
Correlation of Counts of Gypsy Moths (Lepidoptera: Lymantriidae) in Pheromone Traps with Landscape Characteristics

Alexei A. Sharov, Andrew M. Liebhold, and E. Anderson Roberts

ABSTRACT. The effect of landscape characteristics (elevation, slope, aspect, and vegetation) on counts of gypsy moths in pheromone traps was studied in a >5 million ha area in Virginia and West Virginia from 1988 to 1994. Habitat effects on population numbers depend on dominant ecological processes in the area: we define *K*-, *r*-, and *c*-effects as differences in carrying capacity, population growth rate, and colonization rate, respectively, that are associated with different landscape characteristics. To differentiate among these effects, we analyzed individually the following three zones at the expanding front of the gypsy moth population: infested (*K*-effects), transition (*r*-effects), and uninfested (*c*-effects). Among landscape characteristics, elevation was most highly correlated with moth counts. Moth counts increased with increasing elevation in the infested and transition zones (*K*- and *r*-effects) which may be associated with good habitats at high elevation. However, the highest average moth counts in the uninfested zone were found at low elevation. Possibly this was a *c*-effect which resulted from a greater colonization rate in the low-elevation areas where human population densities are greater and the probability of inadvertent transfer of egg masses on human vehicles is increased. The effect of vegetation on moth counts was much less pronounced than the effect of elevation. Moth catches were higher in deciduous and mixed forests than in coniferous forests and nonforested areas. The effect of landscape characteristics on moth captures was stronger in the transition zone than in other zones. *FOR. SCI.* 43(4):483–490.

Additional Key Words: *Lymantria dispar*, elevation, forest type, biological invasion.

GYPSY MOTH, *Lymantria dispar* (L.) is one of the most important forest pest insects in the eastern United States (Doane and McManus 1981). It 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). It annually defoliates millions of hectares of forests causing tree mortality in repeatedly defoliated sites, deterioration of forest aesthetic and recreational values, allergy in humans, and other problems. Two major types of dispersal contribute to the expansion of the gypsy moth range: (1) transportation of egg masses and other life stages by humans, and (2) airborne

dispersal of first-instar larvae (McFadden and McManus 1991). The majority of airborne larvae are deposited within several hundred meters from the source (Mason and McManus 1981), but a small proportion of them can travel as far as 19 km (Taylor and Relling 1986). However, new isolated infestations are always small in size, which is difficult to explain by transfer of windborne larvae. The history of many new infestations can be traced to household moves from the infested zone to the uninfested zone (McFadden and McManus 1991). Thus, gypsy moth dispersal combines long “jumps” due to transportation of egg masses with local colony growth caused by larval dispersal. The area at the expanding popula-

Alexei Sharov is with Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061; Andrew Liebhold is with Northeastern Forest Experiment Station, USDA Forest Service, 180 Canfield St., Morgantown, WV 26505; and Anderson Roberts is with Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061.

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tion front can be separated into three zones: the uninfested zone with few isolated small colonies, the transition zone with larger and partially coalescing colonies, and the infested zone with high-density coalesced populations (McFadden and McManus 1991).

Monitoring and management of gypsy moth populations is often conducted at the regional scale. In 1988–1992 the USDA Forest Service implemented the Appalachian Integrated Pest Management (AIPM) program within an area of 5.18 million ha in the central Appalachian Mountains (Reardon 1991). Reduction of adverse gypsy moth effects on forest ecosystems and slowing the spread of this pest were among the most important objectives of this program. It was succeeded by the Slow-the-Spread (STS) pilot program which was designed only to slow population spread (Leonard and Sharov 1995). In both projects, decisions depended on the location of the area relative to the expanding population front and to landscape characteristics.

A regional approach to population management requires detailed information on the spatial distribution of the target population. In this study we attempted to determine the extent to which male moth counts were correlated with various habitat characteristics, such as elevation, slope, aspect, and vegetation. This correlation (if it exists) can be used for optimization of population monitoring and for improving our understanding of the species' biology (e.g., habitat preferences and dispersal).

