Evaluation of Preventive Treatments in Low-Density Gypsy Moth Populations Using Pheromone Traps

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ABSTRACT Pheromone traps can be used for evaluating the success of treatments that are applied to either eradicate or delay the growth of isolated low-density populations of the gypsy moth, *Lymantria dispar* (L.). We developed an index of treatment success, *T*, that measures the reduction in moth counts in the block treated adjusted by the change in moth counts in the reference area around it. This index was used to analyze the effectiveness of treatments that were conducted as part of the USDA Forest Service Slow-the-Spread of the gypsy moth project from 1993 to 2001. Out of 556 treatments that were applied during this period, 266 (188,064 ha) were selected for the analysis based on several criteria. They included 173 blocks treated with *Bacillus thuringiensis* (Berliner) variety *kurstaki* and 93 blocks treated with racemic disparlure. Analysis using general linear models indicated that disparlure treatments were significantly more effective than *B. thuringiensis* treatments in reducing moth captures. The frequency of repeated treatments in the same area was higher after *B. thuringiensis* than after disparlure applications. Treatments were more successful if the pretreatment moth counts outside of the block treated were low compared with moth counts inside the block.

KEY WORDS gypsy moth, pheromone traps, mating disruption, *Bacillus thuringiensis*, disparlure, eradication

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THE GYPSY MOTH, *Lymantria dispar* (L.), is a serious pest of hardwood forests in northeastern United States (Doane and McManus 1981). It was introduced into North America in 1869 near Boston. Since that time its populations in the United States have reached Virginia, NC, in the south, IN, and Illinois in the west and Wisconsin in the north (Liebhold et al. 1992, Sharov et al. 2002). More than 81 million acres of forests have been defoliated by the gypsy moth since 1924, and >12 million acres of forests have been aerially treated with insecticides since 1970 (USDA Forest Service 2001).

In the 1960s and 1970s most treatments were conducted using conventional synthetic pesticides like carbaryl (sevin) and dylox (trichlorfon). Since 1983, these materials have been increasingly replaced by *Bacillus thuringiensis* variety *kurstaki* (Berliner) and dimilin (diflubenzuron) (Liebhold and McManus 1999). Dimilin is an inhibitor of chitin synthesis and is nontoxic to vertebrate animals, but it kills many arthropod species and hence may affect certain nontarget organisms (Butler et al. 1997). *B. thuringiensis* is a more specific agent than dimilin; it kills mostly lepidopteran larvae (Reardon et al. 1994). In field tests, *B. thuringiensis* protects foliage (Andreadis et al. 1983, Liebhold et al. 1996) and may cause a substantial reduction in gypsy moth numbers (Dubois et al. 1988). Applications of *B. thuringiensis* have also been shown to decrease the numbers of nontarget forest lepidopteran species (Sample et al. 1996, Whaley et al. 1998). Two other treatment agents, gypsy moth nuclear polyhedrosis virus (NPV) and disparlure (synthetic sex pheromone), have no known nontarget effects. However, NPV is not the best choice for preventing defoliation because it requires a long incubation period to cause mortality, its efficacy is not consistent (Podgwaite 1999), and production costs are high. In low-density populations, treatments with NPV may have a very limited effect because host population numbers are not sufficient to sustain an epizootic. Application of the synthetic gypsy moth pheromone disparlure in a slow-release formulation interferes with male search behavior and subsequently decreases the number of fertilized eggs laid by females (Reardon et al. 1998, Leonhardt et al. 1996). Initially this method was tested on high-density gypsy moth populations but results were not satisfactory (Cameron 1981). Later experiments in medium- and low-density populations have proved that disparlure can substantially reduce gypsy moth abundance (Reardon et al. 1998). Operational

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use of disparlure is increasing (Sharov et al. 2002). Its effectiveness is inversely related to population density (Schwalbe et al. 1983, Webb et al. 1988, 1990).

Historically, most treatments of gypsy moth populations have been conducted to prevent defoliation in the current year. Treatments are typically scheduled based on counts of overwintering egg mass populations, which can be used to predict defoliation (Gansner et al. 1985, Liebhold et al. 1993). Operational treatments of outbreak populations usually provide at least partial foliage protection, but they may have limited effects on densities in subsequent years or on the probability of defoliation in the future (Liebhold et al. 1996).

Treatments applied to low-density populations have historically been conducted as part of eradication projects far away from established gypsy moth populations (Dreistadt and Dahlsten 1989). But recently it was suggested that treatment of low-density populations could be used in a barrier zone strategy to slow the spread of gypsy moth populations in North America (Leonard and Sharov 1995). The expansion of gypsy moth population range is enhanced by accidental establishment of isolated colonies just ahead of the moving front. Most of these colonies result from the inadvertent transport of gypsy moth life stages by humans (McFadden and McManus 1991). Isolated colonies grow, coalesce and eventually contribute to the progression of the population front (Sharov and Liebhold 1998a). Thus, it is possible to slow the spread by detecting and eradicating these isolated colonies at very early stages. The term "eradication" in its strict sense may not fully describe this strategy because colonies are often located close to the generally infested area and thus recolonization is possible. Because ≈two-thirds of the potential area in the U.S. with highly susceptible host trees still remains uninfested (Liebhold et al. 1997), slowing gypsy moth spread into these areas generates economic benefits (Leuschner et al. 1996, Sharov and Liebhold 1998b). This idea was implemented in the USDA Forest Service Slow-the-Spread (STS) project which started in 1993 (Leonard and Sharov 1995) and became fully operational in 1999. Initially, most treatment in the STS project used *B. thuringiensis*, but the area treated with disparlure for mating disruption increased from 1.2×10^3 ha in 1993 to 86.2×10^3 ha in 2001 (Sharov 2001).

