

## Spatial Variation Among Counts of Gypsy Moths (Lepidoptera: Lymantriidae) in Pheromone-Baited Traps at Expanding Population Fronts

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**ABSTRACT** Geostatistics were used to quantify spatial variation in captures of adult male gypsy moths, *Lymantria dispar* (L.), in pheromone-baited traps in the central Appalachians. Spatial variation was analyzed in the infested zone, where yearly total capture was >300 moths per trap; the transition zone, where moth capture ranged from 1 to 300 moths per trap; and the uninfested zone, where moth capture was <1 moth per trap. The trend associated with gypsy moth spread was removed in each zone using linear and nonlinear regression. Spatial correlation among trap captures in the transition zone (correlogram sill, 0.544; range, 31.2 km) was much stronger than in the infested (sill, 0.269; range, 23.9 km) and uninfested (sill, 0.222; range, 19.7 km) zones. Additional short-range correlation (range, 1.4 km) was detected in the uninfested zone. Differences in the spatial distribution of male moth populations among the 3 zones may be caused by different dominating population processes in each zone. Other factors, such as trap saturation, also may contribute to the difference in the patterns of moth captures. Obtained zone-specific geostatistical parameters can be used for interpolation of moth captures at unsampled locations and for improving gypsy moth monitoring.

**KEY WORDS** *Lymantria dispar*, geostatistics, biological invasions

ANALYSIS OF THE spatial distribution of insect populations is important for planning pest monitoring programs (Southwood 1978, Taylor et al. 1978), for predicting population density in unsampled locations (Liebhold et al. 1991), for improving pest management strategies (Hughes and McKinlay 1988), and for understanding ecological relationships with different abiotic and biotic factors (Iwao 1970, Hassell and May 1974).

Traditionally, the spatial pattern of populations has been characterized from frequency distributions (Southwood 1978). Most of these studies focused on the mean-variance relationship and were often used to improve sampling designs (Taylor et al. 1978). This approach is based on the assumption that sample values are not correlated; thus, the distance among the samples can be ignored. However, samples separated by small distances should have more similar population densities than samples separated by large distances. The presence of spatial correlation has been demonstrated in a number of studies (Johnson 1989, Schotzko and O'Keefe 1989, Liebhold et al. 1991).

An alternative approach to the use of frequency distributions is to relate the variation among sample counts to intersample distances using variograms, covariance functions, and correlograms

(Rossi et al. 1992, Liebhold et al. 1993). These methods, collectively known as "geostatistics," have been developed historically for geological applications, but they are increasingly used in ecological studies (Rossi et al. 1992). Geostatistics provides information about the range (distance) and strength of spatial correlations among samples. When estimated for different intersample directions, they can be used to detect isotropy (radial symmetry) versus anisotropy (asymmetry) in the population. Anisotropy indicates that aggregations are elongated in a particular direction.

The gypsy moth, *Lymantria dispar* (L.), is one of the most important forest insect pests in the eastern United States (Doane and McManus 1981). It was accidentally introduced to North America near Boston in 1869 and since that time it has been slowly expanding its range to the west and south (Liebhold et al. 1992). The range of the gypsy moth expands largely by accidental transportation of egg masses and other life stages on human vehicles (e.g., during household moves from the infested zone to the uninfested zone) (McFadden and McManus 1991). Larval dispersal then contributes to local spread of growing colonies. This kind of dispersal that combines long "jumps" with local colony growth is called stratified dispersal (Hengeveld 1989). The following 3 zones can be distinguished at the moving population front: the uninfested zone with few isolated small

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colonies, the transition zone with larger and partially coalescing colonies, and the infested zone with high-density coalesced populations (McFadden and McManus 1991).

Gypsy moth populations are monitored mainly using counts of overwintering egg mass populations, and counts of male moths in pheromone-baited traps (Ravlin et al. 1987). Egg mass counts are most reliable for assessing of medium- and high-density populations and are widely used for making decisions concerning aerial suppression of outbreak populations (Ravlin et al. 1987). Pheromone traps are highly sensitive and cost effective at detecting low-density populations (Schwalbe 1981). They are mostly used to detect new isolated gypsy moth infestations and to monitor the expansion of the population front. At high population densities, traps become saturated (Elkinton 1987) and little correlation exists with observed defoliation (Liebhold et al. 1995). However, in recently infested areas, pheromone traps can be helpful in predicting defoliation (Gage et al. 1990) and are essential components of many integrated pest management decision algorithms (Ravlin et al. 1990).

