APPENDIX

For the M step of the EM algorithm given in Section 2.1, we need to maximize $Q(\boldsymbol{\theta}, \boldsymbol{\theta}^\nu)$, which is just $L_c(\mathbf{Y}, \mathbf{Z}, \boldsymbol{\theta})$ with Z_{ij} replaced by w_{ij}^ν. For concise notation we will use p_i for $p(\alpha, \beta, x_i)$, Δ_i for $\Delta(x_i) = c + dx_i$, μ_i for $\mu + c + dx_i = \mu + \Delta_i$, and omit the ranges for $\Sigma_{i=1}^{k} \Sigma_{j=1}^{n_i}$. Recall that if Z_{ij} is known to be 0, then set $p_i = w_{ij} = 0$, and if Z_{ij} is known to be 1, then set $p_i = w_{ij} = 1$. The gradient $\nabla Q(\boldsymbol{\theta}, \boldsymbol{\theta}^\nu)$ is

$$\frac{\partial Q(\boldsymbol{\theta}, \boldsymbol{\theta}^\nu)}{\partial \alpha} = \Sigma\Sigma(w_{ij}^\nu - p_i),$$

$$\frac{\partial Q}{\partial \beta}(\boldsymbol{\theta}, \boldsymbol{\theta}^\nu) = \Sigma\Sigma(w_{ij}^\nu - p_i)x_i,$$

$$\frac{\partial Q(\boldsymbol{\theta}, \boldsymbol{\theta}^\nu)}{\partial \mu} = \Sigma\Sigma[(1 - w_{ij}^\nu)(Y_{ij} - \mu) + w_{ij}^\nu(Y_{ij} - \mu_i)]/\sigma^2,$$

$$\frac{\partial Q(\boldsymbol{\theta}, \boldsymbol{\theta}^\nu)}{\partial c} = \Sigma\Sigma[w_{ij}^\nu(Y_{ij} - \mu_i)]/\sigma^2,$$

$$\frac{\partial Q(\boldsymbol{\theta}, \boldsymbol{\theta}^\nu)}{\partial d} = \Sigma\Sigma[w_{ij}^\nu(Y_{ij} - \mu_i)]x_i/\sigma^2,$$

$$\frac{\partial Q(\boldsymbol{\theta}, \boldsymbol{\theta}^\nu)}{\partial \sigma} = \Sigma\Sigma[-\sigma^2 + (1 - w_{ij}^\nu)(Y_{ij} - \mu)^2 + w_{ij}^\nu(Y_{ij} - \mu_i)^2]/\sigma^3.$$

The Hessian $\mathbf{H}(\boldsymbol{\theta})$ of $Q(\boldsymbol{\theta}, \boldsymbol{\theta}^\nu)$ is block-diagonal with the (α, β) part similar to that for standard logistic regression: The (θ_k, θ_l) elements of $\mathbf{H}(\boldsymbol{\theta})$ are $\Sigma\Sigma h_{ij}(\theta_k, \theta_l; \boldsymbol{\theta})$, where $h_{ij}(\alpha, \alpha; \boldsymbol{\theta}) = -(1 - p_i)p_i$, $h_{ij}(\alpha, \beta; \boldsymbol{\theta}) = -(1 - p_i)p_i x_i$, and $h_{ij}(\beta, \beta; \boldsymbol{\theta}) = -(1 - p_i)p_i x_i^2$. The estimates $(\hat\alpha^{\nu+1}, \hat\beta^{\nu+1})$ are unique (when they exist) and can be found easily by Newton–Raphson iteration of $(\hat\alpha^{\nu+1}, \hat\beta^{\nu+1})' = (\hat\alpha^\nu, \hat\beta^\nu)' - H_{22}(\hat\alpha^\nu, \hat\beta^\nu)^{-1}\nabla Q_2(\boldsymbol{\theta}^\nu, \boldsymbol{\theta}^\nu)$, where $(\hat\alpha^\nu, \hat\beta^\nu)$ are used as starting values and $H_{22}(\alpha, \beta)$ is the 2×2 part of $\mathbf{H}(\boldsymbol{\theta})$ relating to (α, β), and ∇Q_2 is defined analogously.

The estimates $(\hat\mu^{\nu+1}, \hat c^{\nu+1}, \hat d^{\nu+1}, \hat\sigma^{\nu+1})$ are explicitly found by setting $\nabla Q(\boldsymbol{\theta}, \boldsymbol{\theta}^\nu) = 0$; e.g.,

$$\hat\mu^{\nu+1} = \Sigma\Sigma(1 - w_{ij}^\nu)Y_{ij}^\nu/\Sigma\Sigma(1 - w_{ij}^\nu),$$

$$\hat\sigma^{\nu+1} = \frac{1}{N}\Sigma\Sigma[(1 - w_{ij}^\nu)(Y_{ij} - \hat\mu^{\nu+1})^2 + w_{ij}(Y_{ij} - \hat\mu_i^{\nu+1})^2].$$

Following Louis (1982), the sample information matrix $\mathbf{I}(\mathbf{Y})$ (see §2.2) may be computed as $\mathbf{I}(\mathbf{Y}) = -\mathbf{H}(\hat{\boldsymbol{\theta}}) - \mathbf{K}(\hat{\boldsymbol{\theta}})$, where $\hat{\boldsymbol{\theta}}$ is the ML estimate and

$$\mathbf{K}(\boldsymbol{\theta}) = \mathrm{E}[\nabla L_c(\mathbf{Y}, \mathbf{Z}, \boldsymbol{\theta}) \cdot (\nabla L_c(\mathbf{Y}, \mathbf{Z}, \boldsymbol{\theta}))' \mid \mathbf{Y}, \hat{\boldsymbol{\theta}}].$$

The elements of $\mathbf{H}(\hat{\boldsymbol{\theta}})$ relating to (α, β) were given above. The remaining nonzero elements are $H_{\hat\mu\hat\mu} = -N/\hat\sigma^2$, $H_{\hat\mu\hat c} = H_{\hat c\hat c} = -\Sigma\Sigma\hat w_{ij}/\hat\sigma^2$, $H_{\hat\mu\hat d} = H_{\hat c\hat d} = -\Sigma\Sigma\hat w_{ij}x_i/\hat\sigma^2$, $H_{\hat d\hat d} = -\Sigma\Sigma\hat w_{ij}x_i^2/\hat\sigma^2$, and $H_{\hat\sigma\hat\sigma} = -2N/\hat\sigma^2$, where $\hat w_{ij}$ is w_{ij}^ν evaluated at $\boldsymbol{\theta}^\nu = \hat{\boldsymbol{\theta}}$.

