Methods for Monitoring the Spread of Gypsy Moth (Lepidoptera: Lymantriidae) Populations in the Appalachian Mountains

ALEXEI A. SHAROV, ANDREW M. LIEBHOLD,[1] AND E. ANDERSON ROBERTS

Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

J. Econ. Entomol. 90(5): 1259–1266 (1997)

ABSTRACT Gypsy moth, *Lymantria dispar* (L.), is gradually spreading in North America from New England to the west and south. Monitoring this expansion is important for evaluating effects of population management on the rate of gypsy moth spread, for planning areas regulated by domestic quarantine, and for accurate timing of preventive silvicultural measures. Spread rate was measured as the distance between population boundaries in consecutive years. Gypsy moth population boundaries from 1988 to 1995 were estimated in northwestern Virginia and southeastern West Virginia using counts of male moths in pheromone-baited traps. Population boundaries estimated using the 10 moths per trap threshold were most stable in space and time compared with the boundaries estimated for other thresholds ranging from 1 to 300 moths per trap. Thus, the 10 moths per trap threshold is reliable for the monitoring of gypsy moth spread. Local spread rates were significantly autocorrelated in space (range, 80 km) but not in time. The rate of gypsy moth spread decreased from 16.9 km/yr in 1984–1990 to 8.8 km/yr in 1991–1996. An 8-km intertrap distance was adequate for detecting this decline in the rate of gypsy moth spread.

KEY WORDS *Lymantria dispar*, biological invasion, spread rate, monitoring, pheromone traps, autocorrelation

THE GYPSY MOTH, *Lymantria dispar* (L.), was accidentally introduced from France to Medford, MA, in either 1868 or 1869 (Liebhold et al. 1989). Eradication was attempted several times but failed, and the range of the gypsy moth has since spread through most of northeastern North America (Liebhold et al. 1992). The current distribution of the gypsy moth includes most of the northeastern United States and parts of bordering Canadian provinces. Another, discrete population that originated from a secondary introduction exists in Michigan (Dreistadt and Weber 1989). The primary- and secondary-infested regions continue to expand.

The relatively slow rate of spread of the gypsy moth may be related to its limited dispersal ability. Females in North American populations are unable to fly, thus the primary natural mechanism of gypsy moth dispersal is wind-borne movement of 1st instars (Mason and McManus 1981). The expansion of an infested area and the founding of isolated populations also may occur when egg masses or other life stages are accidentally transported on human-made objects (McFadden and McManus 1991, Liebhold et al. 1992).

The gypsy moth feeds on a wide variety of tree species (Liebhold et al. 1995). Thus, it is likely that populations ultimately will invade most of the United States and Canada. However, because the rate of spread is relatively slow, the full range of the potential area will probably not become infested for many years. Prediction of when various areas will become infested would be useful for: proper timing of silvicultural measures which can reduce the adverse impact of gypsy moth defoliation (Gottschalk 1993), planning sampling programs in areas at risk of defoliation, planning areas for quarantine regulation, and planning and evaluating strategies to slow the spread of the gypsy moth (McFadden and McManus 1991).

In 1993, the U. S. Forest Service initiated the Slow-the-Spread (STS) Program, a pilot project designed to test the feasibility of slowing the spread of the gypsy moth over large regions (Leonard and Sharov 1995). The following 3 project areas were established along the advancing front of gypsy moth populations: (1) the Appalachian Mountains in Virginia and West Virginia, (2) northeastern North Carolina, and (3) the upper peninsula of Michigan. The strategy used in this project was to detect and eradicate (or suppress) isolated gypsy moth colonies that occurred just beyond the expanding front of gypsy moth populations. Suppression is considered here as an intermediate step to eradication. However, if the colony is located too close to the population front, there may not be sufficient time to eradicate the colony. Eradication–suppression of newly established colonies should reduce their growth and coalescence and thereby reduce the rate of gypsy moth spread. The Appa-

[1] U.S. Forest Service, 180 Canfield Street, Morgantown, WV 26505.

lachian Integrated Pest Management (AIPM) Project was conducted from 1988 to 1992 in Virginia and West Virginia that was designed to suppress both isolated populations and high-density populations near the expanding front (Reardon 1991). Reduction of gypsy moth spread rate was one of the AIPM objectives which was adopted by STS. However, STS was designed to slow gypsy moth spread while using fewer pesticide applications than in the AIPM project (Leonard and Sharov 1995).

To evaluate the effect of these projects on the rate of population spread, it is important to have reliable methods for measuring population spread rates. Gypsy moth populations are traditionally monitored using any of the following 3 methods: (1) aerial maps of forest defoliation, (2) numbers of overwintering egg masses (Kolodny-Hirsch 1986), and (3) numbers of male moths in pheromone-baited traps (Talerico 1981, Ravlin et al. 1987). Egg mass counts are the most reliable method for assessing densities of medium- and high-density populations; thus they are widely used for decision-making concerning suppression of outbreak populations (Ravlin et al. 1987). Counts of adult males are widely used to detect new isolated gypsy moth infestations because pheromone traps are effective in detecting low-density populations and are less labor-intensive than egg mass sampling (Schwalbe 1981).