The success of treatments targeted against outbreak populations of the gypsy moth is traditionally evaluated by the reduction in egg mass counts and defoliation in treated versus untreated blocks (Twardus and Machesky 1990, Liebhold et al. 1996). These methods are not applicable in low-density populations because egg mass densities cannot be estimated with any accuracy and populations are too low to cause noticeable defoliation. Thus, evaluation of preventive treatments has to be based on alternative methods. Larval counts under burlap bands are a sensitive sampling method at moderate population densities (Reardon et al. 1998, Wallner et al. 1990), but in low-density colonies that are treated within the STS project, even larval numbers under burlap bands are not sufficient for analysis. At these extremely low densities, the only sampling method that is viable is the use of male moth counts in pheromone traps because they are most sensitive to variation among very low population levels.

Another advantage of using pheromone traps for treatment evaluation is that they are inexpensive and thus can be used on an operational basis rather than just in experiments. But the quality of data collected with pheromone traps has been questioned. Liebhold et al. (1995) and Carter et al. (1992) found that the correlation between moth counts in pheromone traps and defoliation was weak in continuously infested areas of high-density populations. However, at these densities many traps become saturated and this may obscure correlations of trap counts with population density (Elkinton 1987). Granett (1974) avoided trap saturation by frequent moth removal and recorded a high correlation between trap catches and population numbers. At low population densities, USDA milk-carton pheromone traps do not become saturated and they are sensitive to changes in population abundance (Schwalbe 1981, Carter et al. 1992, Sharov et al. 1996). In the STS project area, gypsy moth population densities are generally very low and traps are not likely to become saturated.

In this paper we have developed a new method for evaluating treatments of low-density, isolated gypsy moth populations that is based on moth counts in pheromone traps. This method was used to evaluate treatments conducted within the STS project from 1993 to 2001 and to compare the relative effectiveness of *B. thuringiensis* and disparlure treatments. Also, we studied factors that may affect the success of preventive treatments in isolated colonies.

Materials and Methods

Description of Treatments. Treatments of isolated gypsy moth populations were conducted within the STS project area from 1993 to 2001. The STS pilot project started in 1993 in three areas: the Appalachian Mountains in Virginia and West Virginia, coastal plain of North Carolina, and Upper Peninsula of Michigan (Fig. 1). In 1993 to 1995, all treatments were confined to the first two geographic areas. In 1995, the project was expanded to include the Virginia Piedmont, and in 1998 it became a National program and was expanded along the entire population front in the U.S. from Wisconsin to North Carolina (Fig. 1).

Most treatments in the STS project are applied in an "action zone" which is located just beyond the generally-infested area (Leonard and Sharov 1995). A computer algorithm is used to recommend the location of the action zone based on male moth counts in pheromone traps in the previous year (Sharov 2001). The inner boundary of the action zone is close to the 1-moth line that separates areas where the average moth capture rate per season is below and above one moth/trap. This line is estimated using the best cell classification method (Sharov et al. 1995a). The actual boundary of the STS action zone may differ slightly

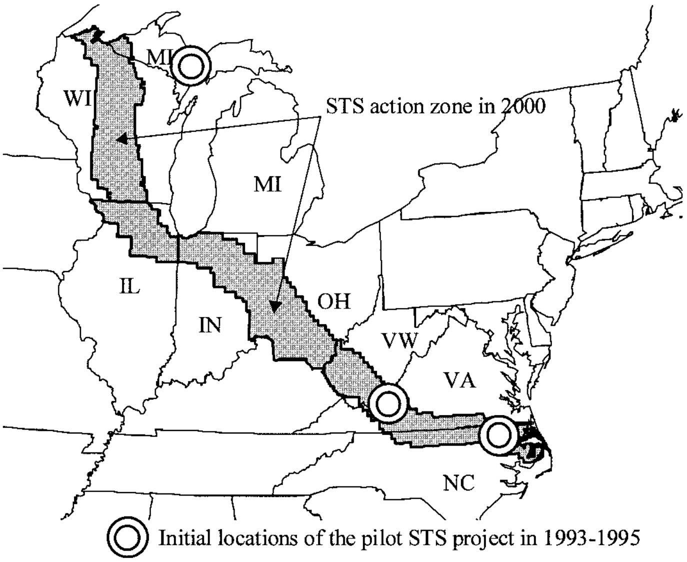

Fig. 1. Map of the action zone in the USDA Forest Service STS project.

from computer recommendations, but usually the difference is small.