With $\hat\mu_i = \hat\mu + \hat\Delta_i$ as above, the (θ_k, θ_l) elements of $\mathbf{K}(\hat{\boldsymbol{\theta}})$ are $\Sigma\Sigma(1 - \hat w_{ij})\hat w_{ij}a_{ij}(\hat\theta_k, \hat\theta_l)$, where $a_{ij}(\hat\alpha, \hat\alpha) = 1$, $a_{ij}(\hat\alpha, \hat\beta) = x_i$, $a_{ij}(\hat\beta, \hat\beta) = x_i^2$, $a_{ij}(\hat\mu, \hat\alpha) = -\hat\Delta_i/\hat\sigma^2$, $a_{ij}(\hat\mu, \hat\beta) = -\hat\Delta_i x_i/\hat\sigma^2$, $a_{ij}(\hat\mu, \hat\mu) = \hat\Delta_i^2/\hat\sigma^4$, $a_{ij}(\hat c, \hat\alpha) = (Y_{ij} - \hat\mu_i)/\hat\sigma^2$, $a_{ij}(\hat c, \hat\beta) = (Y_{ij} - \hat\mu_i)x_i/\hat\sigma^2$, $a_{ij}(\hat c, \hat\mu) = -\hat\Delta_i(Y_{ij} - \hat\mu_i)/\hat\sigma^4$, $a_{ij}(\hat c, \hat c) = (Y_{ij} - \hat\mu_i)^2/\hat\sigma^4$, $a_{ij}(\hat d, \hat\alpha) = (Y_{ij} - \hat\mu_i)x_i/\hat\sigma^2$, $a_{ij}(\hat d, \hat\beta) = (Y_{ij} - \hat\mu_i)x_i^2/\hat\sigma^2$, $a_{ij}(\hat d, \hat\mu) = -\hat\Delta_i(Y_{ij} - \hat\mu_i)x_i/\hat\sigma^4$, $a_{ij}(\hat d, \hat c) = (Y_{ij} - \hat\mu_i)^2x_i/\hat\sigma^4$, $a_{ij}(\hat d, \hat d) = (Y_{ij} - \hat\mu_i)^2x_i/\hat\sigma^4$, $a_{ij}(\hat\sigma, \hat\alpha) = [(Y_{ij} - \hat\mu_i)^2 - (Y_{ij} - \hat\mu)^2]/\hat\sigma^3$, $a_{ij}(\hat\sigma, \hat\beta) = a_{ij}(\hat\sigma, \hat\alpha)x_i$, $a_{ij}(\hat\sigma, \hat\mu) = -a_{ij}(\hat\sigma, \hat\alpha)\hat\Delta_i/\hat\sigma^2$, $a_{ij}(\hat\sigma, \hat c) = a_{ij}(\hat\sigma, \hat\alpha)(Y_{ij} - \hat\mu_i)/\hat\sigma^2$, $a_{ij}(\hat\sigma, \hat d) = a_{ij}(\hat\sigma, \hat c)x_i$, and $a_{ij}(\hat\sigma, \hat\sigma) = [(Y_{ij} - \hat\mu_i)^2 - (Y_{ij} - \hat\mu)^2]^2/\hat\sigma^6$.

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A New Index of Aggregation for Animal Counts

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SUMMARY

new index is described that is especially appropriate for measuring the aggregation of entomological ta in the form of counts per sample unit and that can make use of spatial information when it is ailable. Calculation of the index is based on a comparison of the effort required of individuals in a mple to achieve complete crowding with that to achieve complete randomness. The power of tests randomness based on this index is found to be greater than those based on the index of dispersion, pecially when spatial information is available.

Introduction

ost animals, unlike plants, move. The spatial information usually collected by animal ologists is therefore less precise than the maps of individuals analysed by plant ecologists, hich have inspired the development of powerful methodology (Besag, 1978; Ripley, 1981; iggle, 1983).

Entomological data usually consist of a count, x_i, made in each of n sample units, $i = 1$, ..., n. The spatial coordinate of each individual is rarely recorded; if the sampling device a trap then sampling proceeds over time and the location of each individual is unknown ior to capture. Furthermore, the spatial location of each sample unit may not be recorded reported. For this reason, animal aggregation is often quantified by the relation between mple summary statistics such as the sample mean, $m = \sum_i x_i/n$, and the sample variance, $= \sum_i (x_i - m)^2/(n - 1)$, or statistics derived from m and s^2, such as the moment estimator k, the shape parameter of the negative binomial distribution.

Studies employing variance–mean relationships (Perry, 1981, 1987a), parameters such k (Taylor, Woiwod, and Perry, 1979; Perry and Taylor, 1986; Clark and Perry, 1989), presence–absence data (Perry, 1987b) can provide valid, albeit limited information about imal distributions, even if the spatial locations of sample units are unrecorded. Taylor et (1983) give examples from population-dynamic behaviour; Perry and Taylor (1988) for tistical studies; Woiwod and Perry (1990) from sampling invertebrates. However, draw-cks of such studies are their inability to use any spatial information when it is available, the lack of any direct relationship between the components of the index and the spatial haviour of the individuals concerned. Southwood (1984), Taylor (1986), Perry (1988a), d Cormack (1988) have commented on the need for measures and models of insect gregation to incorporate, where possible, information concerning the movement of ividuals within real spatial frames.

