Optimizing the Use of Barrier Zones to Slow the Spread of Gypsy Moth (Lepidoptera: Lymantriidae) in North America

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ABSTRACT Slowing the expansion of the range of the gypsy moth, *Lymantria dispar* (L.), in North America will reduce the area affected by gypsy moth populations in the future and hence may be economically justified. The rate of range expansion can be reduced by eradication of isolated gypsy moth infestations in a barrier zone that is located just beyond the expanding population front and is slowly shifted in the direction of population spread. We developed a model to optimize the allocation of resources for monitoring and treatment of isolated colonies in a barrier zone. Model parameters were estimated using data collected in the central Appalachian Mountains. The model predicted that the cost of slowing population spread is minimized when the density of pheromone traps and eradication activity within the barrier zone decrease with increasing distance from the population front. Sensitivity analysis indicated that the output was most sensitive to the change of the maximum distance from the population front at which colonies can become established. The present value of predicted costs of all monitoring and treatment in the barrier zone were <1/4 the present value of expected benefits from slowing the spread of the gypsy moth over 25 yr.

KEY WORDS *Lymantria dispar*, biological invasion, barrier zone, optimization, model

THE DOMINANT PARADIGM of pest management during the last 30 yr has been integrated pest management (IPM), which was formulated as a strategy to maintain local pest populations below economic injury levels (Stern et al. 1959). Traditional IPM is a local strategy; it typically has local short-term objectives which are achieved by local intervention measures. Area-wide pest management is a different strategy that considers the large-scale spatial distribution of pest species (Conway 1984). This strategy implies more than just extending local strategies to large areas. Area-wide pest management has long-term objectives, and intervention strategies are planned and implemented on a regional scale. It may include introduction of exotic natural enemies, quarantine, eradication of pest species, barrier zones, or landscape management. Recent examples of area-wide pest management are attempts to eradicate the boll weevil in the United States (Ahouissoussi et al. 1993) and regional control of grasshoppers (Berry et al. 1991). In this article, we describe another area-wide project: slowing the spread of the gypsy moth, *Lymantria dispar* (L.), with a barrier zone.

Gypsy moth was introduced to North America in 1869 near Boston (Liebhold et al. 1989) and is currently distributed throughout most of the northeastern United States, including most of the area of Michigan, West Virginia, and Virginia, and small portions of Wisconsin, Ohio, and North Carolina. The historical rate of population spread in North America ranged from 2.82 to 20.78 km/yr (Liebhold et al. 1992). Both local and area-wide pest management strategies have been used against the gypsy moth (Doane and McManus 1981). The primary strategy of local gypsy moth management is suppression of outbreak populations using aerial application of insecticides. This strategy usually is successful in preventing defoliation and nuisance impacts but it often does not result in substantial decreases in egg mass populations compared with untreated areas (Liebhold et al. 1996). Among area-wide pest management strategies implemented against gypsy moth, there have been several attempts to either eradicate all North American populations or to stop population spread (McManus and McIntyre 1981). However these programs did not result in eradication of the entire population. Neither eradication from North America nor stopping the spread of the gypsy moth is possible because of biological, economic, and environmental constraints. A more realistic strategy is to slow the rate at which gypsy moth populations are spreading to the south and west (McFadden and McManus 1991, Leonard and Sharov 1995). Slowing population spread may result in a decrease in the area affected by the gypsy moth in the near future. Leuschner et al. (1996) showed that the benefits from slowing the

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rate of gypsy moth spread obtained over the next 25 yr may range from 774.8 to $3,801.5 million (present value).

In 1993, the U.S. Forest Service initiated the Slow-the-Spread (STS) pilot project to determine the feasibility of slowing the spread of gypsy moth over large geographical areas (Leonard and Sharov 1995). The project was established immediately ahead of the advancing front of gypsy moth populations in the following 3 areas: (1) the upper peninsula of Michigan, (2) the Appalachian mountains in Virginia and West Virginia, and (3) northeastern North Carolina. The STS project was designed to detect and manage isolated gypsy moth colonies located just beyond the expanding front of gypsy moth populations. Colonies were detected and delineated using grids of pheromone-baited traps (Schwalbe 1981). Suppression 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 portions of Virginia and West Virginia was targeted at both high- and low-density populations (Reardon 1991), but the STS project is targeted only on small isolated colonies located just beyond the expanding population front.

A major challenge in the design of the STS project has been to optimize its strategy (i.e., to find the management decision rules that will yield the maximum effect with minimum cost). Optimization of slowing gypsy moth spread is difficult because different decision rules may be applied in areas that differ in their distance from the population front and in their landscape characteristics. The initial decision rule algorithm used in the STS project was based mainly on intuition. It was not clear what reduction of spread rate could be expected and how it could be affected by any modification of the decision algorithm. Decision rules evolved gradually according to available resources and observed results of previous actions.

