

## Quantitative analysis of gypsy moth spread in the Central Appalachians

Alexei A. Sharov

Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, Va., USA

Andrew M. Liebhold

USDA Forest Service, Morgantown, W.Va., USA

**ABSTRACT:** Gypsy moth, *Lymantria dispar* (L.), is an introduced forest pest in North America that has been expanding its range to the west and south. In attempt to slow its spread, the USDA Forest Service has established several barrier zones in which isolated colonies are detected and eradicated. To evaluate the effect of barrier zones on the rate of gypsy moth spread, we measured the rate of spread as the average distance between population boundaries in consecutive years which were estimated using male moth counts in pheromone traps, egg mass counts, and defoliation maps in the central Appalachian Mts. in 1984-1995. In 1988-1992, the boundary of 1 moth per trap was on average 108.5 km from the boundary of defoliation, and male moth capture rate increased 10 times per 29 km perpendicular to the population front. Since 1990, the average rate of gypsy moth spread declined from 20.78 km/yr to 8.6 km/yr. This reduction of spread rate may have been due to eradication of isolated colonies in the study area that started in 1990. We developed a model of gypsy moth spread that considered establishment of isolated colonies beyond the moving population front. The model predicts that the barrier zone in the Appalachian Mts. should reduce the rate of gypsy moth spread by ca. 53% which is consistent with our data.

### INTRODUCTION

The gypsy moth, *Lymantria dispar* (L.), was accidentally introduced to North America near Boston in 1869 and since that time it has been slowly expanding its range (Liebhold et al. 1989, 1992). The current distribution of the species includes most of the northeastern United States and parts of bordering Canadian provinces. Another, discrete population exists in Michigan that originated from a secondary introduction that was not successfully eradicated. The primary and secondary infested regions continue to expand.

Quantitative analysis of gypsy moth spread would be useful for: (1) proper timing of silvicultural measures which can reduce the adverse impact of gypsy moth defoliation (Gottschalk 1993), (2) planning sampling programs in areas at risk to defoliation, (3) planning areas for quarantine regulation, and (4) for planning and evaluating strategies to slow the spread of the gypsy moth (McFadden & McManus 1991).

In 1993 the USDA 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 & Sharov 1995). The following 3 barrier zones were established along the advancing front of gypsy moth populations: (1) the Appalachian Mts. in Virginia and West Virginia, (2) northeastern North Carolina, and (3) the Upper Peninsula of Michigan. The strategy used in this project is to detect and eradicate (or suppress) isolated gypsy moth colonies that occur just beyond the expanding front of gypsy moth populations. Suppression of newly established colonies should reduce their growth and coalescence, and thereby reduce the rate of gypsy moth spread. A similar program, the Appalachian Integrated Pest Management (AIPM) project, was conducted from 1988-1992 in Virginia and West Virginia and was designed to suppress both

high-density populations and isolated populations near the expanding front. 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.

In order to evaluate the effect of these projects on the rate of population spread it is important to have access to reliable methods for measuring population spread rates. Liebhold et al. (1992) suggested evaluating the rate of gypsy moth spread from the relationship between the year of establishment of quarantine regulations in a county and the distance of the county from the area infested in 1900. The estimated rate of spread varied from 2.82 to 20.78 km/yr. However the method of Liebhold et al. (1992) is not enough accurate for management purposes because it used a county-level spatial resolution and it may be biased due to subjective factors that affect the establishment of quarantine regulations.

More reliable estimates of the rate of spread can be obtained from geographically-distributed population samples. Gypsy moth populations are traditionally monitored using any of 3 methods: (1) aerial maps of forest defoliation, (2) counts of overwintering egg mass populations (Kolodny-Hirsch 1986), and (3) counts 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 and thus they are widely used for making decisions 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 highly sensitive at detecting low-density populations and this method is much less labor-intensive than egg mass sampling (Schwalbe 1981).

Sharov et al. (1995) proposed to estimate the rate of population spread as a distance between population boundaries in 2 consecutive years. A population boundary was defined as an isoline that separates areas with population density generally below and generally above a certain threshold. Threshold density is important when populations are evaluated on a continuous scale rather than as simply presence-absence. The first objective of this study was to implement this method for measuring the rate of gypsy moth spread and to evaluate the effect of population management on the rate of spread.

The second objective was to develop a model of gypsy moth population spread that could be used to test the effect of barrier zones on the rate of expansion of population range. Most models of population spread are based on diffusion equations. For example, the model of Skellam (1951) combines diffusion of organisms with exponential population growth. Reaction-diffusion models that are used for simulating population spread were reviewed by Hastings (1996). Marsula and Wissel (1994) used a diffusion-based model to simulate the management of a barrier zone designed to stop the spread of screwworm populations. However, simple diffusion models are not appropriate for simulation of the spread of gypsy moth populations (Liebhold et al. 1992). There is no continuous wave of population spread. Instead, discrete isolated infestations are established beyond the population front (McFadden & McManus 1991). These infestations apparently originate from egg masses and other life stages transported on human vehicles. Isolated infestations grow in size, coalesce and finally contribute to the expansion of the population front. Discontinuous long-distance dispersal is usually combined with local neighborhood dispersal that makes local infestations grow. Hengeveld (1989) suggested the term "stratified diffusion" or "stratified dispersal" to refer to a combination of different dispersal scales.

