal to the clump area (a colony or a patch of the mosaic). In Figs. 2 and 3 the unit-size $\overset{*}{m}$-m relationships for several basic patterns are shown schematically. I_δ vs. quadrat size relations described by MORISITA (1959) can easily be derived from these relations (2nd columns of Figs. 2 and 3), because I_δ is essentially identical with $\overset{*}{m}/m$.

For detecting the approximate area occupied by a clump, MORISITA (1959) used the index $I_{\delta(u)}/I_{\delta(2u)}$, where $I_{\delta(u)}$ is the value of I_δ calculated for the quadrat of size

u and $I_{\delta(2u)}$ is that for the double-sized quadrat $2u$. In terms of $\overset{*}{m}$ and m, the index equivalent to this can be expressed by

$$\tau_h = \frac{\overset{*}{m}_u}{m_u} \div \frac{\overset{*}{m}_{hu}}{m_{hu}} = \frac{h\overset{*}{m}_u}{\overset{*}{m}_{hu}}, \tag{12}[1]$$

where m_{hu} and $\overset{*}{m}_{hu}$ indicate the mean and mean crowding for the quadrat of h times as large as the size u ($h=2$ in the MORISITA's original index). When the values of τ_h are calculated successively in a sequence of quadrat sizes and plotted against the quadrat sizes, the peak of the curve may suggest that the clump area lies somewhere between the two corresponding quadrat sizes.[2] The behaviour of this index can easily be interpreted by reference to Figs. 2 and 3 (3rd columns). For the use of this index, the quadrat size should be increased successively with a common multiple.

Since the τ_h index does not provide any knowledge on the distribution pattern of clumps, the following index may be more useful for our purpose:

$$\rho_i = \frac{\overset{*}{m}_i - \overset{*}{m}_{i-1}}{m_i - m_{i-1}}, \tag{13}$$

where $i=1, 2, 3, \ldots$ stands for the order of quadrat sizes. For the smallest quadrat size ($i=1$), $\rho_1 = \overset{*}{m}_1/m_1$.

As obvious, this index indicates the ratio of the increment of $\overset{*}{m}$ against m while the quadrat size increases from $(i-1)$th to ith, and hence it takes a constant value as far as the $\overset{*}{m}_u$-on-m_u regression remains to be linear. If the basic component of the distribution is a single individual, the index is identical with $\overset{*}{m}_u/m_u$; it is equal to or larger than unity in random and aggregated distributions respectively. In random or aggregated distribution of territorial individuals, ρ_i takes the value of zero for the quadrat sizes smaller than the territory size, and then it takes the value equal to or larger than unity for the larger quadrat sizes. The same relations also hold for the distributions comprising compact colonies, except that ρ_1 is larger than ρ_2. In random or aggregated distribution of loose colonies, ρ_i takes a vlaue greater than unity for the quadrat size smaller than the colony area, and it drops to a lower level when the quadrat size exceeds the colony area and maintains the value corresponding to the distribution pattern of colonies (i. e. $\rho_i = \overset{*}{m}_{bu}/m_{bu}$). If the intra-colony distribution is uniform, ρ_i for the small quadrat sizes will take the value of zero as before (see Fig. 3, 4th column).

As outlined above, the ρ index may indicate not only the approximate clump area, but also the intra-clump distribution and the distribution pattern of clumps as well. It is advantagious that for this index there is no necessity for keeping the ratio between two successive quadrat sizes being constant in a sequence. Also, it

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[1] Literally this index is identical with the τ index that has been proposed by IWAO and KUNO (1971) for distinguishing the three kinds of density relationships in the mortality processes.

[2] MORISITA (1959) suggested that the value of this index is to be plotted against the larger quadrat size of the two. But it is sometimes better to plot it against the smaller quadrat as seen in the examples given in the next chapter.
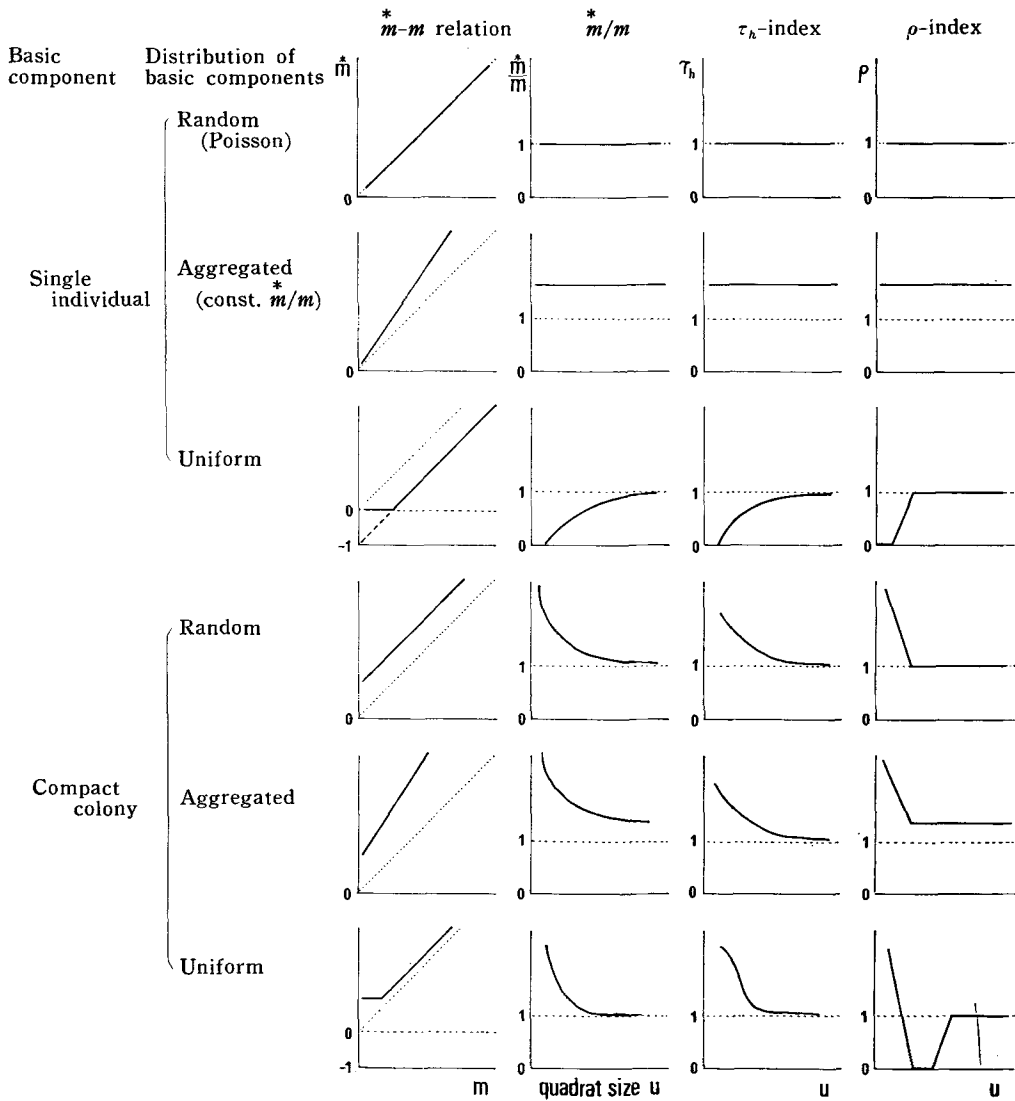
Fig. 2. Schematic representation showing the expected $\overset{*}{m}$-m relationships with successive changes of quadrat sizes (unit-size relation) and changes in pattern indices for various patterns of distributions comprising individuals and compact colonies.

Dotted line in the $\overset{*}{m}$-m graph indicates the Poisson expectation.

should be noted that ρ may serve as an index to detect the spatial correlation between adjacent quadrats: ρ equals unity if there is no correlation (equivalent to the random combination of quadrats), and larger or smaller than unity if positive or negative correlation exists.