Most previous studies of the relationship between gypsy moth abundance or defoliation and habitat characteristics focused on interactions occurring at the stand level (i.e., woodlots of 10–1000 ha). Susceptibility to gypsy moth defoliation generally declines as the proportion of preferred host species decreases (Bess et al. 1947, Houston and Valentine 1977, 1985). Stands located on xeric sites are generally more susceptible than stands on moist sites (Bess et al. 1947, Montgomery and Wallner 1988). According to Bess et al. (1947), in New England, susceptible stands are mostly located either in coastal areas with sandy soils or on mountain ridges. The abundance of natural enemies and the presence of refugia that can protect resting gypsy moth larvae from predation were also considered important components of stand susceptibility (Bess et al. 1947, Campbell 1976, Houston and Valentine 1977).

The relationship between gypsy moth density (or defoliation) and landscape characteristics can only be detected using spatial analysis on a landscape level. Liebhold et al. (1994) were the first to use spatial analysis for landscape characterization of forest susceptibility to the gypsy moth. These authors found that the frequency of defoliation was the highest in pine, oak-pine, and oak-hickory forest types, and lowest in maple-birch-beech and aspen-birch stands and in nonforest areas. The three most susceptible forest types exhibited decreased susceptibility at elevations lower than 200 m. However, this study had several limitations. First, the significance of the relationship between defoliation frequency and landscape characteristics was not tested statistically. Spatial autocorrelation both in defoliation frequency and in landscape characteristics precluded the application of a simple

statistical analysis. Second, defoliation occurs only at very high population density, and thus, this analysis did not provide any information on the behavior of low- and medium-density populations in various habitats. Third, the analysis of defoliation frequency does not provide any clues about ecological processes that determine the effect of various habitats on gypsy moth populations. For example, it remains unknown if population growth rate is higher in frequently defoliated areas than in seldom defoliated areas.

To overcome these limitations we decided to use quantitative measures of gypsy moth abundance rather than defoliation frequency. Monitoring of the gypsy moth is based mainly on two methods: counts of overwintering egg mass populations, and counts of male moths in pheromone-baited traps (Ravlin et al. 1987). Egg mass counts are the most reliable census method in medium- and high-density populations, and thus they are widely used for making decisions concerning aerial suppression of outbreak populations (Ravlin et al. 1987). Pheromone traps are highly sensitive and cost-effective at detecting low-density populations (Schwalbe 1981). Thus they are mostly used to detect new isolated gypsy moth infestations and to monitor the expansion of the population front. In this paper we use historical data on moth counts in pheromone traps primarily because of the large spatial and temporal scope of these data. Although moth counts in pheromone traps had little correlation with observed defoliation in Massachusetts (Liebhold et al. 1995), they can be helpful in predicting defoliation in recently infested areas (Gage et al. 1990) and are essential components of many IPM decision algorithms (Ravlin et al. 1990).

We expected that correlations of moth counts with landscape characteristics would be different in the infested, transition, and uninfested zones because of different ecological processes that dominate in these zones. Colony establishment dominates in the uninfested zone, colony growth dominates in the transition zone, and stationary (equilibrium or cyclic) dynamics are characteristic of the infested zone (Sharov et al. 1996). Habitat effect on population numbers is mediated by these processes and may be zone-specific. Different kinds of habitat effects can be associated with parameters of the logistic population model: K -effect we define as the difference in carrying capacity among habitats (in the infested zone); r -effect is the difference in population growth rate among habitats (in the transition zone). Colonization (immigration) process is not included in the original logistic model, but it can be easily incorporated. Thus, we can consider the c -effect (c from "colonization") which means the difference in colonization rate among geographical points (in the uninfested zone). To separate K -, r -, and c -effects of landscape characteristics on population numbers, these effects should be analyzed individually in the infested, transition, and uninfested zones at the expanding population front.

Adult male gypsy moths can disperse from their eclosion sites whereas females are flightless in North America. As a result, the spatial distribution of male moths may be different from the distribution of reproducing populations, and the value of its analysis can be questioned. Nevertheless, we believe that the analysis of male moth spatial distribution is

important because of the following. First, this is the only method of population monitoring that is currently used in a large geographical area (Michigan, Indiana, Ohio, West Virginia, Virginia, North Carolina, and other states). Egg mass surveys have never been intensively conducted over such large areas. The largest egg mass sampling programs were implemented in coastal New England (1910–1931), in Massachusetts (1985–1991) (Liebhold et al. 1991), and in the AIPM project (1988–1991). The first two programs had large distances between sample locations, and thus spatial resolution was low. Only the AIPM program had sufficient spatial resolution (several samples per 1 km²). However, the sampling program was expensive, and there were not sufficient funds to continue it after 1991. Second, egg mass counts were generally above detectable levels in the infested zone only. In the uninfested and transition zones, moth trapping remains the only reliable monitoring method. Thus, the analysis of the spatial distribution of moth counts is justified.

