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Effect of Quadrat and Core Sizes on Determining the Spatial Pattern of *Criconemella sphaerocephalus*

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Abstract: An unmanaged pasture was sampled on four occasions (A, B, C, D) with five different quadrat sizes for *Criconemella sphaerocephalus* by removing a constant soil core volume of 75 cm^3 (A) and 300 cm^3 (C) from increasing quadrat areas of 0.5–8 m^2, and removing soil core volumes of increasing size—75–1,200 cm^3 (B) and 300–4,800 cm^3 (D)—proportionally with an increase in quadrat area (0.5–8 m^2). Frequency counts of *C. sphaerocephalus* were fitted to six probability distributions. The index of aggregation (b) for Taylor's power law and Morisita's index of dispersion were also calculated where appropriate. Twelve of nineteen of the sampling combinations were best described by negative binomial distribution ($P = 0.05$). *Criconemella sphaerocephalus* appeared more highly aggregated when sampled with constant soil core volumes (A and C) than from increasing soil core volumes (B and D) based on Taylor's index of aggregation (b). Morisita's index of dispersion indicated aggregation at the smallest quadrat area (0.5 m^2) for all sampling occasions (A, B, C, D).

Key words: spatial distribution, Taylor's power law, Morisita's index of dispersion, *Criconemella sphaerocephalus*.

Estimation of nematode field populations is based on soil samples collected from quadrats (specified sampling units distributed in random [9] or, more frequently, regular patterns [1]) throughout the field. Density of the nematode species per unit volume of soil is then determined. The ability to estimate a population accurately, based on a relatively small number of samples, is dependent on the sampling procedure and the horizontal distribution of the organism (8,13,16–18).

The most frequently reported horizontal spatial distribution for nematodes is the negative binomial distribution (8,12,17). The parameter k of the negative binomial distribution has been interpreted as a measure of dispersion (2,6). Previous studies have found k to be dependent on the mean population density (24) and quadrat size (8,18). Noe and Barker (17) used the parameter k to evaluate the overestimation of yield loss caused by *Meloidogyne incognita* (Kofoid & White) Chitwood when yield predictions were based on mean density alone.

Another measure of dispersion developed empirically has been presented by Taylor (21). Taylor (21,22,24) demonstrated with many species of various types of organisms that density and variance were interdependent measures, $S^2 = am^b$. The index b, when Taylor's power law is expressed in logarithms ($\log S^2 = \log a + b \log m$), is dependent on both species behavior and environment. These characteristics may be species specific and of possible value in describing spatial dispersion of populations (23). McSorley et al. (12) applied Taylor's power law to the distribution of 16 nematode genera from three fields. They found estimates of the index b were relatively consistent for each genus when plot size was varied. Boag and Topham (3), when sampling for *Longidorus elongatus* (de Man) Thorne & Swanger, found the index b to vary according to the distance between sampling points.

Morisita proposed that the diversity of the density of an organism per quadrat be used as a measure of dispersion (14). Morisita's index of dispersion can be used to measure distribution within a cluster of organisms (intraclump), distribution of the clusters with respect to other clusters (interclump), and mean clump size (14). The index has been used to measure dispersion within the context of soil-borne pathogens by taking soil core subsamples of constant volume and then increasing quadrat size (1,19).

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TABLE 1. Sample combinations of quadrat area, replication number, and core volume per sampling occasion used to determine populations of *Criconemella sphaerocephalus* in a pasture.

Quadrat area (m^2)	Replications	Core volume (cm^3)/sampling occasion†			
		A	B	C	D
0.5	80	75	75	300	300
1.0	40	75	150	300	600
2.0	20	75	300	300	1,200
4.0	10	75	600	300	2,400
8.0	5	75	1,200	300	4,800

† Samples were taken over a 5-day period with all the samples per sampling occasion collected the same day.

The objectives of this study were to evaluate three indices of dispersion for use in describing the aggregation of nematode populations. Of specific interest was the effect of using a constant soil sample volume with increasing quadrat area versus an increasing soil sample volume with increasing quadrat area on Morisita's index of dispersion. We chose as our model system a plant-parasitic nematode with a wide host range in an unmanaged pasture.