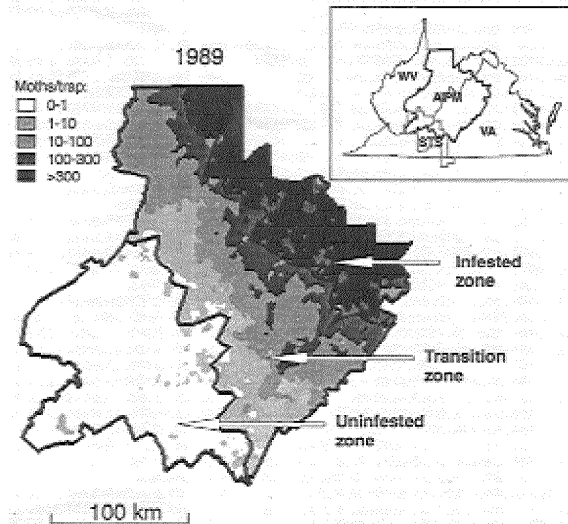
The spatial distribution of gypsy moth egg mass populations was quantified by Liebhold et al. (1991), but no comprehensive analysis of male moth distribution exists. Analysis of male moth spatial distribution is important for understanding the dynamics and spread of low-density populations that cannot be detected using egg mass counts. Attempts to slow the spread of gypsy moths (Leonard and Sharov 1995) should be based on the knowledge of the structure and dynamics of low-density populations.

Variograms of male moth counts were estimated in the central Appalachians (Sharov et al. 1995) and in Massachusetts (Liebhold et al. 1995). However, no attempt was made to differentiate the spatial patterns among the infested, transition, and uninfested zones. In Massachusetts, intertrap distance was large (11.6 km, on average) and did not allow detection of spatial dependence at smaller spatial lags.

This study was conducted to quantify the spatial distribution of male moth populations of *L. dispar* using geostatistical methods. We expected that the presence of stratified dispersal caused the size of gypsy moth colonies to increase with time as the population front moved forward. Thus, we attempted to compare gypsy moth spatial patterns in the infested, transition, and uninfested zones and relate these patterns to ecological processes in these 3 zones (colonization, population growth, and coalescence).

#### Materials and Methods

We used historical pheromone trap data (1988–1994) collected in the Appalachian Mountains in northern Virginia and southern West Virginia.



**Fig. 1.** Appalachian Integrated Pest Management (AIPM) and Slow-the-Spread (STS) project areas. Gypsy moth catches in pheromone-baited traps in 1989 interpolated using median kriging are shown by the gray scale. Boundaries of the infested, transition, and uninfested zones were drawn at thresholds of 1 and 300 moths per trap.

Most data were collected as part of the USDA Forest Service Appalachian Integrated Pest Management (AIPM) and Slow-the-Spread (STS) (Fig. 1) programs (Reardon 1991, Leonard and Sharov 1995). Complete details of male moth trapping were described by Sharov et al. (1995). The basic trap grid had intertrap distances of 2 km in Virginia and 3 km in West Virginia in 1988–1991. Since 1992, a 1-km basic grid was used in the Slow-the-Spread project area for detecting isolated gypsy moth infestations beyond the expanding population front. In small areas where isolated infestations were suspected, intensive trapping grids with intertrap distances of 500 or 250 m were deployed. The location of traps and egg mass samples was recorded using Universal Transverse Mercator coordinates (Snyder 1987).

The spatial distribution of male moth counts was analyzed in the following 3 zones: (1) the infested zone where yearly total moth capture was  $>300$  moths per trap, (2) the transition zone where moth capture ranged from 1 to 300 moths per trap, and (3) the uninfested zone where moth capture was  $<1$  moth per trap (Fig. 1). The thresholds 1 and 300 moths per trap were selected to divide the area into biologically distinct areas. Data obtained in the Appalachian Integrated Pest Management project area from each year from 1988 to 1994 were subdivided into the 3 zones. Only a few traps were located in the infested zone in 1993–1994. Thus, only 2 zones (transition and uninfested) were analyzed in these years. The Slow-the-Spread project area was located entirely in the uninfested zone; thus, it was not subdivided into zones.

The boundaries between zones (Fig. 1) were estimated for each year using the "best cell classification" method (Sharov et al. 1995). This method minimizes the number of grid cells that are misclassified below or above a specific population threshold (we used thresholds of 1 and 300 moths per trap). The best cell classification method was applied to continuous indicator raster maps (1 by 1 km) that coded (0, 1) for each cell if the gypsy moth population was below the threshold value (0) or above the threshold value (1). Indicator maps of male moth counts were generated using indicator median kriging and were subsequently categorized using the cumulative probability function as above or below the threshold value of 0.5 (Sharov et al. 1995). Boundary points were estimated in strips (1 km wide) perpendicular to the general boundary direction with azimuth 147.5° (Sharov et al. 1995). Equal weights (1:1) were used for cell misclassifications of type 1 (occupied cells considered unoccupied) and type 2 (unoccupied cells considered occupied). Then, boundary points were averaged in nonoverlapping blocks of 5 adjacent strips each.

