On the Mathematical Basis of the Variance-Mean Power Relationship

Mutsunori TOKESHI

School of Biological Sciences, Queen Mary and Westfield College, University of London, Mile End Road, London E1 4NS, U.K.

Abstract. The mathematical basis of a widely-known variance-mean power relationship of ecological populations was examined. It is shown that the log variance (S^2) – log mean (m) plot is virtually delimited by two lines $\log S^2 = \log n + 2 \log m$ and $\log S^2 = \log m$, thus increasing the chance that a linear regression line can be successfully fitted, without a profoundly behavioural background. This makes difficult the task of interpreting a successful fit of the power law regression and its parameter b in a biologically meaningful manner. In comparison with the power law regression, Iwao's $\overset{*}{m}$-m regression is structurally less constrained, i.e. has a wider spatial region in which data points can scatter. This suggests that a comparison between the two methods in terms of how good a fit is achieved for a particular data set is largely meaningless, since the power law regression may inherently produce a better fit due to its constrained spatial entity. Furthermore, it could be argued that a successful fit in Iwao's method, when found, is less taxed with mathematical artefacts and perhaps more clearly linked to some biological mechanisms underlying spatial dispersion of populations.

Key words: variance-mean power law, $\overset{*}{m}$-m regression method.

Introduction

The observation that population mean density, μ, is related to variance, V, by a power function,

$$V = \alpha \mu^\beta,$$

constitutes one of very few principles in ecology ('Taylor's Power Law', Southwood 1978) that has been found to be applicable to a wide range of animal species (Taylor 1961; Taylor et al. 1978 1980; Taylor and Woiwood 1980). This relationship can be conveniently described in a linear regression form for logarithmic values of sample variance (S^2) and mean (m);

$$\log S^2 = a + b \log m,$$

where the parameter b was regarded by Taylor (1961) as an 'index of aggregation' which takes a characteristic value for each species, reflecting the balance between opposing behavioural tendencies to move towards or away from centres of population density (Taylor and Taylor 1977). Whilst Taylor and his co-workers have proposed in a series of publications spanning nearly three decades (Taylor 1961, 1984; Taylor and Taylor 1977; Taylor and Woiwood

1980, 1982; Taylor et al. 1978, 1980, 1983, 1988; Perry and Taylor 1985) that behavioural mechanisms are responsible for this remarkably consistent observation, some ecologists have remained sceptical about this view (Iwao 1979; Hanski 1980; Dye 1983; Downing 1986) and considered alternative non-behavioural explanations (Anderson et al. 1982; Thórarinsson 1986; Hanski 1987; Soberon and Loevinsohn 1987; Perry 1988). Because the power law now seems to be part of current ecological thinking with very frequent appearance in population studies (e.g. McArdle et al. 1990; Rosewell et al. 1990), it is considered worthwhile to clarify the mathematical basis of the law itself, the task that has not been done thoroughly. The objective here is to present a simple, general mathematical argument which has been overlooked in the previous debate on this subject and demonstrates that mathematical artefacts divorced from behavioural and/or demographic ecology of organisms play an important role in establishing the above relationship. Furthermore, the power law is contrasted to another well-known regression method, that of Iwao (1968), and possible implications are considered.

Mathematical basis of the power law

Statistically, the sample variance S^2 is defined as

$$S^2 = \frac{\Sigma(x_i - \bar{x})^2}{n-1}, \tag{1}$$

where x_i and $\bar{x}$ are a variate and its mean, respectively, and n is the sample size. This equation can be rewritten as

$$S^2 = \frac{\Sigma x_i^2 - n\bar{x}^2}{n-1}. \tag{2}$$

With fixed values of n and $\bar{x}$, Σx_i^2 assumes a maximum value when one of the variate x_i equals $n\bar{x}$ and all the rest are zero, i.e. max $[\Sigma x_i^2] = n^2\bar{x}^2$, which can be replaced into eqn (2) to give the maximum value of S^2 thus,

