

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

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ABSTRACT Since its introduction near Boston in 1869, the gypsy moth, *Lymantria dispar* (L.), has spread over 1,000 km to the southwest. To measure its current rate of spread through the central Appalachian Mountains we estimated population boundaries, which are lines that separate areas with population densities generally above and below a specific threshold. Population boundaries were estimated in northwestern Virginia and southeastern West Virginia using male moth counts (1988–1994), egg mass counts (1988–1991), and defoliation maps (1988–1994). The boundary of 1 moth per trap was on average 110 km from the boundary of defoliation, and the male moth capture rate increased 10 times per 29 km perpendicular to the population front. Approximately 11 yr separated the time when traps caught 1 moth per trap until defoliation first occurred in the same area. The rates of gypsy moth spread estimated using different census methods and from different population thresholds changed almost synchronously from year to year. Only spread rates estimated from defoliation data had a different temporal pattern. Gypsy moth spread rate declined from 1988 to 1994 by 35%, as measured from time series of spread rates and boundary compression (reduction of the distance between adjacent boundaries). Reduction in gypsy moth spread rate may have been the result of intensive population management in the area.

KEY WORDS *Lymantria dispar*, biological invasions, spread rates

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 to the west and south (Liebhold et al. 1992). Accurate prediction of gypsy moth spread is important for proper timing of silvicultural measures that can reduce the adverse impacts of gypsy moth defoliation (Gottschalk 1989), planning sampling programs in areas at risk to defoliation, planning for areas that require quarantine regulation, and for planning barrier zone programs aimed at slowing the spread of gypsy moth (McFadden and McManus 1991).

In 1993 the USDA Forest Service initiated the Slow-the-Spread (STS) program to determine the feasibility of using integrated pest management (IPM) strategies to slow the spread of gypsy moth over large geographical areas (Leonard and Sharov 1995). The following 3 project areas have been established immediately ahead of the advancing front of gypsy moth populations: (1) in the upper peninsula of Michigan, (2) in the Appalachian Mountains in Virginia and West Virginia, and (3) in northeastern North Carolina. The project strat-

egy is to detect and manage isolated gypsy moth colonies located just beyond the expanding front of gypsy moth populations. Management of newly established low-level infestations can prevent their growth, coalescence, and subsequent contribution to gypsy moth spread. The previous Appalachian Integrated Pest Management (AIPM) program (1988–1992) conducted in Virginia and West Virginia was targeted both at high- and low-density populations. Reduction of gypsy moth spread rate was one of the AIPM objectives adopted by STS. However, STS is designed to slow gypsy moth spread with lower pesticide use and management costs as used in the AIPM project. To evaluate the effect of these projects on the rate of population spread it is important to monitor population spread rates.

We have developed methods for estimating population boundaries, which are the lines that separate the areas where population densities were generally above and below a specific threshold (Sharov et al. 1995). These methods can be used to assess annual gypsy moth spread rates and to detect trends in their change over time.

Gypsy moth populations are mainly monitored using any of 3 methods: (1) aerial maps of forest

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defoliation, (2) counts of overwintering egg masses (Kolodny-Hirsch 1986), and (3) counts of male moths in pheromone-baited traps (Talerico 1981, Ravlin et al. 1987). Defoliation records have a limited value for monitoring gypsy moth spread because they represent only high-density populations that occur in regions with highly susceptible forest types (Liebhold et al. 1994). Egg mass counts are the most reliable method for assessing densities of moderate- and high-density populations and thus they are widely used for making decisions concerning suppression of outbreak populations (Ravlin et al. 1987). Pheromone traps are widely used to detect low-density gypsy moth infestations because they can detect male moths long before other life stages can be found using conventional sampling methods (Schwalbe 1981).

In areas infested by gypsy moth for many years, there is little or no relationship between male moth counts and subsequent defoliation at the same location (Carter et al. 1992, Liebhold et al. 1995). However, in the area along the expanding gypsy moth front, the relationship among male moth counts, egg mass density, and defoliation may be quite different because of the strong population density gradient (Ravlin et al. 1991). Thus, it may be possible to use male moth counts for predicting gypsy moth spread.

The objective of this study was to compare gypsy moth population boundaries estimated from 3 different population measurements: male moth counts, egg mass counts, and defoliation records. The following 4 major questions are addressed here: (1) How long does it take leading-edge populations to reach a specific density level and to cause defoliation? Knowledge of the expected time from 1st detection until initiation of defoliation would be useful for selecting the best silvicultural strategy for specific stands. (2) What distance separates population boundaries derived from various density levels? Many regions where gypsy moth is spreading are not sampled. Knowledge of the distance between population boundaries would allow prediction of the location of unknown boundaries. For example, the boundary of 1,000 egg masses per hectare could be predicted from the boundary of 100 moths per trap. (3) Do population spread rates measured from different population thresholds change synchronously from year to year? If this hypothesis is true, it would allow extrapolation of spread rate dynamics estimated from one population threshold to those derived from other population thresholds. (4) Have gypsy moth spread rates changed over the past 7 yr? If spread rates have reduced, this reduction may be the result of pest management activity in the AIPM and STS projects.