Population spread can be quantified using population boundaries which are the lines that separate areas where population densities are generally above or below a specific threshold (Sharov et al. 1995). Sharov et al. (1996) detected a reduction in the rate of gypsy moth spread in the central Appalachians from 1988 to 1994, which likely resulted from pest management activity in the area (AIPM and STS projects).

Our objectives in this study were (1) to compare spatio-temporal variability of population boundaries estimated from different population thresholds (including male moth counts, egg mass counts, and defoliation) and to select the threshold that is most stable and hence most reliable for monitoring population spread; (2) to analyze the autocorrelation of spread rates in space, time, and among rates derived from different population thresholds; this information is important for planning the spatio-temporal scope of monitoring programs and for measuring change in spread rates; and (3) to assess the accuracy of population spread rates estimated from male moth counts in pheromone traps and to examine the relationship between the accuracy and the density of pheromone traps.

Materials and Methods

Area and Data. Historical pheromone trap data (1984, 1988–1995), egg mass count data (1988–1991), and aerial sketch maps of defoliation (1988–1994) from the Appalachian Mountains in northern Virginia and southern West Virginia were used for analysis. Basic intertrap distance was 3 km in West Virginia and 2 km in Virginia, although intensive trapping grids (1 or 0.5 km) were applied in several places of particular interest. Trap competition may cause a bias in moth counts if traps were located too close (e.g., at 0.5 km). Elkinton and Cardé (1988) found competition between traps separated by ≤80 m, but there were no studies on the competition between traps separated by a large distance (e.g., ≥0.5 km). The area covered by dense grids of pheromone traps was always <5% of the total study area. Thus, we believe that the effect of trap competition on population boundaries was small.

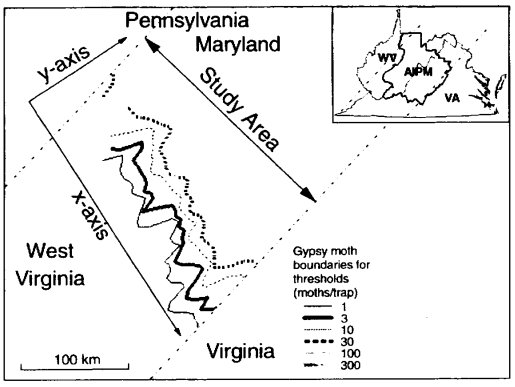

Fig. 1. Study area, its relation to the AIPM project area, and gypsy moth boundaries in 1989 estimated for 6 thresholds of moth counts in pheromone traps. Boundaries are mathematical functions in a rotated Cartesian coordinate system (x-y).

Egg masses were sampled using 0.01-ha fixed-radius plots. The density of samples varied from 4 to 10/1 km^2. Defoliation was recorded using high-altitude optical bar photography (Ciesla and Acciavatti 1982). The threshold for detecting defoliation was ≈30%. Most data were collected as part of the U.S. Forest Service AIPM and STS projects (Reardon 1991, Leonard and Sharov 1995). Complete details of sampling methods were described by Sharov et al. (1995, 1996). The area of analysis was restricted to the mountain region where most historical data were collected (Fig. 1).

Boundary Estimation. A best-cell classification method (Sharov et al. 1995, 1996) was used to estimate "regular" population boundaries. A boundary is considered regular if it has no islands, gaps, or folds. If a grid of cells is applied to the area, then a boundary line classifies some cells as occupied by the population and other cells as unoccupied. The best-cell classification method minimizes the number of grid cells that are misclassified. Population thresholds of 1, 3, 10, 30, 100, and 300 moths per trap; and 1, 3, 10, and 30 egg masses per 0.01 ha were used to estimate boundaries. Defoliation data did not require thresholds. Boundary points were

estimated in 1-km intervals, then averaged in nonoverlapping 5-km blocks. The weights assigned for cell misclassifications of the 1st and 2nd type (the 1st type of misclassification occurred when population was above the threshold but was classified as below the threshold; the 2nd type occurred when the population was below the threshold but was classified as above the threshold) were 1:1 for male moths, 3:1 for egg masses, and 30:1 for defoliation (Sharov et al. 1996). Higher weights for 1st type misclassifications were needed for egg mass density and defoliation because these variables were more spatially aggregated than moth counts in pheromone traps. Selected weights yielded the maximum number of estimated points in population boundaries and minimum variability of these points (Sharov et al. 1996).