The analysis of the unit-size $\overset{*}{m}$-m relation in a single population, however, may not be sufficient for detecting the pattern characteristic of the species. If the data

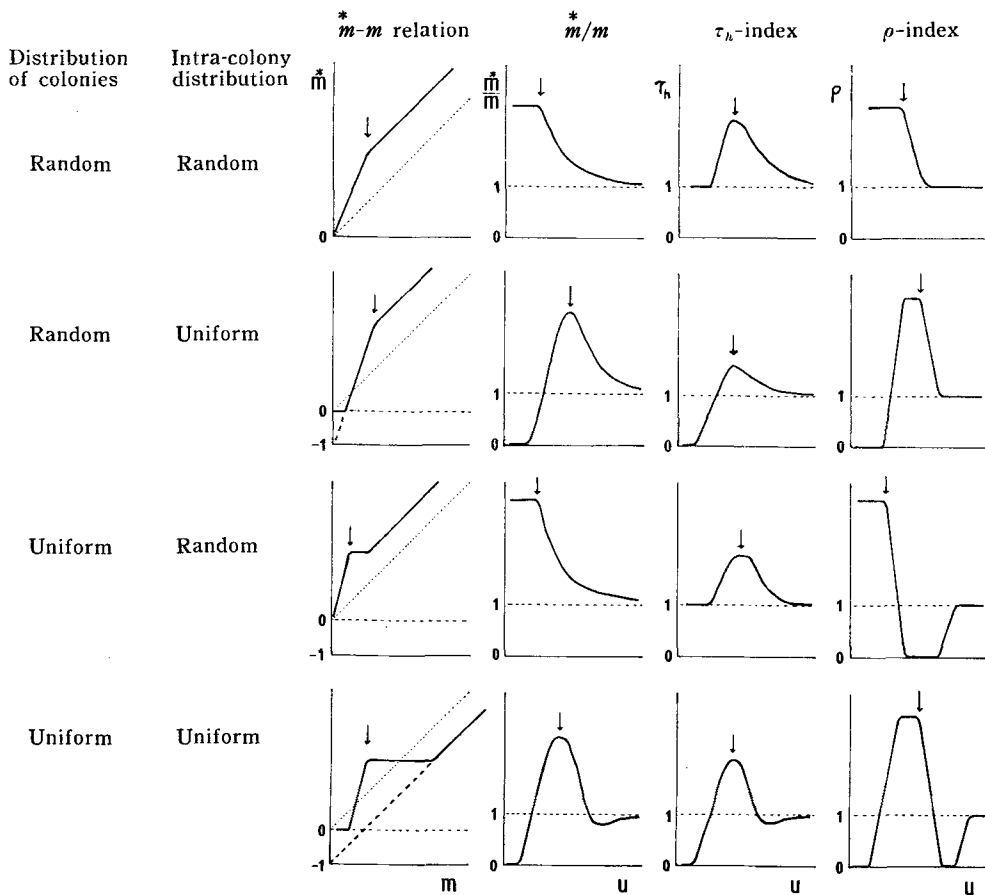Fig. 3. Schematic representation showing the unit-size $\overset{*}{m}$-m relationships and changes in pattern indices for various patterns of distributions comprising loose colonies. Arrow indicates the area occupied by a colony. Aggregated distribution of colonies is different from random distribution of colonies only in such a way that the slope of the regression after quadrat size exceeds the colony area is greater than unity (and hence $\rho > 1$) (See Fig. 2: compact colony models).

on several populations are available, some further information will be obtained from the values of α and β in the series $\overset{*}{m}$-m relations for respective quadrat sizes. If the basic component of the distribution is the single individual or the compact colony, the value of α may not be altered by changing quadrat size. If, however, the distribution is comprising the loose colonies of a fixed mean size in number, the α will increase its value with increasing the quadrat size to the point where the quadrat size exceeds the colony area and then it will take a constant value corresponding to $\overset{*}{m}_c$ at the larger-sized quadrats. The value of β indicates the distribution pattern of basic components, individuals or colonies, for a given quadrat size. If the change of ρ value relates to β rather than α, most probably it is due to the effect of environmental heterogeneity. However, such an interpretation would not be true

if the ρ-graph indicates any tendency for uniformity in the pattern, because β would change with increasing the quadrat size in the uniform distributions of individuals or colonies (see p. 99 and 102).

In the foregoing discussion, it is assumed that any quadrat will never across the boundary of a clump. In practical cases, however, the condition may rarely be satisfied if the clump is not compact enough. Since the effect of cutting the clump through the quadrat edges is difficult to consider theoretically, it will be examined by using the artificially constructed populations in the next chapter.

<div align="center">ANALYSIS WITH ARTIFICIAL POPULATIONS</div>

Random Distribution of Colonies: Intra-Colony Distribution is Random

The four populations conforming the double Poisson (Neyman type A) distribution are constructed, in all of which the number of individuals per colony is a Poisson variate with $m_c = 3$ but the mean number of colonies per 1 cm² varies from 0.1 to 0.4. In compact colony model, the individuals belonging to each colony are treated as if they congregate at the centre of the colony, whereas in loose colony model they are randomly located within the area of 1 cm². An example of the resulting distribution in loose colony model is shown in Fig. 4 A.

As can be seen from Fig. 4 B, the distribution of colonies is well fitted by the Poisson series at any quadrat size. If the colonies are compact and never cut through by the quadrat edges, the $\overset{*}{m_u}$-on-m_u regression for the population with changing quadrat size is parallel with the Poisson line ($\beta' = 1$) and its intercept corresponds to $\overset{*}{m_c}$ ($\alpha' = 3$). If, however, the colonies are loose, the regression is curvilinear; its slope is steep while the quadrat size is smaller than the colony area, and then gradually approaches unity as the quadrat size increases. The regression becomes linear and parallel with the expected line of $\alpha' = 3$ and $\beta' = 1$ for the range of quadrat sizes larger than $4 \sim 8$ cm². In some trials, the regression is on the expected line, but more usually it has a somewhat smaller value of α'. This may be interpreted as follows: The probability that the quadrats lie across the colony boundaries does not become nil even when the quadrat size is considerably large as compared with the colony area, but the degree of spatial correlation between adjacent quadrats becomes negligible. Then the pattern would become equivalent to the random combination of quadrats where the intercept is somewhat smaller than $\overset{*}{m_c}$.

The approximate colony area is difficult to be detected directly from the unit-size $\overset{*}{m}$-m relation, but the ρ value falls sharply when the quadrat size just exceeds the colony area as is expected. The gradual decrease of ρ values in the smaller quadrat sizes would be due to the fact that the actual area occupied by a colony varies from 0.25 to 1.0 cm². At the larger quadrat sizes, its value is stabilized around unity, which also well reflects the spatial pattern of the population (Fig. 4, C and D). As the mean density of the population increases, however, the change of ρ value is
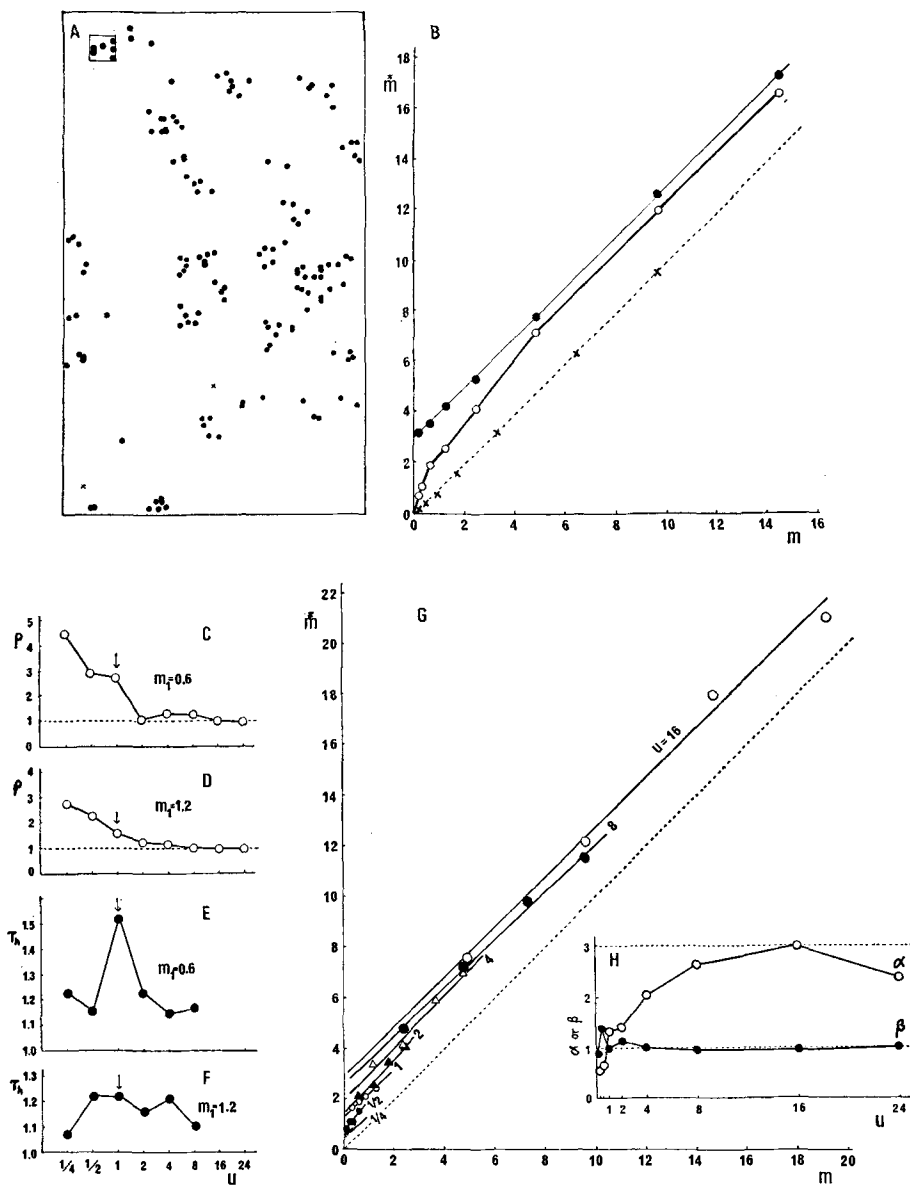
Fig. 4. Analysis of artificial populations conforming the random distribution of loose colonies with random disposition of individuals within colonies.

A: Distribution map for a medium-density population. Rectangle indicates the standard quadrat size ($u=1:1$ cm^2). Mean density (m_1): 0.6/cm^2. Crosses in the figure indicate the incipient colonies comprising zero individual.