Spatial relationships among male moth catches were analyzed using standard the following geostatistical tools: (1) variograms,  $\gamma(h)$ ; (2) covariance functions,  $C(h)$ ; and (3) correlograms,  $\rho(h)$  (Rossi et al. 1992):

$$\gamma(h) = \frac{\sum [z(x) - z(x+h)]^2}{2N(h)} \quad (1)$$

$$C(h) = \frac{\sum z(x)z(x+h)}{N(h)} - M_{-h}M_{+h} \quad (2)$$

$$\rho(h) = \frac{C(h)}{s_{-h}s_{+h}}, \quad (3)$$

where  $h$  is the lag vector that starts at 1 sample location and ends at another sample location,  $z(x)$  is the sample value (e.g., numbers of organisms) at location  $x$ , summation is performed over all pairs of locations  $x$  and  $x+h$  separated by lag vector  $h$ ,  $N(h)$  is the number of these pairs,  $M_{-h}$  and  $M_{+h}$  are the mean of the points that correspond to the tail and head of vector  $h$ , respectively, and  $s_{-h}$  and  $s_{+h}$  are the standard deviations of the tail values and head values of vector  $h$  respectively. The length of vector  $h$  is the distance between 2 samples, and its orientation shows the direction from 1 sample to another sample. Covariance functions,  $C(h)$ , and correlograms,  $\rho(h)$ , were converted to a variogram form using equations:

$$C'(h) = C(0) - C(h) \quad (4)$$

$$\rho'(h) = 1 - \rho(h) \quad (5)$$

Functions  $\gamma(h)$ ,  $C'(h)$ , and  $\rho'(h)$  show the increase of difference in moth counts in traps separated by vector  $h$ , as the length of vector  $h$  increases.

Variograms, covariance functions, and correlograms were estimated using GSLIB software

(Deutsch and Journel 1992). Log transformation,  $\ln(N+1)$ , was applied to male moth counts before analysis. During the Appalachian Integrated Pest Management and Slow-the-Spread programs, traps were often placed at higher densities in areas where isolated populations were detected the previous year. Statistics  $\gamma(h)$ ,  $C(h)$ , and  $\rho(h)$  are sensitive to such sampling bias because areas with high sample densities have a disproportional effect on the result (Isaaks and Srivastava 1989). Thus, we used a "thinning" procedure to remove extra samples from the areas with increased sample density. A grid of cells was superimposed over the area, and a single trap was selected at random if there were  $>1$  trap in the cell. Thinning was done only once, and removed traps were excluded from further analysis. A cell size of 2 by 2 km was used in the Appalachian Integrated Pest Management area in 1988–1994, and a cell size of 1 by 1 km was used in the Slow-the-Spread area (uninfested zone) in 1992–1994. No thinning was applied to intensive trapping blocks in the Slow-the-Spread area in 1992–1994 because trap density was mostly uniform there ( $\approx 4$  traps per square kilometer).

Most geostatistical methods assume ergodicity (constant univariate and bivariate probability distributions) of measured values over the entire space (Isaaks and Srivastava 1989). However, our data violated this assumption and exhibited a strong trend (gradual change of mean moth counts through the area) which was associated with gypsy moth spread from northeast to southwest. Rossi et al. (1992) recommended the use of covariance functions and correlograms rather than variograms for analysis of data with a trend, because they are nonergodic statistics. Nonergodicity refers to the situation when the mean and variance vary through space, in particular,  $M_{-h} \neq M_{+h}$  and  $s_{-h} \neq s_{+h}$ . Covariance functions and correlograms are less sensitive to trends than variograms; however, this does not mean that they are not affected by trend at all. If the value  $z(x)$  at each point  $x$  is a combination of a random autocorrelated variable  $v(x)$  and a trend  $T(x)$  which is independent from  $v(x)$ , then,

$$C_z(h) = C_v(h) + C_T(h), \quad (6)$$

where  $C_z(h)$ ,  $C_v(h)$ , and  $C_T(h)$  are covariance functions for variables  $z$ ,  $v$ , and  $T$ , respectively. If the trend is a linear function in a 1-dimensional space ( $T(x) = bx$ ) and samples are evenly distributed, then

$$C_T(h) = \text{Var}(T)(1 - h/d)^2 \quad (7)$$

where  $\text{Var}(T)$  is the variance of the trend and  $d$  is the length of the sampled interval (see **Appendix**). If space lag,  $h$ , is negligibly small compared with the length,  $d$ , of the sampled area, then the covariance function of the trend (equation 7) is almost constant. In this case, the trend has a very limited effect on the covariance function  $C_z'(h)$  expressed in a variogram form. However, in practical situations, it is common that the area sampled is

not very large and the maximum lag distance  $h$  is only 2 or 3 times smaller than the length of the area sampled. If the maximum lag  $h_{\max} = 0.5d$ , then the covariance function  $C_T(h)$  decreases 4 times as the lag  $h$  increases. This may have a significant effect on  $C_z'(h)$ , especially if the trend is strong ( $\text{Var}(T)$  is large). The same problem may arise with correlograms. Thus, when the sample area is limited, it is better to remove the trend before variograms and correlograms are estimated rather than to rely on nonergodic features of these functions.