Materials and Methods

Area and Data

We used historical pheromone trap data (1988–1994) collected in the Appalachian Mountains in northern Virginia and southern West Virginia. Most data were collected as part of the AIPM and STS programs (Reardon 1991, Leonard and Sharov 1995) (Figure 1). Complete details of male moth trapping were described by Sharov et al. (1995). The location of traps was recorded using Universal Transverse Mercator coordinates (Snyder 1987). The basic trap grid had intertrap distance of 2 km in Virginia and 3 km in West Virginia in 1988–1991. Since 1992, a 1 km grid was used in the STS project area for detecting isolated gypsy moth infestations

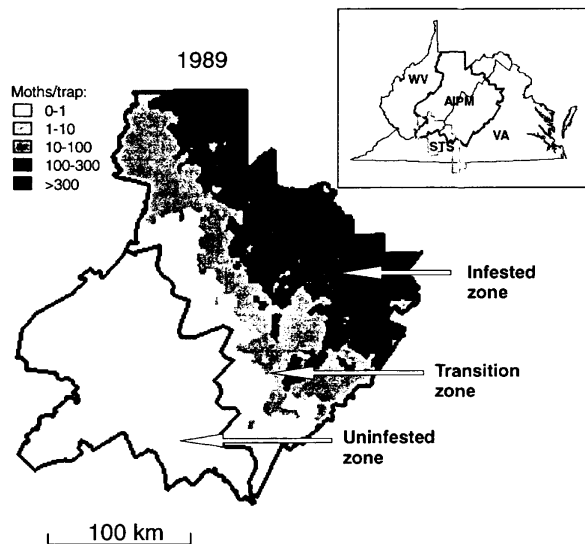


Figure 1. Appalachian Integrated Pest Management (AIPM) and Slow-the-Spread (STS) project areas. Gypsy moth catches in pheromone-baited traps in 1989 interpolated using median kriging are shown by the grayscale. Boundaries of the infested, transition, and uninfested zones were drawn at 1 and 300 moths/trap thresholds.

beyond the expanding population front. High-density trapping grids with <1 km intertrap distance were not included in these analyses.

The spatial distribution of male moth counts was analyzed in three zones: the infested zone where trap capture was >300 moths/trap, the transition zone where trap capture ranged from 1 to 300 moths/trap, and the uninfested zone where trap capture was <1 moth/trap. Data obtained in the AIPM project area from each year from 1988 to 1994 were subdivided into the three zones. Only a few traps were located in the infested zone in 1993–1994. Thus, only two zones (transition and uninfested) were analyzed in these years. The STS project area was located in the uninfested zone only. Thus, it was not subdivided into zones. STS data were more extensive than AIPM data, and therefore we used them instead of data from the uninfested zone in the AIPM area in 1992–1994.

The boundaries between zones were estimated for each year using the “best cell classification” method (Sharov et al. 1995). This method minimizes the number of grid cells that are misclassified below or above a specific population threshold (we used thresholds of 1 and 300 moths/trap). The best cell classification method was applied to continuous 1 × 1 km indicator raster maps that coded (0, 1) for each cell if the gypsy moth population was below the threshold (value = 0) or above the threshold (value = 1). Indicator maps of male moth counts were generated using indicator median kriging and subsequently categorized using the cumulative probability function as above or below the threshold value of 0.5 (Sharov et al. 1995). Boundary points were estimated in strips of 1 km width perpendicular to the general boundary direction with azimuth 147.5° (Sharov et al. 1995).