Optimization of a management strategy often can be most efficiently accomplished through the use of a quantitative population model (Shoemaker 1977). Population spread traditionally has been simulated using diffusion-type models that assume continuous spread of organisms in space (Holmes et al. 1994). However, gypsy moth spread cannot be simulated using diffusion models because its spread is discontinuous. Pheromone trapping grids reveal numerous isolated colonies established just beyond the moving population front (Leonard and Sharov 1995, Sharov and Liebhold, 1997a). These colonies usually originate from egg masses or other life stages inadvertently transported on motor vehicles (McFadden and McManus 1991).

Sharov and Liebhold (1997a) developed an analytical model of population spread that includes the establishment of isolated colonies beyond the population front and growth of these colonies. This model simulated the effect of a barrier zone on the rate of expansion of population range. In this article, we use a different version of that model to investigate optimal strategies of barrier zone management to reduce the rate of gypsy moth spread. The major questions addressed herein are as follows: (1) at what density should pheromone traps be deployed at various distances from the population front (optimization)? (2) how do model parameters affect the estimated optimum distribution of pheromone traps and project cost (sensitivity analysis)? and (3) what are the expected costs of the program and how do they compare with expected benefits?

Model Description and Analysis

Model Description. Our model simulates the movement of the population front of gypsy moths using the colonization dynamics at the leading edge. The population front is defined as the line that separates the area where defoliation is common and the area where defoliation is almost absent (Sharov et al. 1996). Gypsy moth has 2 types of dispersal: (1) long-distance transportation by humans, which results in establishment of small isolated colonies beyond the population front; and (2) relatively short-distance windborne dispersal of 1st instars on silk threads by which isolated colonies increase their area until they coalesce (McFadden and McManus 1991). We assume that long-distance dispersal originates only from the area behind the population front which is at outbreak levels and not from the isolated colonies which are at lower densities and, numerically, represent a small fraction of the population. Defoliation in the main population promotes the dispersal behavior of large larvae. This increases the probability that larvae will pupate on motor vehicles and household items which may be transported to the uninfested area.

In the model, long-distance dispersal is incorporated by an equation for the rate of colonization, $b(x)$, as a function of distance from the population front, x. This is the cumulative dispersal from various locations behind the population front, but it is expressed as a function of distance from the front. We have shown previously that the rate of gypsy moth colonization declined linearly with distance (Sharov and Liebhold 1997a). Thus,

$$b(x) = c \cdot \left(1 - \frac{x}{x_{max}}\right), \quad \text{if } x < x_{max}; \qquad b(x) = 0, \quad \text{if } x \geq x_{max}, \qquad [1]$$

where c is the rate of colony establishment at the population front and x_{max} is the maximum distance at which colonies become established.

Characteristics of a colony (i.e., its area and number of individuals) depends only on colony age. The number of individuals, n_a, per colony of age a increases exponentially with age

$$n_a = n_0 \cdot R^a, \qquad [2]$$

where n_0 is the initial numbers of individuals in a colony and R is the net reproductive rate. The area of the colony is assumed to grow proportionally to the age squared (Skellam 1951)

$$S_a = g \cdot a^2, \quad [3]$$

where g is a growth rate parameter.

The model is a series of difference equations that follows the density, $m_{a,z,t}$, of colonies of age a, at time t, and at spatial location z. We use a 1-dimensional space which is perpendicular to the population front and is oriented in the direction of spread. The probability of colony extinction per time step, $q(a,x)$, depends both on the age of the colony, a, and distance from the population front, x. We assumed that colonies become extinct only as a result of pest management. Although natural extinction of colonies does occur, the model counted only those colonies that successfully established. At each time step, the age of colonies increases by 1 and their density decreases because of eradication:

$$m_{a,z,t+1} = [1 - q(a-1, z - Z[t])]m_{a-1,z,t} \quad \text{for } a > 0, \quad [4]$$

where $Z(t)$ is the location of the population front at time t. The density of newly established colonies equals the rate of colony establishment

$$m_{0,z,t+1} = b[z - Z(t)]. \quad [5]$$

The average density of individuals $N_{z,t}$ at time t, at a spatial location z is

$$N_{z,t} = \sum_a n_a \cdot m_{a,z,t}. \quad [6]$$

By definition, the population front is always located at the farthest point where the average density of individuals is $\geq K$, which is the carrying capacity (the density of defoliating populations). Thus,

$$Z(t) = \max\{z | N_{z,t} \geq K\}. \quad [7]$$

If the historical expansion of the population front, $Z(t-\tau)$, $\tau = 1, 2, \ldots$, is known, then the density of colonies, $m_{a,z,t}$, of age a at location z is equal to the rate of colony establishment a time units ago, $m_{0,z,t-a} = b[z - Z(t-a-1)]$, multiplied by the product of probabilities of colony persistence (equations 4 and 5):

$$m_{a,z,t} = b[z - Z(t-a-1)] \prod_{\tau=1}^{a} \cdot [1 - q(a-\tau, z - Z[t-\tau])]. \quad [8]$$