MATERIALS AND METHODS

A pasture (3,200 m^2) planted to Bermuda grass (*Cynodon* sp.) was divided into a grid of 80 plots (8 × 5 m each). The pasture was sampled four times over a period of 5 days, with each sampling occasion labeled consecutively A, B, C, and D. On each sampling occasion, a total of 155 individual subsample cores were removed according to a binary series of quadrats (0.5–8.0 m^2). Each subsample core was assigned a plot number between 1 and 80 which was chosen at random and with repetition. A quadrat was arbitrarily placed within an assigned plot, then a single core site was arbitrarily selected within the quadrat. The number of replications for each quadrat size decreased as the quadrat size increased. The smallest quadrat size (0.5 m^2) was replicated 80 times, and the largest quadrat size (8.0 m^2) was replicated five times (Table 1).

The soil sample volume was varied on each sampling occasion. Soil volumes were either kept constant (75 and 300 cm^3) during a sampling occasion or increased (75–1,200 cm^3 and 300–4,800 cm^3) in response to increasing quadrat area (Table 1). For the purpose of this study, a sampling group is defined as all the replications with the same quadrat area and soil volume combination taken on the same sampling occasion. There were five sampling groups per sampling occasion for a total of 20 groups. Groups are referred to by the sampling occasion letter (A, B, C, D) and the quadrat area (0.5, 1, 2, 4, or 8 m^2).

For the smallest sampling volume (75 cm^3), samples were retrieved using a soil probe (2.5 cm d) to a depth of 15 cm. All other sample volumes were excavated with a trowel using a wire frame of the correct dimensions to a depth of 15 cm. All samples were processed by elutriation and centrifugation (5). Nematode counts were not adjusted for elutriation efficiency. *Criconemella sphaerocephalus* Taylor, 1936 (20) was the dominant plant-parasitic nematode species present, and only its distribution was evaluated.

The Poisson, negative binomial, Neyman type A, logarithmic with zeros, Poisson with zeros, and Thomas Double Poisson probability distributions were fitted by a FORTRAN program to frequency tables generated from the data (7). Estimates of k for the negative binomial were generated from the FORTRAN program by the method of maximum likelihood. When more than 30% of the samples had 0 counts, k was estimated from the proportion of zeros (6). Determination of goodness-of-fit was by using the chi-square statistic at $P = 0.05$. The parameter k (when appropriate) was regressed against density (adjusted to counts/4,800 cm^3) and the coefficient of determination (r^2) was examined for the degree of correlation. The frequency of zero counts was compared among sampling occasions for constant to increasing soil volumes (A to B and C to D) with the Z-test ($P = 0.10$).

The index of aggregation (b) for Taylor's power law was calculated for each sampling occasion by regressing each