$$S^2_{max} = n\bar{x}^2. \tag{3}$$

Replacing $\bar{x}$ by m following Perry's (1981) notation of the Taylor's power law and taking logarithms of the both sides of this equation, we obtain

$$\log S^2_{max} = \log n + 2 \log m. \tag{4}$$

This effectively defines the maximum value of the log variance for a given combination of n and m. To fit the Taylor's power law we require not only one but several sets of m and S^2, where each S^2 has a theoretical maximum value associated with it, depending on the sample size n and mean m. In ecological studies, however, researchers often try, most reasonably, to employ a fixed value of n as far as possible in a series of sampling (Elliott 1981, 1982a, b) and in any case it falls well within one order of magnitude (Taylor et al. 1980; Drake 1983) which, if converted to logarithm to the base 10, results in a variation of less than 1. Under these circumstances, the equation (4) basically describes a linear relationship between log mean density and the maximum value of log variance with the slope=2 and the intercept=$\log n$ (Fig. 1). Furthermore, as noted by many workers (Taylor 1984; Taylor and Taylor 1977; Taylor and Woiwood 1980, 1982; Taylor et al. 1978, 1980, 1983, 1988; Perry and Taylor 1985; Soberon and Loevinsohn 1987; Perry 1981; Elliott 1981, 1982a, b; Drake 1983), animal populations to which the power law analysis has been applied are substantially over-dispersed (Kemp 1987), i.e.,

$$S^2 > m. \tag{5}$$

Taking logarithms of both sides,

$$\log S^2 > \log m. \tag{6}$$

Equations (4) and (6) together mean that, in ecological investigations, data points for the log mean density-log variance plot are virtually gathered from the restricted region delimited by the upper line (a) and the lower line (b)
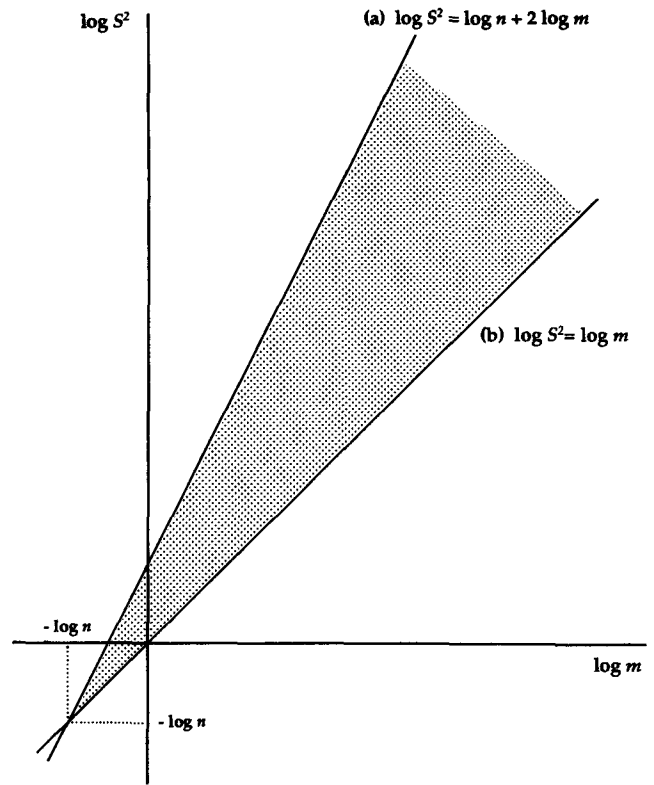

Fig. 1. The theoretical 'sampling space' (shaded area) of ecological data points in the variance-mean regression analysis. Lines (a) and (b) define the upper and the lower boundary of the space, respectively.

in Fig. 1. Furthermore, these data points will not be scattered uniformly within this region but tend to be located away from the boundary lines, in particular the upper one (i.e., $\log S^2 < \log n + 2 \log m$); this is expected because the magnitude of variation encompassed by the majority of ecological data to be analysed in this manner is unlikely to approach such an extreme value as S^2_{max} (i.e. all but one sampled units containing no individual). All these conditions will considerably increase the chance that a linear regression line can be successfully fitted on a log variance-log mean graph. It should here be stressed that no biological background, behavioural nor demographic, has so far been assumed, except that the populations are supposed to be over-dispersed for most of the spatial scales used for investigation, which is a least controversial point and acceptable to both the proponents and critics of the power law (Taylor et al. 1978; Anderson et al. 1982).