Materials and Methods

Area and Data. We used historical pheromone trap data (1988–1994), egg mass count data (1988–

1991), and aerial sketch maps of defoliation (1988–1994) collected in the Appalachian Mountains in northern Virginia and Southern West Virginia. Most data were collected as part of the USDA Forest Service AIPM and STS programs (Reardon 1991, Leonard and Sharov 1995).

Complete details of male moth trapping and egg mass surveys were described by Sharov et al. (1995). Defoliation was recorded using high altitude optical bar photography (Ciesla and Acciavatti 1982) that was collected at the approximate peak period of defoliation. The threshold for detecting defoliation using this method was $\approx 30\%$. Defoliation polygons were digitized in vector format and then converted to a 1×1 km raster grid; a cell was considered defoliated if at least some portion of it was defoliated.

Boundary Estimation. A best cell classification method (Sharov et al. 1995) was used to estimate regular population boundaries. A regular boundary is a mathematical function in a rotated Cartesian coordinate system with the x-axis oriented along the general boundary direction that is selected before analysis. Earlier we used an iterative procedure to fit the general boundary direction to the boundaries of male moth counts in the same area (Sharov et al. 1995). The fitted general boundary azimuth was equal to 147.5° . Boundary analysis is not sensitive to small changes in the general boundary direction, and thus, we used the azimuth of 147.5° as a general boundary for all boundaries estimated in this study.

The area was partitioned into strips (1 km wide and ≈ 200 km long) perpendicular to the general boundary direction. The boundary point was estimated in each strip, and then these points were connected across the strips to form a boundary line. The boundary point was located where the number of 1-km grid cells that were misclassified below or above a population threshold was minimal. Boundary points were averaged in nonoverlapping blocks of 5 adjacent strips each. We used the following thresholds: 1, 3, 10, 30, 100, and 300 moths per trap; 1, 3, 10, and 30 egg masses per 0.01 ha. Indicator maps of male moth counts and egg mass density were generated using indicator median kriging as described in Sharov et al. (1995). Defoliation maps did not require kriging because the presence of defoliation was already coded for all cells in the map.

This method of boundary estimation can be adjusted by using different weights for cell misclassifications of the 1st and 2nd type. The 1st type of misclassification occurred when population levels were above the threshold but were classified as below the threshold; the 2nd type occurred when the population was below the threshold but was classified as above the threshold. Two criteria were used to select appropriate weights: the number of boundary points (=number of strips in which boundary points could be estimated using each population threshold) should be large, and the av-

erage variance of estimated boundary points should be small. Using these criteria, the following relative weights for cell misclassifications of the 1st and 2nd type were selected: 1:1 for male moths, 3:1 for egg masses, and 30:1 for defoliation.

Distribution of Boundary Points. Each boundary was represented as a set of boundary points in a Cartesian coordinate system that was rotated so that the general boundary ran horizontal. Cumulative distributions of Y coordinates of boundary points were estimated and plotted for all population thresholds and all years.

Distance Between Boundaries. The distance between 2 boundaries was estimated at each X coordinate point and then averaged for all points where both boundaries had nonmissing Y values. Population spread rate in year t was measured as the distance between boundaries in years t and $t-1$. We used a general linear model to determine if population thresholds significantly affected temporal patterns of spread rates. A 2-dimensional array of average spread rates $v_{t,i}$ in year t for population threshold i was analyzed. Each population threshold was compared with the other population thresholds combined. We substituted population threshold i by an auxiliary factor $G_j(i)$ defined as: $G_j(i) = 1$ if $j = i$, and $G_j(i) = 0$ if $j \neq i$, and then analyzed its effect on spread rate together with time T as a 2nd factor. The pattern of spread rate change at threshold j was considered different from patterns of spread rate change at other thresholds if the effect of either G_j or $T \times G_j$ was significant. Egg mass thresholds were not compared with other thresholds because time series of egg mass spread rates were too short (3 yr).

The average distance between population boundaries derived from different population thresholds was estimated as the difference between means generated by the general linear model with 2 factors: year and population threshold. Direct averaging was not possible because egg mass boundaries were not available for 1992–1994. The general linear model was selected because it accepted missing data and estimated corrected means.

Spread Rate Change in Time. Two criteria were used for detecting the spread rate change. The direct criterion was the regression slope of average spread rates versus time. First, we determined if spread rates estimated from male moth counts and egg mass counts could be legitimately combined. We used a general linear model to compare spread rates with the following 2 factors: (1) time (1989–1991) and (2) census method (male moth counts versus egg mass counts). Because spread rates depended on neither census method nor its interaction with time, we combined spread rates for all male moth thresholds and egg mass thresholds to evaluate whether they changed with time. Spread rates estimated from defoliation areas were not used in this analysis because they changed in a significantly different pattern than

spread rates estimated from male moth captures and egg mass counts.