The average density of individuals at location z is

$$N_{z,t} = \sum_{a=0}^{\infty} \left\{ n_0 R^a b[z - Z(t-a-1)] \prod_{\tau=1}^{a} \cdot [1 - q(a-\tau, z - Z[t-\tau])] \right\}, \quad [9]$$

and then, the location of the population front at time t can be estimated using equation 7. Thus, we can estimate the location of the population front at time t from a time series of population front locations in previous time steps. The rate of spread is the difference between consecutive locations of the population front: $V(t\text{-}1) = Z(t) - Z(t\text{-}1)$. Numerical simulations showed that the rate of spread always ultimately converged to a stationary value. Therefore, the model can be simplified by assuming a constant rate of spread equal to V_{max} without management, and V with a barrier zone. Thus, time is omitted in all equations below, and the density of colonies and individuals is given at a specific distance from the population front rather than at a specific spatial location:

$$m_{a,x} = m_{a,Z(t)+x,t}, \quad [10]$$

$$N_x = N_{Z(t)+x,t}. \quad [11]$$

where $Z(t) = z_0 + tV$, and V is the rate of spread. According to equations 7 and 11,

$$N_0 = K. \quad [12]$$

The probability of colony eradication, $q(a,x)$, is a control function. However, isolated colonies must be detected before they can be eradicated. Thus, it is impossible to specify a fraction of colonies to eradicate. Alternatively, it is possible to specify the density of traps to be deployed at various distances; then, the proportion of colonies that will be detected and eradicated can be computed from these densities. Given our assumptions about how colonies develop, we can derive a relationship between $q(a,x)$ and the density of traps, T_x, at distance x. If the distribution of traps is random, then the probability, $P_{a,x}$, of detecting a colony of age a at distance x from the population front equals 1 minus the zero term of the Poisson distribution

$$P_{a,x} = 1 - \exp(-S_a T_a), \quad [13]$$

where S_a is the area of the colony (equation 3) and T_x is the density of traps at distance x. By the area of a colony we mean the area of the cloud of male moths that can be detected with pheromone traps. The area of this cloud may be larger than the area of the reproducing population because adult males fly away from their emergence sites whereas females cannot fly.

Equation 13 provides realistic predictions when colonies are small. However, the probability of detecting large colonies is underestimated because traps are typically placed at regular grids rather than at random as assumed by equation 13. Thus, we additionally assumed that all colonies large enough to have ≥ 3 traps on average within their area are detected with a probability of 1.0. Thus,

$$\begin{aligned} P_{a,x} &= 1 - \exp(-S_a T_a) && \text{if } S_a T_x < 3, \\ P_{a,x} &= 1 && \text{if } S_a T_x \geq 3. \end{aligned} \quad [14]$$

In the model, colonies are eradicated 2 yr after their detection because it takes time to confirm the ex-

Table 1. Simulation of spread of gypsy moths in presence of a barrier zone

Time until population front reaches area, yr	Distance from population front, km	Density of colonies (per 10,000 km²) of the following age, yr						Avg density of individuals, no./km²	Trap density, traps/km²	Detection costs, $/km²	Eradication costs, $/km²
		0	1	2	3	—	17				
28	252	0	0	0	0	—	0.0	0.0	0.02	1.28	0.00
27	243	0.5	0	0	0	—	0.0	0.0	0.02	1.28	0.00
26	234	1.1	0.5	0	0	—	0.0	0.0	0.02	1.28	0.00
25	225	1.7	1.1	0.5	0	—	0.0	0.0	0.02	1.28	0.00
24	216	2.3	1.7	1.1	0.2	—	0.0	0.0	0.02	1.28	0.43
—	—	—	—	—	—	—	—	—	—	—	—
9	81	11.5	10.9	10.3	3.3	—	0.0	7.4	0.02	1.28	187.67
8	72	12.1	11.5	10.9	3.6	—	0.0	7.9	0.02	1.28	201.26
7	63	12.7	12.1	11.5	3.8	—	0.0	8.5	0.02	1.28	214.86
6	54	13.3	12.7	12.1	4.0	—	0.0	9.0	0.02	1.28	228.45
5	45	13.9	13.3	12.7	4.2	—	0.0	9.5	0.02	1.28	242.05
4	36	14.6	13.9	13.3	4.4	—	0.0	10.1	0.02	1.28	255.64
3	27	15.2	14.6	13.9	4.6	—	0.0	10.6	0.02	1.28	269.24
2	18	15.8	15.2	14.6	4.8	—	0.0	11.1	0.02	1.28	282.83
1	9	16.4	15.8	15.2	5.0	—	0.0	11.6	0.02	1.28	296.43
0	0	17.0	16.4	15.8	5.3	—	0.0	12.2	0.02	1.28	310.02
Colony area, km		0.0	7.1	28.4	63.9	—	2,052		Total costs:	37.12	3,696.62