A strong trend occurred in counts associated with gypsy moth spread from northeast to southwest in the transition zone. Trend was removed by using residuals from either linear regression:

$$T = b_0 + b_1x + b_2y \quad (1)$$

or logistic regression:

$$T = \frac{\ln(1000)}{1 + \exp[-(b_0 + b_1x + b_2y)]} \quad (2)$$

where T is the trend [predicted log count of males, $\ln(N + 1)$] at sample point with coordinates of x and y , and b_i are regression coefficients. The upper limit of the logistic function was set equal to $\log(1000)$ because trap capacity was ≈ 1000 moths. Logistic regression was performed using the NLIN procedure (SAS Institute 1992). Both regressions (1) and (2) were estimated in each zone individually, and then, the one that yielded highest R^2 was selected. In each zone, we analyzed the effect of the following factors on the residuals of log-transformed male moth counts: elevation, slope, aspect, type of vegetation, and land use/land cover type.

Elevation data (Figure 2) were obtained from U.S. Geological Survey 1:250,000 Digital Elevation Models (DEM) with a resolution of ≈ 90 m (Elassal and Caruso 1983).

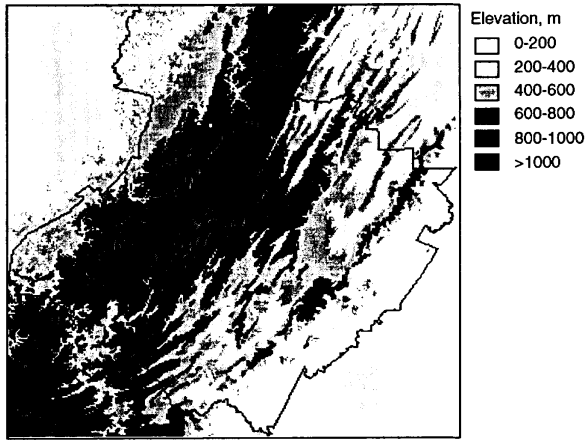


Figure 2. Elevations in the Appalachian Integrated Pest Management area; data from U.S. Geological Survey Digital Elevation Models (Elassal and Caruso 1983).

Elevation at trap locations was estimated from the value of the nearest DEM grid point. We used five categories of elevation (0–250, 250–500, 500–750, 750–1000, and >1000 m). Slope and aspect at sample locations were estimated from the eight nearest DEM points. Four categories of slope (0–5, 5–10, 10–15, and >15°) and eight categories of aspect (with azimuth intervals of 45°) were considered.

Three different vegetation classification maps designated here as FIA1, FIA2, and USGS were used. Forest type data FIA1 was extracted from a 1:7,500,000 scale map published by the Society of American Foresters (Eyre 1980). The map identifies eight forest type groups in the study area: (1) spruce–fir, (2) white–red–jack pine, (3) loblolly–shortleaf

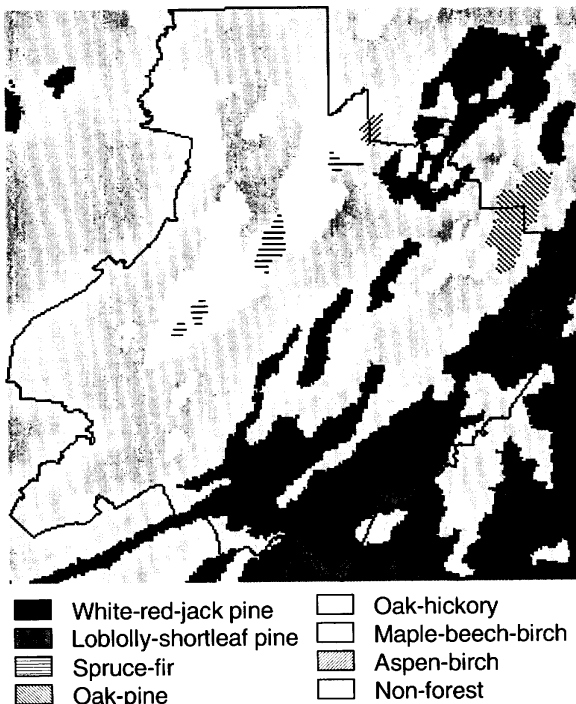


Figure 3. Classification of forest types with large polygons (FIA1) in the Appalachian Integrated Pest Management project area.