In each year t, estimated population boundaries can be viewed as a series of functions in a rotated Cartesian coordinate system with the x-axis oriented parallel to the general boundary direction (Fig. 1). The azimuth of the general boundary direction (147.5°) was estimated by Sharov et al. (1995). The same coordinate system was used for all years. The local boundary point was the y-value of the boundary function at a specific location x. If there was not enough data to estimate a local boundary point, then its value was considered missing, indicated by gaps in lines shown in Fig. 1. Average boundaries were obtained by averaging local boundary points (y-values) along the boundary line. Each average boundary corresponded to a specific year and specific population threshold. Local spread rate was measured as the distance between boundaries (difference in y-values) for the same population threshold in 2 consecutive years. Average spread rates were obtained by averaging local spread rates along the boundary line.

Variability of Population Boundaries. If the population front was parallel to the general boundary direction and moved forward with a constant speed, then boundary points would depend linearly on year. Deviations from the linear function were interpreted as boundary variability in space and time. Local boundary points $B(t,i,x)$ for year t, population threshold i, at location x along the general population boundary were regressed linearly versus years. This regression was estimated separately for each population threshold, and locations were used as replications. Local boundary points may be autocorrelated, which may violate the assumption of independence that is necessary for testing the significance of regression. However, we used regression only to quantify the variability of population boundaries and did not test the statistical significance of regression.

Spread Rate Correlograms. This analysis was performed using male moth counts in pheromone traps to determine if local spread rates were autocorrelated in space, time, and among population thresholds that were used for boundary estimation. Spread rates were arranged in a 3-dimensional array with coordinates: (1) space (distance along the general boundary direction in 5-km intervals), (2) time (6 yr from 1988 to 1994), and (3) population thresholds (6 male moth thresholds). Nonergodic correlograms (Deutsch and Journel 1992) were estimated for each coordinate. An exponential model

$$\rho(h) = c \cdot \exp\left(-\frac{3h}{a}\right), \qquad (1)$$

where $\rho(h)$ is autocorrelation at h intervals in space, time, or population thresholds; c is the sill; and a is the range. Parameters (c and a) were fit to sample correlograms using nonlinear regression (least square method).

Correlograms obtained were used to test if the reduction in spread rates of the gypsy moth was significant. We estimated annual population spread rates from 1988 to 1995 and averaged them along each boundary line. Also, we estimated population boundaries in 1984 and hence were able to estimate the average spread rate in a 4-yr period from 1984 to 1988. Because the reduction in population spread rate may have resulted from eradication of isolated infestations just beyond the expanding population front, we compared spread rates before 1990 (the year when eradication started) and after 1990. Analysis of variance (ANOVA) was used to estimate the F statistic. However, we could not use the standard F distribution for determining the probability, P, because estimated spread rates for adjacent population thresholds were correlated. To test if this difference was significant, we used unconditional gaussian simulations (Deutsch and Journel 1992) to generate 500 replications of local spread rates at the same combinations of space location, time (year), and population threshold at which actual spread rates were estimated. Sample correlograms in space and among population thresholds were used in these simulations. The null hypothesis was that the mean spread rate did not change in time. We used simple kriging with standard values of mean = 0 and variance = 1. The F statistic is invariant to linear transformations ($y = a + bx$) of the response variable. It was not necessary to use the actual mean and variance in gaussian simulations because the change in mean and variance is equivalent to a linear transformation. F statistics were estimated for each simulation, and the proportion of simulated F values that exceeded the sample F value was considered as an error probability (P).

Accuracy of Estimated Spread Rates. Intertrap distance was important in the analysis of the accuracy of estimated spread rates; thus, we wanted to use a relatively uniform distribution of traps. To remove traps that were set too close to each other, a grid (2 by 2 km) was applied to the entire area. If any cell had >1 trap, then we randomly selected only 1 trap in that cell. This thinned set of traps is referenced below as the entire set of traps. Average intertrap distance in this set of traps was ≈2.5 km.

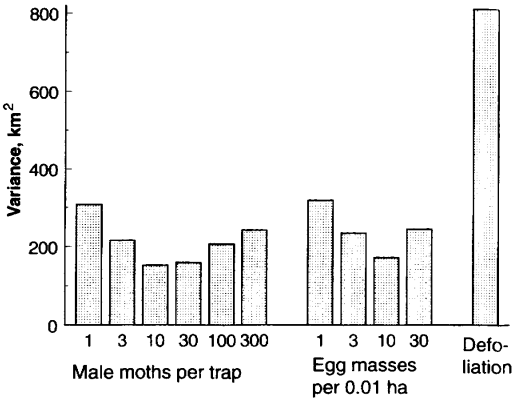

Fig. 2. Variability of local gypsy moth boundaries in space and time measured as the error variance in the linear regression of local boundary values versus time.