Shigesada et al. (1995) developed several models of stratified dispersal in animal populations. The scattered colony model assumes independent growth of a set of colonies which expand in size and simultaneously emit long-distance dispersal propagules. A more realistic coalescing colony model assumes that new colonies become established at a specific distance from the expanding population front. When their boundary reaches the population front, then they coalesce with the primary colony and their area is added to the infested area. Although models of Shigesada et al. (1995) generate reasonable rates of population spread, they are not realistic enough to be used for simulating the effect of barrier zones. For example, according to the coalescing colony model, eradication of offspring colonies can be restricted to a very small area because new colonies are produced at a fixed distance from the population front.

In this paper we developed a new model of stratified dispersal in which colonies can become established at varying distances from the population front. This model is biologically more realistic and provides more meaningful representation of barrier zone strategies.

## MATERIALS AND METHODS

We used historical pheromone trap data (1980, 1984, 1988-1995) egg mass sample data (1988-1991) and defoliation maps in northwestern Virginia and southeastern West Virginia. Most of the data was collected during the Appalachian Integrated Pest Management (AIPM) project, 1988-1992, (Reardon 1991); and Slow-the-Spread (STS) project that started in 1993 (Leonard & Sharov 1995).

Most pheromone traps were the standard 1.9-liter milk-carton design (Schwalbe 1981). In the STS project, delta-traps were used in uninfested areas. All traps were baited with (+) disparlure impregnated dispensers. Traps were placed in regular grids; most grids traps were spaced by 2-3 km. The number of traps placed each year varied from 3,380 to 20,760.

Egg masses were sampled in 0.01 ha plots mostly in the area with male moth counts of 200-300 moths per trap and more. Each year from 11,650 to 45,860 samples were taken. The number of plots within a 1 km<sup>2</sup> area was determined using a sequential sampling plan (Fleischer et al. 1991) and generally ranged from 4 to 10. The number of new egg masses was counted on tree boles, branches and on the ground. Because we were interested in patterns of egg mass distribution larger than 1 km, egg mass counts were averaged in each 1 km<sup>2</sup> cell prior to analysis.

The location of traps and egg mass samples was recorded using Universal Transverse Mercator (UTM) (Snyder 1987) coordinates estimated from locations on standard 1:24,000 topographic maps published by the U.S. Geological Survey.

Preliminary analysis of male moth counts in 3 states (VA, WV, and NC) in 1995 indicated that the pattern of population spread in the Appalachian Mts. is different from that in the coastal plain and piedmont. Because most of data were collected in the mountains, we restricted the analysis to the mountain region (between the lines from Grant Town, Marlon Co., WV to Clendenin, Kanawha Co., WV and from Culpeper, Culpeper Co., VA to Sydnorsville, Franklin Co., VA).

Population boundaries were estimated as follows. The first step was to interpolate moth counts in pheromone traps using median indicator kriging with subsequent E-type estimation (Deutsch & Journel 1992). This method is not sensitive to data distribution and generates unbiased estimates (Deutsch & Journel 1992). Variograms were isotropic and were approximated by an exponential model with the relative nugget of 0.45 and effective range of 20.5 km for male moth counts. For egg mass counts parameters were: relative nugget, 0.58; and effective range, 17.8 km (Sharov et al. 1995). Median indicator kriging was performed on a lattice of 1 × 1 km cells. After E-type values were estimated, we delineated population boundaries using the following population thresholds: 1, 3, 10, 30, 100, and 300 moths per trap and 1, 3, 10, and 30 egg masses per 0.01 ha. Defoliation maps did not require kriging because the presence of defoliation was already coded for all cells in the map.

To estimate population boundaries we used the best cell classification method (Sharov et al. 1995). If a grid of cells is applied to the area, then a boundary line classifies cells into occupied and nonoccupied by a population. Some of these cells may be misclassified: they may be considered occupied whereas in reality they are not and vice versa. The method identifies a line that has no folds and that minimizes the number of misclassified cells. 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 it 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. 1996a).