istence of a colony and to delimit colony boundaries (Leonard and Sharov 1995). Thus, the probability, $q(a,x)$, of eradication of a colony of age a at distance x is equal to the probability of detecting this colony 2 yr earlier when the age of the colony was $(a-2)$ and the distance from the population front was $(x + 2V)$, where V is the rate of spread:

$$q(a,x) = P_{a-2,x+2V}. \qquad [15]$$

The cost of operating the barrier zone is estimated as follows. The 1st step is to estimate the cost per unit area (1 km²) at each distance from the population front. The cost of eradication is proportional to the area treated. The sum of the areas of the colonies to be treated per unit area at distance x from the population front is $\sum_a m_{a,x}S_a q(a,x)$. Because the proportion of area covered with colonies is usually <5%, we ignored possible overlap of colonies. The area of a reproducing population is usually smaller than the area where male moths are caught in pheromone traps; thus, only the central portion of the detected colony should be treated. The fraction of area treated, Q_x, at distance x from the population front is

$$Q_x = w\sum_a m_{a,x}S_a q(a,x), \qquad [16]$$

where w is the proportion of the area of a colony that requires treatment. The cost of managing the barrier zone per unit area at distance x is

$$C_x = Q_x C_{erad} + T_x C_{trap}, \qquad [17]$$

where C_{erad} is the cost of eradication per unit area and C_{trap} is the cost of a trap. Two terms in equation (17) represent eradication and detection costs, respectively. Finally, the total annual cost of the barrier zone per 1 km of its length is

$$C = \sum_x C_x. \qquad [18]$$

The model was built using a Microsoft Excel (Microsoft 1993) spreadsheet (Table 1). Both time and space were discrete. We used a 1-dimensional space oriented perpendicular to the population front. The origin of the spatial axis was assumed to move forward together with the expanding population front so that it always coincided with the front of the area defoliated. Thus, each spatial interval corresponded to a specific distance from the population front (column 2). Time was defined using increments of 1 yr, and space increments were defined as multiples of the annual population spread rate (e.g., 9 km/yr).

The density of colonies of various ages per 10,000 km² is given in columns 3, 4, ... of Table 1. The density of newly established gypsy moth colonies (column 3) decreased linearly with increasing distance from the population front, x, according to equation 1. If colonies were not eradicated, then the density of colonies simply would be shifted diagonally to the right and down (i.e., to the next age class and to the previous distance class). However, the density of colonies decreases because of eradication. The proportion of colonies eradicated corresponds to equations 14 and 15.

The total cost per 1-km of length of the barrier zone was estimated as the sum of detection costs and eradication costs per 1 km² in all distance classes ($37.12 + $3,696.62; see Table 1) multiplied by the width of the distance class which is equal to the annual spread rate of the population (V = 9 km/yr). Thus, the total costs are $33,604/1 km of length of the barrier zone.

Optimization. Optimization of the management program with limited resources can be accomplished using either of 2 methods: (1) maximize the effect at fixed costs or (2) minimize costs at fixed effect. We selected the 2nd method because it was easier to use a target rate of population spread rather than to estimate the rate of spread numerically.

The rate of spread was set to a target rate, and the trap density at various distances from the population front was modified to minimize total costs of the barrier zone per 1 km of length. Equation 12 was used as a constraint. Optimization was performed using Microsoft Excel (Microsoft 1993), the "solver" tool. Before optimization, the density of traps, T_x, was arbitrarily set to 0.02/km^2 at all distances from the population front (Table 1). Several additional initial conditions were used to check if the solution converged to the same function.

Cost-Benefit Analysis. The analysis is based on the work of Leuschner et al. (1996) who estimated benefits of different scenarios of slowing gypsy moth spread. These authors estimated potential economic impacts from the gypsy moth that can be expected in the United States during a 25-yr period assuming a rate of population spread of 2.5, 5, 7.5, 10, 12.5, and 15 miles/yr. Long-term economic analysis should consider inflation to discount future costs and benefits (Clark 1976). Thus, Leuschner et al. (1996) estimated the present value (PV) of impacts as a weighted sum of impacts in a sequence of years with decreasing weights using the inflation rate of 0.04.

In our model, the rates of population spread (V) were different from the values used by Leuschner et al. (1996). Thus, we interpolated impacts (PV) estimated by Leuschner et al. (1996) using a quadratic equation:

$$101.56 + 166.9 \cdot V + 0.8136 \cdot V^2 (R^2 = 100\%). \quad [19]$$

We believe that the value of negative impacts caused by the gypsy moth was overestimated by Leuschner et al. (1996) because these authors assumed residential impacts, which were ≈83% of the total impacts, to occur every year in the entire area occupied by the population. Because gypsy moth outbreaks are episodic, we expect that residential impacts occur only in areas defoliated by the gypsy moth. In the generally infested zone in Virginia and West Virginia, the proportion of area defoliated in 1990–1994 varied from 18 to 34% (21% on average) (unpublished data). Thus, we adjusted economic impacts caused by the gypsy moth multiplying them by $[(1 - p) + p \cdot 0.21]$, where $p = 0.83$ is the proportion of residential impacts from total impacts. Benefits from slowing the spread were estimated as a difference between impacts (PV) caused by gypsy moth populations that spread with the rate of 21 km/yr and with a reduced rate (17, 13, 9, or 5 km/yr).