For comparison, we estimated variograms, covariance functions, and correlograms for the original data and after the trend was removed. Trend was removed by using residuals from either linear regression:

$$T(x) = b_0 + b_1x_1 + b_2x_2, \quad (8)$$

or nonlinear regression with a logistic function:

$$T(x) = \frac{\ln(1,000)}{1 + \exp[-(b_0 + b_1x_1 + b_2x_2)]}, \quad (9)$$

where  $T(x)$  is the trend (predicted log count of males) at sample point  $x$ ;  $x_1$  and  $x_2$  are coordinates of vector  $x = \{x_1, x_2\}$  in meters; and  $b_i$  are regression coefficients. The upper limit of the logistic function was set equal to  $\log(1,000)$  because trap capacity was  $\approx 1,000$  moths. Both regressions (8) and (9) were estimated, and the one that yielded the highest  $R^2$  was selected. Nonlinear regression was performed using the NLIN procedure (SAS Institute 1992). When a logistic function was fit over the entire area, the variance of the residuals in the uninfested zone often was larger than the variance of the original data. Thus, we estimated both linear and nonlinear regressions separately in each zone.

Variograms, covariance functions, and correlograms were estimated in 4 specific directions (N, NE, E, and SE) using an angle tolerance of  $22.5^\circ$  and a band width of 5 km (Isaaks and Srivastava 1989). Angle tolerance was applied only within the band width. An omnidirectional correlogram was also estimated. A lag distance interval of 1 km was used except in intensive trapping grids where a smaller lag interval (0.5 km) was applied. In the Appalachian Integrated Pest Management project area, omnidirectional correlograms (converted to variogram form) of the residuals of log moth counts (after trend removal) were modeled using an exponential model:

$$\rho'(h) = 1 - c_1 \exp(-3h/a_1), \quad (10)$$

where  $c_1$  is the sill (correlation of moth counts at small lag distance), and  $a_1$  is the effective range (distance at which spatial correlation becomes  $<5\%$  of the sill) (Isaaks and Srivastava 1989). The exponential model was fit using a nonlinear regression procedure NLIN (SAS Institute 1992) from correlogram values for lags from 2 to 25 km.

Data from the Slow-the-Spread area, where traps were separated by 1 km in the base grid and

500–250 m in intensive grids, were used to analyze short-range spatial relationships among moth counts. Only an omnidirectional correlogram was estimated from these data after trend removal. The correlogram obtained had 2 nested structures; thus, it was simulated with a nested exponential model:

$$\rho'(h) = 1 - c_1 \exp(-3h/a_1) - c_2 \exp(-3h/a_2), \quad (11)$$

where  $c_2$  and  $a_2$  are the sill and effective range of the 2nd structure. The model was fit using the nonlinear regression procedure NLIN (SAS Institute 1992) for points with lags of  $\leq 25$  km. Correlogram values for  $h < 2$  km were taken from the correlogram estimated from the intensive grid data, and points for  $h \geq 2$  km were taken from the correlogram estimated from the basic grid with a 1-km intertrap distance.

Comparing population patterns in different zones can be facilitated by reducing a variogram to a single number that represents the degree of spatial relationship among population samples. We suggest using the integral of the correlogram,  $\rho(h)$ , over the entire 2-dimensional space as an index of spatial dependence. This integral can be interpreted as the area around a sample point where moth numbers are correlated. If the correlogram is the same in all directions and has an exponential form (10), then

$$I = \int_0^\infty 2\pi h \rho(h) dh = \frac{2\pi}{9} c_1 a_1^2 \quad (12)$$

Integral  $I$  is measured in square kilometers because  $a_1$  is measured in kilometers and  $c_1$  is dimensionless (it is correlation). If either range or sill of the variogram is close to zero, then the integral  $I$  is also close to zero, indicating a weak spatial relationship among points on the plane.

## Results

Logistic models provided a better fit to the trend than linear models in 17 cases, whereas linear models were better in 5 cases (Table 1). The  $R^2$ , which indicates the strength of the trend, was always high in the transition zone and low in the uninfested and infested zones. In the transition zone, the gradient of the trend was always in the NE direction, indicated by positive values of  $b_1$  and  $b_2$ . However, in the infested and uninfested zones, the trend sometimes had a different orientation, as indicated by negative coefficients  $b_1$  and  $b_2$  (Table 1).

Variograms estimated before (Fig. 2) and after trend removal (Fig. 3) exhibited higher noise compared with covariance functions and correlograms. Covariance functions and correlograms tend to exhibit less random fluctuation because they are normalized using means and standard deviations of the tail and head of the lag vector (equations 2 and 3).