The indirect criterion for detecting change in spread rate was boundary compression (the reduction of the distance between low- and high-density population boundaries). A simple model can be used to illustrate that boundary compression can be caused by reduction in population spread rate. We assumed that the proportion of migrants in any gypsy moth population was low, and thus, population densities increased mainly due to reproduction of residents. Gypsy moth populations spread mainly because of inadvertent transportation of egg masses by humans (McFadden and McManus 1991). Only a small proportion of egg masses are transported, and thus our assumption is relevant. Our model differs from the model of Skellam (1951), which assumes all individuals to disperse at the same rate represented by a diffusion coefficient.

Another assumption is that there is no gradient in average habitat quality in the direction of population spread. This assumption is important because otherwise population spread will be nonstationary. According to the map depicted by Gansner et al. (1993), there are no visible changes in forest susceptibility to gypsy moth in the study area in the direction of population spread (from northeast to southwest). Thus, this assumption is true for the study area.

Consider 2 population thresholds expressed as logarithms of population density: $x_0 = \ln(N_0)$ and $x_1 = \ln(N_1)$, $x_1 > x_0$. Boundary locations corresponding to these thresholds in year t are: $B_{t,0}$ and $B_{t,1}$. If population growth is exponential with rate r , then it takes $n = (x_1 - x_0)/r$ years for the population to grow from density x_0 to x_1 . As a result, $B_{t+n,1} = B_{t,0}$. The rate of spread, v , can be measured as:

$$v = (B_{t+n,1} - B_{t,1})/n \\ = r(B_{t,0} - B_{t,1})/(x_1 - x_0). \quad (1)$$

Boundary compression is the condition where the distance between boundaries ($B_{t,0} - B_{t,1}$) declines with time. The denominator ($x_1 - x_0$) in (1) is a constant. Thus, unless r has increased, boundary compression should be associated with the reduction in population spread rate. It is more likely that population growth rate would decrease rather than increase as a result of intensive pest management during the last 7 yr (AIPM and STS projects). Thus, boundary compression should be associated with spread rate reduction.

Other factors, e.g., weather or natural enemies can affect the value of r in individual years, however it is not likely that they will cause a significant trend in r -values over the entire 7-yr study period. If r -value fluctuates but shows no steady increase or steady decline in time, then, according to (1), boundary compression should be associated with the change of population spread rate.

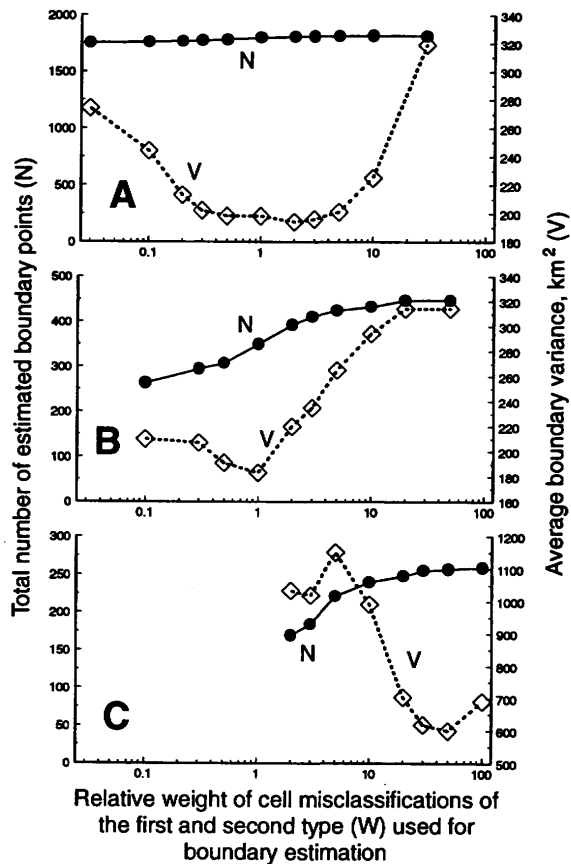


Fig. 1. Number, N , of boundary points estimated, and the average variance, V , of boundaries of male moths (A), egg masses (B), and defoliation (C) and their relation to the relative weight, W , for cell misclassifications of the 1st and 2nd type.

To test for boundary compression, we estimated the average distance between all pairs of adjacent population boundaries (e.g., 1 and 3 moths per trap, 3 and 10 moths per trap) for all years. On a log scale, the difference between 1 and 3 moths per trap is nearly the same as between 3 and 10 moths per trap. Thus, we combined the data for all pairs of male moth thresholds and estimated the regression of interboundary distance versus time. Egg mass data were not used in this analysis because the distance between egg mass boundaries was much shorter than between male moth boundaries, and therefore, interboundary distances were not comparable.