For single samples, ecologists have traditionally assessed spatial pattern by testing the

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null hypothesis that individuals are distributed randomly over an area, their counts following a Poisson distribution. The most extensively used measure of aggregation is probably the Poisson index of dispersion, s^2/m, for which the test statistic, $I = (n-1)s^2/m$, has an approximate χ^2_{n-1} distribution under the null hypothesis, and provides quite a powerful test of randomness (Perry and Mead, 1979).

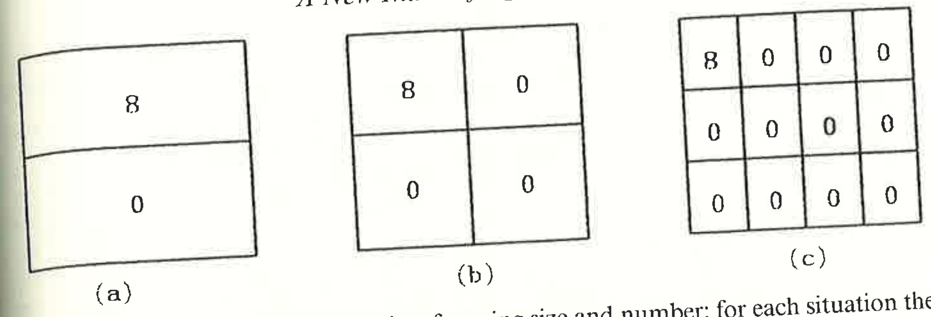
The purpose of this paper is to give details of a new index of aggregation (Perry, 1988b) that seeks to overcome these problems, and to assess the power of tests of randomness based on it. The index is capable of substantial development, but to justify this it must first be shown that it provides a more powerful test of randomness, for a range of sensible alternative hypotheses, than standard methods. The index of dispersion does not provide the only useful standard test, nor is the composite Poisson alternative hypothesis described by Perry and Mead (1979) the only useful alternative, but they provide a useful benchmark against which to assess the new index, and further comparisons are beyond the scope of this paper.

2. A New Index

Since almost all samples of animals display aggregation ($s^2 > m$) rather than regularity ($s^2 < m$), the latter condition is ignored, although the index could be modified easily to account for it. The basis for the index is to measure the aggregation of a sample by comparing the net effort required of individuals in transferring successively from unit to unit to achieve complete crowding, with that required to conform to "randomness", here defined by the condition $s^2 \le m$. For example, consider a sample of *Myzus persicae*, collected by Harrington (1987) in $n = 15$ units, with counts 3, 3, 3, 4, 5, 6, 7, 8, 8, 9, 10, 10, 10, 10, 15, and for which $m = 7.40$, $s^2 = 11.83$. If there were no spatial information available (and assuming it took the same amount of effort for an individual to transfer from its own unit to any of the others) complete crowding could be achieved with minimal effort if all the individuals except those in the unit with the largest count, x_{max}, transferred to that unit—a total of $(\sum_i x_i - x_{max})$ "moves". So the "moves to crowding", *mtc*, are 111 − 15 = 96, in this example. The condition $s^2 \le m$ could be achieved with minimal effort if, successively, an individual from the unit with the largest current count, c_{max}, transferred to that with the current smallest, c_{min}. Each such "move" reduces the sample variance by $2(c_{max} - c_{min} - 1)/(n-1)$. In this example, the condition is achieved after three individuals from the unit initially containing 15 transfer, successively, to each of the units initially containing 3, and, finally, an individual from that same unit (now containing 12 individuals) transfers to one of the four cells currently containing 4. This gives a sample (following transfers) with counts 4, 4, 4, 5, 5, 6, 7, 8, 8, 9, 10, 10, 10, 10, 11; the sample mean is, of course, unchanged, but the sample variance is now 6.54. The "moves to randomness", *mtr*, are thus 4. The index of aggregation, *S*, is formed from some function of *mtr* and *mtc*. That considered in this paper, $S = mtr/(mtr + mtc)$, gives a range between zero and unity, and allows a logit transformation of S: $\ln[S/(1-S)] = \ln(mtr) - \ln(mtc)$, which may be a sensible basis for further analyses. For this example, $S = .040$, indicating a mildly aggregated sample, relatively more close to randomness than complete crowding.

It is clear that the index S can be extended to incorporate available spatial information when the sample units are regularly spaced; true spatial movement then replaces transfers beween sample units, and this is done for a rectangular grid of units in Section 5.

It is admittedly less than ideal to define the condition for randomness in terms of m and s^2, since although the existence of a Poisson distribution implies that the expected values of m and s^2 are equal, the reverse is untrue. However, it is difficult to define an alternative condition, directly in terms of expected frequencies of the Poisson distribution, that would not make calculation of the index unacceptably cumbersome.



ure 1. Imaginary counts in sample units of varying size and number; for each situation the index of aggregation is $S = 1$.

Taylor (1984) discusses proposed attributes of a "perfect coefficient" to measure the gree of nonrandomness. The index described here satisfies most of the requirements, but ay clearly be influenced by the number and size of the sample units. Consider $n = 2$ mple units, each 4 × 2 ft, with eight individuals sampled in one unit and none in the ther (Fig. 1a) for which $S = 1$. If now more information were available, and the counts ad been made in four 2-foot-square units (Fig. 1b), or sixteen 1-foot-square units Fig. 1c), it is clear that $S = 1$ becomes more exceptional and unlikely as the number of nits increases. Whether this is a disadvantage is arguable, but, in any case, the issue oncerns pattern at several scales (see Section 8), which is beyond the scope of this paper.

The concept underlying the index has parallels with the "number of moves" diversity dex of Fager (1972) (see also Lyons and Hutcheson, 1988).

The following two sections investigate tests of randomness using the index S when there no spatial information available.

Tests of Randomness When No Spatial Information Is Available

wo tests are proposed: The first is very quick to compute but approximate; the second is randomisation test.