B: The unit-size $\overset{*}{m}$-m relation for the population shown in A (open circles). Solid circles show the relation for the compact colony model of the same population. Cross symbols indicate the distribution of colony centres.

C and D: The ρ-index plotted against quadrat size for the above population and a high-density population ($m_1=1.2$). Arrow indicates the colony area.

E and F: The τ_h index plotted against quadrat size for the same populations.

G: The series $\overset{*}{m}$-m relations for successive puadrat sizes.

H: The values of α and β in the series $\overset{*}{m}$-on-m regression plotted against quadrat size.

limited to a smaller range and hence the detection of colony area becomes less easy. The same is true for the τ_h index, in which the peak of the curve indicating the colony area becomes obscure in high density populations (Fig. 4, E and F).

The series $\overset{*}{m}$-m relations for respective quadrat sizes in the four populations are shown in Fig. 4 G, and the α and β values calculated for them are plotted against quadrat sizes in Fig. 4 H. The value of β is approximately equal to unity at any quadrat size as is expected. The α value rapidly increases at first and seems to be stabilized at the quadrat size of $8\,cm^2$, but it tends to be somewhat smaller than the expected value of 3. Thus, when the colonies are loose, the distribution pattern of colonies may well be detectable, but the mean crowding for colony size ($\overset{*}{m_c}$) may be more or less underestimated.
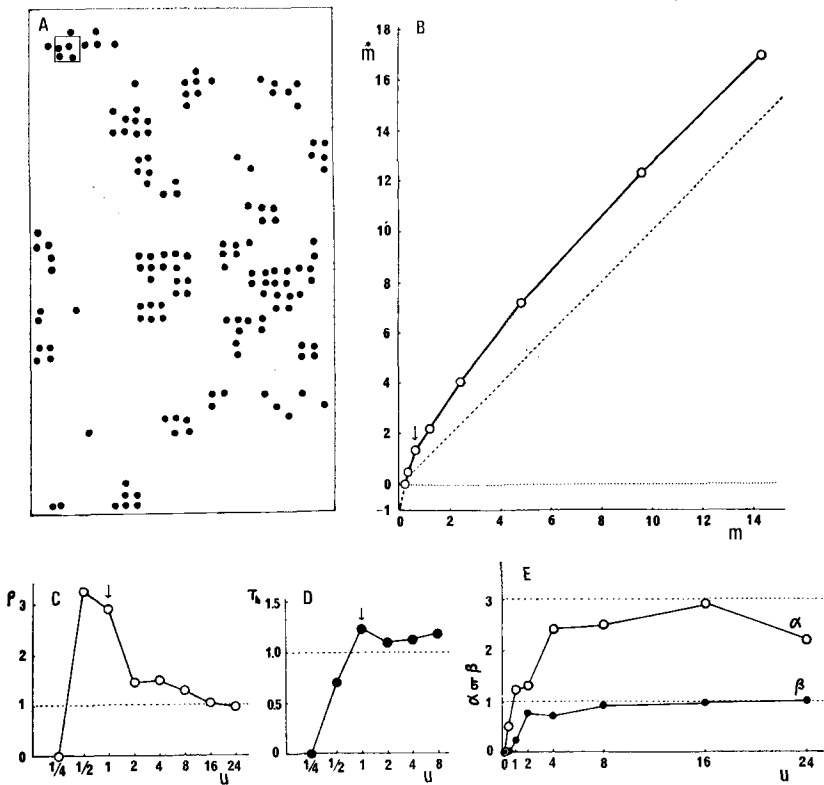

Fig. 5. Analysis of artificial populations conforming the random distribution of loose colonies with uniform intra-colony distribution.

A: Distribution map for a medium-density population ($m_1 = 0.6$).

B: The unit-size $\overset{*}{m}$-m relation for the population illustrated in A.

C: The ρ index plotted against quadrat size.

D: The τ_h index plotted against quadrat size.

E: The values of α and β in the series $\overset{*}{m}$-on-m regression plotted against quadrat size.

Random Distribution of Colonies: Intra-Colony distribution is Uniform

The loose colony model of the double Poisson series mentioned above is modified in such a way that each individual has a territory of $0.25\,cm^2$ without altering the spatial disposition of colonies. Since the number of individuals per colony varies from 1 to 8, the colony area varies from 0.25 to 2.00 with the mean $0.75\,cm^2$ (Fig. 5).

Again it is apparent that the $\overset{*}{m}_u$-on-m_u regression becomes linear at larger quadrat sizes and its slope for this part well indicates the random pattern of colony disposition, but the intercept α' obtained by extrapolation gives a considerably underestimated value of $\overset{*}{m}_c$. The ρ value rises from 0 at the smallest quadrat size to 3 at the next two sizes, then falls sharply, and gradually approaches unity at the larger quadrat sizes. The more gradual change of ρ towards unity in this than in the previous model may be related to the wider variation in colony area. The τ_h index seems to be less indicative for the detection of colony area.

The series $\overset{*}{m}$-m relation for each quadrat size is generally fitted by a linear regression, but the slope β changes progressively from 0 at the quadrat size 0.25 to unity at the sizes 16 and 24 as is anticipated (see p. 102). It is obvious that in this type of model the distribution of individuals approaches the completely uniform pattern when the mean density is very high, and hence the regression would be curvilinear if such a crowded population is included in the series.
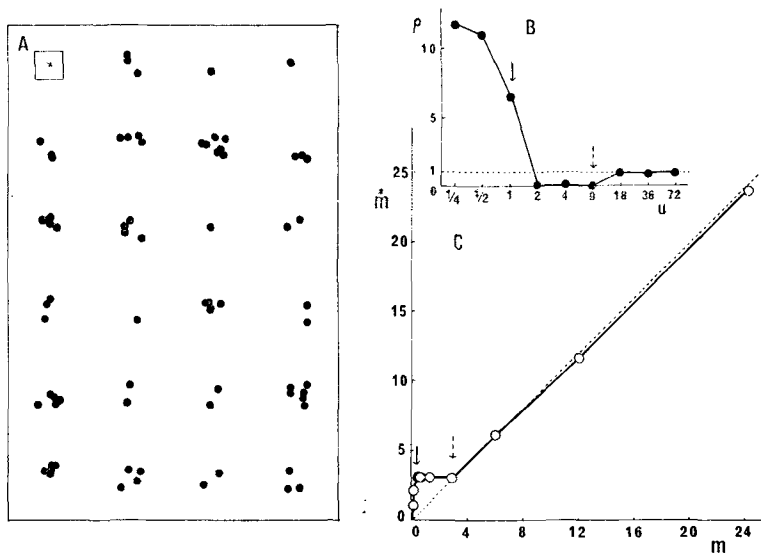

Fig. 6. Analysis of an artificial population conforming the completely uniform distribution of loose colonies with random distribution of individuals within colonies.
A: Distribution map. B: The ρ index plotted against quadrat size.
C: The unit-size $\overset{*}{m}$-m relation. Arrow with broken line indicates the quadrat size at which every quadrat contains one colony.

Uniform Distribution of Colonies

An extreme case is the completely uniform distribution of colonies. Fig. 6 shows such a pattern where the number of individuals per colony is a Poisson variate with the mean 3 and the disposition of individuals within colonies is also random. The ρ value drops to zero when the quadrat size exceeds the colony area and then it becomes unity when every quadrat contains the same number of colonies.
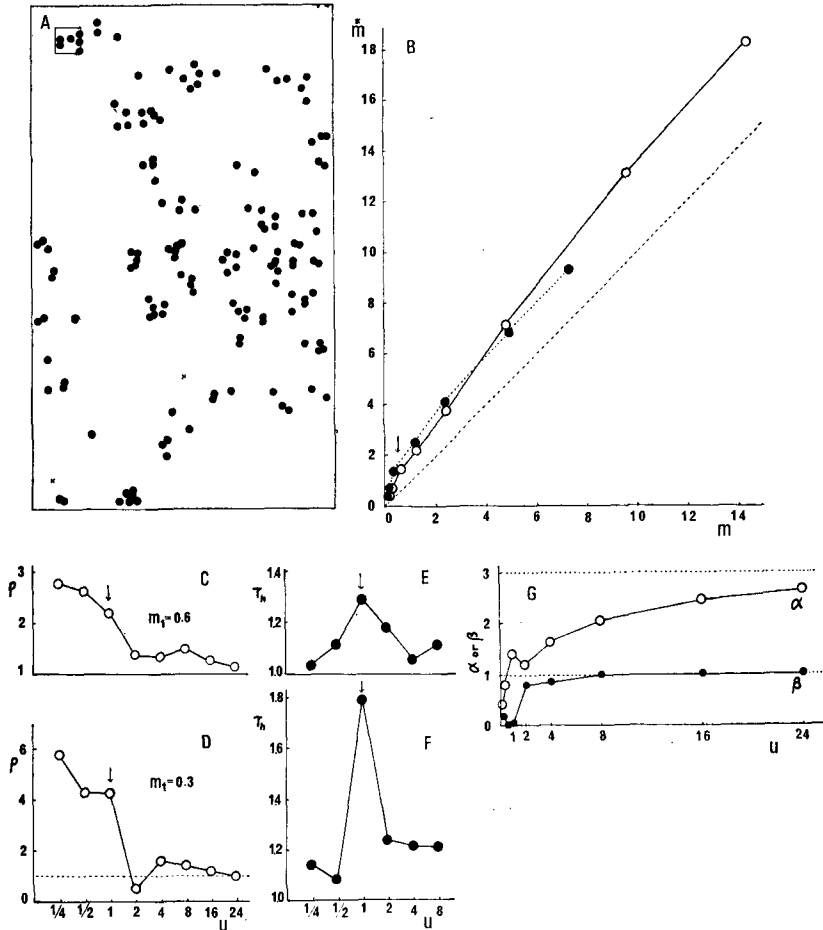

Fig. 7. Analysis of artificial populations conforming the non-overlapping (positive binomial) distribution of loose colonies with random disposition of individuals within colonies.