Given this 'sampling space', it is theoretically possible to obtain a linear regression with any value for the parameter (=slope) b as long as a *finite* number of points are located in this space, although, without further constraints, b is most likely to fall in the range of 1.0-2.0; this agrees with previous analyses of empirical data. On the other hand,

a universal statistical tendency to approach randomness (i.e. the line log S^2 = log m) as density decreases (small m) may also increase the chance of producing $b \geq 2$ on this constrained graph. Among a set of data points, those points with smaller values of m will tend to lie closer to the line log S^2 = log m and, depending on the values of m with which randomness is achieved for a given data set, there is always a possiblity that b becomes larger than 2. Similarly, if the values of n associated with larger m are on average larger than those associated with smaller m among a set of data points, then the fitted regression line is likely to have a steeper slope b. Here, there are three general observations to be made, which closely relate to Downing's (1986) view on the value of b:

—Fitting of a linear regression is likely to be more successful if

(i) there are more data points.

(ii) data points are scattered over a wider range of mean density.

(iii) data points on the whole are located closer to the intersection ($-$log n, $-$log n) of the two boundary lines (i.e. inclusion of samples with low mean densities).

Discussion

It is apparent from above that the establishment of the power law relationship is greatly facilitated by mathematical artefacts coupled with ecological common sense (fixed sample size, over-dispersion) and that the successful fit of a regression line to data cannot by itself be interpreted as a concrete proof of behaviour-based density dependence of spatial distribution as has often been argued (Taylor 1984; Taylor and Taylor 1977; Taylor et al. 1980, 1983; Elliott 1981, 1982a, b; Drake 1983). Whilst this need not negate the involvement of behavioural mechanisms in the process (indeed behaviour may be reinforcing this relationship, together with demographic stochasticity [sensu Anderson et al. 1982], sampling regimes employed, etc.), the use of the power law as a behavioural model in ecology should be treated with caution, because of an inherent difficulty in separating behavioural or other ecological components from the mathematical artefacts described here. The difficulty is, the degree to which mathematical artefacts play a part is likely to vary from one set of data to another depending on the number, values and scatter, etc., of data points, the aspect that has been overlooked in most empirical studies. Thus a comparison between different species/ seasons/areas, etc. poses a serious problem: what proportion of the difference in parameter b between particular data sets can be ultimately attributed to behaviour, not to underlying mathematics and chance?

It is worth noting that the constrained nature of the

spatial domain on a log variance-log mean plot, in particular the upper boundary line, will also apply to theoretical (contagious) relationships such as the negative binomial and the Neyman's distribution, as long as there is no substantial, arbitrary variation in n across data; uniformly large n will not in itself free a variance-mean relation from the mathematical constraints considered here. In other words, the fact that theoretical distributions all approximate a straight line (Kuno 1991) does not mean that linearity of these relations is completely independent of mathematical artefacts on a log variance/mean graph. As with empirical data, interpretation of b for theoretical data remains an elusive matter, without fully knowing the range of b values encountered under different parameter conditions for a particular theoretical relationship.

It should here be stressed that the above analysis provides solely the general mathematical framework of the power law and is not intended as a complete explanation of why particular empirical data have achieved a highly significant linear regression with r^2 exceeding 0.99 or even 0.999, for example; such an explanation naturally rests with a case-by-case analysis. An important point to note, however, is that any explanation conceived, whether behavioural or demographic (e.g. Anderson et al. 1982; Taylor and Taylor 1977; Perry 1988; Hanski and Woiwood 1993), always operates in addition to the mathematical constraints demonstrated above.