Simple Model of Population Spread. A simple model of gypsy moth population spread was de-

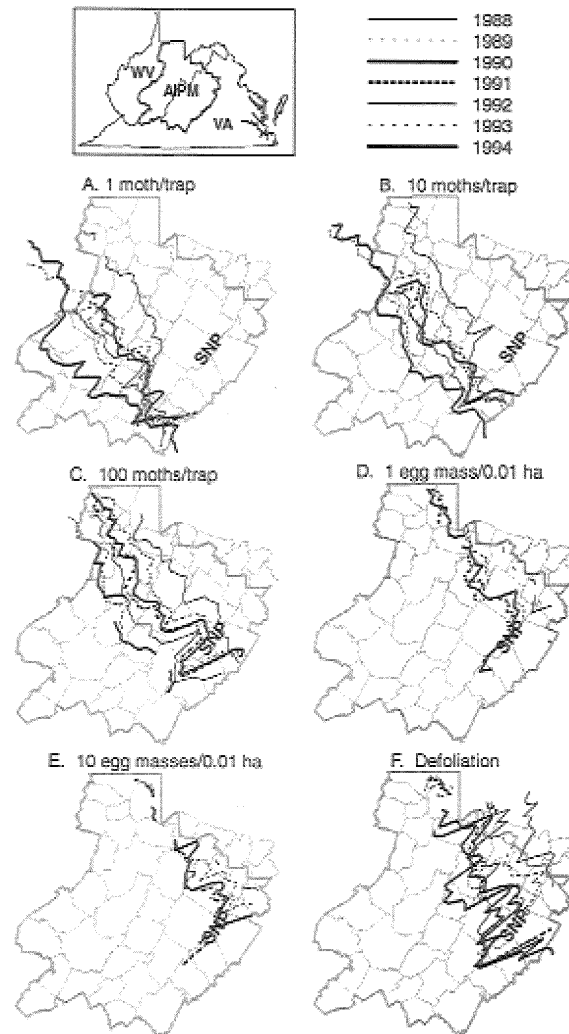


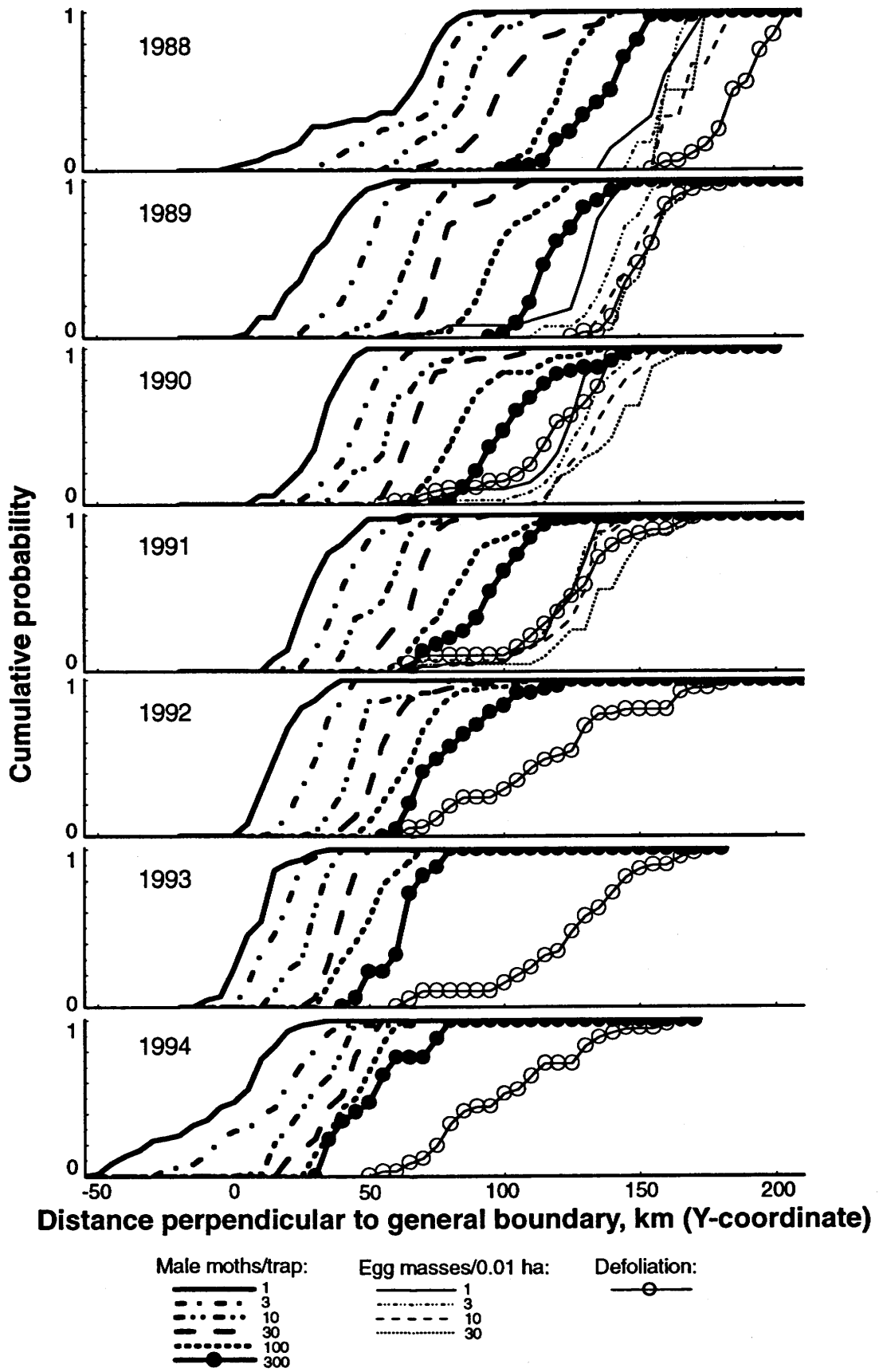
Fig. 2. Population boundaries of male moths (A–C), egg masses (D and E) and defoliation (F) in the Appalachian Integrated Pest Management (AIPM) area in 1988–1994 (egg mass boundaries were estimated in 1988–1991 only). The mountain ridge (Blue Ridge Mountains) along the Shenandoah National Park (SNP) caused the deformation of several population boundaries.