Treatment blocks were selected using a computer algorithm based on the analysis of moth counts in pheromone traps (Sharov 2001). The algorithm searched for areas where moth counts in traps were abnormally high compared with neighboring areas indicating the presence of an isolated colony. Occasionally, additional factors (e.g., presence of life stages, quarantine regulations, landscape characteristics, etc.) were taken into account. Selection of treatment agents was largely subjective. In most cases, disparlure treatment for mating disruption was recommended if the maximum moth count in traps was <50 per trap, however occasionally several blocks with higher moth captures were treated with disparlure. Disparlure was also the preferred treatment in blocks where sensitive nontarget invertebrates were thought to be present. Most other blocks were treated with *B. thuringiensis.*

A total of 556 treatments were applied in the STS project from 1993 to 2001, and the total area treated was 345,259 ha. *B. thuringiensis* treatments consisted of double or single aerial applications at 24 to 30 BIU/ha of an aqueous formulation; the rate of spray was 4.68 liters/ha. Mating disruption with racemic disparlure was accomplished with aerial application of Hercon pheromone flakes, formulation Disrupt II, with a sticker (Gelva-2333, Solutia Inc., Springfield, MA) at a dose of 37.5 to 75 g (AI)/ha. These doses have been previously demonstrated to be effective against gypsy moth populations with densities ≤15 egg masses/ha (Webb et al. 1988, Leonhardt et al. 1996). Other treatment agents included dimilin and NPV (Gypchek). However, the use of these agents was limited because dimilin is a nonselective pesticide that may affect other nontarget invertebrates (Butler et al. 1997), and Gypchek is produced in small amounts. The number of blocks treated with these two agents was not sufficient for analysis; thus, we will not consider them further in this paper.

Selection of Treatments for Analysis. For statistical analysis, we selected a subset of treatments that satisfied the following three criteria: (1) the treated block was located outside of the generally-infested area; (2) the area of the block (A) was ≥ 1 km^2; (3) the minimum density of traps (D) in the year before treatment and in the evaluation year was ≥ 1 km^{-2} in small blocks ($1 \leq A \leq 5$ km^2) or $D \geq 0.5$ km^{-2} in large blocks ($A > 5$ km^2). The evaluation year was the year of treatment for *B. thuringiensis,* but the following year for disparlure.

The first criterion excluded treatments in continuously infested area because their population behavior in response to treatments would be expected to vary considerably from that of isolated colonies beyond the population front that were the focus of this study. A treatment block was considered to be outside of the generally infested area if it was beyond the inner boundary of the STS action zone, or if the distance to the inner boundary of the STS action zone was <10 km. The latter condition was necessary to include those blocks that were located outside of the STS action zone but still in an area with relatively low population density (Sharov et al. 1996).

The second criterion was important because male moths disperse, and thus, moth capture in a pheromone trap represents the average population abundance in a relatively large area around the trap (Mastro 1981). If a treatment block is too small, then moth counts in pheromone traps would not be a good representation of population abundance in the treated block. Our experience suggested that blocks smaller than one km^2 could not be reliably evaluated based on pheromone trap data.

Table 1. Number and total area of treatment blocks analyzed

State	*B. thuringiensis*		Disparlure		Total	
	N	Area, ha	N	Area, ha	N	Area, ha
Illinois	11	2,373	1	567	12	2,939
Indiana	0	0	6	2,519	6	2,519
North Carolina	12	10,388	18	7,846	30	18,234
Ohio	0	0	2	1,659	2	1,659
Virginia	36	39,156	35	20,318	71	59,474
Wisconsin	91	64,478	14	7,556	105	72,034
West Virginia	23	21,888	17	9,317	40	31,205
Total	173	138,282	93	49,782	266	188,064

The third criterion was needed because proper evaluation of treatment success required a sufficient number of traps. Treatments with *B. thuringiensis* were evaluated using trap data collected in the same year as application, but disparlure treatments were evaluated using data in the year after application. Disparlure treatments applied in 2001 would be evaluated in the fall of 2002, and because these data were not yet available, they did not satisfy the third criterion. In large treatment blocks ($A \geq 9$ km^2), the actual density of traps in the treatment block was used. The equation for trap density, D, in small blocks ($A < 9$ km^2) was

$$D = \frac{N + 0.1\ (N_n - N)}{A + 0.1\ (A_n - A)}, \qquad [1]$$

where N is the number of traps within the block treated, N_n is the number of traps within 3 km from the center of the block treated, A is the area of the block, and $A_n = 9\pi$ km^2 is the area of a 3-km circle. Neighboring traps that were not located in the treated block were given a weight of 0.1. We selected a low weight value to reduce the effect of traps located outside of the treated block.

Three blocks treated with disparlure in 1993 in Virginia and West Virginia were treated again with *B. thuringiensis* in 1994. Hence, evaluation was not possible in the year after treatment. Thus, we did not include these blocks in the analysis although they satisfied all three criteria discussed above.

A Total of 266 treatments were analyzed (188,064 ha), including 173 blocks treated with *B. thuringiensis* (138,282 ha) and 93 blocks treated with disparlure (49,782 ha) (Table 1). Among blocks treated with *B. thuringiensis,* 13 received one application, and 160 had two applications. Among blocks treated with disparlure, 89 received the dose of 75 g/ha, and four received 37.5 g/ha.