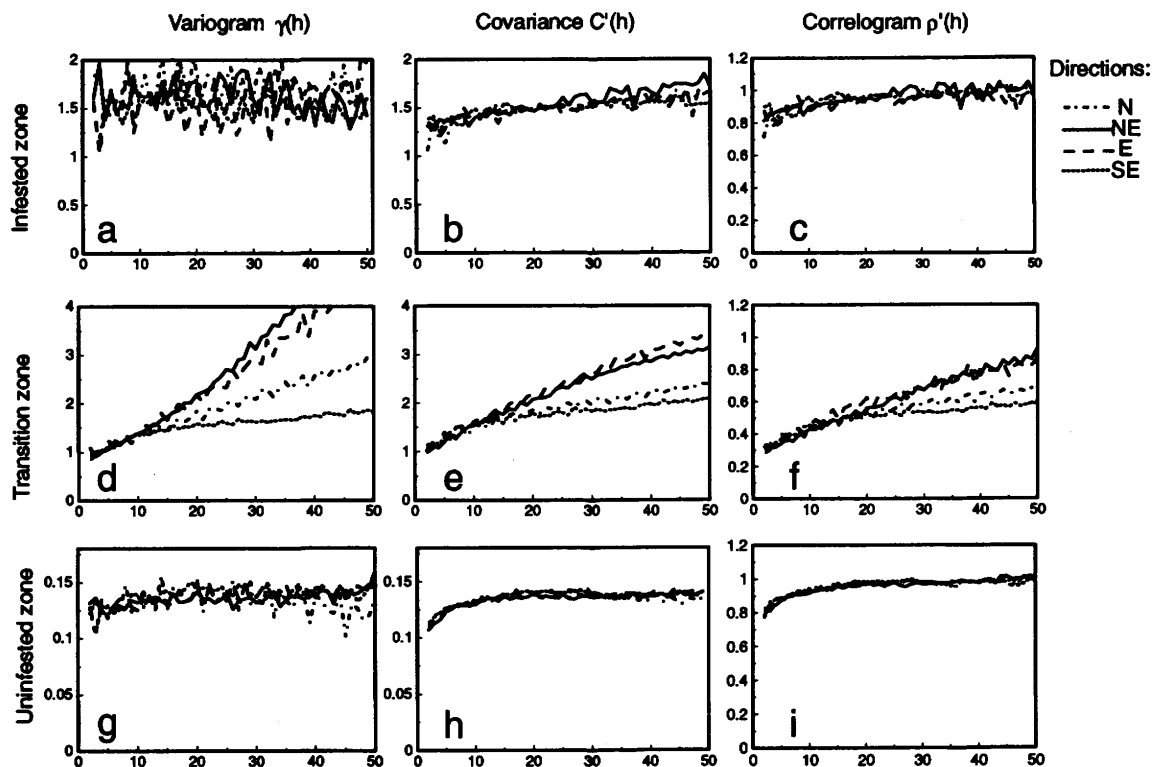
**Table 1. Parameters of trend in gypsy moth male counts (equations 8 and 9)**

Zone	Area	Year	No. traps	Best model	R <sup>2</sup> , %	b <sub>0</sub>	b <sub>1</sub> × 10 <sup>-6</sup> , m <sup>-1</sup>	b <sub>2</sub> × 10 <sup>-6</sup> , m <sup>-1</sup>
I	AIPM	1988	853	LG	12.6	90.06	-4.56	-19.78
I	AIPM	1989	1,372	LG	8.6	-97.53	13.89	21.05
I	AIPM	1990	1,832	LG	2.0	-40.99	3.69	9.49
I	AIPM	1991	1,722	LN	2.9	-16.57	1.39	5.09
I	AIPM	1992	1,450	LG	6.5	-47.88	2.41	11.33
T	AIPM	1988	2,908	LN	49.6	-92.50	36.62	16.87
T	AIPM	1989	3,098	LG	56.7	-90.12	24.58	17.52
T	AIPM	1990	2,593	LG	43.4	-87.38	21.12	17.44
T	AIPM	1991	2,334	LG	46.3	-92.48	22.87	18.41
T	AIPM	1992	1,772	LG	49.5	-112.75	28.58	22.45
T	AIPM	1993	587	LG	68.1	-165.04	48.11	32.23
T	AIPM	1994	1,546	LG	56.0	-103.38	25.53	20.83
U	AIPM	1988	2,863	LG	6.2	-113.58	19.50	23.02
U	AIPM	1989	2,220	LG	5.6	-42.95	20.85	6.51
U	AIPM	1990	2,316	LG	1.2	36.88	-4.34	-9.15
U	AIPM	1991	2,419	LN	0.2	4.51	-0.34	-0.99
U	AIPM	1992	2,622	LG	5.2	-61.48	21.65	10.86
U	AIPM	1993	2,216	LN	0.4	-0.70	0.73	0.11
U	AIPM	1994	1,764	LN	3.0	-10.31	1.93	2.28
U	STS	1992	9,459	LG	0.5	-52.89	5.14	11.02
U	STS	1993	12,571	LG	2.5	-85.87	8.95	18.62
U	STS	1994	13,222	LG	5.1	-80.98	14.90	16.71