rived from average distances between boundaries. The model was based on the assumption that population spread rate is constant and does not depend on the population threshold used for boundary estimation:

$$B'_{t+\Delta t, j} = B_{t, i} + D_{t, j} + v \cdot \Delta t \quad (2)$$

where $B'_{t+\Delta t, j}$ is the predicted boundary location

Fig. 3. Distribution of gypsy moth population boundaries in the Central Appalachians in 1988–1994 estimated using different population thresholds. Boundaries were considered in the rotated coordinate system with the x-axis oriented along the general boundary direction (azimuth = 147.5°). The origin of this coordinate system was selected arbitrarily. Each curve in these graphs shows the proportion of boundary points that have Y coordinate less than the specified value.



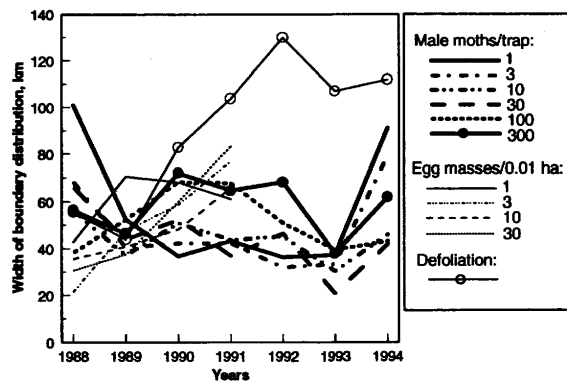


Fig. 4. Width of population boundary distributions estimated as a 95% CI for individual points ($2 \cdot 1.96 \cdot SD$).

(Y coordinate) in year $t + \Delta t$ for population threshold j , $B_{t,i}$ is the actual location of population boundary in year t for threshold i , $D_{i,j}$ is the average distance between boundaries for thresholds i and j in the same year, and v is the rate of population spread. The rate of spread, v , is positive if spread direction coincides with the boundary Y coordinate, and is negative for the opposite direction of population spread.

The accuracy of the model was tested separately for boundary averages and for local boundary points. Boundaries were predicted using (2) for the current year and future years ($\Delta t \geq 0$); if $\Delta t = 0$, then the predicted boundary always corresponded to a higher population threshold ($j > i$). In this way, each pair of boundaries was used only once. Defoliation boundaries were excluded from the analysis because the pattern of defoliation spread was different from the spread of male moths and egg masses.

Results

Population Boundaries. The total number of boundary points (N) estimated from male counts for all thresholds and all years did not depend on relative weights of cell misclassifications (W) of the 1st and 2nd type (Fig. 1A); the uniform grid of pheromone traps resulted in successful estimation of boundaries at nearly every location. Average boundary variance (V) was low in the interval of relative weights from 0.2 to 5. We selected the relative weight of $W = 1.0$, which was in the approximate center of this interval (log scale).

The total number of boundary points estimated from egg mass counts was relatively low when we used a relative weight of $W = 1.0$ (Fig. 1B). Thus, we selected a higher value of $W = 3.0$, despite a slightly higher variance at $W = 3.0$ than at $W = 1.0$. Additional boundary points estimated using $W = 3.0$ were located mainly in the Shenandoah National Park (SNP) further to the southwest than other boundary points (Fig. 2), and thus, they increased the variance. This high variance reflects

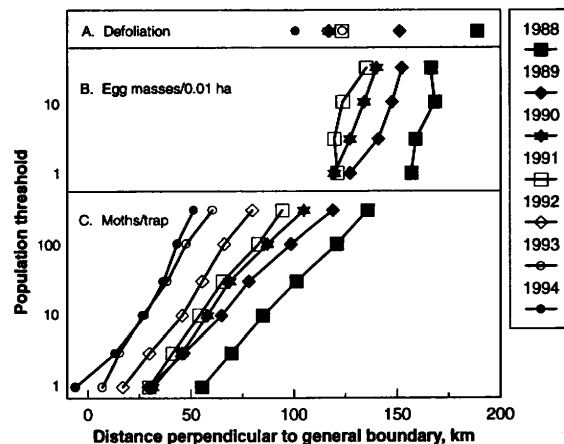


Fig. 5. Average gypsy moth population boundaries of defoliation (A), egg masses (B), and male moths (C) (Y coordinates averaged along the boundary) in different years and for different population thresholds.

the high natural variability of egg mass boundaries, rather than any flaw of the method. The total number of boundary points estimated from defoliation records stopped increasing with increasing relative weight at $W = 10$ (Fig. 1C). However, the average boundary variance reached a minimum at higher values of W (from 30 to 50). We selected the value of $W = 30$.