In relation to the Power Law, it is interesting to see the mathematical basis of the $\overset{*}{m}$-m method (Iwao 1968, 1970, 1972, 1979; Iwao and Kuno 1971), another well-known regression method for analysing aggregation patterns that Taylor has criticised as offering unsatisfactory fit to real data (Taylor 1984; Taylor et al 1987). Iwao (1968) proposed that Lloyd's (1967) mean crowding $\overset{*}{m}$ is linearly related to the mean m:

$$\overset{*}{m} = a + bm, \qquad (7)$$

where a and b are constants. Since $\overset{*}{m}$ is defined as

$$\overset{*}{m} = m + S^2/m - 1. \qquad (8)$$

With a fixed value of m, the maximum value of $\overset{*}{m}$ is obtained when S^2 is maximised, i.e. equaion (3). Substituting and rearranging (with $\bar{x} = m$),

$$\overset{*}{m}_{max} = (n + 1)m - 1. \qquad (9)$$

Similarly, combining equation (5) with (8),

$$\overset{*}{m} > m. \qquad (10)$$

Equations (9) and (10) define the upper and the lower boundary, respectively, of the effective sampling region on the $\overset{*}{m}$-m plot (Fig. 2). With n typically assuming 10 or more in most ecological studies, the space where data points can scatter on this plot is much larger than the corresponding
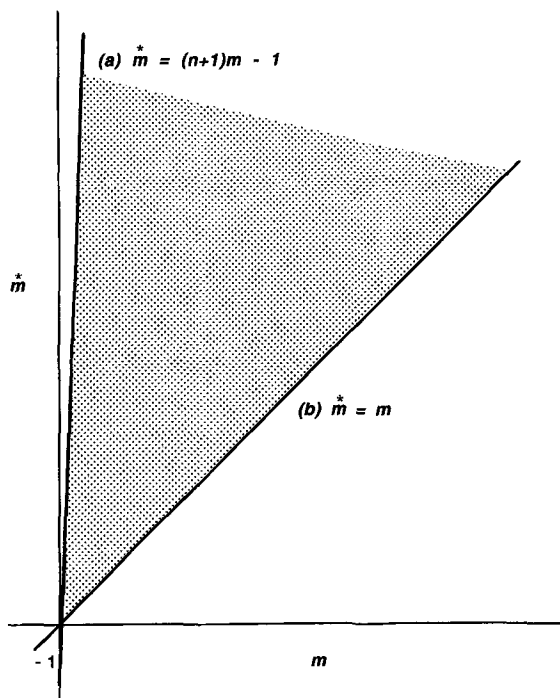
Fig. 2. The theoretical' sampling space' (shaded area) of ecological data points in the $\overset{*}{m}$-m regression analysis. Lines (a) and (b) define the upper and the lower boundary, respectively.

Fig. 3. $\overset{*}{m}$-m regression of a chironomid community. The regression line is: $\overset{*}{m}=1.13$ (±0.37, 95% C.L.) $+1.32$ (±0.013) m.

coefficient of determination were obtained for the power law regression ($r^2=0.933\pm0.042$ [1 SD]) than for the $\overset{*}{m}$-m regression ($r^2=0.865\pm0.158$ [1 SD]), although three out of eight species had a slightly higher value of r^2 with the $\overset{*}{m}$-m regression (Table 1). It can generally be argued that a

space on the log variance-log mean plot; note that as n increases, the upper boundary line infinitely approaches the m axis. It then follows that constraints of the data sampling space are less pronounced in the Iwao's regression than in the Taylor's and it is all too natural that the latter generally demonstrates a better fit of linear regression than the former with respect to a particular data set (e.g. Drake 1983). For example, data from a freshwater chironomid community (Tokeshi 1986, 1995; Tokeshi and Townsend 1987) reveal that, on average, higher values of

Table 1. Coefficient of determination (r^2) in Taylor's (log $S^2=$ $a+b$ log m) and Iwao's ($\overset{*}{m}=\alpha+\beta m$) regression analyses for different species of chironomid.