A: Distribution map for a medium-density population (m_1=0.6).

B: The unit-size $\overset{*}{m}$-m relations for low- and medium-density populations (solid and open circles, respectively).

C and D: The ρ index plotted against quadrat size for the low- and medium-density populations, reespectively.

E and F: The τ_h index plotted against quadrat size for the two populations corresponding to C and D.

G: The values of α and β in the series $\overset{*}{m}$-m relation plotted against quadrat size.

Since in this case the colony size is the Poisson variable, the $\overset{*}{m_u}$-on-m_u regression becomes to be on the Poission line at large quadrat sizes. The range of quadrat sizes at which $\overset{*}{m_u}$ equals zero, of course, depends on the colony density of the population.

A more realistic situation would be that the colonies are distributed nearly at random but without overlapping (i. e., the positive binomial distribution of colonies). When the double Poisson populations (p. 108) are modified in this way, we get the unit-size $\overset{*}{m}$-m relation and the ρ-graph as illustrated in Fig. 7. Although the $\overset{*}{m_u}$-m_u relation is very similar to that of the double Poisson model, the ρ-graph tends to have a trough after the quadrat size exceeds the colony area. In a series of distributions of this type, the value of β is nearly equal to zero for the range of quadrat sizes that are smaller than the colony area and then approaches unity at larger quadrat sizes, which resembles the trend in the afore-mentioned model of randomly-distributed colonies with uniform intra-colony distribution. Distinction between the both kinds of patterns would be possible by the use of ρ-graph.

Aggregated Distribution of Colonies as a Mosaic of Different-Density Subareas

When the four artificial populations of the double Poisson series (p. 108) are
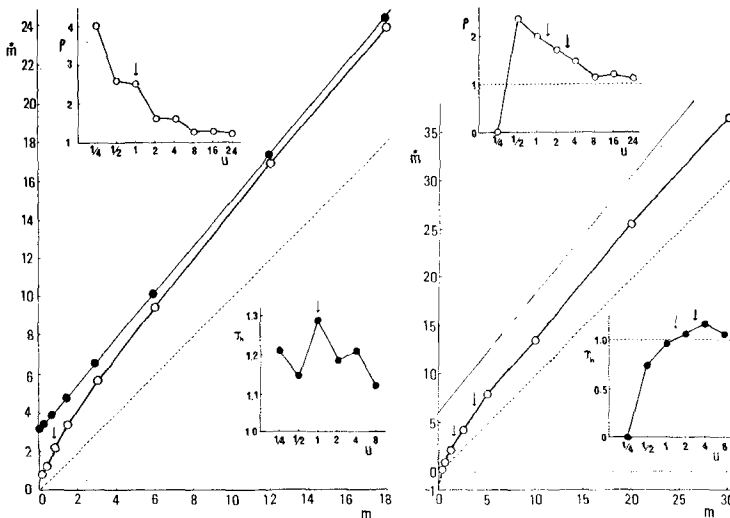

Fig. 8. The unit-size $\overset{*}{m}$-m relation and the graphs of ρ and τ_h against quadrat size in two artificial populations comprising aggregatively-distributed colonies.
Left: Aggregated distribution of colonies with random disposition of individuals within colonies (open circles). Solid circles indicate the relation for compact colony model.
Right: Aggregated distribution of colonies with uniform disposition of individuals within colonies. Solid line in the $\overset{*}{m}$-m graph shows the relation expected for compact colony model. Thin and thick arrows indicate the average and maximum colony areas, respectively.

combined together to form a mosaic pattern, we get the unit-size $\overset{*}{m}$-m relation as shown in Fig. 8 (left) for the quadrat sizes smaller than each subarea. In the compact colony model, it is expected from eq. (9) that the intercept of the regression does not change (i. e., $\alpha'=3$) and the slope β' would be somewhere around 1.197, which agree well with the observed values $\alpha'=2.998$ and $\beta'=1.198$.

In the loose colony model, the regression is curvilinear and the slope for the range of larger quadrat sizes is approximately parallel with that for the compact colony model as is expected ($\alpha'=2.106$, $\beta'=1.217$). The ρ-graph is rather step-wise; the first and third drops of ρ vlaues are due to incidental clumping of individuals in the model population.

The effect of uniform arrangement of individuals within colonies is examined using another population comprising aggregatively-distributed colonies where the colony size varies from 1 to 12 with the mean 6 and each individual has a territory of 0.25 cm². The unit-size $\overset{*}{m}$-m relation and ρ-graph well indicate the distribution pattern of this population (Fig. 8, right). The gradual decrease of ρ value over the range of quadrat sizes 1~8 cm² is consistent with a wide variation in the colony area ranging from 0.25 to 3.00 cm².

Double-Clumped Distribution: Colonies are Distributed Randomly within Large Clumps

In the four populations comprising the randomly-distributed colonies (p. 108), the distribution of colonies in quadrats of 4 cm² is changed to the aggregated pattern conforming the negative binomial series with $k \doteqdot 1$ (i. e., $\beta \doteqdot 2$), without appreciable change of distribution at the quadrat sizes of smaller than 1 and larger than 16 cm². This means that the colonies are distributed randomly within loose clumps and these clumps are distributed rather regularly over the area (Fig. 9).

In this case, the unit-size $\overset{*}{m}$-m relation shows a convex pattern, and the ρ-graph is step-wise, indicating the presence of double clumps as well as rather regular arrangement of larger clumps. It is noted that the ρ value at quadrat sizes 4~8 ($\doteqdot 2$) rightly indicates the distribution pattern of individuals to be expected. The τ_h index fails to show the presence of clumps of 4 cm².

As to the series relation, the value of β changes from 1 at the quadrat size 1 cm² to approximately 2 at 4 cm² but the value of α does not change significantly as compared with that for the double Poisson model (1.79 vs. 1.97). This type of change corresponds to the increase of colony density within large clumps in high-density populations. Instead, if we assume the negative binomial with a common p, the random distribution of large clumps having a fixed mean size, we may have the regression with $\beta=1$ and a larger value of α. Thus, the attainable value of α would be governed by larger clumps if colonies are distributed in clumps having a fixed mean size. The former (constant α with change of β) may be expected when the large clumps are due to local differences of habitat conditions, and the latter is
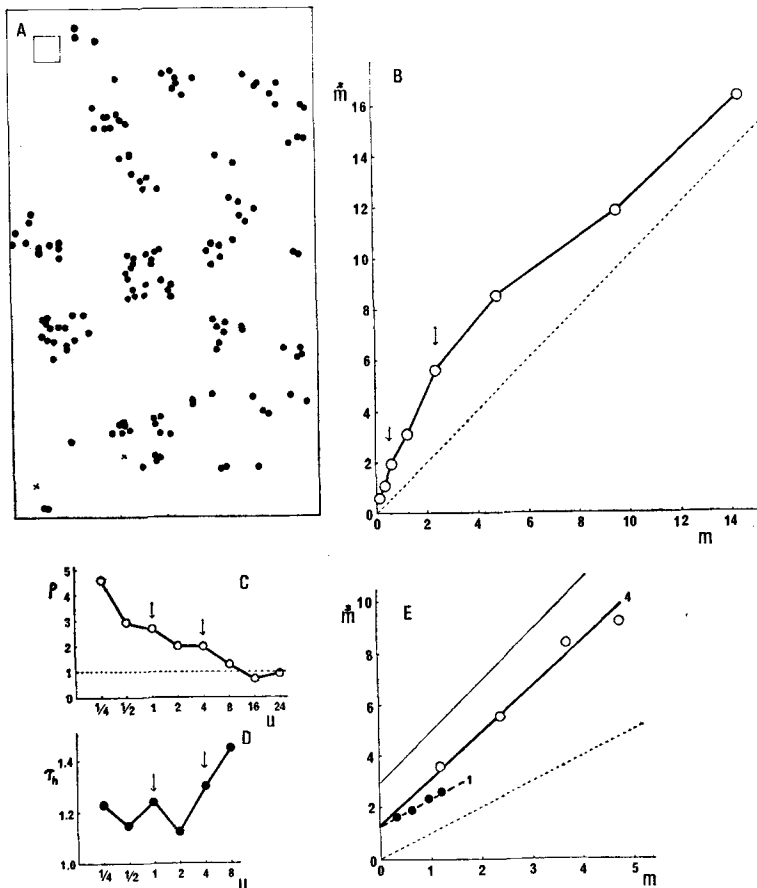
Fig. 9. Analysis of artificial populations where loose colonies are distributed randomly in large clumps.

In this model, the distribution pattern changes from the Neyman type A at $u=1$, through the negative binomial with a common k ($k_c=1$) at $u=4$, again to the Neyman type A at $u=16$ and 24.