The cost of slowing the spread was estimated as follows. For simplicity, the spread of the gypsy moth from Michigan was not considered by Leuschner et al. (1996), and we followed this simplification. The length of the barrier zone (from Lake Erie to the Atlantic Ocean) is ≈1,000 km. The cost of the entire program (PV) over 25 yr is equal to the cost of the barrier zone per 1 km of length (predicted by the model) multiplied by 1,000 km of length and by the discount term, $[1 - \exp(-\alpha T)]/\alpha$, where $T = 25$ yr is the duration of the program, and $\alpha = 0.04$ is the inflation rate.

Model Parameters

Sharov and Liebhold (1997a) estimated several parameters from historical trap data in the AIPM and STS areas: $c = 0.0017$, the maximum colonization rate per year per 1 km^2 at the population front; $x_{max} = 250$ km, the maximum distance from the population front at which new colonies can be established; and $R = 5.51$, the net rate of population increase per year. Parameter R was adjusted (Sharov and Liebhold 1997a) so that the model showed the same rate of uncontrolled population spread (≈21 km/yr) that was observed in 1966–1990 in the area with a mean minimum January temperature of >7°F (Liebhold et al. 1992). Liebhold et al. (1992) used degrees fahrenheit in the analysis, but erroneously indicated that temperature was measured in centigrade.

Initial population numbers, n_0, in an isolated colony are not known. We doubt that many colonies may start from a single egg mass because of the low probability of mating (Sharov et al. 1995). A more realistic estimate of the average initial number of egg masses that may start a new colony is $n_0 = 5$. We found that this parameter had no effect on optimization results because it only scaled the density of the individuals, N_x.

In the Appalachian Mountains, the spread rate of gypsy moth populations was ≈21 km/yr before 1990 and ≈9 km/yr after 1990 (Sharov and Liebhold 1997b). This decline may be associated with eradication of isolated colonies just beyond the population front that was started in 1990. In this model, we assumed the uncontrolled rate of spread, V_{max} = 21 km/yr. We used target rates of population spread varying from 5 to 17 km/yr. A separate spreadsheet was used for each target rate of spread.

The average density of organisms at the population front, K = 139,659 per km^2, is not a parameter because it is a function of other model parameters (x_{max}, c, R, and V_{max}). It was estimated as the value of N_0 using equations 9 and 11 and assuming no population management ($q(a,x) = 0$), and a rate of spread of V_{max}.

Little information is available that can be used for estimating the rate of growth of colony area, g, because colonies usually are not detected until several years after their establishment; thus, the year of establishment is unknown. Most colonies are suppressed or eradicated immediately following detection so that it is impossible to monitor their growth. Also, there are substantial fluctuations in colony size among years because of fluctuating environmental conditions. In the study area, we found the following 3 colonies for which sufficient data existed to trace their growth over several years: (1) the intersection of Rockbridge, Botetourt, and Bedford counties (VA); (2) near Sugarloaf Mountain (Bote-

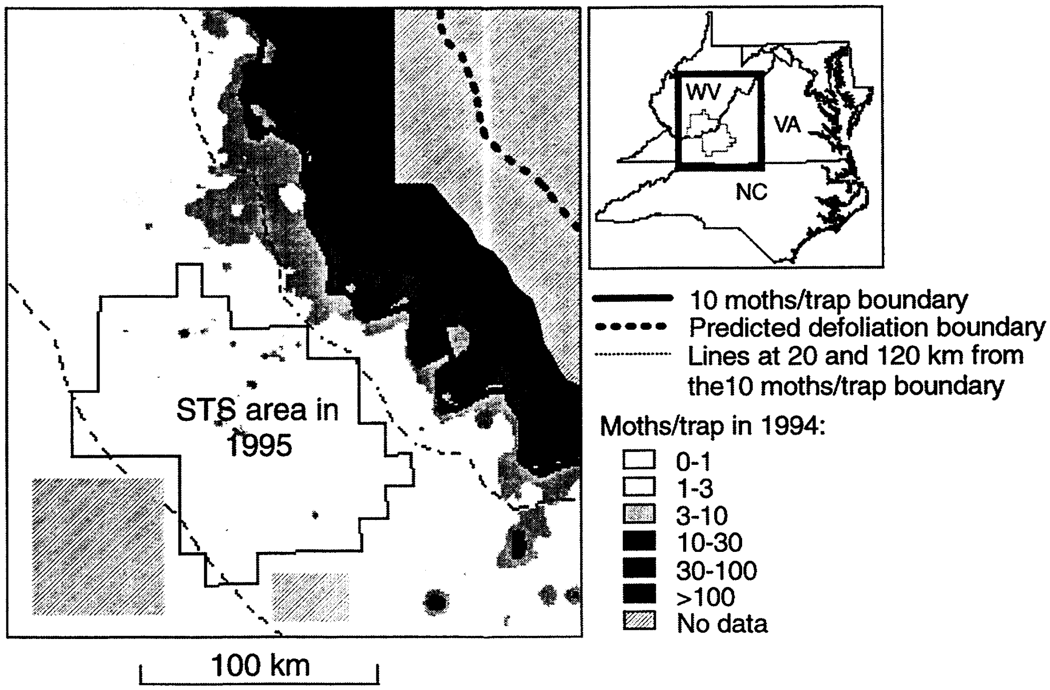

Fig. 1. Location of the STS project area in 1995 relative to the 10 moth/trap line in 1994.