Boundary points were estimated in 5-km intervals. All population boundaries were functions in a rotated Cartesian coordinate system with x- and y-coordinates shown in Fig. 1. We used the same coordinate system for all boundaries so that they could be compared easily. The origin was selected arbitrarily so that x- and y-values were positive. The y-coordinate coincided with the

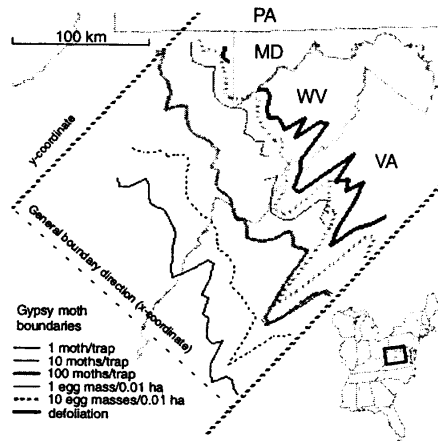


Fig. 1. Gypsy moth population boundaries estimated using best cell classification method from moth counts in pheromone traps, egg mass samples, and defoliation map in 1989.

border of the study area and had the azimuth of 42.7°. Average boundary location was estimated as the average y-value for all boundary points.

Population spread rate was measured using the following 2 methods: (1) as the difference between average boundary locations for the same population threshold in 2 consecutive years and (2) as the average difference between local boundary points. These 2 measures would coincide if boundaries had no missing values. However, boundary lines were not always complete, and thus, these measures were different. Boundaries in 1984 had more than a half points missing, and this caused a considerable difference in estimates of spread rate obtained from 2 methods. Spread rates were estimated using male moth counts in pheromone traps for 6 population thresholds (1, 3, 10, 30, 100, and 300 moths per trap) and then averaged for all thresholds. Population monitoring was irregular before 1988; thus, there were no data between 1980 and 1984, and between 1984 and 1988. Thus, we estimated the average rate of population spread in each 4-yr interval as the distance between population boundaries at the beginning and end of the interval divided by 4.

To detect the reduction in the spread rate of gypsy moth populations we compared average spread rate before and after the start of pest management activity directed at slowing population spread. We expect that the reduction in population spread rate resulted mainly from eradication of isolated infestations just beyond the expanding population front, which started in 1990. Thus, we grouped spread rates into 2 categories: before 1990 and after 1990.

#### ANALYSIS OF GYPSY MOTH SPREAD

Average boundary values plotted against the distance along the y-coordinate (see Fig. 1) show the progression of the population front (Fig. 2). In 1988-1992, the distances between average boundaries estimated using different population thresholds generally remained the same from year to year (Fig. 2). Accumulated average distances between adjacent boundaries from 1 moth per trap to: 3, 10, 30, 100, 300 moths per trap, 1, 3, 10, 30 egg masses per 0.01 ha, and defoliation were 13.9, 28.4, 40.1, 54.7, 69.0, 92.4, 97.8, 104.6, 109.6, and 108.5 km, respectively. One order of magnitude increase in male moth counts occurred over a distance of  $\approx 29$  km across the population front. Egg mass boundaries were much closer to each other than male moth boundaries (Fig. 2). The average rate of population spread during that period was 10.4 km/yr. Thus, it took  $\approx 11$  yr for gypsy moth populations to grow from 1 moth per trap to the first defoliation.

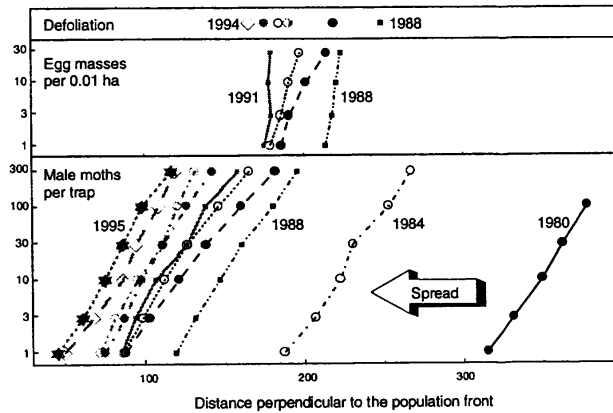


Fig. 2. Average gypsy moth population boundaries (y-coordinates averaged along each boundary) in different years and for different population thresholds (moth counts, egg mass counts, and defoliation). Distance perpendicular to the population front is measured from an arbitrarily selected point beyond the population front. Unlabeled lines represent data for the years (in chronological order) between those indicated on the graph.

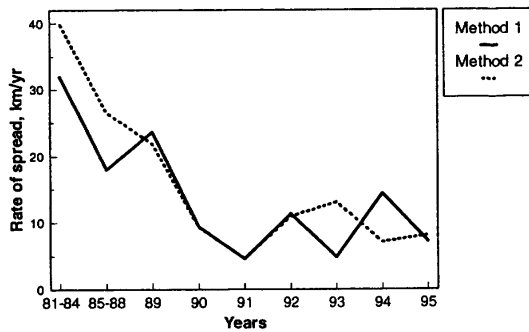


Fig. 3. The rate of gypsy moth spread estimated from 6 thresholds of moth counts as the difference between averaged boundaries (method 1) and as the average difference between local boundary points (method 2).