For all combinations of five sample sizes, n = 10, 20, 50, 100, and 500, with eleven lues of a Poisson parameter, θ = .5, 1, 2, 3, 5, 7.5, 10, 17.5, 25, 35, and 50, a sample of oisson random deviates was simulated 10,000 times, using the Numerical Algorithms roup GO5CAF generator (NAG Ltd, 1988). The value of S was calculated for each mulation and the values ordered; S_{95}, the 95th centile of the resulting frequency distrition, is tabulated for each combination of n and θ in Table 1. It was found that S_{95} was proximated closely for each combination of n and θ by

$$S_{95}(n,\theta) = \frac{.212}{\sqrt{\theta n}} \exp\left\{\left(\frac{3.68}{2.28+\sqrt{n}}\right) + \left(\frac{.204}{\sqrt{\theta} - .198}\right) + \left(\frac{.898}{\sqrt{\theta n} - .729}\right)\right\}.$$

is enables a quick, approximate test of randomness for any given sample to be conucted. The procedure is to replace θ in the above formula by m and to reject the null pothesis of randomness at the 5% level if the calculated value of S from the sample ceeds $S_{95}(n, m)$. The actual size of the test using this method was estimated by simulating mples of Poisson random deviates for combinations of values of n and θ, carrying out e test procedure, and recording the percentage of times out of 40,000 simulations the ll hypothesis was rejected. The results are shown in Table 2; the test procedure is not commended for values of $\theta \le 3$ when $n \le 20$, or for any values of $\theta \le 1$. Two-thirds of e tabulated values were within two standard errors of 5%, and the test seems adequate as informal, rough guide to indicate nonrandomness. Results with values other than those

Table 1
95th centile of 10,000 simulations for the index of aggregation with no spatial information, S_{95}. Value of S_{95} above, corresponding value of mtr/(mtr + mtc) below.

n	θ = .5	1	2	3	5	7.5	10	17.5	25	35	50
10	.500 1/2	.250 1/4	.143 2/14	.107 3/28	.0755 4/53	.0606 4/66	.0505 5/99	.0350 6/167	.0300 6/200	.0242 7/289	.0199 9/453
20	.250 1/4	.143 3/21	.0789 3/38	.0588 3/51	.0426 4/94	.0345 5/145	.0293 6/205	.0215 7/325	.0177 8/453	.0146 9/615	.0122 12/983
50	.111 2/18	.0698 3/43	.0408 4/98	.0314 5/159	.0227 6/264	.0182 7/385	.0158 8/506	.0114 9/787	.00949 12/1,265	.00794 14/1,764	.00678 17/2,508
100	.0678 4/59	.0421 4/95	.0262 5/191	.0194 6/309	.0146 7/478	.0115 9/785	.0100 10/998	.00742 13/1,752	.00611 15/2,457	.00516 18/3,487	.00440 22/5,001
500	.0245 6/245	.0156 8/512	.00981 10/1,019	.00751 11/1,465	.00536 13/2,423	.00425 16/3,769	.00380 19/4,994	.00275 24/8,717	.00234 29/12,408	.00193 34/17,615	.00164 41/25,063

Table 2
Percentage of simulations for which the quick test of randomness, with no spatial information, indicated rejection of the null hypothesis when true

n	θ = 1	2	3	5	7.5	10	17.5	25	35	50
10				4.48	5.59	4.95	5.08	4.99	4.72	5.09
20				4.21	5.22	4.77	4.29	4.70	5.01	4.78
50	4.24	5.04	4.94	5.15	5.15	5.03	5.10	5.10	5.13	4.87
100	5.45	4.76	4.90	4.36	5.06	5.15	5.32	4.87	5.31	5.05
500	5.38	5.69	4.36	4.93	4.84	5.01	4.95	4.89	5.03	5.00

...ulated values of n and θ appeared similar. For the data given in the previous section, ...calculated value of S was .040 and $S_{95}(15, 7.4)$ was .0436, so the quick test would (just) ...t reject the null hypothesis of randomness at the 5% level. Interestingly, the index of ...spersion test statistic for these data is $I = 22.4$, corresponding to a probability level of ...out 7.5% under the associated chi-squared test.

A less quick, but potentially more accurate method, and one that gives an estimated ...obability under the null hypothesis, is provided by a randomisation test (see, e.g., Besag ...d Diggle, 1977). In this, each of the total number of individuals, $\Sigma_i x_i$, in the sample is ...allocated randomly to one of the n sample units, and the value of S for this randomised ...mple, say S_{rand}, is calculated and stored. The procedure is repeated r times and the ...oportion of the r occasions for which $S_{\text{rand}} \geq S$ gives a probability of the actual value of ...under the null hypothesis of randomness. For the data in the previous section, out of ...,000 randomised samples, in 571 of them $S_{\text{rand}} \geq .040$, the actual value of S, giving a ...obability level of $P = .0571$.

Of the two tests, the former is recommended solely for use in the field, where only a ...nd calculator may be available. For general use, where access to high-speed computers is ...ailable, the latter test is accurate, acceptably fast, and easy to program; the next section ...vestigates its power.