pine, (4) oak–pine, (5) oak–hickory, (6) maple–beech–birch, and (7) aspen–birch, and (8) nonforest (Figure 3). Only eight traps occurred in the aspen–birch group, so this group was excluded from the analysis. Each forest type group includes multiple forest types, and these types include various tree species (Eyre 1980), among which there are hosts both favorable and unfavorable to the gypsy moth. Despite the generic nature of this classification, it can be useful for identification of areas susceptible to gypsy moth defoliation (Liebhold et al. 1994). The FIA2 map classified the same area but it was primarily derived from remotely sensed data (Zhu and Evans 1992). This map is characterized by much more localized discontinuity than the FIA1 map; thus, it was not possible to present it in a gray-scale format. The FIA2 map uses the same categories of forest as FIA1, except there were no aspen–birch stands. Only a few traps (from 8 to 23) occurred in the spruce–fir group, so this group was excluded from the analysis. USGS is 1:250,000 land use/land cover data provided by the U.S. Geological Survey (1986). Spatial resolution of USGS data was 250 m. USGS data have several dozens of categories of land use/land cover, from which we selected only four that were useful for the analysis of gypsy moth distribution: deciduous forest, coniferous forest, mixed forest, and nonforest (all other categories combined).

Effect of six factors (elevation, slope, aspect, FIA1, FIA2, and USGS) on residuals of log moth counts was quantified using the one-way analysis of variance (ANOVA). The significance of effects in ANOVA models could not be tested using standard threshold values of the *F*-statistic because both the factor and the response variable were autocorrelated. Thus, we used a Monte-Carlo approach to test the significance. Unconditional Gaussian simulation of moth counts at trap locations (Deutsch and Journel 1992) was performed using an exponential variogram model with parameters specific to each zone: infested, transition, and uninfested (Sharov et al. 1996). In each of 500 unconditional simulations, we generated male moth counts at each trap location assuming the null hypothesis of no correlation between moth catch and local factors in the study area. Then simulated moth counts were compared with actual factor values at same locations using the *F*-statistic (ANOVA). The distribution of these *F*-statistics was used to test the null hypothesis; if the experimental *F*-statistic was beyond the upper confidence limit (one-tail chi) of simulated *F*-statistics, then the effect of the factor was considered significant. A Bonferroni correction of error probability was used: $P = 0.05/6 = 0.008$ because six *F*-statistics (for six factors) were tested simultaneously. The upper confidence limit of simulated *F*-statistics were determined from the histogram.

If an effect on residuals of log moth counts, *Y*, was significant, then we estimated average *Y*-values for each factor category (e.g., for each elevation class). As a result, we obtained the array of averages $Y_{t,i}$, where *t* is year and *i* is factor category. These averages were summarized using the general linear model (GLM) with weights equal to the number of observations $N_{t,i}$ in year *t* that fall into category *i*. This analysis was performed for each zone individually. If the factor showed no significance in the GLM, then the effect of

the factor was not consistent among the years. When the GLM indicated a significant effect of a factor, then weighted averages Y_i were estimated for each factor category i .

Because elevation was found to have the strongest effect on moth counts, we used the two-factor GLM to separate this effect from effects of other factors (slope, aspect, vegetation). First, averages were estimated for each combination of elevation classes with categories of a second factor for each year when the effect of the second factor was significant. Years were again used as replications, and the number of observations in each year was used as the weight. If the second factor (and/or its interaction with elevation) was significant, then we considered that it was correlated directly with moth counts rather than indirectly mediated by elevation. This analysis does not take into account possible correlations among years. It indicates the consistency of factor effects in different years rather than statistical significance.

Results

Logistic models provided a better fit to the trend than linear models in all cases except for the infested and uninfested zones in 1991, and for the transition zone in 1988. Regression coefficients and R^2 values were published earlier (Sharov et al. 1996).

Most of the significant effects of local factors on the residuals of log moth counts were detected in the transition zone (Table 1). The proportion of significant effects was 7% in the infested zone, 48% in the transition zone, and 19% in the uninfested zone.

Among the factors, elevation (E) and land use/land cover (USGS) had the most significant effects on moth counts. Elevation was significant in 10 cases and USGS was significant in 8 cases. R^2 values for these two factors were highest

Table 2. Test for consistency of local factor effects on the residuals of log moth counts in different years.