A: Distribution map for a medium-density population.

B: The unit-size $\overset{*}{m}$-m relation.

C and D: The ρ and τ_h indices plotted against quadrat size, respectively.

E: The series $\overset{*}{m}$-m relations for the quadrat sizes 1 and 4. Thin line indicates the expected line for compact colony model.

more likely when the clumpiness is related to the intrinsic properties of the species concerned.

Regularly-Spaced Double Clumps

Fig. 10 A shows a regularly-spaced double-clumped pattern. The individuals are distributed randomly within small colonies of 1cm² in area each, but both the small colonies within large clumps of 16 cm² in area and the large clumps themselves are distributed without overlapping. The distribution of large clumps, however, is more

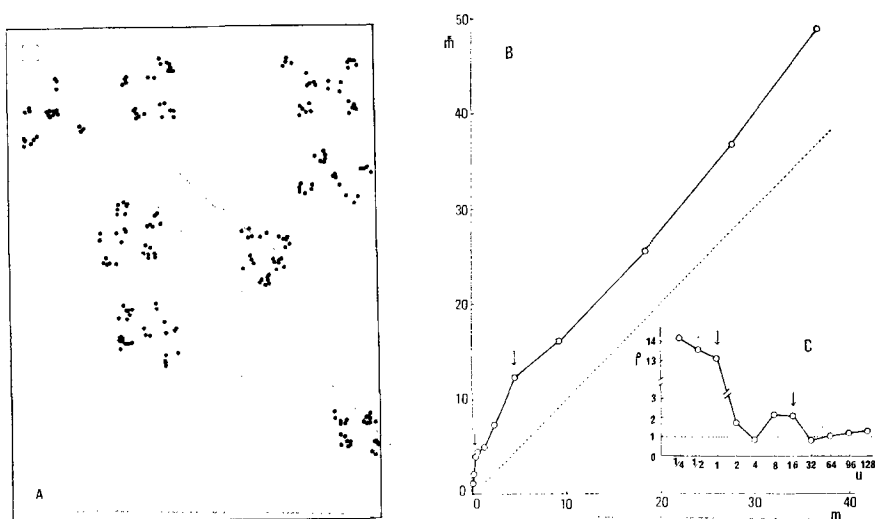Fig. 10. Analysis of an artificial populations comprising the regularly-
spaced double clumps.

A: Distribution map. B: The unit-size $\overset{*}{m}$-m relation.
C: The ρ index plotted against quadrat size.

or less aggregative over the space.

The regression of $\overset{*}{m}_u$ on m_u appears to be similar to that for above-mentioned example (Fig. 9), but the ρ-graph shows a somewhat different pattern as seen in Fig. 10 B and C. The two scales of clumpings are well reflected by the corresponding sharp drops of ρ values, and the existence of two troughs in the graph indicates the regular disposition of small colonies and that of large clumps respectively. The upward trend of ρ values beyond unity at the large quadrat sizes is consistent with the non-random dispersion of large clumps.

Thus, relatively complex pattern of distribution would be detectable by using the graph of ρ value against quadrat size; uniform arrangement of individuals, colonies and large clumps results in the saw-toothed pattern, whereas random or aggregated distribution of them gives the step-wise pattern.

As shown above, the conclusions on theoretical basis are generally supported by the results obatined in the analysis of artificial populations. It becomes evident, however, that in the distribution comprising loose colonies the value of α' obtained by extrapolation in the unit-size $\overset{*}{m}$-m relation would underestimate the true value of $\overset{*}{m}_c$ to some extent even if the $\overset{*}{m}_u$-on-m_u regression becomes to be linear at large quadrat sizes. Similarly, α in the series $\overset{*}{m}$-m relation may be somewhat smaller than $\overset{*}{m}_c$ even at the quadrat size sufficiently larger than the colony area. The clump area seems to be be better detected by ρ index than by τ_h index, and the variation in clump area would be indicated by successive decrease in ρ value over the range

of two or more quadrat sizes.

APPLICATION TO BIOLOGICAL POPULATIONS

Rice Stem Borer Larvae

The total 9 distribution maps of the second-generation larvae of the rice stem borer, *Chilo suppressalis*, in paddy fields were examined. Eight of them were unpublished data kindly supplied by Mr. T. SUGINO of Shizuoka Agricultural Experiment Station and the remaining one was taken from KOJIMA and OKAMOTO (1957).

Generally speaking, the unit-size $\overset{*}{m}$-m relation is cuvilinear, but it becomes approximately linear for the range of quadrat sizes larger than 2 or 4 rice hills. In the two examples shown in Fig. 11, the slope of the regression β' is nearly 1.0 in one population (Kochi) and 1.6 in the other (Shizuoka 7C). The values of β' in all the other cases fall in intermediates between these two. The value of α' estimated from the linear part of the regression lies somewhere around 10 in most cases. The ρ-graph indicates the existence of clumps (often double clumps) of 4~16 rice hills in area.

The $\overset{*}{m}$-m relation for the series of populations is well fitted by a linear regression at each of successive quadrat sizes. The values of α and β thus calculated are
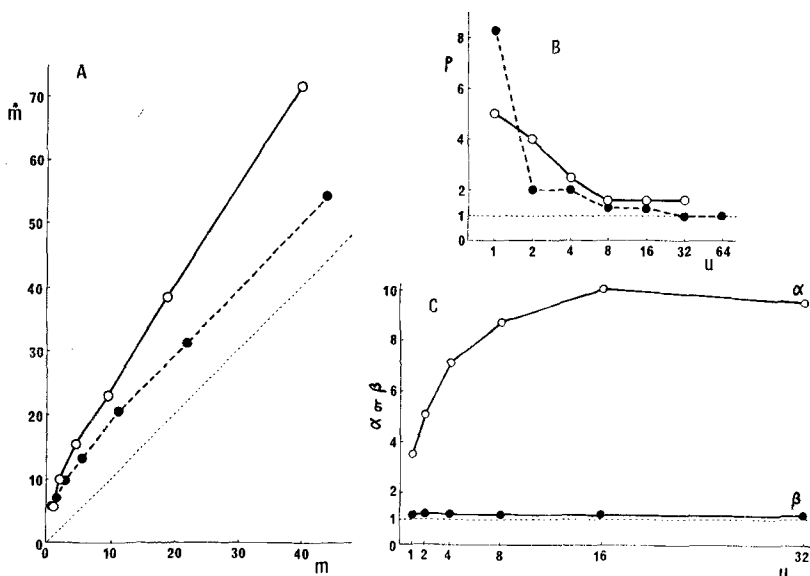

Fig. 11. Analysis of distribution pattern of the second-generation larvae of the rice stem borer, *Chilo suppressalis*. (Data from SUGINO, unpnblished, and KOJIMA and OKAMOTO, 1957)

A: The unit-size $\overset{*}{m}$-m relations for two populations, Shizuoka 7C and Kochi. (u=1 a hill of rice plants)

B: The ρ index plotted against quadrat size for the two populations above.

C: The values of α and β in the series $\overset{*}{m}$-m relation plotted against quadrat size. (Data for 9 populations).

plotted against quadrat sizes in Fig. 11 C. It is remarkable that the value of β remains to be fairly constant at a level close to unity over the range of quadrat sizes used. The value of α, on the other hand, rapidly increases at first and gradually approaches an asymptotic value of about 10 at quadrat size of 16 hills. The pattern is thus very similar to the random distibution of loose colonies.

These results may suggest that the larval colonies are distributed nearly at random or with a weak tendency for aggregation and the colony area would be less than 16 hills (possibly 4~8). The colony size (strictly, the mean crowding for colony size distribution $\overset{*}{m}_c$) is indicated by $\alpha \doteqdot 10$, but the true value of $\overset{*}{m}_c$ would be considerably larger than this as mentioned earlier (p. 110). These conclusions are consistent with the fact that the female moths lay egg masses (av. 40~60 eggs per mass) nearly at random over the field (KONO, 1958; ÔTAKE, 1961), and that the average distance of larval dispersal from an egg mass is 37.7 cm with the maximum of 106 cm, which may correspond to 4~16 rice hills (MIYAMOTO, 1951).