tourt County, VA); and (3) Peters Mountain (Giles County, VA). The area of each of these colonies was measured on a 1-km^2 raster map generated from moth counts in pheromone traps interpolated using median kriging with subsequent E-type estimation (Deutsch and Journel 1992). We used the threshold of 3 moths per trap to delineate the boundary of a colony because lower moth catches often represent moth migrants that came from distant areas. Colony 1 was 1st detected in 1986, and by 1990 had an area of 321 km^2. Colony 2 was 1st detected in 1986, and by 1990 had an area of 128 km^2. Colony 3 was 1st detected in 1990, and by 1993 had an area of 55 km^2. We assumed that these colonies were established 1 yr before 1st detection. Parameter g was estimated using equation 3 individually for each colony, then averaged; $g = 7.1\ km^2 \cdot yr^{-2}$.

The proportion, w, of colony area that requires treatment was adjusted so that the total area treated was the same as in the Virginia–West Virginia portion of the STS project, which was 10,815 ha in 1994 and 8,863 ha in1995. This portion of the STS area is used as an example because that project was apparently successful in that region (Sharov and Liebhold 1997b). In 1994–1995, the STS project area in Virginia–West Virginia was located mainly between 20 and 120 km from the line of 10 moths per trap (Fig. 1). The average distance between the line of 10 moths per trap and defoliation boundary in 1988–1994 was ≈80 km (Sharov et al. 1996). Thus, the STS area was located between 100 and 200 km from the defoliation front. The length of the barrier zone along the population front was ≈130 km. Within this area, pheromone traps were deployed in a 1-km grid. We used the model to simulate this design of the barrier zone, and determined that the sum of areas of colonies detected annually was 231.7 ha per 1 km of length of the barrier zone, or 30,121 ha for the entire barrier zone (130 km). Parameter $w = 0.33$ was estimated as the ratio of the area actually treated in 1994–1995 to the predicted sum of areas of colonies detected annually.

Average trapping costs in the STS project in 1994–1995 were \$64 per trap, and average treatment costs were \$25/acre (\$6,177/km^2); both estimates include overhead costs (D. Leonard, USDA Forest Service, Ashville, NC, personal communication). In some cases, >1 yr of treatment is necessary to eradicate a population. However, this factor is already included in parameter w, which was adjusted to the actual area treated. Eradication costs also should include costs associated with using high-density trap grids for delimiting infestation boundaries and for posttreatment evaluation. The STS project implements 500-m trap grids for this purpose. The delimiting area is historically larger than the treatment area by a factor $1/w \approx 3$. Thus, for each 1 km^2 treated, there should be 12 traps for delimiting and 4 traps for evaluation. This is a total of 16 traps that

Table 2. Characteristics of model-generated barrier zones designed for different target spread rates of gypsy moth populations

Target rate of spread, km/yr	No. traps per unit length of barrier zone, no./km[a]	Area treated per unit length of barrier zone, km^2/km	Width of barrier zone, km	Costs of barrier zone per unit length, $/km/yr	Avg costs of barrier zone, $$/km^2/yr$	% trapping costs[b]
17	8.3	0.21	51	2,059	40.38	36.4
13	19.9	0.54	104	5,134	49.36	35.5
9	32.4	0.97	144	9,078	63.04	33.8
5	46.4	1.50	190	13,790	72.58	32.7

[a] These are traps used for detecting colonies; traps used for delimiting colonies and for evaluating treatments are not included.
[b] Trapping costs including the cost of all traps used for various purposes (detection, delimitation, and treatment evaluation).

cost $1,024. The total costs for eradication were estimated as ≈$7,200/1 km^2.

Results

Optimal Management of the Barrier Zone. Following optimization procedure, the total number of traps and the total area treated per 1-km of length of the barrier zone increased with decreasing target rate of population spread (Table 2). In total the number of traps varied from 8.3 to 46.4/1 km of length of the barrier zone, and the area treated varied from 0.21 to 1.50 km^2.