Index of Treatment Success. Treatment success was evaluated by comparing the reduction in moth counts in the block treated adjusted for the natural change in moth counts in the reference area around it. Moth counts were interpolated in a 500-m grid using median indicator kriging with subsequent E-type estimation (Deutsch and Journel 1992). Ordinary kriging was not appropriate because the distribution of moth counts in traps was not normal. The advantage of the median indicator kriging with E-type estimation compared with lognormal kriging was that it provided unbiased estimates. Interpolated moth counts were averaged in "treatment cells" and "reference cells" in a 24 × 24 km area around the treatment block (Fig. 2). Other treated blocks, as well as a 1.5-km buffer area directly around all treated blocks, were not included in the reference cells.

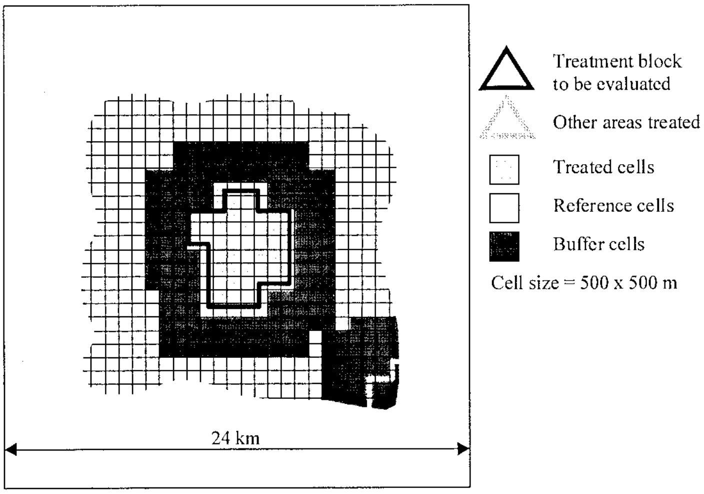

Fig. 2. Example of treated, reference, and buffer areas used for estimating the index of treatment success.

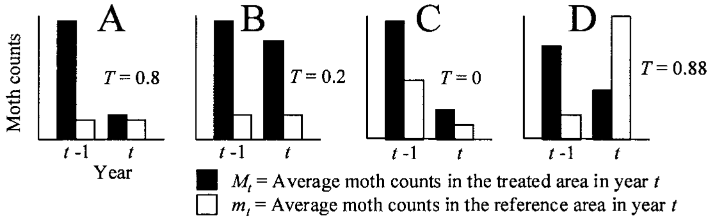

Fig. 3. Hypothetical examples of estimating the index of treatment success, T.

The index of treatment success, T, was estimated as:

$$T = 1 - \frac{M_t \cdot \max\,(m_{t-1},\ 0.05)}{M_{t-1} \cdot \max\,(m_t,\ 0.05)} \qquad [2]$$

where M_t and m_t were average moth counts in year t in the treatment block and in the reference area around it, respectively. If the average moth counts in reference cells were too low, they could not be estimated with satisfactory accuracy. To avoid an unpredictable effect on the index T, average moth counts in the reference cells were bounded by the value of 0.05 in equation 2.

Index T indicates the proportion reduction in moth counts in pheromone traps caused by the treatment. A value of $T = 0$ corresponds to no treatment effect, $T = 1$ corresponds to complete removal of the population. A negative index of treatment success indicates an increase of population numbers in the block. Treatments were considered successful if $T > 0.67$, partially successful if $0.33 < T < 0.67$, and unsuccessful if $T < 0.33$. These threshold values for indexes of treatment success were selected based on the analysis of moderate to high-density populations reported by Liebhold et al. (1996). In their study, most treatments resulted in ≈threefold decrease in egg mass density. Dimilin treatments were slightly more effective, and *B. thuringiensis* treatments were less effective. These levels of mortality are usually considered satisfactory in field trials (Dubois et al. 1988).

A successful treatment did not necessarily mean that the colony had been eradicated. If the initial population numbers were high, then several successful treatments may be needed to eliminate the target population.

Four hypothetical situations are presented in Fig. 3 to illustrate the meaning of index T. In situation A, moth counts in the block treated were reduced five times, and moth counts in the reference area did not change; index $T = 0.8$ indicates that the treatment was successful. In situation B, moth counts in the treatment block declined just slightly; index $T = 0.2$ indicates that the treatment was not successful. In situation C, moth counts in the block decreased four times after treatment, but the same change in moth counts was observed in the reference area. Thus, the decrease in moth counts was apparently not caused by the treatment; index $T = 0$ indicates that the treatment was not successful. In situation D, moth counts in the block treated were reduced by 50% only, but moth counts in the reference area quadrupled; index $T = 0.88$ indicating that the treatment was successful.