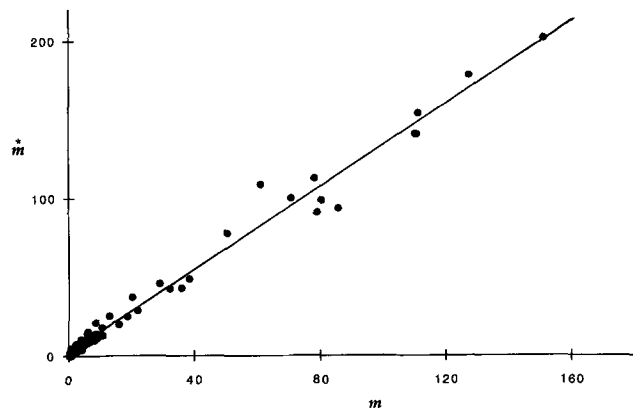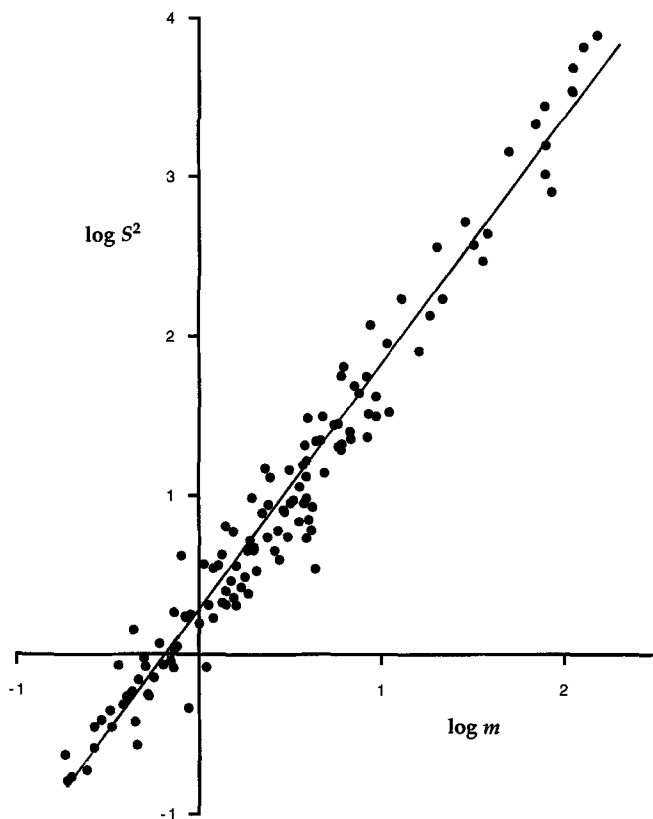| species	r^2	
	Taylor's	Iwao's
Tvetenia calvescens (Edwards)	0.97	0.89
Eukiefferiella ilkleyensis (Edwards)	0.93	0.89
Cricotopus annulator Goetghebuer	0.89	0.82
Cricotopus bicinctus (Meigen)	0.97	0.98
Orthocladius obumbratus Johannsen	0.96	0.99
Rheocricotopus chalybeatus (Edwards)	0.86	0.51
Thienemanniella majuscula (Edwards)	0.91	0.85
Rheotanytarsus curtistylus (Goetghebuer)	0.97	0.99

Fig. 4. Log (variance)-log (mean) regression of a chironomid community. The regression line is: log $S^2=0.253$ (±0.045, 95% C.L.) $+1.54$ (±0.05) log m.