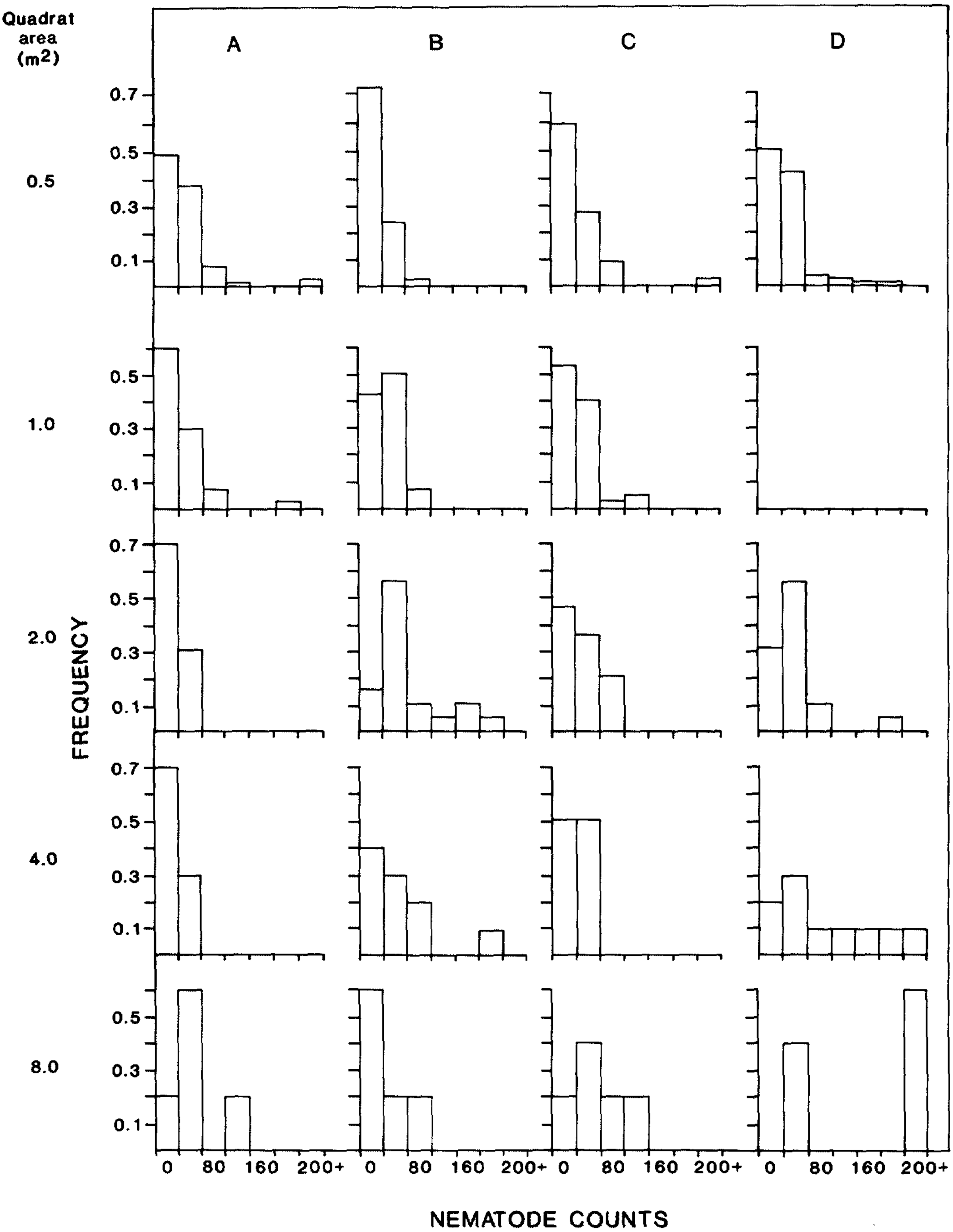

FIG. 1. Frequency distribution for counts of *Criconemella sphaerocephalus* when sampling with a binary series of quadrats and a constant sample volume (sampling occasions A and C) or an increasing sample volume with increasing quadrat size (sampling occasions B and D). Soil volume sampled for A was 75 cm^3, B was 75–1,200 cm^3, C was 300 cm^3, and D was 300–4,800 cm^3.

group's variance against its mean ($\log S^2 = \log a + b \log m$). In this relationship S^2 is the sample variance, log a is the Y intercept, b is the rate determining parameter or index value, and m is the sample mean. The index values were used only for intersampling occasion comparisons. It was not valid to compare sampling occasion b

TABLE 2. Frequency distribution describing the population density of *Criconemella sphaerocephalus* in a pasture as affected by quadrat area and soil volume.

Sampling occasion	Quadrat area (m^2)	Mean	Variance (10^3)	k of the negative binomial	Distributions†
A	0.5	43.4	59.2		NAF
	1.0	12.3	0.869	0.20	NB‡, NTA
	2.0	3.8	0.0549	0.28	NB, NTA‡, L0, TDP
	4.0	1.5	0.0055		NAF
	8.0	22.0	1.670		NAF
B	0.5	4.7	0.122	0.16	NB‡, NTA
	1.0	12.3	0.346	0.47	NB‡, NTA
	2.0	42.5	3.71	0.54	NB‡
	4.0	36.0	3.93	0.45	NB‡, NTA
	8.0	12.0	0.583		NAF
C	0.5	20.4	4.42	0.15	NB‡
	1.0	11.8	0.549	0.28	NB‡
	2.0	16.0	0.609	0.18	NB‡
	4.0	8.0	0.157	0.51	P, NB, P0, NTA‡, L0
	8.0	31.0	1.39	0.63	NB‡, P0
D	0.5	15.8	1.11	0.27	NB‡
	2.0	24.8	1.80	0.49	NB‡, NTA
	4.0	89.0	9.32	0.63	NB‡, NTA
	8.0	248.0	59.7		P‡

† Distributions are represented by the following abbreviations: Poisson = P; negative binomial = NB; Poisson with zeros = P0; Neyman type A = NTA; logarithmic with zeros = L0; Thomas Double Poisson = TDP. When the data were not adequately fitted by any of the distributions examined (chi-square test with $P = 0.05$), the abbreviation NAF was used.