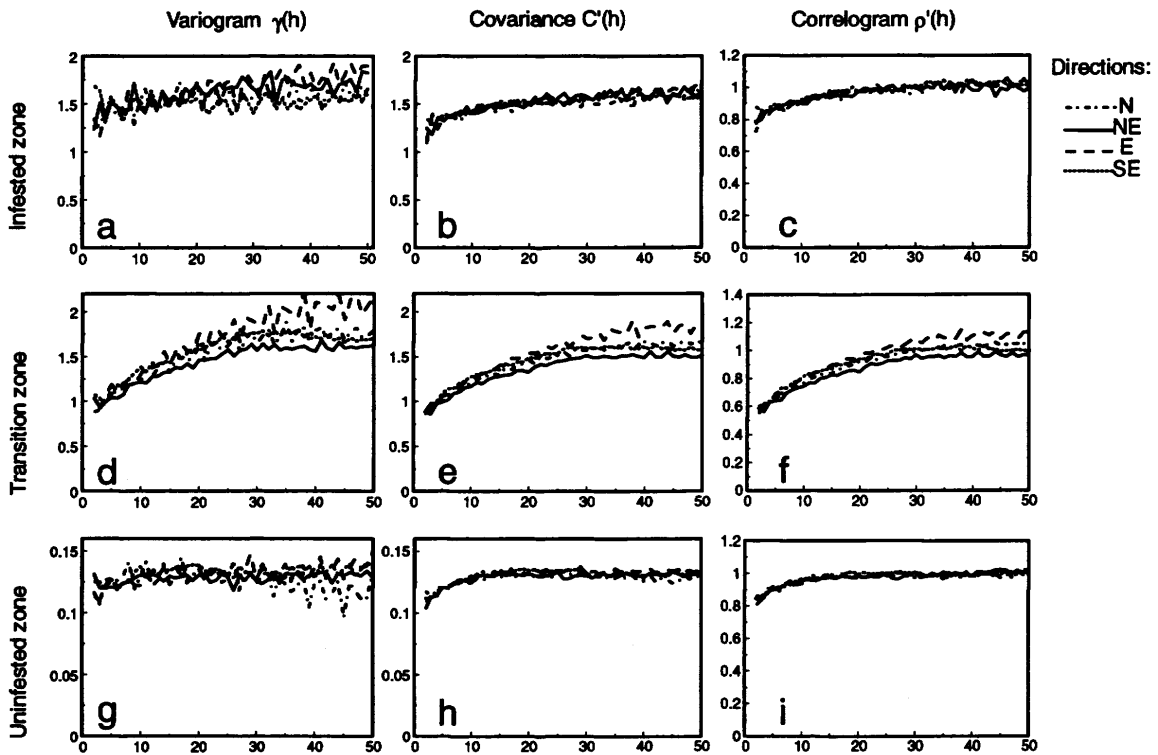
I, infested zone; T, transition zone; U, uninfested zone. AIPM, Appalachian Integrated Pest Management project area; STS, Slow-the-Spread project area. LN, linear model; LG, logistic model.

Trend removal had a limited effect on the shape of variograms, covariance functions, and correlograms in the infested and uninfested zones (Figs. 2 and 3). This is not surprising because the trend

was very weak in these 2 zones. Trend was strong in the transition zone; thus, spatial relationships changed significantly after its removal. The major changes were observed in the variogram because



**Fig. 2.** Variograms, covariance functions (in variogram form), and correlograms (in variogram form) of log gypsy moth counts in pheromone traps in the Appalachian Integrated Pest Management area (trend is not removed).



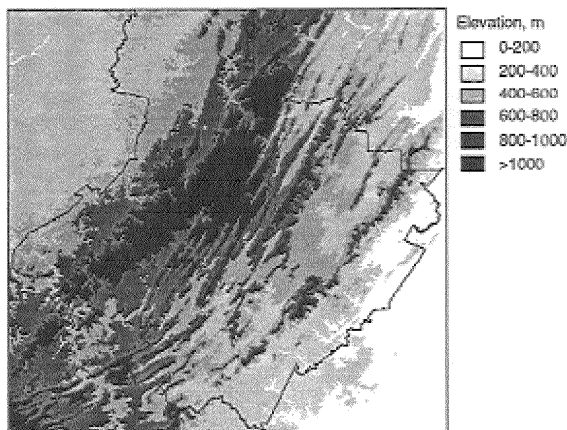
**Fig. 3.** Variograms, covariance functions (in variogram form), and correlograms (in variogram form) of the residuals of log gypsy moth counts in pheromone traps after trend removal in the Appalachian Integrated Pest Management area.