comparison of goodness-of-fit between these two methods is largely meaningless, since the power law regression is more facilitated by mathematical artefacts (i.e. narrower spatial domain) than Iwao's regression. It may in turn be suggested that a significant fit in the $\overset{*}{m}$-m regression (whether it is linear or slightly curvilinear matters little in the present consideration), if found, can be more clearly linked to some underlying ecological processes. For the chironomid community mentioned above, a single regression line on the $\overset{*}{m}$-m plot gives a very good fit to the entire community data ($r^2 = 0.99$, Fig. 3), probably suggesting that species in this assemblage do not possess strongly species-specific patterns of dispersion. Interestingly, a power-law regression analysis of the same data has yielded a slightly lower level of goodness-of-fit ($r^2 = 0.96$, Fig. 4), which may be a fairly uncommon case in view of the above reasoning. In summary, the $\overset{*}{m}$-m method is at least *expected* to be less taxed with mathematical artefacts than the power law method. These and other points may require further clarification, quite apart from the practice of goodness of fit comparisons which seems to have overshadowed analyses in this direction (cf. Perry and Taylor 1988; Kemp 1988). In conclusion, despite past criticisms and various proposals, Iwao's method remains as a valid approach to analysing dispersion patterns of populations (cf. Kuno 1991), perhaps structurally less constrained than Taylor's method, as demonstrated here.

References

Anderson, R. M., D. M. Gordon, M. J. Crawley and M. P. Hassell (1982) Variability in the abundance of animal and plant species. *Nature* **296**: 245–248.

Downing, J. A. (1986) Spatial heterogeneity: evolved behaviour or mathematical artifact? *Nature* **323**: 255–257.

Drake, C. M. (1983) Spatial distribution of chironomid larvae (Diptera) on leaves of the bulrush in a chalk stream. *J. Anim. Ecol.* **52**: 421–437.

Dye, C. (1983) Insect movement and fluctuations in insect population size. *Antenna* **7**: 174–178.

Elliott, J. M. (1981) A quantative study of the life cycle of the net-spinning caddis *Philopotamus montanus* (Trichoptera: Philopotamidae) in a Lake District stream. *J. Anim. Ecol.* **50**: 867–883.

Elliott, J. M. (1982a) A quantative study of the life cycle of the case-building caddis *Odontocerum albicorne* (Trichoptera: Odontoceridae) in a Lake District stream. *Freshwat. Biol.* **12**: 241–255.

Elliott, J. M. (1982b) The life cycle and spatial distribution of the case-building caddis Agriotypidae) and its caddis host *Silo pallipes* (Trichoptera: Goeridae). *J. Anim. Ecol.* **51**: 923–941.

Hanski, I. (1980) Spatial patterns and movements in coprophagous beetles. *Oikos* **34**: 293–310.

Hanski, I. (1987) Cross-correlation in population dynamics and the slope of spatial variance—mean regressions. *Oikos* **50**: 148–151.

Hanski, I. and I. P. Woiwood (1993) Mean-related stochasticity and population variability. *Oikos*, **67**: 29–39.

Iwao, S. (1968) A new regression method for analyzing the aggregation pattern of animal populations. *Res. Pop. Ecol.* **10**: 1–20.

Iwao, S. (1970) Problems of spatial distribution in animal population ecology. pp. 117-149. *In* G. P. Patil (ed.) *Random counts in biomedical and social sciences.* Pennsylvania State University Press, Philadelphia.

Iwao, S. (1972) Application of the $\overset{*}{m}$-m method to the analysis of spatial patterns by changing the quadrat size. *Res. Popul. Ecol.* **14**: 97–128.

Iwao, S. (1979) The $\overset{*}{m}$-m method for analysing the distribution pattern in biological populations. pp. 215-228. *In* G. P. Patil and M. L. Rosenzweig (eds.) *Comtemporary quantitative ecology and related ecometrics, Stat. Ecol.* **12**. International Co-operative Publication House, Maryland.

Iwao, S. and E. Kuno (1971) An approach to the analysis of aggregation pattern in biological populations. pp. 461–513. *In* G. P. Patil et al. (eds.) *Statistical ecology*, Vol. 1. Pennsylvania State University Press, Philadelphia.

Kemp, A. W. (1987) Families of discrete distributions satisfying Taylor's power law. *Biometrics* **43**: 693–699.