Factor ^a	Zone ^a	Number of years	F^b	df	P
E	I	2	10.73	4, 5	0.011
E	T	5	45.97	4, 20	0.000
E	U	3	7.16	4, 10	0.005
S	T	4	38.05	3, 12	0.000
FIA2	T	4	12.25	5, 18	0.000
USGS	T	5	25.25	3, 16	0.000
USGS	U	3	5.53	3, 8	0.024

^a See footnotes to Table 1.

^b General linear model (GLM) analysis of averages obtained from those years where factor effect was significant; sample numbers were taken as weights.

in the transition zone, intermediate in the infested zone, and lowest in the uninfested zone (Table 1). The average R^2 value for elevation was 3.7% in the infested zone, 8.3% in the transition zone, and only 1.3% in the uninfested zone. The average R^2 value for land use/land cover followed the same pattern: 1.0% in the infested zone, 2.1% in the transition zone, and 0.5% in the uninfested zone.

The effect of elevation on male moth counts was consistent among years (Table 2). It had a strong nonlinear effect in the transition zone, and a much weaker effect in other zones (Figure 4). In the transition zone, moth counts increased with elevation increasing from 0–250 m to 750–1000 m; however, further increase in elevation had no significant effect on moth abundance. The average difference among log moth counts at low (0–250 m) and high (750–1000 m) elevation was 1.25, which corresponds to $e^{1.25} = 3.5$ times difference in actual moth counts. In the infested zone, moth counts were low in the lowest elevation class (<250 m) and equally high in all higher elevation classes. In the uninfested zone, elevation had an opposite effect on moth counts: the highest moth counts were found at low elevation.

Table 1. Effect of elevation, slope, aspect, and vegetation on the residuals of log moth counts in pheromone traps.

Zone ^a	Area ^b	Year	Significance of factor effects ^c						R^2 , %	
			E	S	A	FIA1	FIA2	USGS	E	USGS
I	AIPM	1988	+	–	–	+	–	–	9.2	2.2
I	AIPM	1989	–	–	–	–	–	–	2.7	0.3
I	AIPM	1990	–	–	–	–	–	–	0.8	1.4
I	AIPM	1991	+	–	–	–	–	–	3.3	0.6
I	AIPM	1992	–	–	–	–	–	–	2.3	0.4
T	AIPM	1988	–	+	–	–	+	+	3.1	1.5
T	AIPM	1989	–	–	–	–	–	+	0.9	1.4
T	AIPM	1990	+	+	+	–	+	+	12.7	3.4
T	AIPM	1991	+	+	–	–	+	–	8.5	1.3
T	AIPM	1992	+	–	–	–	–	+	6.5	1.5
T	AIPM	1993	+	–	–	–	–	–	14.8	2
T	AIPM	1994	+	+	–	+	+	+	11.3	3.7
U	AIPM	1988	+	–	–	+	+	+	2.6	0.7
U	AIPM	1989	–	–	–	–	–	–	0.1	0.5
U	AIPM	1990	–	–	–	–	–	–	0.6	0.4
U	AIPM	1991	–	–	–	–	–	–	0.9	0.2
U	STS	1992	+	–	–	–	–	–	1.8	0.3
U	STS	1993	+	–	–	–	–	+	3.1	0.6
U	STS	1994	–	–	–	–	–	+	0.3	0.6

^a I, infested zone; T, transition zone; U, uninfested zone.

^b AIPM, Appalachian Integrated Pest Management project area; STS, Slow-the-Spread project area.

^c E, elevation; S, slope; A, aspect; FIA1, forest type classification with large polygons; FIA2, forest type classification with small polygons; USGS, land use/land cover classification.

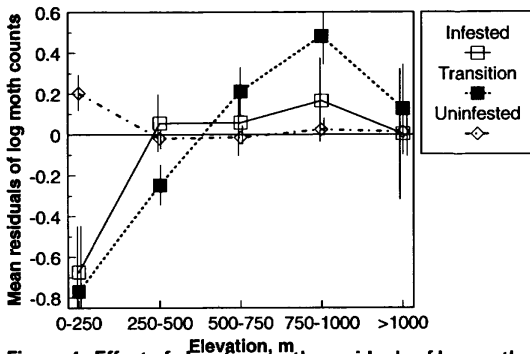


Figure 4. Effect of elevation on the residuals of log moth counts after trend removal. Vertical lines are confidence intervals ($P = 0.05$).