The accuracy of population spread rates, estimated from male counts in pheromone traps, was evaluated using a modified Tukey jackknife method (Sokal and Rohlf 1981), which provides the estimate of the standard error of any statistic Y. Statistic Y is estimated from the complete sample, which is then subdivided into n equal portions (often each portion is represented by a single sample). The corresponding statistic Y_i is estimated based on sample data with each portion of the observations i left out in turn. Pseudovalues, ϕ_i, are computed as

$$\phi_i = nY - (n - 1)Y_i. \quad (2)$$

The jackknifed estimate of the statistic Y is then simply the average of pseudovalues, and the standard eror of Y is estimated as the standard deviation of pseudovalues divided by $\sqrt{n}$.

The original jackknife method is valid for independent and identically distributed data, although moth counts are spatially dependent. Spatial dependence among moth counts may result from moth dispersal, growth of isolated colonies, or effect of autocorrelated landscape characteristics such as elevation and vegetation (Sharov et al. 1997). Because of spatial dependence, the distribution of moth counts depended on trap location and neighboring locations have similar distributions. In the original jackknife method, the spatial distribution of samples is ignored, thus space coordinates are not considered when the entire sample is subdivided into n portions. In the modified jackknife method, we subdivided the entire sample so that each portion of sample points was uniformly distributed over the area. Then each site with its specific mean and variance of moth counts was equally represented in all portions of samples. As a result, pseudovalues (equation 2) were independent random variables with the same distribution (see Appendix). Thus, they could be used to estimate the standard error of Y.

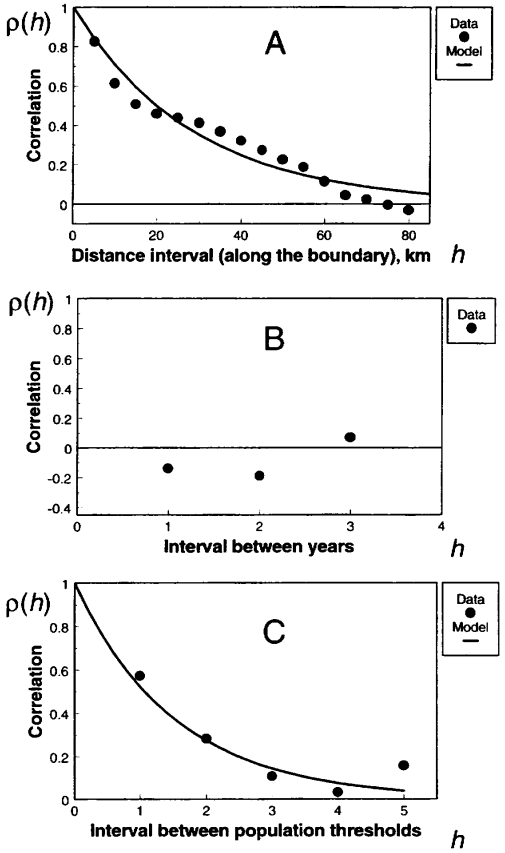

Fig. 3. Correlograms of local gypsy moth spread rate in space (A), time (B), and for different population thresholds (C).

To apply the Tukey jackknife method, the entire set of traps in each year was subdivided into 8 equal groups so that each group uniformly covered the entire area. These groups were obtained using the following algorithm: (1) a grid (15 by 15 km) was applied to the entire area; (2) in each cell, 1/8 of randomly selected traps was designated to the 1st subset, then 1/7 of the remaining traps was designated to the 2nd subset, and so on. The grid ensured more uniform distribution of traps than would be expected from random trap selection. Population spread rates were estimated from the entire set of traps and from 8 subsets pooled but 1 subset left out in turn (7/8 of the entire set). Then the standard error of the spread rate was estimated according to the Tukey method (Sokal and Rohlf 1981).

To measure the effect of intertrap distance on the accuracy of estimated spread rates, we estimated spread rates using each 1/8 portion of traps. Then the standard deviation (=standard error) of

spread rates obtained from all subsets of data points was estimated.

Results

Variability of Population Boundaries. The variance of residuals in the linear regression of local boundary points versus time shows the variability of boundaries in space and time (Fig. 2). Among all thresholds of male moth counts, the lowest variability in boundary points was detected for 10 moths per trap, and the highest variability was detected for 1 moth per trap. The variability of egg mass boundaries was lowest for 10 egg masses per 0.01 ha and relatively high for 1 egg mass per 0.01 ha. Defoliation boundaries exhibited the highest variability in space and time.

Spread Rate Correlograms. Autocorrelation of local population spread rates in space was high for distance intervals <20 km (Fig. 3A). Then it declined gradually with increasing distance. Correlogram sill, c, in equation (1) was not significantly different from 1, which indicated no high-frequency noise (no nugget effect). Thus, we used $c = 1$ for fitting correlogram range. The range of the correlogram was estimated as $a = 86$ km.