Population spread rates estimated using both methods declined during the census period (Fig. 3). In 1981-1990, the average rate of spread was 26.5 km/yr (average from 2 methods), whereas in 1991-1995, the average rate of spread was 8.6 km/yr. Liebhold et al. (1992) estimated the rate of uncontrolled population spread (without barrier zones) in areas with mean minimum temperature < 7°C (our study area satisfies this requirement) as 20.78 km/yr in 1966-1990 which is close to our estimates for 1981-1990. It is hard to tell which estimate of the uncontrolled spread rate is more accurate. Liebhold et al. (1992) used a less accurate method, but they analyzed a longer period. In this paper we will use the result of Liebhold et al. (1992) because it gives a more conservative estimate of the reduction in the rate of population spread (59% reduction).

#### MODEL OF GYPSY MOTH SPREAD

Our model of gypsy moth spread considers 3 zones at the expanding population front: the infested zone which is assumed to be a source of long-distance dispersal, the transition zone where new colonies become established, and the uninfested zone where no colonies exist (Fig. 4). We

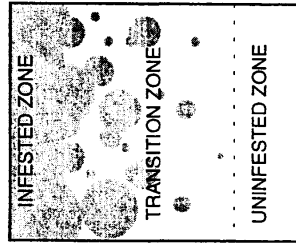


Fig. 4. Three zones at the expanding population front.

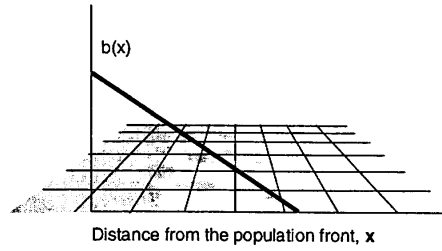


Fig. 5. The probability of colony establishment,  $b(x)$ , decreases with increasing distance,  $x$ , from the front of the infested zone.

assumed that the rate of colony establishment,  $b(x)$ , decreased with increasing distance,  $x$ , from the front of the infested zone (Fig. 5).

Average population density,  $N$ , is the mean number of individuals per unit area. The front of the infested zone is defined as a line where the average population density  $N$  reaches the carrying capacity,  $K$ . For simplicity, our model is built in one dimension which is considered perpendicular to the moving population front. The front of the infested zone is located at the point where  $N = K$ . Colonies grow with time and the value of  $N$  increases respectively. As a result,  $N$  becomes eventually  $>K$ , and the front of the infested zone moves forward to the point where the new value of  $N = K$ .

At distance  $x$  from the front of the infested zone, colonies of various age are present. The average population density can be estimated as the integral of the density of colonies of various ages multiplied by the number of individuals in these colonies. The number of colonies of age  $a$  at distance  $x$  is equal to the colonization rate at time  $t-a$  where  $t$  is current time. We assume that the rate of spread has reached its asymptotic value, and therefore, it is constant. Then, at time  $t-a$ , the distance from the front was  $x+av$ ; and colonization rate at that time (which equals to the number of colonies of age  $a$  at present time) was equal to  $b(x+av)$ , where  $b(x)$  is the number of new colonies established annually at distance  $x$  from the population front, and  $v$  is the rate of spread. Then the average population density  $N(x,v)$  at distance  $x$  from the front of the infested zone is:

$$N(x,v) = \int_0^{\infty} b(x+av) \cdot n(a) \cdot da \quad (1)$$

where  $n(a)$  is the number of individuals in a colony of age  $a$ . The front of the infested zone is the point where the average population density reaches the carrying capacity,  $K$ :

$$N(0,v) = K. \quad (2)$$

Combining equations (1) and (2) we get a traveling wave equation:

$$\int_0^{\infty} b(av) \cdot n(a) \cdot da = K \quad (3)$$

This equation can be used for estimating the spread rate,  $v$ , if functions  $b(x)$  and  $n(a)$  are specified explicitly. The rate of colony establishment decreased linearly with the distance from the front of the infested zone (data supporting the linearity of this function is presented below). Thus,

$$b(x) = \max \left[ 0, c \cdot \left( 1 - \frac{x}{x_{\max}} \right) \right] \quad (4)$$

where  $x_{max}$  is the maximum distance at which colonies can become established (=width of the transition zone), and  $c = b(0)$  is the maximum rate of colony establishment in the area adjacent to the infested zone. We assume that the number of individuals in a colony,  $n(a)$ , grow exponentially with colony age  $a$ :

$$n(a) = n_0 \cdot \exp(ra) \quad (5)$$

where  $n_0$  is the initial number of individuals in a new colony, and  $r$  is the intrinsic rate of increase.