European Chafer Larvae

BURRAGE and GYRISCO (1954) described the distribution of the larvae of the European chafer, *Amphimallon majalis*, in 3 pasture plots of 25 by 25 feet each. As shown in Fig. 12 (left), the unit-size $\overset{*}{m}$-m relation in either plot is well fitted by a
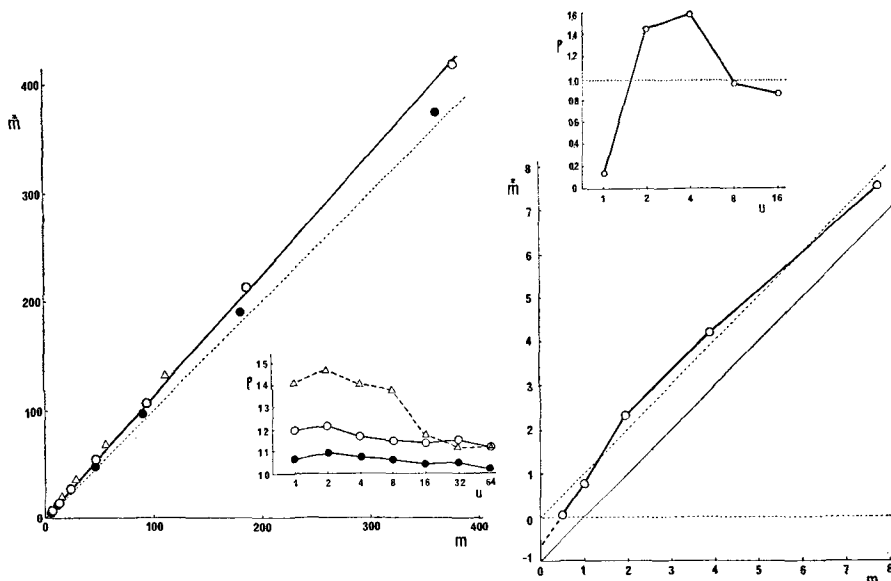

Fig. 12. Analysis of distribution patterns of two species of insects, the larvae of the European chafer, *Amphimallon majalis* and the eggs of the azuki bean weevil, *Callosobruchus chinensis*.
Left: *Amphimallon* (Data from BURRAGE and GYRISCO, 1954; $u=1 : 1\,\mathrm{ft^2}$). Open and solid circles and triangle indicate the plots A, C and D respectively.
Right: *Callosobruchus* (Data from NAKAMURA, 1968; $u=1 :$ one bean)

linear regression with a small positive value of α'. The slope β' is nearly equal to unity in Plot C but slightly larger in the other two. The ρ-graph indicates that there are clumps of area of ca. 8 sq. ft. in Plot D, the area of the lowest mean density, but no such structure in the other two. Inspection of distribution maps suggests that in either plot there is a weak gradient of density over the area rather than distinctive clumpings of individuals. Thus, it seems likely that the chafer larvae distribute themselves with a weak tendency of contagiousness, which may be related to local differences in the environmental conditions.

It is noted that in this instance the unit-size relation in a single population and the series relations for successive quadrat sizes can roughly be represented by a single linear regression of $\overset{*}{m}$ on m ($\alpha' \doteqdot 0$, $\beta' \doteqdot 1.1$).

Azuki Bean Weevil Eggs

The ovipositing female of the asuki bean weevil, *Callosobruchus chinensis*, tends to avoid the azuki beans on which eggs have already been laid. This results in an uniform distribution of eggs per bean under uncrowded condition (IWAO, 1968, IWAO and KUNO, 1971). NAKAMURA (1968) observed the oviposition behaviour of three females that were introduced singly into the arena of 64 by 64 cm on which 64 beans were placed equidistantly. Fig. 12 (right) shows the unit-size $\overset{*}{m}$-m relation for the eggs laid by one female during the 8-hour period (No. 2 of his experiments). It is noted that the distribution is regular at one-bean unit but it becomes to be aggregative at larger units, and also that the regression has a turning point at 4-bean unit. The ρ-graph shows a peak at 4-bean unit. The pattern resembles the colonial distribution with uniform intra-colony disposition. According to NAKAMURA, the female tends to lay eggs successively on neighbouring beans, but the peak at 4 bean unit in the ρ-graph might suggest that the area covered by one chain of ovipositional acts is not large.

Rhizomatous Sedges

PHILLIPS (1954) analyzed the spatial pattern of a rhizomatous sedge, *Eriophorum augustifolium*, by using the GREIG-SMITH's method. In most cases, the grid was composed of 256 units of 10 cm squares. She interpreted the results of such analysis with reference to the method of spread by rhizomes of this plant. According to her, the fundamental pattern in dispersion of shoots is as follows: (1) clumping of daughter rhizomes round a parent stock, which gives rise a primary peak in the mean-square curve at the quadrat size 4~16. It sometimes involves a small subsidary peak at quadrat size 1, 2, or 4, and this may be resulted from the presence of backward rhizomes that are shorter than the forward rhizomes; (2) a larger clumping of shoots consisting of three or four season's growth from a single plant, which corresponds a secondary peak at quadrat size 32~128; (3) a heterogeneity of environ-
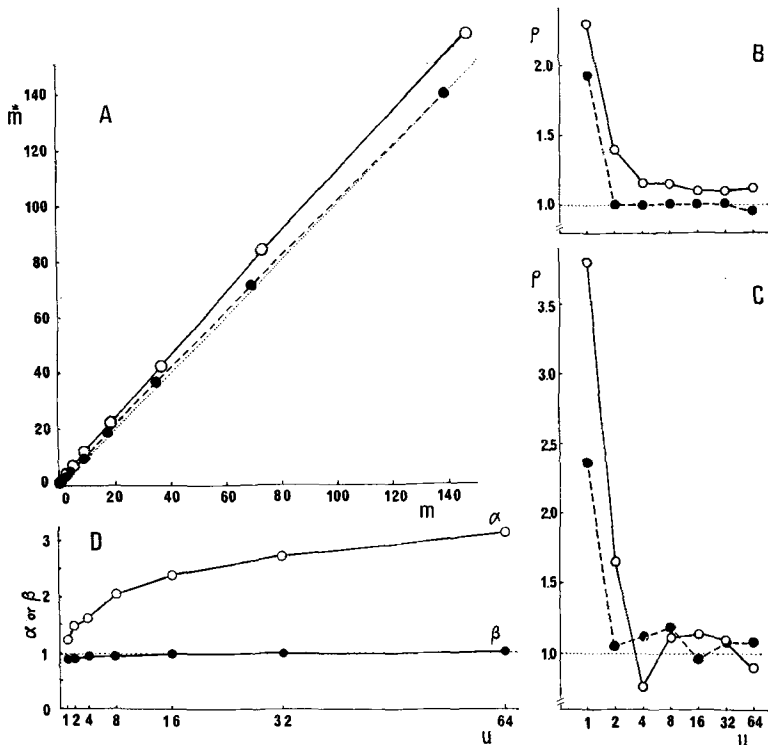
Fig. 13. Analysis of distribution pattern of a rhizomatous sedge, *Eriophorum angustifolium* (Data from PHLLIPS, 1954).

A: The unit-size $\overset{*}{m}$-m relation for two populations. ($u=1 : 100cm^2$)

B and C: 4 examples of graphs of ρ index against quadrat size.

D: The values of α and β in the series $\overset{*}{m}$-m relation plotted against quadrat size (based on 9 populations).

ment at a still larger scale. The clumpiness due to (2) or (3), however, was lacking or undetectable in some communities examined.

The unit-size $\overset{*}{m}$-m relations, calculated from her data, indicate that small clumps between quadrat sizes of 1 and 16 (usually 1, 2, or 4) present in all of the nine sets of her data, but the existence of larger clumps are noticeable in only four of them (Fig. 13 A, B, C). There is no indication of regular arrangement of individuals within clumps, but clumps themselves tend to be regularly spaced in some cases. The series $\overset{*}{m}$-m relation for each of successive quadrat sizes is well fitted by a linear regression ($r^2=0.96\sim0.998$). The changes of α and β with changing quadrat size are shown in Fig. 13 D. The value of β indicates a tendency for underdispersion at small quadrat sizes $1\sim8$ and random pattern at larger quadrat sizes. The value of α increases rapidly at first and then tends to be stabilized gradually. These changes of α and β resesmble those of the positive binomial distribution of colonies or the randomly distributed colonies within which individuals are distributed rather regularly. Since the ρ-graphs do not suggest regular disposition of individuals within

colonies, the pattern observed is more likely to be the regular arrangement of colonies. This inference is consistent with PHILLIP's observation. The small value of α indicates that each clump would be consisting of several shoots. Thus, the pattern detected seems to correspond with the clumping of daughter rhisomes round a parent plant (PHILLIP's (1)), and the presence of larger clumps (2) and (3) seems not to be fundamental to this species. In relation to this, it should be noted that the mean-square graph tends to increase at larger quadrat sizes even when colonies are distributed at random without any larger clumpiness (see p. 124).

In another species of sedge, *Carex arenaria*, however, there seems to exist a triple-clump structure. Fig. 14 A shows the unit-size $\overset{*}{m}$-m relation for this species in a dune (GREIG-SMITH's data cited by BARTLETT, 1971). The ρ-graph shows three peaks at quadrat sizes 1, 4, and 16, and clumps of small and intermediate scales tend to be distributed regularly. GREIG-SMITH mentioned in his comment for BARTLETT's paper that the rhizome (of this plant) grows in a straight line and aerial shoots are produced at approximately equidistant node along it, and that the number of shoots per node is mostly one but occasionally two. Therefore, the peak at quadrat size 1 may be due to occasional appearance of two shoots at a single node, and the second and third peaks may perhaps be related with the development of rhizome system over one or more seasons. Since the regression of $\overset{*}{m}_u$ on m_u becomes to be linear with $\alpha'=1.5$ and $\beta'=1.0$ at quadrat sizes larger than 16 units, it is inferred that the clumps of 40×40 cm in the average area, within which several shoots tend to form regularly-spaced double clumps, are distributed randomly over the grid area $(2.4\times2.4$ m$)$.