... Power of Randomisation Test When No Spatial Information Is Available

...he methodology for determining the power of the randomisation test based on S when ...o spatial information is available, and the class of alternatives to the null hypothesis of ...ndomness, follows closely that used by Perry and Mead (1979), who investigated the ...ower of the index of dispersion test. Briefly, the alternative consisted of an infinite mosaic ...f contiguous squares of unit side, each containing a Poisson distribution of individuals ...ith density either λ (dense squares) or μ (sparse squares), the dense squares occurring ...ndomly with probability s. The squares were sampled with a circular quadrat of radius r ...$\leq$ .5), randomly "thrown" onto the mosaic, which therefore overlapped up to four ...uares. The distribution of X, the count per quadrat, was therefore Poisson with parameter ...ependent on quadrat area (πr^2), areas of overlap, and densities of overlapped squares. In ...is study, a random Poisson deviate (with the appropriate parameter) was simulated for ...ch quadrat "thrown" and the procedure repeated n times to give a sample, for which the ...dex, denoted S_{H_1}, was calculated. This was repeated 10,000 times to yield a frequency ...stribution of S_{H_1}. For the corresponding null hypothesis, 10,000 samples of size n were ...awn from a Poisson distribution with parameter $[\lambda s + (1 - s)\mu]\pi r^2$, to yield a frequency ...stribution of the index, denoted S_{H_0}, with 95th centile denoted $S_{H_0}(95\%)$. The power for ...test of size 5% was then obtained by finding the percentage of values $S_{H_1} \geq S_{H_0}(95\%)$. ...he results, for various combinations of values of λ, μ, s, and r, given in Tables 3 and 4,

Table 3
Power (percent) of the index of aggregation, S, test in the absence of spatial information

		λ/μ			
		2	3	5	11
$n = 20$, $s = .5$, $\lambda + \mu = 60$					
r	.15	14.33	32.40	61.10	87.14
	.20	23.86	60.02	88.93	98.87
	.25	36.70	79.54	98.15	99.88
	.30	50.95	92.09	99.62	99.98
	.35	63.75	97.05	99.85	100.00
	.40	74.97	98.66	99.96	100.00
	.45	83.01	99.59	99.96	100.00
$n = 20$, chessboard pattern (see Perry and Mead, 1979), $\lambda + \mu = 60$					
r	.15	11.80	25.14	48.45	76.80
	.20	16.64	41.83	73.45	93.91
	.25	23.82	57.90	83.13	97.93
$n = 40$, $s = .5$, $\lambda + \mu = 60$					
r	.15	20.59	52.43	87.07	99.09
	.20	37.03	83.58	99.32	99.98
	.25	57.25	97.03	99.96	100.00

Table 4
Power (percent) of the index of aggregation, S, test in the absence of spatial information

$n = 20$, $s = .5$, $r = .25$, $\lambda/\mu = 2$

	$(\lambda + \mu)/2$				
	7.5	15	30	45	60
Power	10.07	16.76	36.73	58.95	73.89

$n = 20$, $s = .5$, $r = .20$, $\lambda/\mu = 3$

	$(\lambda + \mu)/2$				
	10	20	30	40	60
Power	16.29	36.76	55.97	74.02	92.69

$n = 20$, $r = .2$, $\lambda/\mu = 3$, $\lambda + \mu = 60$

	s						
	.2	.3	.4	.5	.6	.7	.8
Power	69.71	69.72	67.05	58.16	47.28	34.40	22.16

$n = 20$, $s = .5$, $\lambda/\mu = 3$, $(\lambda + \mu)/2 = 1.2r^2$

	r							
	.5	.45	.4	.35	.3	.25	.2	.05
Power	34.25	39.70	41.14	47.41	49.54	53.38	56.19	70.80

$n = 20$, $s = .5$, $\lambda/\mu = 2$, $(\lambda + \mu)/2 = 1.875r^2$

	r					
	.5	.45	.4	.35	.3	.25
Power	25.10	25.35	28.11	33.50	34.18	37.21

be directly compared with the results for identical combinations for the index of ersion test reported by Perry and Mead (1979) in their Tables 1–4. (Note that in Perry Mead's Table 1, the power for $\lambda/\mu = 2$, $n = 40$ was 21.59, not 28.30 as given; also, 2 of their Table 2 should have been labelled $\lambda/\mu = 3$, not $\lambda/\mu = 2$.) In almost all cases test based on the index of aggregation is more powerful than that based on the index dispersion, usually by at least 2% and by over 10% in one case. It behaves much as the ex of dispersion does as regards variation in power with λ, μ, r, and s, and so conforms adly with the conclusions for that test drawn by Perry and Mead (1979). We might ect that if any available spatial information were incorporated in the index of aggregan, then this might lead to a further increase in power; this is investigated in the next two tions.

The Index of Aggregation with Spatial Information

nsider a rectangular grid of equally spaced sample units with $j = 1, \ldots, a$ rows and $k =$ …, b columns (so the sample size is $n = ab$), with counts x_{jk}. For example, the previous zus *persicae* data of Harrington (1987) were actually collected at 10-metre intervals on $a = 3$, $b = 5$ grid marked out along the side of a cabbage field, as shown in Table 5a. ere is little evidence of extreme clustering, although the larger counts seem to occupy its near one of the "diagonals" of the grid.

One obvious way to incorporate such information into the index of aggregation, S, is to nsider a single "move" to comprise an individual moving from its current unit to any ghbouring unit, along a row or column but not diagonally; "effort" and "movement" e then synonymous.

Now, the minimal movement for complete crowding must be calculated allowing the ssibility that any unit may act as "host" for the individuals from other units, not just

Table 5

a. Actual counts of *Myzus persicae* on an equally spaced 5 × 3 grid

	k				
j	1	2	3	4	5
1	8	6	5	9	10
2	3	3	10	15	7
3	10	10	4	8	3

b. Final configuration after six moves, using the algorithm to achieve $s^2 \leq m$ (see text)

	k				
j	1	2	3	4	5
1	8	6	5	9	10
2	4	5	9	13	8
3	9	9	4	8	4

c. Artificial initial configuration of counts identical to those in (**a**) but with more obvious clustering

	k				
j	1	2	3	4	5
1	5	6	7	10	8
2	3	3	10	9	10
3	4	3	8	10	15

that cell with the maximum value of x_{jk}. If all individuals not in unit (j, k) move to that unit then complete crowding is achieved with a net movement of $\sum_{j'} \sum_{k'} x_{j'k'}(|j - j'| + |k - k'|) = c(j, k)$ say, so the value of *mtc*, the moves to crowding, is the minimum of $c(j, k)$ over all values of j and k. In our example, although the maximum value of x_{jk} occurs at $j = 2$, $k = 4$, for which $c(2, 4) = 213$, the minimum of $c(j, k)$ is 206, for $j = 2$, $k = 3$. So $mtc = 206$.