The traveling wave equation (3) combined with (4) and (5) yields the equation that can be used for estimating the maximum rate of population spread  $v = v_{max}$  (without barrier zones):

$$\frac{cn_0 V}{r^2} \cdot \left[ \exp\left(\frac{r}{V}\right) - \frac{r}{V} - 1 \right] = K \quad (6)$$

where variable  $V = v_{max}/x_{max}$  represents the rate of population spread,  $v_{max}$ , relative to the maximum distance at which isolated colonies can be established,  $x_{max}$ . Equation (6) includes this relative population spread rate,  $V$ , only, and thus, spread rate  $v_{max}$  is always proportional to  $x_{max}$ . Equation (6) cannot be solved analytically and thus, we used numerical methods to estimate  $V$ .

The relative population spread rate,  $V$ , increased with increasing values of  $cn_0/K$  (Fig. 6). The value of  $cn_0/K$  is the density of organisms in newly established colonies just beyond the front of the infested zone ( $cn_0$ ) relative to the total number of organisms at the front of the infested zone ( $K$ ). It quantifies the intensity of colonization process. We expect this value to be very small ( $<0.1$ ) in most dispersing populations because establishment of new colonies is a rare event and the initial number of individuals ( $n_0$ ) is usually small.

The relationship between relative spread rate,  $V$ , and the intrinsic rate of increase,  $r$ , is almost linear (Fig. 6) in contrast to the diffusion model of Skellam (1951) which predicts that spread rate is proportional to the square root of the intrinsic rate of increase. This means that the intrinsic rate of increase has a much stronger effect on population spread rate in our model than in diffusion-based models.

Now we will assume that a barrier zone starts at distance  $x_0$  from the front of the infested zone and extends to the end of the transition zone. The relative width of a barrier zone,  $W$ , is defined by its proportion of the width of the transition zone:

$$W = \frac{x_{max} - x_0}{x_{max}} \quad (7)$$

Eradication of all colonies in a barrier zone is equivalent to truncating the tail of the colonization function,  $b(x)$ , at  $x \geq x_0$  (Fig. 7). This truncated function can be used in the traveling wave equation (3) to estimate the rate of population spread,  $v$ , in the presence of a barrier zone. We will consider reduction of population spread rate due to the barrier zone as a fraction of the spread rate without barrier zone,  $v_{max}$ :

$$R = \frac{v - v_{max}}{v_{max}} \quad (8)$$

The relationship between the reduction in the rate of population spread,  $R$ , and the relative width of the barrier zone,  $W$ , was studied using the equation:

$$(1 - R + QW) \cdot \exp\left[\frac{Q(1 - W)}{1 - R}\right] + R - \exp(Q) = 0 \quad (9)$$

where  $Q = rx_{max}/v_{max}$ . Equation (9) was derived from 2 traveling wave equations (3) with non-truncated and truncated  $b(x)$  functions. Equation (9) cannot be solved analytically, and thus, we used numerical methods to estimate  $R$  as a function of  $W$  for different values of parameter  $Q$  (Fig. 8).

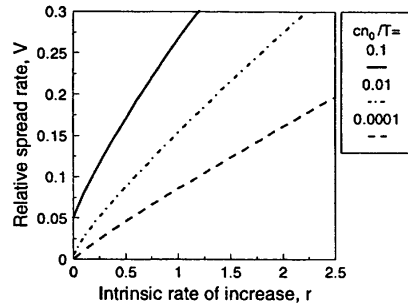


Fig. 6. Relative population spread rate ( $V = v_{\max}/x_{\max}$ ) predicted by the model as a function of intrinsic rate of increase,  $r$ , and parameter  $cn_0/T$ .

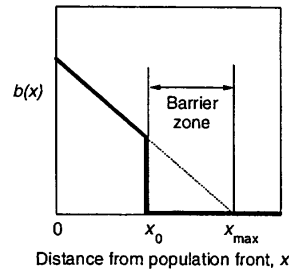


Fig. 7. The function of the probability of colony establishment,  $b(x)$ , becomes truncated beyond distance  $x_0$  from the front of the infested zone if a barrier zone is set in the area from  $x_0$  to  $x_{\max}$ .

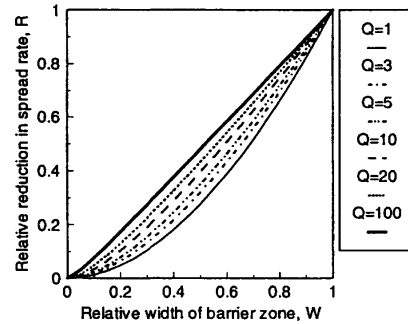


Fig. 8. Relative reduction in spread rate,  $R = (v_{\max} - v)/v_{\max}$ , predicted by the model.

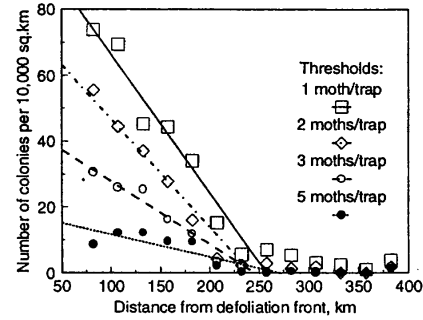


Fig. 9. Number of gypsy moth colonies detected at different distances from the front of the infested zone using 1, 2, 3, and 5 moths per trap as detection thresholds.