‡ Distribution representing the best fit by the chi-square test.

values with the value of 1.0 (representing a random distribution), since quadrat sizes were nonuniform.

Morisita's index was calculated for each group according to the equation

$$I_\delta = q \Sigma X_i(X_i - 1)/T(T - 1),$$

where X_i is the number of individuals in the i-th quadrat unit (i = 1, 2, q), q is the number of quadrat (sampling) units, and $T = \Sigma X_i$ (14). Mean clump size is estimated by plotting the smallest quadrat against the next quadrat size ($I_{\delta x}/I_{\delta 2x}$) (14). When the process is repeated for each of the quadrats, peaks will occur where quadrat size and mean clump size are approximately equal.

TABLE 3. Index of aggregation for populations of *Criconemella sphaerocephalus* in a pasture using Taylor's power law.

Sampling† occasion	log a‡	b§	$P < F$‖	r^2#	Standard error (b)
A	1.67	2.55	0.003	0.97	0.277
B	8.28	1.65	0.002	0.97	0.166
C	4.34	1.89	0.110	0.63	0.840
D	18.69	1.44	0.005	0.99	0.099

† Means and variances for the five quadrat areas sampling occasion were used in the regressions.

‡ y-intercept of the equation log variance = log a + b log mean.

§ Index of dispersion.

‖ *Probability of the F-test, reject for $P > 0.05$.*

Coefficient of determination.

RESULTS

Frequency count histograms are presented in Figure 1. Population estimates of the mean and variance for each of the sampling groups ranged from 1.5 to 2.5 × 10^3 and 5.5 to 59.7 × 10^3, respectively (Table 2). Twelve of the nineteen sampling groups were best described by the negative binomial distribution. Groups A-2 and C-4 were best described by the Neyman type A distribution, although they were also adequately fit by the negative binomial distribution. Group D-8 was best described by the Poisson distribution, although only five samples were fitted to the distribution. The frequency counts of the remaining four groups (A-0.5, A-4, A-8, B-8) did not correspond to any of the tested distributions with $P = 0.05$. Estimates of the parameter k for the negative binomial distribution, where appropriate, ranged from 0.15 to 0.63. No relationship of the k values to each group's density estimate was apparent. There was a significant correlation at $P = 0.05$ between quadrat size and k values ($r^2 = 0.533$).

The frequency of zeros in sampling occasion A for the quadrat sizes 0.5, 1.0, 2.0, 4.0, and 8.0 m^2 were 0.49, 0.60, 0.70, 0.70, and 0.20, respectively. The frequency of zeros in sampling occasion B for the quadrat sizes 0.5, 1.0, 2.0, 4.0, and 8.0 m^2 were 0.75, 0.43, 0.15, 0.40, and 0.60, respectively. There was a significant difference between frequencies of zero in A and B for the quadrat sizes 2.0, 4.0, and 8.0 m^2 ($P = 0.05$). The frequency of zeros in sampling occasion C for the quadrat sizes 0.5, 2.0, 4.0, and 8.0 m^2 were 0.60, 0.45, 0.50, and 0.20, respectively. The frequency of zeros in sampling occasion D for the quadrat sizes 0.5, 2.0, 4.0, and 8.0 m^2 were 0.49, 0.30, 0.20, and 0.20, respectively. There was a significant difference between frequencies of zero in C and D for the 4.0-m^2 quadrat size ($P = 0.05$).

The index value b of Taylor's power law, indicated greater aggregation for A and C ($b = 2.55$ and 1.89, respectively) than for B and D ($b = 1.65$ and 1.44, respectively) (Table 3). Data for sampling occasions A, B, and D gave satisfactory regression equations with coefficients of determination of 0.97, 0.97, and 0.99, respectively. The *F*-test of the analysis of variance was significant at $P = 0.05$.