Equation 2 was used for *B. thuringiensis*, because its effect could be evaluated in the year of application. But the effect of disparlure could not be evaluated using traps in the year of application because few if any males would be captured in the presence of pheromone treatments. Thus, we evaluated disparlure treatments using a modified index of treatment success:

$$T = 1 - \frac{M_{t+1} \cdot \max\,(m_{t-1},\ 0.05)}{M_{t-1} \cdot \max\,(m_{t+1},\ 0.05)}, \qquad [3]$$

Treatment success was analyzed using a general linear model (SAS 1996; Proc GLM). The transformed index T, $-\log(1.01 - T)$, was modeled as a function of the following factors: (1) treatment method (agent, number of applications of *B. thuringiensis*, or dose of disparlure); (2) area of the block treated; (3) distance to the generally-infested area; (4) log-transformed maximum pretreatment moth counts in the treatment block, $\log(N_{\max} + 1)$; and (5) log-transformed ratio X of the average pretreatment moth counts in the reference area to the average pretreatment moth counts in the treatment block, $\log(X + 0.01)$. The equation for transforming index T was selected according to the following two criteria: it is monotonic, and makes the distribution of T-values closer to normal. Distance to the generally infested area was calculated as the distance to the inner boundary of the STS action zone. Because there was a tendency to use disparlure in blocks with lower population density, it was important to use factor (4) in the analysis, which would adjust the results to possible effects of the initial population density. Factor (5) was selected during preliminary exploratory analysis according to its strong effect on index T. Incorporation of this factor in the GLM was important for increasing the sensitivity of analysis to other factors. Factors (2–5) were covariates. Adjusted means, Z, of the transformed index T generated by GLM were back-transformed as $T = 1.01 - 10^{-Z}$.

A potential problem with comparison of treatment success in blocks treated with *B. thuringiensis* and disparlure was that evaluation of *B. thuringiensis* blocks was conducted in the year of treatment, whereas the evaluation of disparlure blocks was conducted in the year after treatment. Consequently, different equations (2 and 3) were used to estimate the index of treatment success for different agents. To avoid uncertain conclusions, we used equation 3 for *B. thuringiensis* treatments in addition to disparlure treatments and repeated the GLM analysis.

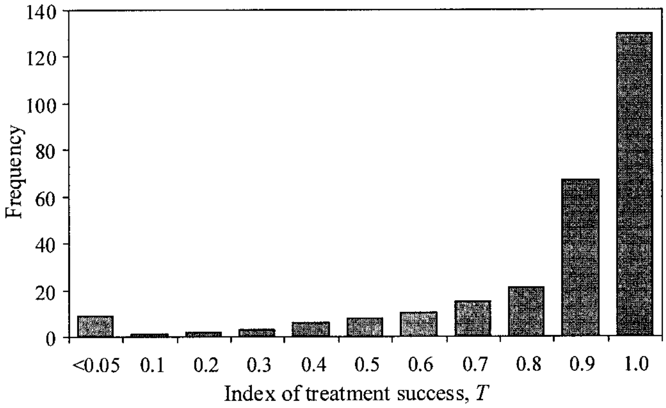

Fig. 4. Frequency distribution of the index of treatment success.

Retreatment Statistics. Another indicator of treatment success is the frequency of repeated treatments in the same area. Overlapping of treatment blocks was determined using raster maps with a 100-m resolution. The proportion of blocks retreated at least partially was compared among blocks treated initially with *B. thuringiensis* and disparlure using contingency table analysis. The same method was used to analyze the relationship between the index of treatment success (treatments were classified into five groups $T = -2.00$–0.67, 0.67–0.89, 0.90–0.96, 0.97–0.99, and 1.00) and the probability of repeated treatment.

Results

Index of Treatment Success. Estimated indexes of treatment success for each treatment block are available on-line (Sharov 2001). The distribution of the index of treatment success, *T*, was highly skewed to the right (Fig. 4). Most treatments had values of *T* close to 1.0 indicating successful suppression of gypsy moth colonies. Out of 266 treatments, 226 (85.0%) were successful, 25 (9.4%) were partially successful, and 15 (5.6%) were not successful. The proportions of successful, partially successful, and not successful treatments were almost equal in blocks treated with *B. thuringiensis* and disparlure (Fig. 5).

Before comparing the success of *B. thuringiensis* and disparlure treatments, we checked if the number of *B. thuringiensis* applications and disparlure dose had any effect. The GLM analysis showed that the index of treatment success did not depend significantly on either the number of *B. thuringiensis* applications (Table 2, A), or disparlure dose (Table 2, B). This result should not be interpreted as a proof that the number of *B. thuringiensis* application or disparlure dose has no effect on treatment success because the number of blocks that received one application of *B. thuringiensis* (11) or 37.5 g/ha dose of disparlure (4) was rather low. The only purpose of this analysis was to show that all *B. thuringiensis* treatments in this study could be considered as one homogeneous group and all disparlure treatments as another group.

The GLM analysis (Table 2, C) indicated that two factors had a significant effect on the index of treatment success *T*: (1) treatment agent, and (2) the ratio *X* of pretreatment moth counts in the reference area to moth counts in the treatment block. Adjusted av-

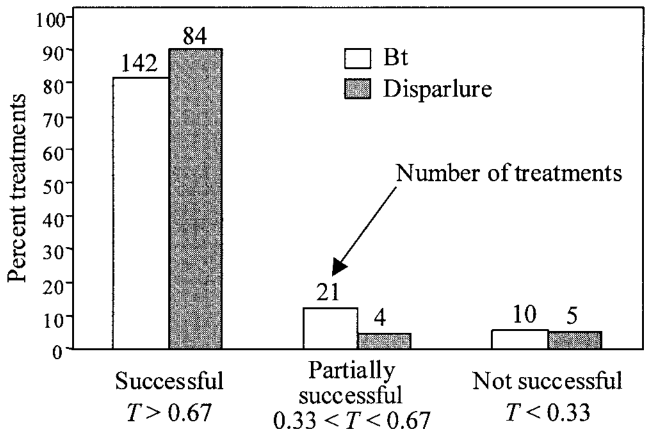

Fig. 5. Percent successful, partially successful, and nonsuccessful treatments with *B. thuringiensis* and disparlure.