Population boundaries estimated using selected relative weights (W) are shown in Fig. 2.

Distribution of Boundary Points. Cumulative probability distributions of population boundaries in 1988–1994 are shown in Fig. 3. Egg mass boundary distributions often had a long tail to the left (Fig. 3). This tail corresponded to gypsy moth infestations in the SNP, which happened to be further to the southwest than infestations in other areas (Fig. 2). Boundaries for male moths and egg masses generally did not overlap (Fig. 3). The boundary for 1 egg mass per 0.01 ha was mostly located to the northeast of the boundary for 300 moths per trap. Defoliation boundaries were most closely associated with the boundary of 30 egg masses per 0.01 ha in the fall of the same year (Fig. 3).

The majority of distributions were similar: they were S-shaped and had a width (95% CI for individual points) of ≈ 40 – 50 km (Fig. 4). In 1988 and 1994 the distribution of 1 moth per trap boundary was wider (≈ 90 – 100 km) than usual. Distributions of defoliation boundaries were very wide in 1991–1993 (>100 km). This was probably related to general decline in gypsy moth density in these years.

Distance Between Boundaries. The distances between average boundaries estimated using different population thresholds generally remained the same from year to year (Fig. 5). In 1991, the boundaries for 1 and 3 egg masses per 0.01 ha were in inverse order. This resulted from averaging the boundaries that had missing values located in

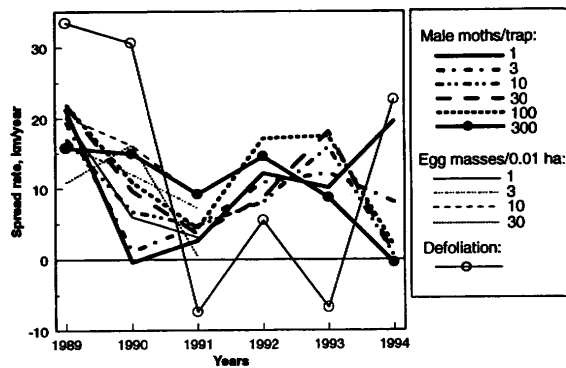


Fig. 6. Average gypsy moth spread rates (averaged along the boundary) in different years and for different population thresholds.

different regions. One order of magnitude increase in male moth counts occurred over a distance of ≈ 29 km perpendicular to the general boundary direction. Egg mass boundaries were much closer to each other than male moth boundaries (Figs. 3 and 5). The defoliation boundary moved less regularly between years when compared with male moth and egg mass boundaries (Fig. 5).

Gypsy moth spread rates measured using different population thresholds generally followed the same temporal pattern: maximum spread rate occurred in 1989, declined and then increased again in 1992–1993 (Fig. 6). The average spread rate estimated from all male moth thresholds was 10.4 km/yr.

Comparison of spread rate dynamics obtained using different population thresholds showed that the effect of the auxiliary factor G_j (used to separate threshold j from other thresholds) alone was never significant. This means that the average spread rate measured using any specific population threshold was not different from the average spread rate measured using all other thresholds. Thus, only the interaction of time T with G_j is shown in Table 1. Spread rates of defoliation changed in a significantly different pattern than spread rates measured using male moth data ($F = 12.31$). When male moth data were analyzed alone (with defoliation data excluded), spread rates estimated using 1 moth per trap had a significantly different temporal pattern as compared to other thresholds ($F' = 5.11$). No other significant differences were detected.

Spread Rate Change in Time. The general linear model showed that spread rates measured using male moth counts were not significantly different from spread rates measured using egg mass counts. The effect of census method was characterized by $F = 0.34$ ($df = 1, 24; P = 0.57$) and the interaction of census method with time was characterized by $F = 2.40$ ($df = 2, 24; P = 0.112$). Because of the lack of significant differences, we combined spread rates estimated from male moth counts and egg mass counts.

Table 1. Consistency of population spread rate dynamics estimated from different population thresholds

Population threshold	F	F'
1 moth per trap	1.35	5.11**
3 moths per trap	0.40	0.70
10 moths per trap	0.40	0.30
30 moths per trap	0.50	0.62
100 moths per trap	0.46	0.48
300 moths per trap	0.61	1.25
Defoliation	12.31***	Not used

F and F' are F statistics for interaction of time T with auxiliary factor G_j , which separates population threshold j from other thresholds, in a general linear model analysis of gypsy moth spread rates. F was estimated using all population thresholds ($df = 5, 42$), whereas F' was estimated using all thresholds except defoliation ($df = 5, 36$). Significant interaction (**, $P < 0.01$; ***, $P < 0.001$) indicates that spread rate dynamics at population threshold j differs significantly from the spread rate change estimated from the other population thresholds combined.