variograms are particularly sensitive to the presence of a trend (Rossi et al. 1992). Covariance functions and correlograms also were affected by trend removal. Before trend removal, their range was large, especially in the NE direction. A large range existed because  $C_T(h)$  decreased with increasing lag  $h$  (equation 7). After trend removal, the range of covariance functions and correlograms was reduced. Anisotropy also changed after trend

removal. Before trend removal, the maximum variation was observed in the NE direction (Fig. 2 d-f), which approximately coincided with the trend gradient (Fig. 1), and minimum variation was observed in the perpendicular direction (SE). Without trend, the lowest variation was observed in the NE direction (Fig. 3 d-f), which is the direction of mountain ridges in the central Appalachians (Fig. 4). This anisotropy was obscured by the trend in the original data.

In the Appalachian Integrated Pest Management area, the omnidirectional correlogram had the largest sill (0.544) and range (31.2 km) in the transition zone (Table 2). In the infested and uninfested zones, the sill of the correlogram was  $\approx 1/2$  of that in the transition zone. The effective range was intermediate in the infested zone and lowest in the uninfested zone.

Omnidirectional correlograms obtained in the Slow-the-Spread area (Fig. 5) were similar to the correlogram in the uninfested zone within the Appalachian Integrated Pest Management area (Fig. 3i). However, Slow-the-Spread correlograms showed relatively strong spatial dependence at short lags ( $h < 2$  km) which was not detected in the Appalachian Integrated Pest Management data because of large intertrap distances. This short-range correlation was represented by the 2nd nested structure in the correlogram model with effective range of 1.4 km (Table 2).



**Fig. 4.** Elevations in the Appalachian Integrated Pest Management area; data from U.S. Geological Survey Digital Elevation Models (Elassal and Caruso 1983).

**Table 2. Parameters of omnidirectional correlograms of the residuals of log moth counts in pheromone traps after trend removal**

Zone	Area	No. nested structure <i>i</i>	Correlogram parameters		Degree of spatial relationship, km <sup>2</sup> <i>I</i>	<i>R</i> <sup>2</sup> , %
			Sill <i>c</i> <sub><i>i</i></sub>	Range, km <i>a</i> <sub><i>i</i></sub>		
I	AIPM	1	0.269	23.9	107.3	97.3
T	AIPM	1	0.544	31.2	369.7	98.9
U	AIPM	1	0.222	19.7	60.1	98.9
U	STS	1	0.242	17.1	49.4	} 99.8
U	STS	2	0.294	1.4	0.4	

See footnotes to Table 1 for abbreviations.

The degree of spatial relationship, *I*, among moth counts in the transition zone were >3 times stronger than in the infested and uninfested zones (Table 2).

### Discussion

Correlograms of log moth counts showed significant differences in spatial distributions of moth populations in the infested, transition, and uninfested zones. These differences are consistent with the hypothesis of stratified dispersal of gypsy moths. In the uninfested zone, the short-range correlogram component (range, 1.4 km) corresponds to the average size of new infestations as they are detected with pheromone traps. Male moths can fly away from eclosion sites (Schwalbe 1981); thus, the size of reproducing populations (where other life stages are present) is likely smaller. The long-range (range, 17–20 km) correlogram component was weak in the uninfested zone. Autocorrelation over long distances might be associated with different phenomena such as individual large colonies, autocorrelation of landscape characteristics that affect population establishment, or long-distance male moth dispersal from high-density areas.

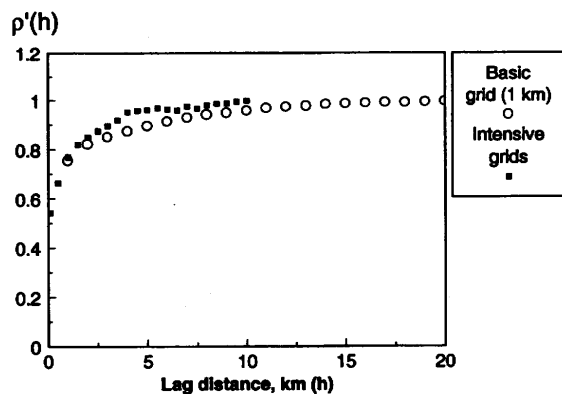
The strongest spatial autocorrelation in moth counts was detected in the transition zone. The range of the correlogram was large (31.2 km), re-

flecting the size of large colonies or colony aggregations. The large sill of the correlogram (0.544) indicates high variation in average population densities among different areas in the transition zone. This means that high-density patches are separated by gaps with very low population density. This type of spatial pattern may result from varying times of initial colonization and differential population growth in favorable and unfavorable sites. The latter explanation seems to be more realistic than the former, because gypsy moth colonies in the transition zone persist for a relatively long time and colonization history becomes less important. Further study of the correlation of moth abundance with local factors (e.g., elevation, vegetation) will show if this hypothesis is true.