Table 2. General linear model (GLM) analysis of transformed index of treatment success, T

Dependent variable	Factor*	Sum of squares	df	F	P
A $-\log(1.01 - T)$, equation (2) for *B. thuringiensis*	Num. applications	0.02	1	0.08	0.776
	Area of the block	0.36	1	1.31	0.254
	Distance	1.00	1	3.69	0.056
	$\log(N_{\max} + 1)$	0.01	1	0.04	0.849
	$\log(X + 0.01)$	4.41	1	16.23	<0.001
	Error	45.38	167		
B $-\log(1.01 - T)$, equation (2) for disparlure	Disparlure dose	0.11	1	0.32	0.576
	Area of the block	0.15	1	0.42	0.518
	Distance	1.32	1	3.81	0.054
	$\log(N_{\max} + 1)$	0.62	1	1.79	0.184
	$\log(X + 0.01)$	5.60	1	16.18	<0.001
	Error	30.12	87		
C $-\log(1.01 - T)$, equation (2) for *B. thuringiensis*, and (3) for disparlure	Treatment agent	5.51	1	18.24	<0.001
	Area of the block	0.28	1	0.93	0.335
	Distance	0.08	1	0.27	0.607
	$\log(N_{\max} + 1)$	0.76	1	2.52	0.114
	$\log(X + 0.01)$	12.39	1	41.01	<0.001
	Error	78.54	260		
D $-\log(1.01 - T)$, equation (3) for *B. thuringiensis* and disparlure for $5 \leq N_{\max} \leq 50$.	Treatment agent	6.5388	1	22.16	<0.001
	Area of the block	0.4732	1	1.6	0.207
	Distance	0.7229	1	2.45	0.119
	$\log(N_{\max} + 1)$	0.9636	1	3.27	0.072
	$\log(X + 0.01)$	11.0028	1	37.29	<0.001
	Error	57.8391	196		
E $-\log(1.01 - \mathrm{T})$, equation (3) for *B. thuringiensis* and disparlure	Treatment agent	6.14	1	17.85	<0.001
	Area of the block	0.02	1	0.05	0.827
	Distance	0.69	1	2.01	0.158
	$\log(N_{\max} + 1)$	1.42	1	4.13	0.043
	$\log(X + 0.01)$	18.16	1	52.85	<0.001
	Error	77.67	226		

* Factors: X = ratio of pre-treatment moth counts in the reference area to moth counts in the treatment block; $N_{\max}$ = pretreatment maximum moth counts in traps; Treatment agent = *B. thuringiensis* versus disparlure, Distance = distance to the generally-infested area, km.

erages of the transformed index of treatment success generated by the GLM were 1.070 ± 0.042 (±SE) for *B. thuringiensis* and 1.394 ± 0.060 for disparlure. Back transformation yielded the following values: $T = 0.925$ for *B. thuringiensis* and $T = 0.970$ for disparlure. Because the index of treatment success means mortality because of treatment, the survival $(1 - T)$ is ≈two times lower for disparlure than for *B. thuringiensis*, indicating that disparlure was two times more effective in reducing gypsy moth numbers.

Treatment success was not related to pretreatment population density measured by log maximum moth counts in traps, $\log(N_{\max} + 1)$, $P = 0.114$ (Table 2C). Although blocks with high densities were more frequently treated with *B. thuringiensis* than with disparlure (Fig. 6), this should not obscure our estimates of

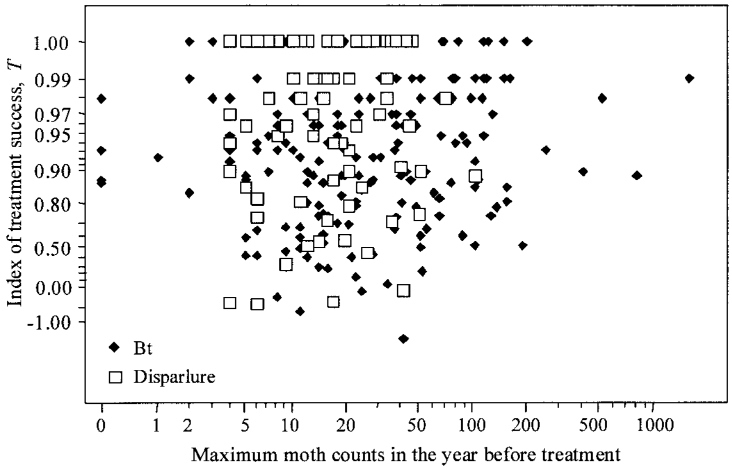

Fig. 6. Index of treatment success for *B. thuringiensis* and disparlure treatments as a function of log maximum moth counts in the block before treatment.