Following optimization, the model specified placing traps in the distant portion of the area where new colonies may be established (Fig. 2A). This portion is called a barrier zone. Within the barrier zone, trap density gradually declined with increasing distance from the population front. The highest trap density always was at the edge of the barrier zone closest to the approaching population front. As the target spread rate decreased, traps were located over a wider range of the barrier zone and closer to the advancing population front. Location of the far end of the barrier zone did not depend on the target spread rate. The upper estimates of trap density (Fig. 2A) nearly coincided for all target spread rates, indicating that the optimal density of traps within a barrier zone depends mostly on the distance from the population front and not on the target spread rate. The maximum trap density was ≈0.35 traps per 1 km^2.

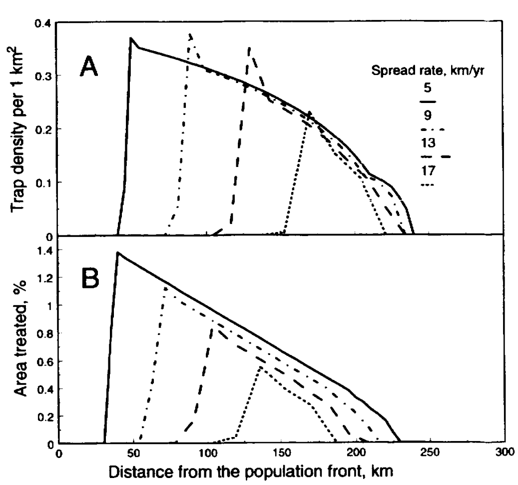

Fig. 2. Optimal density of pheromone traps (A) and proportion of area treated with pesticides (B) generated by model using target population spread rates varying from 5 to 17 km/yr.

The area where eradication activity should occur was slightly closer to the population front than was the trapping area (Fig. 2B). This was because treatment occurred 2 yr after initial detection of the population, and during this time the population front moved forward. Within the barrier zone, the percentage of the area treated decreased with increasing distance from the population front. The proportion of area treated was generally <3%. This proportion was highly dependent on the distance from the population front and was mostly unrelated to the target spread rate (Fig. 2B).

To estimate potential cost savings from optimizing the management of the barrier zone in the STS project, we compared optimized costs with costs predicted by the model that simulates the strategy implemented in the STS project (i.e., 1 trap per 1 km^2 set at distances from 100 to 200 km from the population front). Simulated costs of the STS strategy are $12,546/1 km of length. According to the model, this strategy slows the rate of population spread to 10 km/yr. After optimization for the same target rate of spread, the costs were reduced to $8,006/1 km of length of the barrier zone, which is 36.2% lower than the cost of the barrier zone before optimization.

Sensitivity Analysis. Table 2 compares optimal barrier zone strategies for various target spread rates. The cost of the barrier zone per unit length increased with decreasing target spread rate. The cost per unit area had a trend to increase with decreasing target spread rate (Table 2). This may be explained by the increases in trapping and eradication activity near the population front (Fig. 2). Thus, average costs per unit area of the barrier zone increases as this zone becomes wider.

Model parameters c, x_{max}, g, R, and w were individually increased by 10%, then the barrier zone was optimized with each set of parameter values. The change in predicted total costs of the barrier zone did not exceed 10%, which indicates

Table 3. Predicted change in cost of management of barrier zone that resulted from a 10% increase in value of individual model parameters

Model parameter that was increased by 10%	Cost of barrier zone per unit length, \$/km/yr	% change in cost
(Control)	9,078	0.0
x_{max}	9,790	7.8
c	9,771	7.6
g	9,565	5.4
R	9,034	−0.5
w	9,776	7.7

moderate sensitivity of the model to the change of parameters. The largest effect (7.8% increase in total costs) was observed from the change of parameter x_{max}, the maximum distance at which colonies are established (Table 3). The change of parameters w and c caused a slightly smaller response. Parameter R had almost no effect on the optimized costs of the barrier zone.

Modification of parameters did not change the qualitative pattern of allocation of trapping and eradication activities in the barrier zone (Fig. 3).

Cost–Benefit Analysis. Predicted costs of the barrier zone per 1 km of length (Table 2) were used to estimate the costs (PV) of a nation-wide barrier zone over 25 yr (Fig. 4). The costs were <1/4 the predicted benefits that could be obtained from slowing gypsy moth spread at all analyzed target rates of spread.

Discussion

Every model simplifies reality to some extent, and our model is no exception. There are many additional factors that may change the outcome of the optimization. Parameters of the model may change because of spatial heterogeneity in the habitat. Long-distance dispersal of male moths may create a background of moth catches that make it more difficult to detect isolated gypsy moth colonies. Nevertheless, this model captures the important features of the system and is capable of meaningful predictions. The model was robust; its qualitative behavior did not change because of variation in parameter values (Fig. 3).