Parameter  $Q$  can be interpreted as follows. The ratio  $x_{\max}/v_{\max}$  equals the amount of time a location exists in the transition zone (without any population management). Then,  $Q$  is the net rate of increase,  $r$ , multiplied by time in the transition zone. Thus,  $\exp(Q)$  is the ratio of population numbers in a colony established at the front of the transition zone when it reaches the infested zone to the initial population numbers when it was established. Unless population numbers increase at least 3 times in isolated colonies in the transition zone, population spread will be continuous and dynamics would closely follow that of a simple diffusion. Thus, the value of  $Q$  should be  $\geq 1$ . The predicted efficiency of a barrier zone in slowing population spread increases with increasing values of parameter  $Q$  (Fig. 8). Thus, the higher is the intrinsic rate of increase,  $r$ , the greater is the percent reduction in the rate of population spread caused by a barrier zone.

Model parameters:  $c$ ,  $x_{\max}$ ,  $n_0$ ,  $r$ , and  $K$  were evaluated as follows. We considered defoliating populations as the major source of long-distance dispersal which leads to establishment of isolated colonies. Thus, the front of the defoliated area was considered as the front of the infested zone in our model. The maximum distance from the population front,  $x_{\max}$ , at which colonies can become established was estimated from male moth counts in grids of pheromone-baited traps in 1984 and in 1988-1995. In order to count isolated colonies, we selected traps that caught  $N$  or more moths and then grouped these traps if they were separated by less than 4 km (4 km was selected because it was larger than the maximum intertrap distance in most grids). These groups were counted in each year. Colonies may coalesce closer to the population front. Thus, we



restricted the counting of colonies to the area beyond the 1 moth per trap boundary. The number of detected colonies was divided by the area covered by pheromone traps that was estimated as the area of the 4-km buffer zone set around all traps used in the analysis. Data from all years were pooled together.

Previously we found that the boundary of 10 moths per trap is the most stable in space and time and therefore, it is most reliable for monitoring of population spread (Sharov et al. 1996b). The average distance from the 10 moth per trap boundary to the area where defoliation first occurs was  $\approx 80$  km. Thus, the distance from a colony to the defoliation front was estimated as the distance from the center of mass of a cluster of traps to the 10 moths per trap boundary plus 80 km.

Gypsy moth colonies detected using pheromone traps cannot be directly interpreted in the model because the majority of them disappear naturally over time, whereas colonies in the model grow continuously. However, we can assume that the number of colonies that will eventually become established is proportional to the number of detected colonies.

The number of colonies detected decreased almost linearly with increasing distance from the population front (Fig. 9). Lower thresholds,  $N$ , resulted in a larger number of colonies detected. However, the maximum distance from the defoliation front did not change considerably with male count threshold and was  $\approx 250$  km. Thus, we assume that  $x_{\max} = 250$  km.

We could not determine parameter  $c$  from Fig. 9 because we did not know what proportion of detected colonies would become established. Thus, we decided to rely on the number of eradicated colonies in the STS project area in VA and WV. The number of treatment blocks was 5, 12, and 7, and the project area was 12,443; 12,649; and 10,147 km<sup>2</sup> in 1993-95, respectively. This makes the rate of colony establishment in the STS area equal to 0.00068 per km<sup>2</sup>.

Parameter  $c$  equals the rate of colony establishment just beyond the front of the defoliation area. The average distance from the center of the STS project area in VA and WV to the boundary of 10 moths per trap was  $\approx 70$  km in 1993-95. Thus, the distance from the STS area to the defoliation front was  $\approx 150$  km. Assuming the linear function  $b(x)$  (eqn. 4), parameter  $c$  was estimated as  $0.00068 \cdot x_{\max} / (x_{\max} - 150) = 0.0017$ .

The initial population numbers  $n_0$  in isolated colonies was not known. We doubt that a colony may start from 1 egg mass because of the low mating probability (Sharov et al. 1995a). Our expectation of the average initial number of egg masses that may start a new colony is  $n_0 = 5$ .

The carrying capacity,  $K$ , was taken equal to 200,000 egg masses per 1 km<sup>2</sup> because we previously showed that the defoliation boundary (detected at  $\approx 30\%$  level) was mostly located between the boundaries of 10 and 30 egg masses per 0.01-ha plot (Sharov et al. 1995).