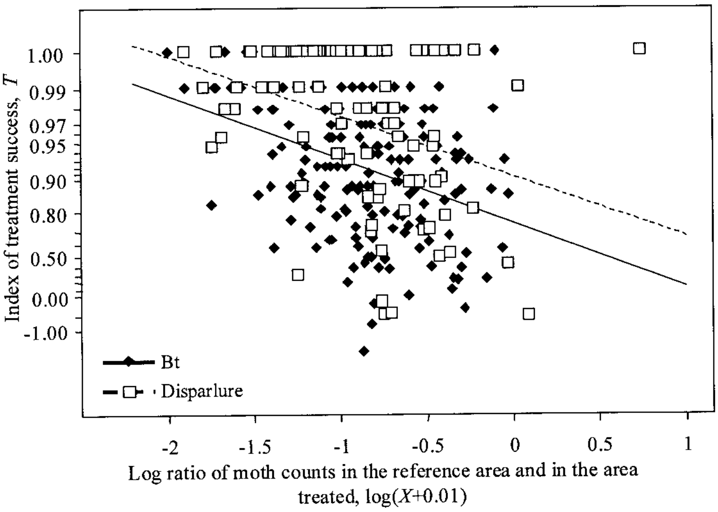

Fig. 7. Regression of transformed index of treatment success versus log-transformed ratio of moth counts outside and inside of treated block. Regression equations are $-\log(1.01 - T) = 0.591 - 0.526 \cdot \log(X + 0.01)$ for *B. thuringiensis* treatments and $-\log(1.01 - T) = 0.973 - 0.498 \cdot \log(X + 0.01)$ for disparlure treatments.

relative effectiveness of these methods for two reasons. First, in the GLM analysis, the net effect of each factor is evaluated. The result is adjusted automatically to possible effects of all other factors in the model. Second, pretreatment density had no detectable effect on treatment success (Fig. 6; Table 2C). To double-check that pretreatment density does not affect our conclusions, we selected a subset of data ($n = 202$) with maximum pretreatment moth counts in traps from 5 to 50 and repeated the GLM analysis. The results (Table 2D) were very similar to those with all data.

Treatment success was lower in blocks with a greater ratio, $X = m_{t-1}/M_{t-1}$, of pretreatment moth counts in the reference area to moth counts inside the block (Fig. 7). Regression lines in Fig. 7 were statistically significant both for *B. thuringiensis* ($R^2 = 0.123$; $t = 4.91$; df = 171; $P < 0.001$) and disparlure ($R^2 = 0.133$; $t = 3.74$; df = 91; $P < 0.001$). Low values of the ratio X indicated that populations were well isolated and well delineated (i.e., the treatment block covered the entire area with high moth counts and almost no moths were captured around it). In blocks with low X values, treatments appeared more successful than in blocks with higher X values (i.e., not well isolated or not well delineated).

GLM analysis of the index of treatment success that was estimated using equation 3 both for *B. thuringiensis* and disparlure treatments yielded similar results (Table 2E). Again, effects of the treatment agent and ratio X were significant. Adjusted averages of the transformed index of treatment success generated by the GLM were 1.022 ± 0.051 (±SE) for *B. thuringiensis* and 1.376 ± 0.063 for disparlure. Back transformation yielded the following values: $T = 0.915$ for *B. thuringiensis* and $T = 0.968$ for disparlure. Disparlure treatments were more effective than *B. thuringiensis*.

Retreatment Statistics. Out of the 232 blocks treated in 1993 through 2000, 64 (28%) were retreated later (through 2001) at least partially. Blocks that were initially treated with *B. thuringiensis* were retreated more frequently (54 out of 139, 38.9%) than blocks initially treated with disparlure (10 out of 93, 10.8%). The difference is statistically significant ($\chi^2 = 22.0$, df = 1, $P < 0.001$); this gives an additional evidence that disparlure was more effective than *B. thuringiensis* applications. Some blocks were retreated several times and the total number of repeated treatments was 81. More than half of repeated treatments covered <20% of the area treated initially (Fig. 8). Additional treatments were usually only needed to clean up populations at the margins of the block. Only 19 repeated treatments (23%) covered >50% of the area treated initially.

The percent of retreated blocks decreased with increasing index of treatment success, T (Fig. 9). The relationship is statistically significant ($\chi^2 = 47.4$, df = 4, $P < 0.001$). This means that blocks treated with no

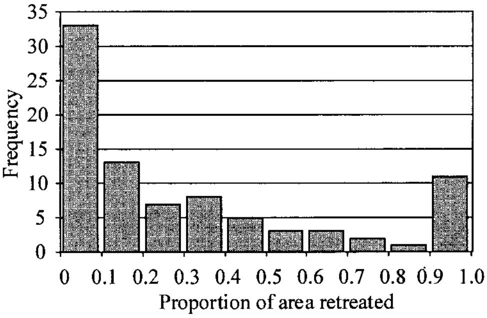

Fig. 8. Frequency distribution of the proportion of blocks that were retreated.