Three Species of Herbs in a Secondary Grassland

CAIN and EVANS (1952) studied the distribution patterns of the goldenrod, *Solidago rigida*, the bush clover, *Lespedeza capitata*, and the blazing star, *Liatris squarrosa*, in an old-field community in Michigan. Likewise the above-mentioned sedges, *Solidago* propagtes itself by creeping rhizomes. It shows a double-clump pattern: the individual shoots within small clumps and small clumps within large clumps tend to be distributed regularly, and large clumps themselves are distributed conatgiously over the field (Fig. 14, B).

In contrast, *Lespedeza* and *Liatris* have no rhizome system and they propagate themselves by seeds. They tend to form clumps of varying size due to localized dispersal of offspring round parents, though some plants occur singly or in pairs. In *Liatris*, the $\overset{*}{m}_u$-on-m_u regression becomes approximately linear at quadrat sizes of between 2 and 16 m^2 with a large β' value (Fig. 14, D). The ρ-graph indicates the presence of clumps of $1/2\sim2$ m^2 in area and the individuals are distributed rather regularly within such clumps. The inspection of distribution map (EVANS, 1952: Fig. 2) indicates the existence of clumps larger than 16 cm^2 in area, and hence the
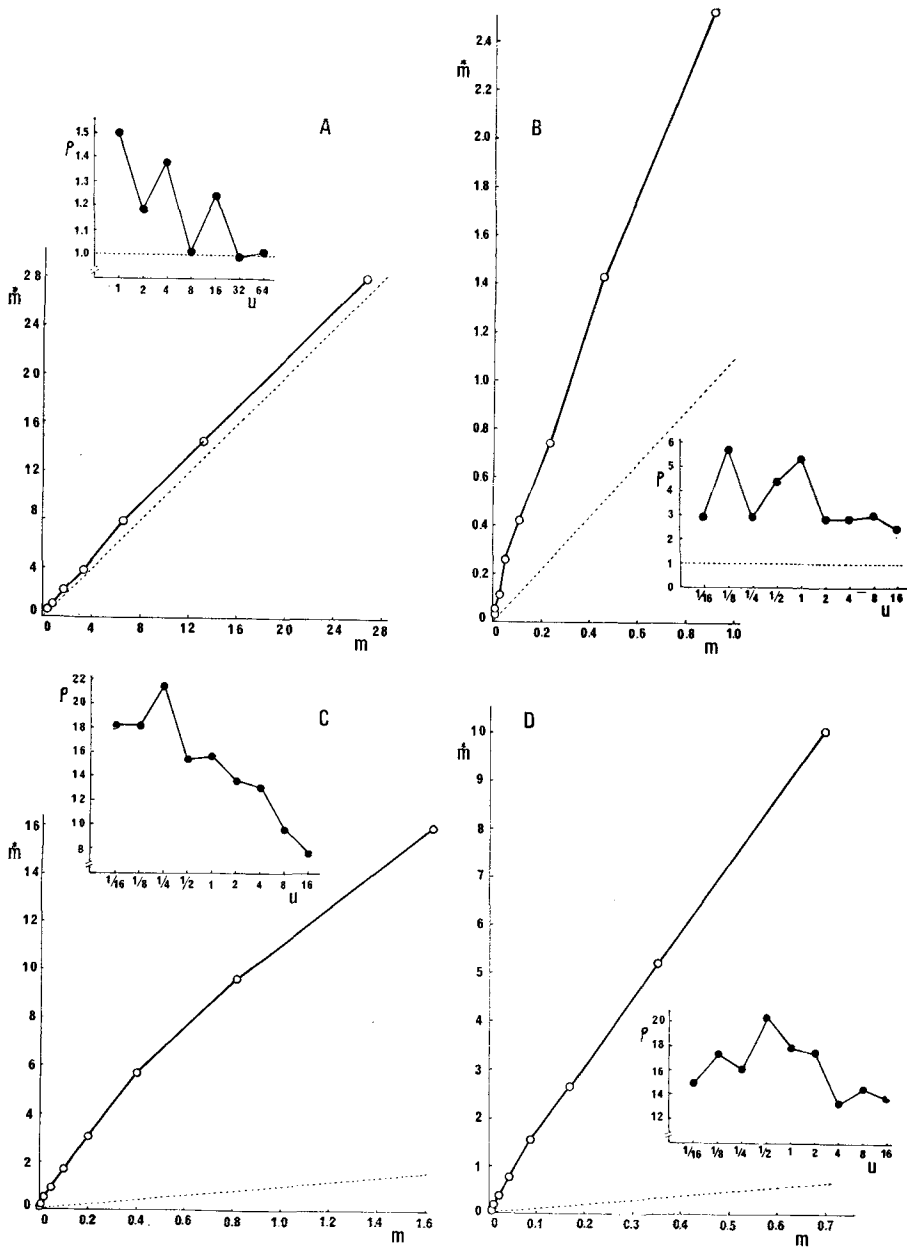
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Fig. 14. Analysis of distribution patterns of 4 species of plants.

A: Rhizomatous sedge, *Carex arenaria* (Data from BARTLETT, 1971; $u=1 : 100 \, \text{cm}^2$)
B: Goldenrod, *Solidago rigida* (Data from CAIN and EVANS, 1952 ; $u=1 : 1 \, \text{m}^2$)
C: Bush clover, *Lespedeza capitata* (Ditto)
D: Blazing star, *Liatris squarrosa* (Ditto)

regression would become less steeper if we take larger quadrat sizes. The pattern in *Lespedeza* is essentially similar to that in *Liatris*, but it seems to be more variable in clump area, which is indicated by the curvilinear $\overset{*}{m}_u$-m_u relation and the progressive decrease of ρ value over the range of quadrat sizes used (Fig. 14, C). Since there are larger clumps as in *Liatris* (EVANS, *l. c.*: Fig. 1), it is necessary to examine the distribution in the larger-sized quadrats in order to detect the pattern more satisfactorily.

DISCUSSION

It is clear that the $\overset{*}{m}-m$ relationship obtained by changing quadrat size in a single population (the unit-size relation) provides a useful basis for the analysis of spatial structure of biological populations. The linearity of the regression of $\overset{*}{m}_u$ on m_u indicates that the change of quadrat size in this range is equivalent to the change of mean density without any alteration in the fundamental pattern of distribution. If there are clumps or territories, the regression would become curvilinear. The approximate area of territory (or exclusive area in some other form) occupied by individual may be indicated by the quadrat size corresponding to the intercept of the regression on m_u-axis, at least in some cases. In the distribution comprising loose colonies, the regression would show a linearity after the quadrat size becomes sufficiently larger than the colony area: the slope β' for this part of the regression would rightly indicate the distribution pattern of colonies over the space, but the extrapolated value of the intercept α' may be more or less smaller than the expected value of $\overset{*}{m}_c$, the mean number of other individuals per individual per colony. The spatial disposition of individuals within colonies is suggested by the unit-size $\overset{*}{m}-m$ relation for the quadrat sizes smaller than the colony area. If the clumpiness in the distribution is largely due to local heterogeneity of the environment, the clump may be much more variable in size than in those stemmed from the intrinsic properties of the species concerned, which results in an irregular pattern of the $\overset{*}{m}_u$-m_u relation.

To detect the approximate area of clump or colony as well as the spatial pattern of individuals within clumps, it is convenient to use the τ_h index, which is equivalent to MORISITA (1959)'s $I_{\delta(s)}/I_{\delta(2s)}$, or the ρ index proposed here. As far as the cases examined here are concerned, the latter seems to be somewhat better for these purposes. Other advantages of ρ over τ_h index are: (1) that ρ indicates the distribution pattern of clumps themselves; (2) that it serves as an index for spatial correlation among neighbouring quadrats; and (3) that, for comparison of ρ values in a sequence of quadrat sizes, it is not necessary to keep the ratio of two successive quadrat sizes being constant. Thus the most of the information ontained by the unit-size $\overset{*}{m}-m$ relation can be summarized by the graph of ρ values plotted against the quadrat size. It is noted, however, that the range of either ρ or τ_h values to be

taken becomes narrower as the density of the population increases. It is due to the fact that mean crowding is concerned only with the quadrats occupied by individuals and hence the change of $\overset{*}{m}_u$ per unit change of m_u is larger in low-density populations than in high-density ones. Some indication on the colony size is obtainable through the inspection of $\overset{*}{m}_u$-on-m_u regression, though it gives an underestimate of $\overset{*}{m}_c$. The degree of underestimation may depend of the compactness of clumps as well as the distribution pattern of clumps.