The intrinsic rate of population increase,  $r$ , can be estimated from egg mass counts. However, egg masses can be counted with acceptable accuracy only in moderate- or high-density populations. Thus, they could not be counted in isolated low-density colonies beyond the population front. Furthermore, we think that extrapolation of  $r$ -values from high- to low-density populations is dangerous because population dynamics at low densities may differ substantially from population dynamics at higher densities (Campbell & Sloan 1978, Elkinton & Liebhold 1990). Thus, we adjusted parameter  $r$  until the model gave a rate of population spread that matched rates observed in nature.

We assume that the initial rate of spread  $v_{\max} = 20.78$  km/yr at  $t = 0$  represents uncontrolled population spread. Parameter  $r = 1.706$  was estimated numerically using equation (6). This means that isolated populations increase their numbers  $\exp(r) = 5.51$  times per year.

Now we can substitute parameter values into eqn. (9) and estimate the effect of the STS barrier zone in VA and WV on the rate of gypsy moth spread. Currently, the barrier zone starts at a distance of  $\approx 100$  km from the defoliation front, and its width is also  $\approx 100$  km. The width of the transition zone is  $x_{\max} = 250$  km and thus, the distant portion (50-km band) is not covered by the barrier zone. However, isolated colonies are detected and eradicated even beyond the barrier zone by a different agency (USDA Animal and Plant Health Inspection Service). Thus, we can consider that the width of the barrier zone is 150 km. Then,  $W = 150/250 = 0.6$ . Parameter  $Q = r x_{\max} / v_{\max} = 1.706 \cdot 250 / 20.78 = 20.52$ . Substituting these values into equation (9), we predict relative reduction of population spread rate  $R = 0.543$  (54.3%).

The actual rate of gypsy moth spread in the central Appalachian Mountains has declined by 59%, which is close to that predicted by the model.

## DISCUSSION

Studies of biological invasions were always based on qualitative (presence-absence) data (Elton 1958, Hengeveld 1989). Extensive historical data on gypsy moth abundance gave us a unique opportunity to study the spread of this species at a quantitative level over a large area. We have developed new methods for analysis of the progression of population boundaries estimated at various thresholds: 6 thresholds of male moth counts in pheromone traps, 4 thresholds of egg mass counts, and defoliation. Our methods are based on estimation of population boundaries (Sharov et al. 1995), which are mathematical functions in a rotated coordinate system. This is a powerful quantitative method that can be used for documenting and predicting the rate of spread of any introduced exotic organisms.

The average locations of population boundaries estimated from various thresholds form a profile of the traveling wave of the spreading population (Fig. 2). The distance from the boundary of 1 moth per trap to defoliation was 108.5 km, and it took  $\approx 11$  yr for a population to build up until defoliation first happened. Log-transformed population numbers increased linearly in space (Fig. 2) which is the result of the exponential population growth. Male counts in pheromone traps are indirect measures of population numbers and they are not necessary proportional to the population density. Several factors may distort proportionality: moth dispersal, saturation of pheromone traps (Elkinton 1987), and competition between traps and natural females for male attraction. However, trap saturation becomes important only at high capture rates, and competition between traps and natural females was shown to be non-significant (Elkinton & Carde 1984). Thus, we think that moth counts in traps are more or less proportional to the density of males in the area, but the density of males does not necessarily correspond to the density of reproducing populations because of possible long-distance dispersal of male moths. Mark-recapture experiments were used to analyze short-range dispersal of male moths (Elkinton & Carde 1980), however long-distance dispersal requires additional studies.

The rate of spread of gypsy moth populations was reduced by 59% after 1990, the year when eradication of small isolated colonies has started beyond the expanding population front. The model of stratified dispersal suggests that eradication of isolated colonies may be the cause of the observed reduction in the rate of population spread.

However, we should be cautious in interpreting these data. First, the barrier zone strategy was implemented consistently only in the STS project that started in 1992. In the previous AIPM project, eradication of small isolated colonies was conducted simultaneously with intensive suppression of outbreak populations. Suppression activity may have also contributed to the reduction of gypsy moth spread rate in the area. Second, population spread rate exhibited considerable fluctuations in time (Fig. 3). Thus, the accuracy of estimated reduction in the spread rate of gypsy moth populations is not high.

It is interesting to compare our results with historical data on gypsy moth spread. A barrier zone was established in 1923 from Canada to Long Island along the Hudson River Valley to prevent the spread of gypsy moth to the west (McManus & McIntyre 1981). This zone was managed until 1941 when it finally became generally infested. Later in 1953-1958, another barrier zone was operated along the Adirondack Mountains and Allegheny plateau. These barrier zones did not stop the advance of population front, but spread rates were very low (2.82 km/yr) during that time as compared with the periods from 1900 to 1915 (9.45 km/yr) and from 1966 to 1990 (20.78 km/yr) (Liebhold et al. 1992). Despite of limitations of the method used by these authors to estimate the rates of population spread, results suggest that the barrier zone along the Hudson River may have significantly contributed to slowing gypsy moth spread.