The slight anisotropy detected in the transition zone is probably related to habitat patches elongated in northeast–southwest direction parallel to mountain ridges in the area (Fig. 4). High-elevation areas were defoliated more often than low-elevation areas in Pennsylvania (Liebhold et al. 1994). Thus, we can expect that population growth is probably greater at high elevations, and the anisotropy in trap capture in the transition zone possibly resulted from the anisotropy in elevation.

The correlogram of log moth counts in the infested zone indicated a weaker spatial relationship than in the transition zone. Probably, this resulted from colony coalescence. The sill of the correlogram is low (0.269), indicating high random variability in population densities. We can hypothesize that population dynamics in this area becomes stationary (equilibrium or cyclic) and, therefore, local factors become less important. For example, in a favorable site, the population may collapse because of viral epidemics and have a lower density than another population in an unfavorable site. Saturation of pheromone traps at high moth density (Elkinton 1987) is another factor that may reduce spatial relationship among moth counts (Liebhold et al. 1995).

It is interesting to compare spatial structure of male moth populations with egg mass populations studied by Liebhold et al. (1991). Those authors found relatively strong spatial dependence at different spatial scales. The range of large-scale spatial dependence varied from 20 to 100 km, whereas



**Fig. 5.** Correlograms of the residuals of log gypsy moth counts in pheromone traps after trend removal in the uninfested zone in the Slow-the-Spread project area in 1992–1994.

the range of small-scale contagions varied from 250 m to  $\approx 1$  km. All plots analyzed by Liebhold et al. (1991) were within the infested zone according to our terminology. Pheromone traps exhibited little spatial dependence in these areas, probably because of trap saturation and intensive moth dispersal (Liebhold et al. 1995). Thus, in the infested zone, egg mass counts represent the spatial structure of reproducing populations better than moth counts in pheromone traps.

The spatial range of  $\approx 100$  km in egg mass populations found by Liebhold et al. (1991) indicated the presence of large-scale trends (trend was not removed, and variograms were used rather than covariance functions and correlograms). However, this trend was different from the one studied here because it was not associated with population spread. It would be interesting to reexamine egg mass data with trend removed and using nonergodic covariance functions and correlograms. In addition to large-scale trends, 2 spatial structures were detected in egg mass populations, one with the range of 20–40 km and the other with the range of 0.25–1 km (Liebhold et al. 1991). The 1st structure corresponds well to the range of male moth correlograms in the infested zone (this study). However, we could not detect the 2nd short-range spatial structure in moth counts because of the large intertrap distance in the infested zone, and trap saturation effect.

Results obtained in this study can be used in gypsy moth monitoring programs in the following ways. First, the precision of mapping of gypsy moth counts in pheromone traps can be improved if variograms used for kriging in the infested, transition, and uninfested zones are zone-specific. Variogram parameters (Table 2) can be used for kriging moth counts in the central Appalachian Mountains. However, in other regions (e.g., North Carolina or Michigan), variograms may be different and should be estimated from local data. We did not detect any anisotropy in moth spatial distribution in the infested and uninfested zones, but slight anisotropy was found in the transition zone. This anisotropy will probably have a very limited effect on interpolation results and, we believe, it can be ignored in most cases.

Second, the variogram estimated in the uninfested zone can be used to improve the design of trap grids used for detection of isolated low-density populations. Eradication of these populations is expected to reduce the rate of gypsy moth spread (Leonard and Sharov 1995). Early detection of these populations allows eradication when their size is still small. The correlogram estimated using gypsy moth counts in the uninfested zone suggests that the average size of isolated colonies is  $\approx 1.4$  km. Thus, intertrap distance should be not  $< 2$  km to ensure high probability of detection of gypsy moth colonies.

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### Appendix

Equation 7 was derived assuming a linear trend,  $T(x) = bx$ , and uniform distribution of sample locations in the interval of size  $d$  (from  $-0.5d$  to  $0.5d$ ). Covariance function of this pure trend was estimated using the equation:

$$\begin{aligned}
 C_T(h) &= \frac{1}{d-h} \int_{-0.5d}^{0.5d-h} T(x)T(x+h) dx \\
 &\quad - T(-h/2)T(h/2) \\
 &= \frac{1}{d-h} \int_{-0.5d}^{0.5d-h} b^2x(x+h) dx \\
 &\quad + 0.25b^2h^2 \\
 &= \frac{1}{12}b^2d^2(1-h/d)^2. \tag{13}
 \end{aligned}$$

Variance of the trend is estimated as:

$$\text{Var}(T) = \frac{1}{d} \int_{-0.5d}^{0.5d} T(x)T(x) dx = \frac{1}{12}b^2d^2. \tag{14}$$

Combining these 2 equations, we get the result:

$$C_T(h) = \text{Var}(T)(1-h/d)^2. \tag{15}$$