Effect of slope was significant (Table 1) and consistent among years (Table 2) in the transition zone only. However, the effect of slope was not consistent when combined with elevation (Table 3). This means that the effect of slope is mostly mediated by elevation.

Aspect and forest type classification FIA1 had significant effects on moth counts in only a few data sets (Table 1). Consistency of these effects could not be tested because of the lack of replications in different years. No further analysis has been done with these two factors.

The FIA2 forest classification map performed better for predicting moth counts than FIA1. It had significant effects on residuals of log moth counts in the transition zone only (Table 1), and these effects were consistent among years (Table 2). However, the effect of FIA2 was not consistent when analyzed together with elevation (Table 3). This means that the effect of FIA2 is mostly mediated by elevation.

The land use/land cover (USGS) classification yielded the best results among all classifications of vegetation. It was consistent among years in the transition zone and nonconsistent in the uninfested zone (Table 2). Analysis of the combined effect of USGS and elevation indicated that USGS had a consistent direct effect on moth counts (Table 3). Moth counts were lower in nonforest areas than in deciduous and mixed forests (Figure 5). In coniferous forests, moth counts were low, but the error was too large for any comparison to be possible.

Discussion

This is the first paper in which gypsy moth counts in pheromone traps have been related to landscape characteristics. The problem of relating spatially autocorrelated vari-

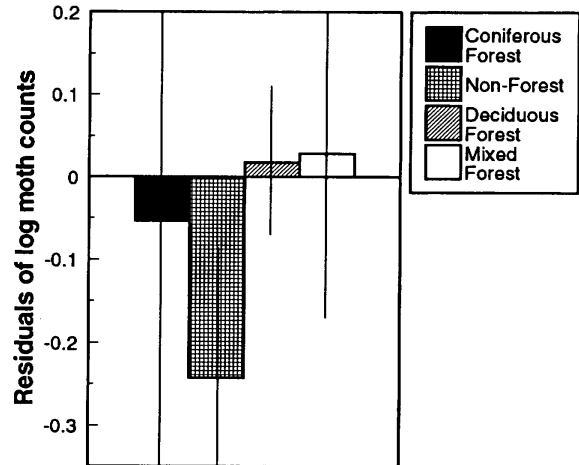


Figure 5. Effect of land use/land cover (USGS) on the residuals of log moth counts after trend removal in the transition zone; elevation effect excluded. Vertical lines are confidence intervals ($P = 0.05$).

ables was solved by the use of unconditional Gaussian simulations in order to test statistical hypotheses. Liebhold et al. (1994) did not use this method; thus, they could not test if the relationships between defoliation and landscape characteristics were significant. Also, for the first time we showed that the effect of landscape characteristics on population numbers was different among three zones at the expanding population front (infested, transition, and uninfested). These differences are related to the dominating ecological processes in each zone.

Among all local factors, elevation had the strongest effect on male moth counts. In the infested and transition zones, moth counts increased with elevation, which is consistent with studies of defoliation on a stand level (Bess et al. 1947, Houston and Valentine 1977) and on a landscape level (Liebhold et al. 1994). However, our study provides important additional information on the effect of elevation on gypsy moth populations. The elevation effect was only strong in the transition zone. In the infested and uninfested zones, this effect was often nonsignificant (Table 1), and in the uninfested zone it was opposite the relationship that was observed in the other zones (Figure 4).

Elevation is related to several ecological factors which may affect the performance of gypsy moth populations. High elevation sites usually have xeric soils which are associated with susceptible stands (Montgomery and Wallner 1988).

Table 3. Combined effect of elevation and other local factors on the residuals of log moth counts in different years and zones.

Factor ^a	Zone ^a	Number of years	Factor		Factor × Elevation		Elevation	
			F^b	P	F^b	P	F^b	P
S	T	4	0.59	0.623	0.60	0.834	9.88	0.000
FIA2 ^c	T	4	2.21	0.060	—	—	27.78	0.000
USGS	T	5	3.01	0.035	0.86	0.585	8.38	0.000
USGS	U	3	0.44	0.724	0.38	0.963	1.42	0.246

^a See footnotes to Table 1.

^b General linear model (GLM) analysis of averages obtained from the years where factor effect was significant (elevation effect was not necessary significant in these years); numbers of samples were taken as weights.