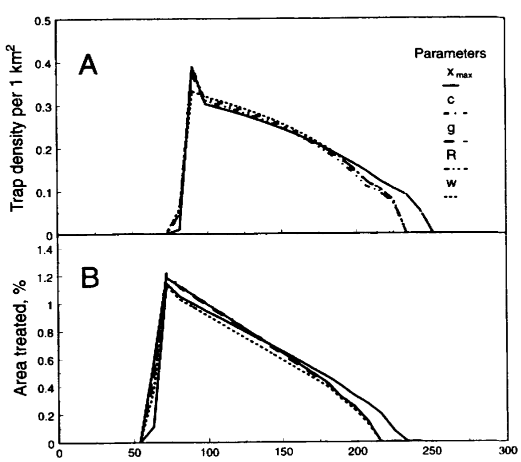

Fig. 3. Optimal density of pheromone traps (A) and proportion of area treated with pesticides (B) at target population spread rate of 9 km/yr predicted by model after model parameters were individually increased by 10%.

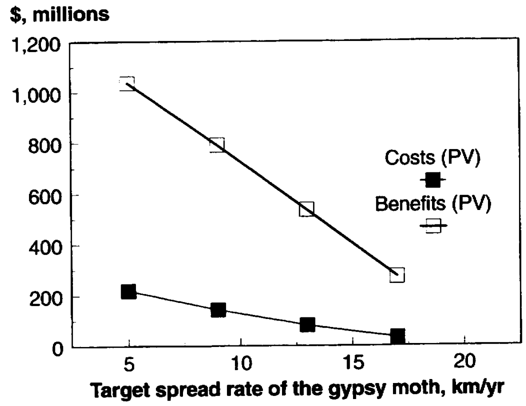

Fig. 4. Predicted costs (generated by the model) and benefits (modified from Leuschner et al. 1996) of slowing gypsy moth spread in period of 25 yr (present value).

This model described the optimal design of a barrier zone for a specified target rate of population spread. However, it did not specify the optimal target rate of spread. Optimization of the target spread rate is an important problem, but is was beyond the scope of this article because it would require a different model.

Optimal Management of the Barrier Zone. The design of the STS project has been gradually evolving in response to results obtained. Initially, in 1992, the barrier zone in Virginia–West Virginia was placed too far (≈120 km) from the population front. Until 1996 it remained in the same place while the population front has advanced. As of 1996, the barrier zone started at ≈100 km from the population front, which is close to the beginning of the optimal barrier zone for the target rate of spread V = 9 km/yr (Fig. 2A).

Optimization may yield a considerable reduction of costs of slowing the spread of gypsy moth populations. Simulated costs of the barrier zone in Virginia–West Virginia, as it was designed in 1994–1995, were 36.2% higher than the costs of the barrier zone with the optimal design. This difference in costs resulted from unnecessarily high trap densities used in the STS project. In 1996, following recommendations from this analysis, the trap density was reduced to 0.25 km^{-2} in most of the area.

The major qualitative result of the model was that more intensive trapping and eradication should be conducted in the proximal portion of the barrier zone than in the distal portion. At distances of 100, 150, and 200 km from the population front, the optimized model specified annual treatment of 1.0, 0.6, and 0.2% of the area, respectively (Fig. 2B). These values can be used for selecting areas to be treated. The following algorithm is suggested for selecting treatment areas. First, the area of the barrier zone is separated into several zones according to the distance from the population front (e.g., 75–125, 125–175, and 175–225 km). In each zone, a cumulative distribution of male moth counts in pheromone traps is estimated from the map generated from sample data. Then, thresholds are estimated from this distribution that correspond to the 1.0, 0.6, or 0.2% of the area with highest moth counts. Finally, areas where moth counts exceed the specific threshold are planned for treatments.

Historical treatments in the STS project area were distributed uniformly through the entire barrier zone. This occurred because it was assumed that early management of gypsy moth populations in the distal portion of the STS area was most important for the reduction of population spread rate. According to the model, the efficiency of the project will increase if more treatments are made near the population front.

Sensitivity Analysis. The model was most sensitive to the change of the maximum distance from the population front at which new colonies can become established (x_{max}). This parameter was previously estimated with sufficient accuracy (Sharov and Liebhold 1997a); thus, it is unlikely that variability in this parameter has a strong effect on simulation results. We are more concerned about parameters c (the rate of colony establishment), g (the rate of colony growth in size), and w (the proportion of colony area that requires treatment), the values of which we consider as preliminary estimates. Parameter g was evaluated from only 3 well-documented colonies, all located in the continuous forested area at high elevation, which is most favorable for gypsy moth reproduction and spread (Liebhold et al. 1994, Sharov et al. 1997). As a result, the value of parameter g may have been overestimated.

The net reproductive rate, R, did not affect the cost of slowing population spread. This can be explained by the assumption that the cost of eradication depended on the area treated rather than on the population density. It is likely that eradication costs increase with increasing population density as follows from the model of Sharov and Colbert (1996). However, sufficient data to support this hypothesis is not available.

Cost–Benefit Analysis. Our model suggests that the potential costs of slowing gypsy moth spread are <1/4 the potential benefits at all target rates of population spread from 5 to 17 km/yr (Fig. 4). This finding suggests that the transition of the STS into a national project is feasible and should be considered. It may be possible to increase the intensity of STS by setting lower target spread rates (e.g., 5 instead of 9 km/yr).

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