Whereas the minimal movement for complete crowding can be found easily by enumeration, the minimal movement required for the condition for "randomness" ($s^2 \leq m$) is found most efficiently using an algorithmic approach. We believe that, for all but pathological cases, the following algorithm leads to the condition in the fewest possible moves, and this appears to have been the case in all the tests carried out: (1) Calculate the current differences between each possible pair of neighbouring units, choose that pair with the largest difference, and move one individual from the unit of the pair (denoted the "donor" unit) with more individuals to the unit of the pair (denoted the "receiver" unit) with fewer; (2) if more than one donor–receiver pair exist with the same difference choose that whose receiver currently has the fewest individuals; (3) if there is still a choice among several possible donor–receiver pairs choose that whose receiver has the neighbour with the smallest count; (4) if this fails to select a unique pair choose that whose receiver has the set of neighbours with the smallest average count; (5) if this still fails to select a unique pair, make a random choice among those available; (6) after a move has been made return to (1). In practice, there is rarely a need to invoke the full algorithm, and even when step (5) has been necessary the calculated value of *mtr* has never differed. For example, it may be verified that for the data in Table 5a, $mtr = 6$, and the random choice necessary on move 3 has not affected *mtr*, or indeed the "final configuration" shown after move 6 in Table 5b, when s^2 has been reduced to 7.0.

The value of S with spatial information is calculated, as previously, from $mtr/(mtr + mtc) = 6/212 = .0283$. It should be emphasised that the values of *mtr*, *mtc*, and S found here are all different from, and cannot be compared to, those values found for the index when no spatial information was available, in Section 2.

A randomisation test, carried out in an exactly analogous way to the test described in Section 3 (the total individuals are randomised spatially over the *ab* sample units), is available for the index of aggregation with spatial information. For the data in Table 5a, out of 10,000 randomised samples, 342 gave values of $S_{\text{rand}} \geq .0283$, the actual value of S, yielding a probability of .0342 under the null hypothesis. By utilizing the spatial information the power of the index of aggregation has been increased still further over the index of dispersion, in this case enabling the null hypothesis to be rejected at the 5% level. (A similar randomisation test applied to the index of dispersion gave a probability of .0739 under the null hypothesis.)

For a sample with identical counts, but more obvious clustering, we might expect the power of the test to increase further. For example, the counts in Table 5c differ from those in Table 5a only in position, the largest having been artificially displaced to the right. For these, $mtr = 9$, $mtc = 194$, $S = .0443$, and the probability under the null hypothesis was reduced to .003. It should again be emphasised however, that although $s^2 \leq m$ in the final configuration, this does not imply that the counts in the final configuration are distributed at random. The next section assesses how the power is affected by incorporating spatial information into the index.

6. Power of Randomisation Test When Spatial Information Is Available

To assess the power of the index when spatial information is available, the basic methodology of Section 4 was used, except that for each sample, instead of randomly and

Table 6

Power (percent) of the index of aggregation, S, test with (first entry) and without (in parentheses) spatial information

	d							
	.125	.25	.5	.75	1	1.5	2.75	3
$r = .2,\ s = .5,\ \lambda = 40,\ \mu = 20$								
$a \times b$								
5 × 4	10.47 (9.30)	19.94 (17.68)	24.33 (22.31)	23.88 (23.41)	23.28 (23.86)	26.24 (26.40)	22.09 (22.88)	24.50 (25.52)
10 × 2	15.04 (12.26)	22.46 (18.95)	23.36 (20.42)	23.22 (22.59)	25.21 (25.43)	23.94 (24.87)	24.57 (25.17)	23.82 (24.22)
8 × 5	19.40 (16.44)	33.00 (29.15)	37.32 (34.70)	37.12 (36.17)	37.45 (37.09)	38.19 (38.28)	36.10 (36.49)	36.91 (37.58)
20 × 2	31.24 (25.27)	37.67 (33.49)	36.67 (34.08)	38.48 (37.38)	37.76 (37.66)	36.61 (37.62)	36.88 (37.24)	35.74 (36.92)
$r = .2\ \ s = .5,\ \lambda = 45,\ \mu = 15$								
$a \times b$								
5 × 4	19.51 (17.03)	42.98 (38.18)	54.40 (51.66)	55.66 (55.77)	57.90 (58.32)	57.57 (57.90)	57.79 (59.54)	55.84 (58.08)
10 × 2	32.27 (27.97)	49.94 (44.09)	55.41 (51.37)	57.11 (56.08)	56.56 (57.36)	57.15 (57.27)	58.45 (59.98)	55.96 (56.53)
8 × 5	40.49 (36.16)	67.70 (63.47)	79.29 (76.76)	80.52 (80.13)	77.91 (77.83)	82.00 (81.85)	82.85 (84.21)	77.69 (78.30)
20 × 2	61.74 (55.38)	76.73 (70.87)	80.50 (77.59)	81.51 (80.25)	78.36 (78.20)	81.28 (81.93)	81.67 (83.08)	79.20 (79.21)
$r = .25,\ s = .5,\ \lambda = 40,\ \mu = 20$								
$a \times b$								
5 × 4	12.25 (10.48)	26.60 (23.42)	34.28 (31.93)	34.75 (33.64)	36.07 (36.62)	37.09 (37.88)	35.68 (36.85)	36.55 (36.94)
10 × 2	19.33 (15.47)	31.12 (26.19)	36.98 (34.18)	36.10 (35.08)	37.29 (36.87)	36.06 (36.49)	35.64 (36.43)	37.21 (37.41)
8 × 5	25.29 (21.58)	46.23 (40.75)	55.74 (52.19)	55.11 (53.56)	57.08 (57.21)	56.86 (57.24)	55.90 (56.68)	55.07 (55.89)
20 × 2	43.31 (36.12)	53.83 (46.84)	57.63 (53.98)	58.00 (56.75)	55.78 (55.60)	55.72 (56.77)	56.10 (56.25)	53.74 (54.87)
$r = .25,\ s = .5,\ \lambda = 45,\ \mu = 15$								
$a \times b$								
5 × 4	25.97 (22.51)	56.13 (52.27)	72.20 (70.12)	75.76 (75.53)	74.53 (74.72)	78.94 (79.45)	79.09 (80.42)	75.51 (77.15)
10 × 2	38.69 (33.45)	62.35 (57.16)	75.42 (72.24)	76.81 (76.38)	74.92 (74.80)	77.40 (78.93)	77.34 (78.85)	73.63 (74.83)
8 × 5	48.69 (44.53)	81.99 (79.85)	93.06 (91.85)	95.67 (95.33)	89.71 (89.64)	95.17 (95.22)	96.25 (96.84)	89.63 (90.12)
20 × 2	70.45 (67.10)	87.51 (83.74)	94.45 (92.98)	95.01 (94.55)	91.16 (90.97)	95.65 (95.99)	95.65 (95.95)	89.82 (90.21)