Population spread rates exhibited almost no autocorrelation in time (Fig. 3B). It was not possible to fit an exponential model to the sample correlogram.

There was a relatively strong correlation [$\rho(1) = 0.57$] among spread rates estimated using neighboring male moth population thresholds (Fig. 3C). However, correlation was weak for $h > 2$. Correlogram sill was $c = 1$ and the range was estimated as $a = 4.6$ intervals between population thresholds, which corresponded to >10 times difference in moth catches. Thus, there is little correlation in spread rates estimated using population thresholds that differ >10 times in magnitude (e.g., 3 and 100 moths per trap).

Average spread rate of gypsy moths was 16.9 km/yr before 1990 and 8.8 km/yr after 1990. The sample value of the F statistic was $F = 17.9$ with df = 1, 46. The mean square error (MSE) was 41.84 km^2. Among 500 unconditional simulations, only 5 had $F > 17.9$. Hence, the probability that the null hypothesis is correct was $P = 0.01$. The 0.95 quantile for the simulated F distribution was $F = 9.92$, indicating that the reduction of gypsy moth population spread rate was significant. When data from 1984 were excluded, the F statistic was $F = 6.5$ and the probability of accepting the null hypothesis increased to $P = 0.126$. Data from 1984 was important for detecting the decrease in gypsy moth spread rates; significance was lost after exclusion of these data. Thus, 8–9 yr of data was the minimum for detecting the decrease in gypsy moth spread rates.

Accuracy of Estimated Spread Rates. The standard error for average spread rates (local spread rates averaged along the boundary line) were estimated using the Tukey method, then averaged over the years separately for each threshold of moth counts. These average standard error varied from 1.4 to 2.1 km (Fig. 4), which was 13–21% of the annual spread rate of the gypsy moth. There was no significant difference in the standard error of average spread rates estimated from various population thresholds ($F = 0.96$; df = 5, 30; $P = 0.457$). The mean standard error, estimated as the mean of 36 squared standard error of average spread rates (6 yr × 6 population thresholds), was equal to 3.74 km^2.

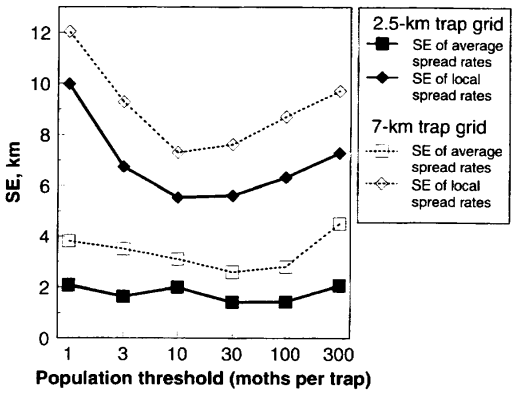

Fig. 4. Standard errors for average population spread rates and local spread rates estimated from trap grids with 2.5-km and 7-km intertrap distances.

The standard error for local spread rates were first averaged along each boundary line (square root from the average squared standard error of local spread rates). These averages were further averaged over the years separately for each threshold of moth counts. The final averages varied from 5.5 to 9.9 km (Fig. 4). There were significant differences in the standard error of local spread rates estimated from various population thresholds ($F = 7.21$; df = 5, 30; $P < 0.001$). Local spread rates estimated from the threshold of 10 moths per trap were most accurate (smallest standard error), and local spread rates estimated from the threshold of 1 moth per trap were least accurate.

The standard error of average spread rates estimated from a subset of traps with a 7-km intertrap distance varied from 2.6 to 4.5 km (Fig. 4). These standard errors were 1.9 times greater than the standard error for average spread rates estimated from the entire set of traps with a 2.5-km intertrap distance. The mean standard error, estimated as the mean of 36 squared standard errors of average spread rates (6 yr × 6 population thresholds), was equal to 14.75 km^2.

The standard error for local spread rates, estimated from 7-km trap grids, were averaged along each boundary line and then averaged over the years separately for each threshold of moth counts. The final averages varied from 7.3 to 12.0 km (Fig.

4). They were 1.3 times greater than the standard error of local spread rates estimated from the entire set of traps with a 2.5-km intertrap distance.

Discussion

Variability of Population Boundaries. Gypsy moth population boundaries estimated from male moth counts were most variable for the threshold of 1 moth per trap. This is likely the result of windborne dispersal of male moths. The high male moth catches in the study area likely arose mostly from locally reproducing gypsy moth populations, whereas low male catches (1–3 moths per trap) in many cases may have represented migrants. Wind speed and direction during the male moth flight period varied in space and time and may have caused the high fluctuations of population boundaries estimated from low male capture thresholds.