A regression equation of gypsy moth spread rates versus time was $v = 13.9 - 1.5t$, where t is time measured since 1989. The regression slope was significant ($P < 0.01$), and the correlation between spread rate and time was $r = -0.375$.

The regression equation of the distance between adjacent gypsy moth boundaries estimated using male moth thresholds versus time was: $\Delta B = 17.55 - 1.01t$, where t is time (years) measured since 1988 (Fig. 7). The regression slope was significant ($P < 0.001$), and the correlation between ΔB and t ($r = -0.533$) was stronger than between v and t . Assuming a 1.01 km annual compression of adjacent boundaries, we can expect that in 6 yr (from 1988 to 1994) the distance between boundaries was reduced by 6.06 km, that is by 35% (95% CI = 17–53%). According to model (1), this reduction of inter-boundary distance indicates a proportional reduction in population spread rate from 1988 to 1994.

Simple Model of Population Spread. 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

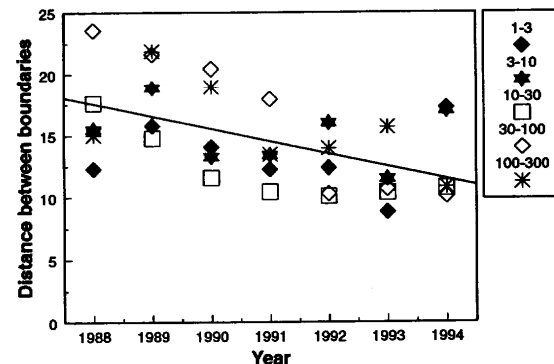


Fig. 7. Regression of distances between adjacent male moth boundaries, ΔB , versus time t measured since 1988 ($\Delta B = 17.55 - 1.01t$). Data points represent different population thresholds for male moths per trap.

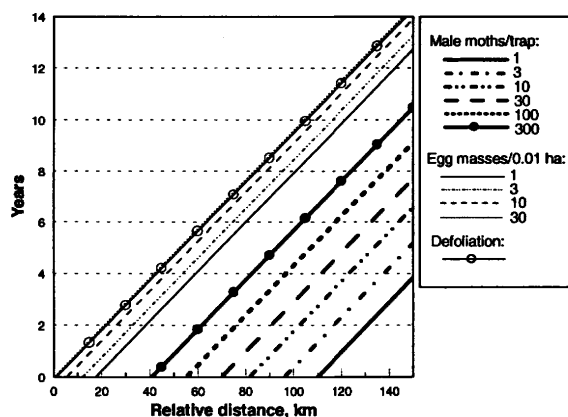


Fig. 8. A nomogram for predicting gypsy moth spread in space and time. Horizontal distance between the lines is equal to the distance between boundaries estimated using different population thresholds. Vertical distance between the lines shows the number of years it takes for the population to grow from one threshold to another. This nomogram assumes a constant rate of population spread of 10.4 km/yr.

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. These distances together with the average estimated population spread rate (10.4 km/yr) were used to predict population boundaries in space and time (equation 2).

Prediction of population boundaries can be simplified using a nomogram (Fig. 8) derived from equation 2. The starting point is the bottom of the nomogram where the line corresponding to the current population level crosses the horizontal line: year = 0. From this point it is possible to move upward (in time) or horizontally (in space). If we move upward and cross the line for population threshold i , then the vertical distance to the intersection corresponds to the number of years left until the population will reach threshold i . In the same way, moving to the right and left, it is possible to predict the distance separating the population boundaries for each threshold, i .

The error of average population boundaries predicted using the nomogram (standard deviations of predicted values from actual values) was 8.1 km. The error of predicted time intervals was $8.1/10.4 = 0.8$ yr, where 10.4 km/yr is the average population spread rate. The error of predicted local boundary points was 20.1 km. The corresponding error in time was $20.1/10.4 = 1.9$ yr.

Discussion

The region in the Central Appalachians used in this study is dominated by mountain ridges and valleys running from southwest to northeast. Another feature that is characteristic to that region is the intensive management of gypsy moth populations that has occurred from 1989 to present (Anonymous 1993, Leonard and Sharov 1995). In

many adjacent areas to the southeast and to the northwest, the terrain is different and the intensity of pest management activities has been lower, and thus the results from this research should not be automatically extrapolated to these areas. However, our methodology is readily applicable to other areas and even to other introduced pest species.

Our methods are based on estimation of regular population boundaries (Sharov et al. 1995), which are mathematical functions in a rotated coordinate system. All methods for analysis of mathematical functions can be applied to regular population boundaries. Thus, estimation of regular boundaries is a powerful quantitative method that can be used for documenting and predicting the rate of spread of introduced exotic organisms.

Distribution of Boundary Points. The extensive variation in local boundary points (Fig. 4) is probably related to the variation in habitat quality for the gypsy moths. In favorable habitats, populations may advance further than in less favorable habitats.