independently throwing n quadrats, a complete rectangular grid of $n = ab$ quadrats (a rows and b columns), whose centres were equally spaced a distance d apart, was thrown randomly onto the mosaic. For integral values of d each quadrat will overlap different squares but with identical areas of overlap, and there will be lack of independence between overlapped squares within the grid unless $d > 1 + 2r$. Hence comparability is possible between the results in Section 4 and these only if d is both relatively large and noninteger. But samples in which spatial information is important—i.e., in which clustering is apparent—are, for the class of alternatives considered here, generated by values of d substantially smaller than unity, because the scale of pattern is then larger than the interquadrat distance. Therefore, for a fair comparison, the power of the test was calculated from 10,000 samples with spatial information under null and alternative hypotheses, and then, for each sample, the counts were retained but the spatial information was discarded, and the power recalculated. This was done for various combinations of d, λ, μ, s, r, a, and b, and the results are given in Tables 6 and 7.

For values of $d < 1$, as expected, the incorporation of spatial information increased power, often by 4% and sometimes by up to 6%. Further, as d increased, so that the scale of pattern was equal to or less than the interquadrat distance, the gain in power became negligible, and sometimes was even slightly negative. Shape of grid was important when $d < .25$, power being larger for longer, thinner grids, which were more likely to overlap to more squares than the squarer-shaped grids. For both spatial and nonspatial forms of test, power increased with d for $d < 1$, because for small d there was a greater chance that all quadrats within the grid overlapped squares of the same Poisson parameter, λ or μ, yielding small values of S. As expected, the agreement between results for the nonspatial test for $d = 2.75$ and those for corresponding parameter values given in Table 3 was good, but note also some large differences in power between integral $d = 3$ and noninteger $d = 2.75$. Insofar as the comments above relate to the nonspatial form of S, they would probably give a good guide also to the behaviour of the index of dispersion test under the same sampling regime and class of alternatives.

To summarise, the test based on S with no spatial information generally provided a more powerful test than the index of dispersion, itself quite powerful against the class of alternatives considered. When spatial information was available, and the scale of pattern

Table 7
Power (percent) of the index of aggregation, S, test with (first entry) and without (in parentheses) spatial information

		d			
		.5	.75	1	1.5
$r = .2$, $\lambda = 45$, $\mu = 15$, $a = 5$, $b = 4$					
s	.2	56.24 (52.39)	61.30 (60.74)	61.54 (61.22)	64.18 (65.33)
	.3	62.62 (58.51)	67.14 (65.92)	64.31 (65.55)	68.26 (69.65)
	.5	53.22 (49.43)	53.75 (53.19)	56.76 (57.09)	57.94 (59.53)
	.7	33.40 (31.43)	35.38 (33.64)	33.76 (34.60)	33.95 (33.84)
	.8	22.58 (21.06)	21.72 (21.10)	20.93 (21.03)	21.09 (21.60)
$s = .5$, $\lambda = 45$, $\mu = 15$, $a = 5$, $b = 4$					
r	.05	65.82 (63.36)	67.45 (66.71)	69.16 (69.57)	67.61 (67.91)
	.2	53.86 (49.98)	56.57 (55.81)	56.22 (56.66)	54.63 (56.40)
	.3	46.81 (40.58)	49.74 (46.60)	50.30 (49.55)	48.94 (49.53)
	.4	40.32 (36.07)	43.45 (41.98)	42.07 (41.31)	42.46 (43.61)
	.5	32.37 (27.48)	36.09 (34.23)	35.90 (34.34)	33.78 (34.81)

large relative to the interunit distance, there was a further increase in power for S test.

Further Examples

(1941) gave, in his Table 4, the number of *Popillia japonica* larvae in each of three are-foot units selected at random from within contiguous plots measuring 6 ft × 5 ft 1.5-ft margins on each side. The methodology developed in Section 5 is valid only for ally spaced units; for other situations (e.g., rectangular units) alternative methodology t be developed. However, in this case the degree of unequal spacing of the centres of plots is slight and has been ignored. Choosing randomly one of the three counts from h plot yields the data in Table 8. Clearly, counts in rows 1–4 (Table 8a) are much ller than those in rows 5–8 (Table 8b), so the more interesting tests of randomness are se within the two sets of $a = 4$ rows and $b = 8$ columns. For Table 8a the 421 individuals e $m = 13.2$ and $s^2 = 18.4$. For the traditional index of dispersion chi-squared test on degrees of freedom, $I = 43.3$ with $P \approx .08$; a randomisation test with 10,000 samples e $P = .0696$. For the index of aggregation, $mtr = 11$, $mtc = 1{,}285$, $S = .00849$, and the domisation test with 10,000 samples gave $P = .0336$. (The nonspatial version of S would e given a higher probability, of .0686.) For Table 8b the 747 individuals have $m = 23.3$ d $s^2 = 31.3$; $I = 41.6$ with $P \approx .10$, and the randomisation test for the index of dispersion e $P = .0985$. For the index of aggregation, $mtr = 16$, $mtc = 2{,}191$, $S = .00725$, and the domisation test gives $P = .0199$. (Again, the nonspatial version of S gives a higher bability of .0670.) Both examples demonstrate data for which the hypothesis of random-s is rejected at the 5% level by the index of aggregation, but not by the index of persion. Of course, a fuller analysis of Bliss' data would account for pattern at different les.