## ACKNOWLEDGMENTS

We thank E. Anderson Roberts for providing access to data-base of gypsy moth counts, Shelby J. Fleischer and Frank C. Curriero for discussion of the manuscript. This research was funded by the Grant No. 95-37313-1892 from the USDA, Cooperative State Research, Education, and Extension Service.

## REFERENCES

- Campbell, R.W. & R.J. Sloan, 1978. Numerical bimodality among North American gypsy moth populations. *Environ. Entomol.* 7: 641-646.
- Deutsch, C.V. & A.G. Journel, 1992. *GSLIB. Geostatistical software library and user's guide*. Oxford University, Oxford.
- Elkinton, J.S., 1987. Changes in efficiency of the pheromone-baited milk-cartoon traps as it fills with male gypsy moths (Lepidoptera: Lymantriidae). *J. Econ. Entomol.* 80: 754-757.
- Elkinton, J.S. & R.T. Carde, 1980. Distribution, dispersal and apparent survival of male gypsy moths as determined by capture in pheromone-baited traps. *Environ. Entomol.* 9: 729-737.
- Elkinton, J.S. & R.T. Carde, 1984. Effect of laboratory-reared female gypsy moths, *Lymantria dispar* L. (Lepidoptera: Lymantriidae), on the capture of males in pheromone-baited traps. *Environ. Entomol.* 13: 1377-1385.
- Elkinton, J.S. & A.M. Liebhold, 1990. Population dynamics of gypsy moth in North America. *Annu. Rev. Entomol.* 35: 571-596.
- Elton, C.S., 1958. *The ecology of invasions by animals and plants*. London, Methuen.
- Fleischer, S.J., F. W. Ravlin & R.C. Reardon, 1991. Implementation of sequential sampling plans for gypsy moth (Lepidoptera: Lymantriidae) egg masses in eastern hardwood forests. *J. Econ. Entomol.* 84: 1100-1107.
- Gottschalk, K.W., 1993. *Silvicultural Guidelines for forest stands threatened by the gypsy moth*. USDA For. Serv. Gen. Tech. Rep. NE-171.
- Hastings, A., 1996. Models of spatial spread: is the theory complete? *Ecology* 77: 1675-1679.
- Hengeveld, R., 1989. *Dynamics of Biological Invasions*. Chapman & Hall, London, New York.
- 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. & 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*. USDA For. Serv. Gen. Tech. Rep. NE-213.
- Liebhold, A.M., J.A. Halverson & G.A. Elmes, 1992. Gypsy moth invasion in North America: a quantitative analysis. *J. of Biogeogr.* 19: 513-520.
- Liebhold, A., V. Mastro & P.W. Schaefer, 1989. Learning from the legacy of Leopold Trouvelot. *Bull. Entomol. Soc. Amer.* 35: 20- 21.
- Marsula, R. & C. Wissel, 1994. Insect pest control by a spatial barrier. *Ecol. Modell.* 75/76: 203-211.
- McFadden, M.W. & 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 & T.L. Payne, (eds.) *Forest insect guilds: Patterns of interaction with host trees* USDA For. Serv. Gen. Tech. Rep. NE-153.
- McKendrick, A.G., 1926. Applications of mathematics to medical problems. *Edinburgh Math. Soc. Proc.* 44: 98-130.
- McManus, M.L. & T. McIntyre, 1981. Introduction. Pp. 1-7. In: C.C. Doane & M.L. McManus (eds.) *The gypsy moth: Research toward integrated pest management*. USDA Tech. Bull. 1584.
- Ravlin, F.W., R.G. Bellinger & 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. and Manage.* 39: 107-112.
- Schwalbe, C.P., 1981. Disparlure baited traps for survey and detection. Pp. 542- 548. In: Doane, C.C. and M.L. McManus (eds.) *The gypsy moth: Research toward integrated pest management*. USDA Tech. Bull. 1584.
- Sharov A.A., E.A. Roberts, A.M. Liebhold & 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 & E.A. Roberts, 1996a. Gypsy moth (Lepidoptera: Lymantriidae) spread in the Central Appalachians: Comparison of population boundaries obtained from male moth capture, egg mass counts & defoliation records. *Environ. Entomol.* 25: 783-792.

- Sharov, A.A., A.M. Liebhold & E.A. Roberts, 1996b. Methods for monitoring the spread of gypsy moth (Lepidoptera: Lymantriidae) populations in North America. *J. Econ. Entomol.* (in press).
- Shigesada, N., K. Kawasaki & Y. Takeda, 1995. Modeling stratified diffusion in biological invasions. *Amer. Natur.* 146: 229-251.
- Skellam, J.G., 1951. Random dispersal in theoretical populations. *Biometrika* 38: 196-218
- Snyder, J.P., 1987. *Map projections-a working manual*. U.S. Geol. Surv. Prof. Pap. 1395.
- 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*. USDA Tech. Bull. 1584.