Boundaries estimated from male moth counts and egg mass counts generally did not overlap. The median of the boundary for 300 moths per trap was always much further to the southwest than the median of 1 egg mass per 0.01 ha (Fig. 3). Thus, egg mass densities became detectable (>1 egg mass per 0.01 ha) only in the area where pheromone trap catches were so high that the traps became partially or completely saturated (Elkinton 1987).

Detectable defoliation ($>30\%$) is usually expected in the area with >20 – 30 egg masses per 0.01 ha in the previous year (Gansner et al. 1985, Liebhold et al. 1993). Defoliation boundaries obtained in this study are most close to the boundary of 3 egg masses per 0.01 ha in the previous year (Figs. 3 and 5). This difference may partially be the result of different weights (W) of grid cell misclassifications used for estimating boundaries of egg mass populations and defoliation areas.

Distance Between Boundaries. Gypsy moth spread rates derived from different population thresholds generally followed the same temporal pattern, except for defoliation spread rates. This suggests that the changes in population spread rates measured at low population thresholds are nearly the same as changes in spread rates at high population thresholds. Male moth spread rates could probably be extrapolated to predict the spread rates of egg mass populations, however the time series of egg mass spread rates available during this period was too short (3 yr) to make a meaningful comparison.

Synchronous changes in spread rates estimated using different population thresholds can be explained using our model (equation 1). In this model, spread rate, v , is proportional to the rate of population growth r . It is reasonable to assume that growth rates of populations at various densities (except very high densities at which defoliation

occurs) are affected in a similar way by some global external factor, e.g., weather (Miller et al. 1989, Williams and Liebhold 1995). This may result in synchronous changes in spread rate.

Rates of spread of defoliation were significantly different from rates estimated from counts of gypsy moth males and egg masses. Dynamics of defoliation are apparently driven by processes different than those that determine population spread. Possibly, this is because defoliating populations are affected by a different set of factors than populations with lower densities (Campbell 1981). For example, viral epizootics usually do not occur in low-density populations (Doane 1970) and, therefore, would have no effect on spread rates measured using low-density thresholds. However, they often occur in defoliating populations and may affect the boundaries of defoliated areas. Defoliation boundaries are probably not reliable for the analysis of population spread over short intervals.

Spread Rate Change in Time. Regression analysis of gypsy moth spread rates and interboundary distances indicated a reduction of population spread rates in the Central Appalachians from 1988 to 1994. Statistical tests (correlation and error probability) showed that boundary compression criterion was a more precise indicator of population spread rate reduction than direct regression of spread rates versus time. This can be explained by equation 1, where spread rate v is proportional to population growth rate r , which may fluctuate considerably from year to year. The distance between neighboring boundaries does not depend on r , and therefore, it is more stable.

The reduction of gypsy moth spread rate might be explained by intensive pest management activities that occurred as part of the AIPM and STS programs in 1989–1994. Several hundred thousand hectare were sprayed with pesticides during this period (Anonymous 1993). Suppression of defoliating populations probably had a minor effect on gypsy moth spread rates because many high-density populations that were not treated may have become a source for inadvertent transport of egg masses from infested to uninfested areas. A more extensive reduction of spread rate would be expected from eradication (or suppression) of low-density populations just ahead of the moving population front. Three low-density populations (beyond the boundary of 100 moth per trap) were treated in 1990. From 1991 to 1994, the number of treated low-density populations was 11, 13, 5, and 9, respectively.

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 and 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 Alle-

gheny 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). These spread rates were calculated from the change in regulated area as determined by the USDA federal quarantine. There is not adequate data from that period to estimate population boundaries. Nevertheless, spread rate estimates obtained by Liebhold et al. (1992) suggest the barrier zone may have significantly contributed to slowing gypsy moth spread.

Simple Model of Population Spread. The nomogram (Fig. 8) can be considered the most simple model for predicting gypsy moth population spread. It can be used for planning preventive management activities designed to reduce or delay the impact of gypsy moth in newly infested areas and can predict the estimated number of years until defoliation can first be expected to occur in the area. It is based on empirical analysis of population progression and it does not consider any local factors, e.g., elevation. Also, it does not account for possible trends in spread rate over time. Because of its simplicity, it has large errors in predicting local population changes, however, it gives reasonable precision when analyzing average population boundaries. Average boundaries were predicted with 8-km error, which seems reasonable for planning silvicultural measures, sampling programs, and quarantine areas. This model can be considered a starting point for developing more sophisticated models. Subsequent models should be compared with this model to see if they provide any gains in accuracy.

The nomogram is specific to the studied area and time period. In other regions or in other years, population spread as well as the distance between boundaries may vary. However, the nomogram can be adjusted for other regions if historical information on the movement of population boundaries is available. Population spread rate may change significantly over time (Liebhold et al. 1992). These changes can be attributed to the pest management policy of individual states, quarantine regulations, or to the advance of the population front into areas with different forest type, climate and other factors.

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