While the index of aggregation was developed for insect counts, it can be useful for other anisms, such as plants, especially if no map is available. Thompson (1958) gave counts *Solidago rigida* in square metre quadrats in his Figure 4B2. The data are sparse: for $= 16$, $b = 16$, $n = 256$, only 80 individuals were counted, with $m = .3125$ and $= .3725$. $I = 304$ (χ^2_{255}, $P \approx .018$), while a randomisation test with 10,000 samples gave $= .0316$. For the index of aggregation, $mtr = 5$, $mtc = 621$, $S = .00799$, and the ndomisation test gives $P = .0229$.

Table 8
Counts of Popillia japonica *from Bliss* (1941)

(a)	9	5	9	18	13	13	11	17
	17	12	16	5	11	13	10	17
	9	19	14	8	13	14	15	13
	14	19	14	6	9	18	21	19
(b)	28	28	21	25	23	16	18	31
	30	34	25	31	22	14	18	24
	29	23	30	20	16	19	20	18
	24	30	30	27	21	21	17	14

Conclusion

any authors have emphasised that the detection of nonrandomness is of little interest cause so few observed sets of animal data are random (Taylor, Woiwod, and Perry, 78). It is more illuminating to estimate and describe the spatial pattern and, if possible, to model it. But any measure of aggregation should be capable of demonstrating sensitively nonrandomness. This paper, introducing the new index of aggregation, S, seeks only to make a case for further studies of S involving modelling and estimation. Of particular interest will be the relationship between S and Taylor's power law, now used extensively to derive efficient sampling schemes (Taylor et al., 1988). Also, Wiens (1989) and other ecologists have recently reemphasised the need for studies of populations to incorporate several spatial scales. Bliss' (1941) method, rediscovered by Greig-Smith (1952) and developed by Mead (1974), has been revitalised by the work of Gérard (1970), Chessel and de Belair (1973), and Chessel (1978, 1979). [See Chessel and Gautier (1984) for a brief review and Chessel and Croze (1978) for an application to presence–absence data.] Further work is required to develop the index of aggregation to allow for several spatial scales. Thioulouse (1987) gives practical examples for cabbage-stem flea-beetles, and Perry (1989) for various species. The third, and crucial, area for development is the generalisation to allow diagonal moves or nonequally spaced grids, which would be difficult algorithmically, and the further generalisation to allow locations in full two- or three-coordinate space. The power of the tests based on S seems sufficient to justify such studies.

The computation required is not excessive; that required for the data in Table 8a reported in Section 7, including 30,000 randomised samples, totalled less than 22 minutes CPU time on a μVaxII. The software was written in DEC's Vax FORTRAN 77, and is machine-dependent only to a minor degree. Mark 13 of the NAG FORTRAN library is required. The software is available free on request, by e-mail or on floppy disc or magnetic tape.

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Résumé

Un nouvel indice est décrit qui est spécialement approprié pour mesurer l'agrégation de données entomologiques se présentant sous la forme de comptages par unité d'échantillonnage, et qui peut faire usage de l'information spatiale lorsqu'elle est disponible. Le calcul de cet index est basé sur la comparaison de l'effort qui serait nécessaire aux individus pour atteindre la concentration complète à celui pour atteindre une distribution totalement aléatoire. La puissance des tests de dispersion aléatoire basés sur cet indice se révèle plus grande que celle des tests basés sur l'indice de dispersion, spécialement lorsque l'information spatiale est disponible.

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...stimation of von Bertalanffy Growth Curve Parameters from Recapture Data

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SUMMARY

...imple method of constructing estimating functions for parameters in the von Bertalanffy growth ...del $E[y(t)] = L[1 - \exp(-Kt)]$ is presented for tag–recapture data when the age of the animal is ...nown. The estimating functions are unbiased under very general distributional assumptions ...vided K does not vary between animals. Simulations of growth in lobsters and whelks indicate ...t the method performs well provided the initial capture times and recapture intervals vary over ...sonable ranges. Comparison is made with methods based on least squares, which have been shown ...be generally inconsistent.

...Introduction

...e von Bertalanffy growth curve is used extensively in fisheries and other areas to model ...e growth of an animal as a function of age from some origin t_0. If $y(t)$ represents the ...wth measurement (which we refer to as length for convenience) after time t, then for a ...gle animal the model assumes

$$E[y(t)] = L[1 - \exp(-Kt)] \tag{1}$$

...r positive parameters L and K. With this parameterisation L is referred to as the ...ymptotic or maximum length of the animal, while K regulates the expected percentage ...f maximum length achieved after a particular age. There has been discussion in the ...erature about whether such interpretations are biologically meaningful [see, for instance, ...night (1968)].

If the available data consist of pairs $(y(t), t)$ and the parameters L and K are assumed to ...e the same for each animal, then the estimation problem may be approached by relatively ...andard nonlinear regression methods, possibly using reparameterisation to improve ...mputational and statistical properties (Kimura, 1980; Gallucci and Quinn, 1979; ...atkowsky, 1986). More realistically, one might assume that the parameters L and K ...ary between animals according to some distribution, in which case one has a ...ndom-coefficients model and interest centres on the estimation of properties of the ...stribution; see, for instance, Sainsbury (1980) and Palmer, Phillips, and Smith (1991).

We are concerned in this paper with recapture data for which the age of the animal is ...known, so that the available data consist of the lengths at each capture and the time ...crements between measurements. For a single recapture, we observe for each animal the

...ey words: Distribution-free estimation; Growth curves; Simulation; Tag–recapture data; Unbiased estimating functions.