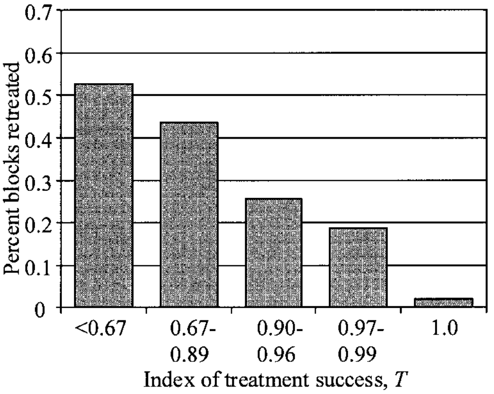

Fig. 9. The probability of repeated treatments in blocks with various values of the index of treatment success for the initial treatment.

or partial success had a higher chance of retreatment than blocks treated successfully.

Discussion

In this paper we have demonstrated that pheromone traps can be used for evaluating the success of treatments in isolated low-density populations of the gypsy moth. This method of treatment evaluation can be incorporated as a routine procedure in pest-management programs. It is already a major component of the STS data analysis (Sharov 2001). However, this method has several limitations:

1. It should not be used in high-density populations because traps become saturated and would not represent population abundance (Liebhold et al. 1995, Elkinton 1987).
2. It may yield biased results if high-density populations are located nearby (this may happen if only a portion of the infested area was treated) because male moths may disperse to the treated block.
3. In the case of disparlure treatment, this method cannot be used in the year of application. This delays treatment evaluation by 1 yr.
4. Even in areas of predominantly low-density populations, long-range dispersal of male moths from outbreak areas may affect the relationship between moth counts in pheromone traps and local population abundance. In this case, this method of evaluation may give biased results. However, in continuously monitored areas it is always possible to use additional data collected in another year to compensate for the effect of moth dispersal.

Results of treatment evaluation in the STS project demonstrated that mating disruption with disparlure was more effective against isolated low-density populations of the gypsy moth than *B. thuringiensis* treatments. This conclusion is drawn both from the difference in the index of treatment success and in the frequency of consecutive treatments in the same area. The evidence comes mostly from colonies with maximum trap catches <50 moths. But disparlure may appear effective even at higher population densities as indicated by four successful treatments ($T > 0.67$) in colonies with maximum moth catches ranging from 52 to 107.

The efficacy of *B. thuringiensis* depends on the timing of applications (treatment should coincide with the peak of second instars in the population) and on weather conditions (Reardon et al. 1994). In the STS project, the timing of applications was always carefully determined based on a phenology model (Sheehan 1992) and observations of egg hatch in the field. Although we don't have a record of exact weather during each treatment, we believe that every effort was made to make treatments at favorable conditions. Thus, we think that the efficacy of *B. thuringiensis* was not affected by application timing or weather more than in any other operational project.

This is the first large-scale evaluation of gypsy moth disparlure treatments in an operational system, and it confirms the effectiveness of this method. Disparlure can be used only as a preventive pestmanagement tool because it does not disrupt mating in high-density populations that may defoliate the forest. In contrast to traditional gypsy moth management programs, STS is preventive. Thus, development of mating disruption has become a key element to the success of STS (Sharov et al. 2002). Target-specific tactics such as mating disruption will continue to be critical in STS to protect unique habitats and rare, threatened or endangered species that occur within the project area.

The current cost of disparlure treatments at 75 g (AI)/ha ($64/ha) is approximately the same as a double application of *B. thuringiensis* ($64–69/ha) (D. Leonard, unpublished). The recommended dose for operational disparlure in the STS project has been recently lowered to 37.5 g (AI)/ha, thus reducing the cost to $42/ha (D. Leonard, unpublished). Tests are underway that could result in further cost reduction in the future by using lower doses of pheromone and/or wider swaths. Thus, pheromone treatments appear not only effective but also cost-efficient.

The results of this study suggest also that *B. thuringiensis* applications were generally more successful at reducing population levels in isolated low-density colonies than in the continuous, high-density populations analyzed by Liebhold et al. (1996). The effect of preventive treatments in low-density populations may be magnified because of reduced mating success of females (Sharov et al. 1995b). If gypsy moth populations are suppressed below the density threshold that supports mating and population growth, then they are more likely to become extinct without further intervention. However, it is difficult to compare these studies because of the difference in objectives and in the density of gypsy moth populations.

The index of treatment success, *T*, decreased with increasing ratio, *X*, of pretreatment moth counts in the reference area to moth counts in the block itself. This result indicates that treatments are more successful if colonies are well isolated or delineated (i.e., no part of a colony escapes the treatment). If a block was not well delineated (e.g., because of insufficient trap density), then some portion of a population would survive and start growing in the following year. This would result in a lower effect of treatment.

Proper delineation of treatment blocks is an important component of the STS project strategy. Because gypsy moth is a dangerous invasive pest species, there was a tendency in the past to eradicate isolated colonies as soon as they are detected. Results of this paper show that it is worthwhile to postpone the treatment and delineate the colony with a dense grid of pheromone traps (i.e., with 500 m intertrap distance). The grid should be larger than the colony itself so that traps in outside rows capture no or very few moths. This ensures the treatment to be well targeted and more successful.

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