Kemp, A. W. (1988) Response (in 'Families of distributions for repeated samples of animal counts'). *Biometrics* **44**: 888–890.

Kuno, E. (1991) Sampling and analysis of insect populations. *Annu. Rev. Entomol.* **36**: 285–304.

Lloyd, M. (1967) Mean crowding. *J. Anim. Ecol.* **36**: 1–30.

McArdle, B. H., K. J. Gaston and J. H. Lawton (1990) Variation in the size of animal populations: patterns, problems and artefacts. *J. Anim. Ecol.* **59**: 439–454.

Perry, J. N. (1981) Taylor's power law for dependence of variance on mean in animal populations. *J. R. Stat. Soc., Ser. C (Appl. Stat.)* **30**: 254–263.

Perry, J. N. (1988) Some models for spatial variability of animal species. *Oikos* **51**: 124–130.

Perry, J. N. and L. R. Taylor (1985) Adés: new ecological families of species-specific frequency distributions that describe repeated spatial samples with an intrinsic power-law variance-means property. *J. Anim. Ecol.* **54**: 931–953.

Perry, J. N. and L. R. Taylor (1988) Families of distributions for repeated samples of animal counts. *Biometrics* **44**: 881–888.

Rosewell, J., B. Shorrocks and K. Edwards (1990) Competition on a divided and ephemeral resource: testing the assumptions. I. Aggregation. *J. Anim. Ecol.* **59**: 977–1001.

Soberon M., J. and M. Loevinsohn (1987) Patterns of variations in the numbers of animal populations and the biological foundations of Taylor's law of the mean. *Oikos* **48**: 249–252.

Southwood, T. R. E. (1978) *Ecological methods.* Chapman & Hall, London.

Taylor, L. R. (1961) Aggregation, variance and the mean. *Nature* **189**: 732–735.

Taylor, L. R. (1984) Assessing and interpreting the spatial distributions of insect populations. *Annu. Rev. Entomol.* **29**: 321–357.

Taylor, L. R., J. N. Perry, I. P. Woiwod and R. A. J. Taylor (1988) Specificity of the spatial power-law exponent in ecology and agriculture. *Nature* **332**: 721–722.

Taylor, L. R. and R. A. J. Taylor (1977) Aggregation, migration and population mechanics. *Nature* **265**: 415–421.

Taylor, L. R., R. A. J. Taylor, I. P. Woiwod and J. N. Perry (1983)

Behavioural dynamics. *Nature* **303**: 801–804.

Taylor, L. R. and I. P. Woiwod (1980) Temporal stability as a density dependent species characteristics. *J. Anim. Ecol.* **49**: 209–224.

Taylor, L. R. and I. P. Woiwod (1982) Comparative synoptic dynamics. I. Relationships between inter- and intra-specific spatial and temporal variance/mean population parameters. *J. Anim. Ecol.* **51**: 879–906.

Taylor, L. R., I. P. Woiwod and J. N. Perry (1978) The density dependence of spatial behaviour and the rarity of randomness. *J. Anim. Ecol.* **47**: 383–406.

Taylor, L. R., I. P. Woiwod and J. N. Perry (1980) Variance and the large scale spatial stability of aphids, moths and birds. *J. Anim. Ecol.* **49**: 831–854.

Thórarinsson, K. (1986) Population density and movement: a critique of Δ-model. *Oikos* **46**: 70–81.

Tokeshi, M. (1986) Resource utilization, overlap and temporal community dynamics: a null model analysis of an epiphytic chironomid community. *J. Anim. Ecol.* **55**: 491–506.

Tokeshi, M. (1995) Randomness and aggregation: analysis of dispersion in an epiphytic chironomid community. *Freshwat. Biol.* (in press)

Tokeshi, M. and C. R. Townsend (1987) Random patch formation and weak competition: coexistence in an epiphytic chironomid community. *J. Anim. Ecol.* **56**: 833–845.