Morisita's index of dispersion for determining mean clump size for each sampling occasion is presented in Figure 2. Mean clump size of sampling occasion A (constant soil volume with increasing quadrat area) showed a peak at or before the smallest quadrat size. Sampling occasion C (constant soil volume with increasing quadrat area) showed initial clumping at or below the smallest quadrat size, but indicated a random distribution between 2 and 4 m^2. At the largest quadrat size, the value of the index increased again, indicating the possibility of additional clumps. With B (increasing core volume proportionally with quadrat area), there was an aggregated pattern at or below the smallest quadrat size which became random as quadrat size increased and then regular at quadrat sizes ≥ 2 m^2 (index < 1.0). No representation of D is shown because incorrect soil volumes were collected for the 1-m^2 quadrat size. Therefore, all three sampling occasions (A, B, and C) had a mean clump size for the nematode of 0.5 m^2 or smaller. In addition, sampling occasion C showed a clump size at 8 m^2 or greater. Sampling occasion B indicated a regular distribution of the nematode at the 2-m^2 and larger quadrat areas.

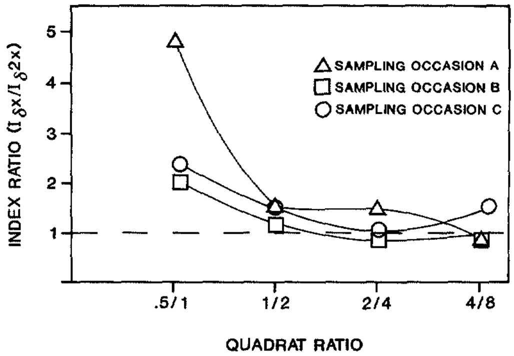

FIG. 2. Determining the average clump size of *Criconemella sphaerocephalus* in a pasture by using Morisita's index (I_δ). The ratio of $I_{\delta x}/I_{\delta 2x}$ is plotted against a binary series of quadrats, where x and 2x are consecutive quadrat sizes in the series.

DISCUSSION

The spatial pattern of plant-parasitic nematodes often appears aggregated based on estimates of the parameter k of the negative binomial distribution. The unmanaged pasture was specifically chosen for this study to minimize the possible influence of tillage practices and plant spacing on nematode aggregation. Our results, which show 14 of 19 groups as adequately described by the negative binomial distribution, are consistent with other studies of plant-parasitic nematodes (1,3,8). A previous study found that *Criconemella* spp. were best described by the Neyman type

A distribution (10). The Neyman type A distribution has been used to describe distributions with both random clusters per sampling area (intraclump) and random distribution of clusters (interclump) (4). The negative binomial distribution has been used to explain several mechanisms of aggregation, including heterogeneity and clustering (4). Spatial heterogeneity within a field due to environmental, edaphic, or topographic features would affect the interclump pattern of nematodes. Distribution of *Criconemella* spp. is affected by moisture levels (15), habitat (11), and plant species (10). The field sampled in this study contained a water-soaked area coincident with the highest sample counts.

The parameter b of Taylor's power law was useful for indicating degree of aggregation. The nematode populations in constant core volumes appeared more highly aggregated than in cores of increasing volume. Morisita's index was used to indicate aggregation of sampling occasions and also mean clump sizes. The sampling occasions all showed clumping at or below the smallest quadrat area (0.5 m^2). The smallest of the increasing core volumes (75–1,200 cm^3) was regularly distributed at the higher quadrat sizes. The larger of the constant core volumes (300 cm^3) showed a second mean clump size beginning at the 8-m^2 quadrat, although the quadrat sizes were not large enough to characterize the second clump size. The quadrat series was not small enough to characterize precisely the intraclump mean cluster size of the nematode population.

It is indicated in this study that the use of constant core volume versus increasing core volume, with respect to quadrat area, will affect the magnitude of aggregation and determination of mean clump size. If either of these two factors are to be used to estimate yield loss, then the effect of sampling methods needs consideration.

LITERATURE CITED

1. Alby, T., J. M. Ferris, and V. R. Ferris. 1983. *Hoplolaimus galeatus* in soybean fields. Journal of Nematology 15:418–426.