Among male catch thresholds tested, the least variable population boundary was detected for 10 moths per trap. Thus, use of this threshold appears optimal for quantifying the progression of the population front and for planning specific pest management activities (e.g., defining the area where isolated colonies should be detected and eradicated).

The variability in egg mass population boundaries was similar to that of male moth boundaries. The threshold of 10 egg masses per 0.01 ha yielded the most stable boundaries among all egg mass density thresholds tested. However, egg mass sampling is expensive compared with pheromone traps, thus is a less desirable sampling method for estimating boundaries over large areas.

Defoliation boundaries were unstable. High variability may have resulted from the low proportion of total area that became defoliated, and spatial heterogeneity in stand susceptibility. Thus, defoliation maps did not provide sufficient accuracy for monitoring gypsy moth spread. However, they may be useful for approximating spread rates if other data are not available.

Spread Rate Correlograms. Local spread rates of the gypsy moth were correlated within the distance range of 86 km along the boundary line. If spread rate is estimated in a small area (e.g., 30–50 km), then it may be considerably affected by local conditions; thus, it may not be representative of spread rates over larger areas.

Spread rates estimated from similar population thresholds (Fig. 3C) were correlated. However, there was almost no correlation among spread rates estimated from population thresholds that differed >10 times. This is probably the result of spatial separation of these populations.

Population spread rates estimated at different population thresholds can be considered as replications for monitoring the spread of gypsy moths. However, these replications are not entirely independent, as shown above. Sharov et al. (1996) detected a decrease in gypsy moth spread rate, but the statistical test was not accurate because it assumed independence among all estimated population spread rates. In this article, we applied more accurate and powerful methods (unconditional simulation) of analysis that confirmed the decrease in gypsy moth spread rates.

We hypothesize that the reduction in the rate of gypsy moth spread resulted mostly from eradication of isolated colonies just beyond the population front. However, other factors also may contribute the reduction of the spread rate. A new fungal pathogen, *Entomophaga maimaiga* (Humber, Shimazu & Soper), which appeared in North America in late 1980s, caused additional mortality in gypsy moth populations (Hajek et al. 1996). Thus, it could affect the rate of gypsy moth spread. Initially, *E. maimaiga* was confined to New England but did not reach the leading edge of gypsy moth populations until 1992 (Hajek et al. 1996). However, the rate of gypsy moth spread declined earlier (in 1990), suggesting that the fungus was not the most important factor affecting the spread. Weather factors can modify the rate of gypsy moth spread in individual years, but they are not likely to affect the average rate of spread over 4–5 yr because there were no obvious long-term trends in weather conditions in the study period.

As with many other large-scale experiments, this experiment on slowing population spread had no real control. The Appalachian Mountains have unique topography and vegetation; thus, it is impossible to find an area with similar conditions. Also, historical data collected in areas adjacent to the Appalachian Mountains are not sufficient to quantify the dynamics of population spread. Extensive data on gypsy moth spread were collected in Michigan (Gage et al. 1990), but the climate and topography are very different. Thus, Michigan cannot be considered as a control.

In experiments that have no direct control, it is very important to have a theory that supports experimental results. We have developed a model that considers the spread of gypsy moth populations via establishment of isolated colonies beyond the expanding front (Sharov and Liebhold 1997). This model predicts that eradication of isolated colonies should result in a 53% reduction in the rate of spread, which is comparable with the actual reduction of spread.

Accuracy of Estimated Spread Rates. The use of 2.5-km trap grids resulted in relatively high accuracy of estimated average spread rates (SE = 13–21% of the annual spread rate of the gypsy moth). It is important to select appropriate intertrap distance for the grid of traps designed for monitoring gypsy moth spread. As the intertrap distance increases, the accuracy of spread rate estimates decreases. However, it is important to identify the magnitude of accuracy that is necessary for solving the problem. If natural variability of a measured value is high, then the measurement error represents a small portion to the overall error of average

estimates, and there is little need to achieve high measurement accuracy.

We can estimate the maximum intertrap distance needed for detecting the decrease in gypsy moth spread rate that was obtained from 1984 to 1995. The mean standard error in the ANOVA used for detecting the decrease in the average population spread rate was 41.84 km^2. It can be separated into 2 portions associated with accuracy of the estimation of the average spread rate (MSE = 3.23 km^2), and natural variability of average spread rates in time and among population thresholds (MSE = 41.84 − 3.23 = 38.61 km^2). The 1st portion increases with increasing intertrap distance, whereas the 2nd portion does not depend on trap spacing. For example, the 1st portion increased to 4.75 km^2 when a 7-km trap spacing was used instead of a 2.5-km spacing. According to the simulated F distribution, the difference in spread rates will remain significant even if the total mean standard error is equal to 75.3 km^2. Then, the 1st portion of the mean standard error can be as large as 75.3 − 38.61 = ≈36.7 km^2.