GREIG-SMITH's (1952) method for detecting the clump area is based on the application of an analysis of variance to the grid sample. It is said that the mean area of clump can be suggested by peak(s) in the graph relating the mean square to quadrat size. Since the mean square allocated to a particular quadrat size u is equivalent to $m_u(2\overset{*}{m}_u - \overset{*}{m}_{2u} + 1)$ except for the largest quadrat size of one-half of the grid area, its value tends to increase with increasing the quadrat size without any appreciable peak, unless the clumps themselves are distributed more or less regularly (see Fig. 15). The point has already been mentioned by GREIG-SMITH himself and
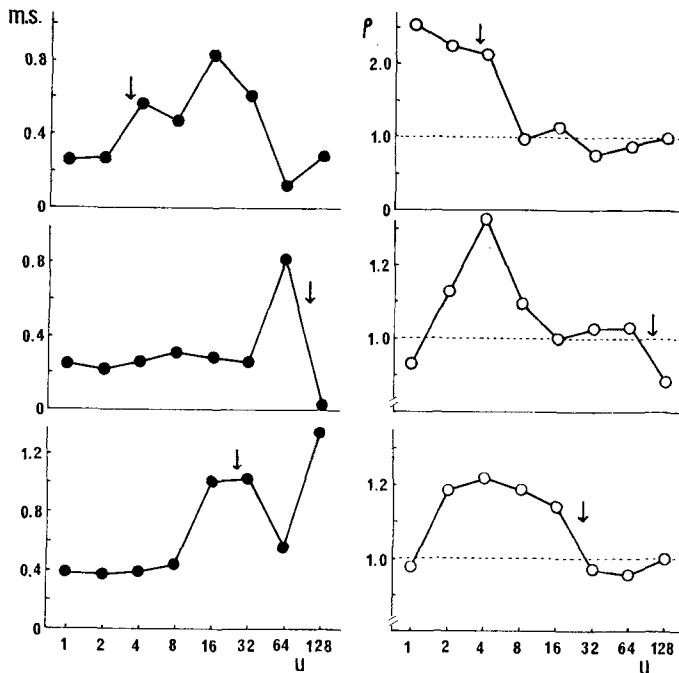

Fig. 15. Comparison between the GREIG-SMITH's analysis of variance and the present method for the detection of clumps in the 3 types of distributions given by GREIG-SMITH (1952).
Left: Mean square (m.s.) plotted against quadrat size (redrawn from GREIG-SMITH's tables). Right: The ρ index plotted against quadrat size. From upper to bottom: Random distribution of loose colonies (GREIG-SMITH's expt. 3), mosaic of irregularly-shaped patches (his expt. 5), and mosaic of similarly-shaped patches (his expt. 6).
Arrow indicates the mean area of clump shown by GREIG-SMITH.

by THOMPSON (1958). It is, therefore, questionable to use this method for the analysis of spatial pattern, though it is still widely used by plant ecologists (e. g., GREIG-SMITH, 1964 ; KERSHAW, 1964 ; ANDERSON, 1971). GREIG-SMITH's method seems to be effective for detecting the approximate area of clump of the mosaic distribution. This is not surprising because this type of distribution is similar in nature to non-overlapping distribution of loose colonies. As shown in Fig. 15, ρ values calculated form GREIG-SMITH's examples indicate even better the clump areas. In addition, ρ-graph suggests that individuals are distributed rather uniformly within clumps in both the mosaic of irregularly-shaped patches and that of similarly-shaped patches. This is not contradictory with GREIG-SMITH's description of experimental procedure (throwing discs) and results. In the mosaic of irregularly-shaped patches, ρ-graph suggests the presence of two scales of clumpiness. This may be due to the fact that different-density patches form narrow bands, so that the probability of cutting each patch through the edges of quadrat is markedly different in different direction.

Thus the $\overset{*}{m}$-m method presented here yields more information than GREIG-SMITH's does. Also, GREIG-SMITH's method can only be applied to the grid of contiguous quadrats, but the present method as well as MORISITA's are, in principle, usable not only for grid sample but also for random samples that are taken with quadrats of different sizes.

As mentioned above, a considerable amount of information on the spatial distribution pattern can be obtained through the inspection of the unit-size $\overset{*}{m}$-m relationship in a single population. It is sometimes possible to infer the general pattern characteristic of the species concerned after examining the unit-size relation for one or few populations. But such an inference involves a considerable danger.

On the other hand, we have developed the method for analyzing the spatial patterns based on the $\overset{*}{m}$-m relationship for a series of population at a given quadrat size. The knowledge obtained by its application is only valid for the quadrat size used, however. The changes in the series $\overset{*}{m}$-m relation with changing quadrat size are also considered here for some basic distribution patterns.

Since the information obtained from the unit-size relation and that from the series relation are complementary, a much fuller understanding of the species mode of spatial distribution would be obtainable if we examine both the unit-size relations for several populations and the series relations for successive quadrat sizes among them. The combined use of these relationships may suggest, for instance, that the presence of loose clumps detected by the unit-size relation is either due to colonial nature intrinsic to the species or due to clumpiness related with the heterogeneous conditions of the habitat, and that $\beta > 1$ in the series relation is related either with increase in colony size or that in colony density at high-density populations.

Finally, it may be worthwhile to mention briefly the application to the sampling

design. GÉRARD and BERTHET (1971) gave the equation for relative precision in sampling the clumped populations, where the quadrat size as well as the number of quadrats to be taken are incorporated as variables. Their equation is based on the assumption that the distribution follows the negative binomial series and its parameter k is invariant over the range of quadrat sizes to be taken. Since it is a rather special case that k (corresponds to $\overset{*}{m}_u/m_u$) remains constant for different quadrat sizes and for diflerent populations, their equation is limited in its applicability.

As has been shown in a previous paper (IWAO and KUNO, 1968), the relative precision, defined as D=standard error/mean, in the simple random sampling is shown by:

$$D_u = \sqrt{\frac{1}{n_u} \left(\frac{\alpha_u+1}{m_u} + \beta_u - 1\right)}, \tag{14}$$

where u denotes the quadrat size used, n_u the number of quadrats sampled, and α_u and β_u are the intercept and the slope of the regression in the series $\overset{*}{m}$-m relation for quadrat size u. If we put $u=1$ for the quadrat size taken as a standard, $m_u = um_1$ and, if sampling is made for the same total area, $n_u = n_1/u$. Then the above equation can be written as,

$$D_u = \sqrt{\frac{u}{n_1} \left(\frac{\alpha_u+1}{um_1} + \beta_u - 1\right)}. \tag{15}$$

Then we have

$$\frac{D_u}{D_1} = \sqrt{\frac{\alpha_u+1+(\beta_u-1)um_1}{\alpha_1+1+(\beta_1-1)m_1}}, \tag{16}$$

which gives a criterion for the comparison of relative precision when the same total area is sampled by two different quadrat sizes: the size u is better if $D_u/D_1 < 1$. The equation given by GÉRARD and BERTHET is a special case of eq. (15), in which $\alpha_u = 0$ and β_u does not change with u and equals $1+1/k$.

The number of quadrats to be sampled for attaining a fixed level of precision D_u can easily be derived from eq. (14):

$$n_u = \frac{1}{D_u} \left(\frac{\alpha_u+1}{um_1} + \beta_u - 1\right). \tag{17}$$

If we denote the cost for taking one quadrat of size u as C_u, the relative cost for a given D in the sampling with two different quadrat sizes 1 and u can be shown by

$$\frac{C_u n_u}{C_1 n_1} = \frac{C_u}{C_1} \frac{\alpha_u+1+(\beta_u-1)um_1}{u\{\alpha_1+1+(\beta_1-1)m_1\}}. \tag{18}$$

The size u is better if $C_u n_u/C_1 n_1 < 1$.

SUMMARY

A method for the analysis of spatial pattern using quadrats of different sizes is developed on the basis of the relationship of mean crowding ($\overset{*}{m}$) to mean density (m). The $\overset{*}{m}$-on-m regression obtained by successive changes in quadrat size in a single population (unit-size relation) shows a characteristic pattern according to the

type of distribution. By aid of the ρ-index proposed here, we can distinguish the random, aggregated and uniform distributions of the basic components (individual or group of individuals). The ρ serves as an index of spatial correlation between neighbouring quadrats, and it also provides information on the approximate area occupied by clump (colony), distribution pattern of individuals within clumps, and possibly the distribution pattern of clumps themselves.

Even in a specified type of distribution, the unit-size $\overset{*}{m}$-m relation is not necessarily identical with the $\overset{*}{m}$-m relation for a series of populations at a particular quadrat size (series relation). The changes in the series $\overset{*}{m}$-m relationship with successive changes of quadrat sizes are also considered for some basic patterns of distributions. The combined use of the unit-size and the series $\overset{*}{m}$-m relations for a set of populations of the species under study may provide a satisfactory picture of the spatial pattern characteristic of the species.

Application of the method is illustrated by using distribution data of several species of animals and plants. The advantage of the present method over other methods are discussed, and the formulae for determining the optimum quadrat unit in sampling surveys are given.

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枠面積の変化に対応した $\overset{*}{m}$-m 関係と
それに基づく空間分布の解析

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　一定面積の枠を用いた時の分布様式解析に $\overset{*}{m}$-m 関係が有効なことは，すでに示した通りであるが，一般に枠の大きさが変れば分布の特性も変化する。単一の分布において枠サイズを順次かえていった時期待される $\overset{*}{m}$-m 関係は分布様式に応じて特徴的なパターンを示し，ここで提出したρ示数を併用することによって，コロニー（あるいは他のかたまり）構造の有無，1コロニーの占める面積やその変異，コロニー内での個体の分布，またコロニー自体の分布様式などについて知見がえられる。ρ 示数は近接枠間の 個体数の相関の有無を検出するにも役立つ。コロニーあたり個体数については $\overset{*}{m}$-m グラフから示唆がえられようが，これは過小評価になる。

　いく組かの分布データがあれば，上記の枠サイズ関係と同時に，各枠サイズについての組間の $\overset{*}{m}$-m 関係が利用できるから，一層詳しい分布様式の解析が可能になる。いく種かの昆虫と草本の分布解析への適用例を示し，またサンプリング調査における最適枠サイズ決定の方法についても触れた。