2. Anscombe, F. J. 1950. Sampling theory of the negative binomial and logarithmic series distributions. Biometrika 37:358–382.

3. Boag, B., and P. B. Topham. 1984. Aggregation of plant parasitic nematodes and Taylor's power law. Nematologica 30:348–357.

4. Boswell, M. T., J. K. Ord, and G. P. Patil. 1979. Chance mechanisms underlying univariate distributions. Pp. 3–156 *in* J. K. Ord, G. P. Patil, and C. Taillie, eds. Statistical distributions in ecological work. Fairland, MD: International Co-operative Publishing House.

5. Byrd, D. W., K. R. Barker, H. Ferris, C. J. Nusbaum, W. E. Griffin, R. H. Small, and C. A. Stone. 1976. Two semi-automatic elutriators for extracting nematodes and certain fungi from soil. Journal of Nematology 8:206–212.

6. Elliott, J. M. 1979. Statistical analysis of samples of benthic invertebrates. The FerryHouse, Ambleside, Cumbria, UK: Freshwater Biological Association publication no. 25. P. 157.

7. Gates, C. E., and F. G. Etheridge. 1970. A generalized set of discrete frequency distributions with FORTRAN program. Mathematical Geology 4:1–24.

8. Goodell, P., and H. Ferris. 1980. Plant-parasitic nematode distributions in an alfalfa field. Journal of Nematology 12:136–141.

9. Heltshe, J. F., and T. A. Ritchey. 1984. Spatial pattern detection using quadrat sampling. Biometrics 40:877–885.

10. Hoffman, J. K., and D. C. Norton. 1976. Distribution pattern of some Criconematinae in different forest associations. Journal of Nematology 8:32–35.

11. Knobloch, N., and G. W. Bird. 1978. Criconematinae habitats and *Lobocriconema thornei* n. sp. (Criconematidae: Nematoda). Journal of Nematology 10:61–70.

12. McSorley, R., W. H. Dankers, J. L. Parrado, and J. S. Reynolds. 1985. Spatial distribution of the nematode community on Perrine Marl soils. Nematropica 15:77–92.

13. McSorley, R., and J. L. Parrado. 1982. Estimating relative error in nematode numbers from single soil samples composed of multiple cores. Journal of Nematology 14:522–529.

14. Morisita, M. 1959. Measuring the dispersion of individuals and analysis of the distributional patterns. Member of the Faculty of Science, Kyushu University, No. 80, Series E (Department of Biology) 2: 215–235.

15. Nesmith, W. C., E. I. Zehr, and W. M. Dowber. 1981. Association of *Macroposthonia xenoplax* and *Scutellonema brachyurus* with peach tree short life syndrome. Journal of Nematology 13:220–225.

16. Nicot, P. C., D. I. Rouse, and B. S. Yandell. 1984. Comparison of statistical methods of studying spatial patterns of soil-borne plant pathogens in the field. Phytopathology 74:1399–1402.

17. Noe, J. P., and K. R. Barker. 1985. Overestimation of yield loss of tobacco caused by the aggregated spatial pattern of *Meloidogyne incognita.* Journal of Nematology 17:245–251.

18. Noe, J. P., and C. L. Campbell. 1985. Spatial

analysis of plant-parasitic nematodes. Journal of Nematology 17:86–93.

19. Schuh, W., R. A. Frederiksen, and M. J. Jeger. 1986. Analysis of spatial patterns in sorghum downy mildew with Morisita's index of dispersion. Phytopathology 76:446–450.

20. Tarjan, A. C. 1966. A compendium of the genus *Criconemoides* (Criconematidae: Nematoda). Proceedings of the Helminthological Society of Washington 33:109–125.

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

22. Taylor, L. R. 1971. Aggregation as a species characteristic. Pp. 357–377 *in* G. P. Patil, E. C. Pielou, and W. E. Waters, eds. Statistical ecology. Philadelphia: University of Pennsylvania Press.

23. Taylor, L. R. 1979. The negative binomial as a dynamic ecological model for aggregation and the density dependence of k. Journal of Animal Ecology 48:289–304.

24. Taylor, L. R. 1984. Assessing and interpreting the spatial distributions of insect population. Annual Review of Entomology 29:321–357.