Finally, we need to relate the accuracy of spread rate estimation and the intertrap distance. As the trap density decreased 8 times (intertrap distance increased from 2.5 to 7 km), the mean standard error increased only 3.9 times (from 3.74 to 14.75 km^2). The sample size had a relatively small effect on the accuracy of the estimate of the spread rate compared with the effect of sample size on the accuracy of the mean value; the mean standard error of the mean value is inversely proportional to the sample size (Taylor 1984). The MSE of the spread rate may grow faster with increasing intertrap distances >7 km than at intertrap distances <7 km. However, it is unlikely that it will grow faster than the mean standard error for the mean value. To make a conservative estimate, it is assumed that the MSE is inversely proportional to the density of traps when traps are separated by >7 km. Then, to obtain the MSE = 36.7 km^2 necessary for detecting the decrease in spread rates, the intertrap distance should be $7 \times \sqrt{36.7/14.75} = 11$ km. We can thus detect change in gypsy moth spread rates even if the intertrap distance was 11 km. In practical situations it may not be rational to increase the intertrap distance beyond 8 km because some traps may become damaged, resulting in lost data.

Strategies for monitoring the spread of the gypsy moth may vary depending on objectives. In this study, our primary objective was to detect the reduction in the rate of population spread over short time periods (≈10 yr). However, our results can be used for adjusting the monitoring strategy for different objectives and different temporal and spatial scales.

It is not clear if our results can be extrapolated to other areas affected by the gypsy moth. The pattern of gypsy moth spread may depend on the terrain, habitat fragmentation, and other factors. However, our results give a reliable starting point for developing strategies for monitoring the spread of gypsy moths in other regions. These programs can be adjusted later using data obtained in those specific areas.

Acknowledgments

We thank Frank C. Curriero (U. S. Forest Service, Morgantown, WV), Shelby J. Fleischer (Pennsylvania State University, University Park) and Joseph S. Elkinton (University of Massachusetts, Amherst) for discussion of the manuscript. This research was funded by the U.S. Forest Service, Forest Health Contract No. 08-94-53-01 and by Grant No. 95-37313-1892 from the USDA Cooperative State Research, Education, and Extension Service.

References Cited

Ciesla, W. M., and R. E. Acciavatti. 1982. Panoramic aerial photography for mapping gypsy moth defoliation. U. S. For. Serv. For. Pest Manage. Methods Appl. Group Rep. 83-1.

Deutsch, C. V., and A. G. Journel. 1992. GSLIB. Geostatistical software library and user's guide. Oxford University Press, Oxford.

Dreistadt, S. H., and D. C. Weber. 1989. Gypsy moth in the northeast and Great Lakes states, pp. 229–256. *In* D. L. Dahlsten and R. Garsia [eds.], Eradication of exotic pests. Yale University Press, New Haven.

Elkinton, J. S., and R. T. Cardé. 1988. Effect of intertrap distance and wind direction on the interaction of gypsy moth (Lepidoptera: Lymantriidae) pheromone-baited traps. Environ. Entomol. 17: 764–769.

Gage, S. H., T. M. Wirth, and G. A. Simmons. 1990. Predicting regional gypsy moth (Lymantriidae) population trends in an expanding population using pheromone trap catch and spatial analysis. Environ. Entomol. 19: 370–377.

Gottschalk, K. W. 1993. Silvicultural guidelines for forest stands threatened by the gypsy moth. U. S. For. Serv. Gen. Tech. Rep. NE-171.

Hajek, A. E., J. S. Elkinton, and J. J. Witcosky. 1996. Introduction and spread of the fungal pathogen *Entomophaga maimaiga* (Zygomycetes: Entomophthorales) along the leading edge of gypsy moth (Lepidoptera: Lymantriidae) spread. Environ. Entomol. 25: 1235–1247.

Kolodny-Hirsch, D. M. 1986. Evaluation of methods for sampling gypsy moth (Lepidoptera: Lymantriidae) egg mass populations and development of sequential sampling plans. Environ. Entomol. 15: 122–127.

Leonard, D. S., and A. A. Sharov. 1995. Slow The Spread project update: developing the process for evaluation, pp. 82–85. *In* S.L.C. Fosbroke and K. W. Gottschalk [eds.] Proceedings, USDA Interagency Gypsy Moth Research Forum 1995. U. S. For. Serv. Gen. Tech. Rep. NE-213.

Liebhold, A., V. Mastro, and P. W. Schaefer. 1989. Learning from the legacy of Leopold Trouvelot. Bull. Entomol. Soc. Am. 35: 20–21.

Liebhold, A. M., J. A. Halverson, and G. A. Elmes. 1992. Gypsy moth invasion in North America: a quantitative analysis. J. Biogeogr. 19: 513–520.

Liebhold, A. M., K. W. Gottschalk, R.-M. Muzika, M. E. Montgomery, R. Young, K. O'Day, and B. Kelly. 1995. Suitability of North American tree species to

the gypsy moth: a summary of field and laboratory tests. U. S. For. Serv. Gen. Tech. Rep. NE-211.

Mason, C. J., and M. L. McManus. 1981. Larval dispersal of the gypsy moth, pp. 161–202. *In* C. C. Doane and M. L. McManus [eds.], The gypsy moth: research toward integrated pest management. U. S. Dep. Agric. Tech. Bull. 1584.

McFadden, M. W., and M. E. McManus. 1991. An insect out of control? The potential for spread and establishment of the gypsy moth in new forest areas in the United States, pp. 172–186. *In* Y. N. Baranchikov, W. J. Mattson, F. P. Hain, and T. L. Payne [eds.], Forest insect guilds: patterns of interaction with host trees. U. S. For. Serv. Gen. Tech. Rep. NE-153.

Ravlin, F. W., R. G. Bellinger, and A. E. Roberts. 1987. Gypsy moth management programs in the United States: status, evaluation and recommendations. Bull. Entomol. Soc. Am. 33: 90–98.

Reardon, R. C. 1991. Appalachian gypsy-moth integrated pest-management project. For. Ecol. Manage. 39: 107–112.

Schwalbe, C. P. 1981. Disparlure-baited traps for survey and detection, pp. 542–548. *In* C. C. Doane and M. L. McManus [eds.], The gypsy moth: research toward integrated pest management. U. S. Dep. Agric. Tech. Bull. 1584.

Sharov, A. A., and A. M. Liebhold. 1997. Model of slowing population spread with a barrier zone. Ecol. Appl. (in press).

Sharov A. A., E. A. Roberts, A. M. Liebhold, and F. W. Ravlin. 1995. Gypsy moth (Lepidoptera: Lymantriidae) spread in the Central Appalachians: three methods for species boundary estimation. Environ. Entomol. 24: 1529–1538.

Sharov, A. A., A. M. Liebhold, and E. A. Roberts. 1996. Spread of gypsy moth (Lepidoptera: Lymantriidae) in the central Appalachians: comparison of population boundaries obtained from male moth capture, egg mass counts, and defoliation records. Environ. Entomol. 25: 783–792.

1997. Correlation of counts of gypsy moths (Lepidoptera: Lymantriidae) in pheromone traps with landscape characteristics. For. Sci. (in press).

Sokal, R. R., and F. J. Rohlf. 1981. Biometry, 2nd ed. Freeman, New York.

Talerico, R. L. 1981. Defoliation as an indirect means of population assessment, pp. 38–49. *In* C. C. Doane and M. L. McManus [eds.], The gypsy moth: research toward integrated pest management. U. S. Dep. Agric. Tech. Bull. 1584.

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

Received for publication 11 July 1996; accepted 20 March 1997.

Appendix

We show that pseudovalues (equation 2) in the Tukey jackknife method are independent random variables with the same distribution if sample points are regularly distributed in space and sample values have site-specific distributions.

Let us assume that the rate of spread, Y, is a linear function of sample values, x_i. The actual relationship may be nonlinear, but the linear approximation can be used if the variability of sample values is not very large. Thus,

$$Y = \sum_{i=1}^{N} x_i w_i,$$

where w_i are coefficients (we don't call them weights because they can be negative). The entire sample is subdivided into n portions that evenly cover the entire area. Then the spread rate is estimated from the entire sample but one portion is excluded at a time:

$$Y' = \frac{n}{n-1} \sum_{i=1}^{N(n-1)/n} x_i w_i$$

where Y' is the spread rate estimated from samples $i = 1, \ldots, N(n-1)/n$ (they are ordered so that samples excluded from analysis go last). The multiplier $n/(n-1)$ is used to compensate for the reduction of the number of samples, so that $E(Y') = E(Y)$. Values of w_i will be almost the same for retaining samples because the proportion of excluded samples is small.

Then, the Tukey pseudovalue is equal to:

$$\phi = nY - (n-1)Y' = n \sum_{i=1}^{N} x_i w_i - \frac{(n-1)\cdot n}{(n-1)} \sum_{i=1}^{N(n-1)/n} x_i w_i = n \sum_{i=N(n-1)/n+1}^{N} x_i w_i.$$

The pseudovalue is equal to the contribution of excluded samples, $i = N(n-1)/n$, to the estimated spread rate Y. Now it is clear that pseudovalues are independent because they are estimated from nonoverlapping subsets of samples. A pseudovalue is a linear combination of a large number of individual samples. The distributions of individual samples become combined; thus, all pseudovalues have almost identical distributions so that the Tukey method can be used to assess the standard error of the estimated spread rate.