^c Interaction of FIA2 × Elevation was excluded from the model because not all combinations of factor values were present.

These stands have a high proportion of preferred tree species (e.g., chestnut oak, *Quercus prinus* L., and white oak, *Q. alba* L.), numerous refugia in which gypsy moth larvae can escape predation (Houston and Valentine 1977, 1985). Smith (1989) found that the white-footed mouse, *Peromyscus leucopus*, which is the major predator of gypsy moth pupae, has abundant alternate food (blueberries) at high elevations, and therefore it does not prey on gypsy moths as intensively as at low elevations. Also, elevation may have a direct effect on gypsy moth populations via predominant deposition of dispersing insects, or by positive geotaxis of flying male moths. Many flying insects are aggregated on mountain tops because of positive geotaxis (Johnson 1969).

Our study was not designed to evaluate the role of each individual factor associated with elevation. Thus, it is possible that the effect of elevation on gypsy moth numbers may vary in different regions. For example, gypsy moth is very abundant in coastal sites with sandy soils in New England despite their low elevation (Bess et al. 1947, Montgomery and Wallner 1988).

The highest ridges in the study area are covered predominantly by maple-beech-birch forests (Figures 2 and 3). Maples (*Acer* spp.), beeches (*Fagus* spp.), and many birch species (*Betula* spp.) are not favored hosts for the gypsy moth (Twery 1991). This was probably the reason why no significant increase in male moth counts was found at elevations above 750 m (Figure 4). A similar nonlinear effect of elevation on gypsy moth-caused defoliation frequency was found in Pennsylvania (Liebhold et al. 1994): defoliation frequency at 200–400 m was higher than at 0–200 m, but did not increase in most forest types at elevation above 400 m.

In the uninfested zone, moth catches were highest at low elevation. Probably, moth abundance in this zone depended more on the rate of colony establishment (*c*-effect) rather than on the rate of population growth. Most colonies in the uninfested zone had been established a few years ago, and there was little time for their growth. Colony establishment rate is likely related to the probability of inadvertent transportation of gypsy moth life-stages by humans (e.g., on vehicles). Human population density is higher at low elevations in this region, and this may cause a higher probability of colony establishment there.

Slope and aspect were not directly correlated with moth counts. Although slope had a significant effect in the transition zone, this effect was mediated by elevation.

Vegetation characteristics (FIA1, FIA2, and USGS) had surprisingly little effect on moth counts. Only USGS had a consistent direct effect on moth counts in the transition zone. The lack of effect of vegetation characteristics does not necessarily mean that vegetation is not important in the spatial distribution of gypsy moth populations. The most probable explanation is that existing vegetation maps do not provide useful classifications of habitat quality for the gypsy moth. Each category of forest type or land use/land cover includes both susceptible and resistant species to the gypsy moth. The proportion of these species may vary and thus these categories are poor predictors of host quality. Another problem was the low spatial resolution of the vegetation

maps. Only USGS maps had sufficient resolution (250 m) to represent the forest mosaic, and this may have been the reason why the USGS effect on moth counts was strongest. Male moth counts in deciduous and mixed forest stands were higher than in nonforested areas. This can be explained by the presence of host trees in deciduous and mixed stands.

Tree species composition is not the only factor that determines habitat quality for the gypsy moth. Soil characteristics that affect physiological conditions of trees or abundance of predators may be more important than tree species composition. For example, Liebhold et al. (1996) found in Japan that gypsy moths are more abundant in larch stands than in oak stands in spite of the fact that oak foliage is of equal suitability as larch. The explanation was that there were more small mammal predators in oak stands than in larch stands. Elevation is correlated not only with tree species composition but also with soil types, predator activity, and climate, all of which may influence gypsy moth dynamics. Thus, it may happen that elevation is a better predictor of habitat quality for the gypsy moth than tree species composition.

The weak effect of vegetation on moth counts could be alternatively explained by intensive moth dispersal. Long-distance dispersal of males is definitely present in gypsy moth populations. For example, bimodal moth flight in the Michigan Upper Peninsula resulted from moth migration over Lake Michigan (Pijanowski, personal communication). The proportion of moths that undergo long-distance dispersal is not known. If moth dispersal was intensive, then it would be difficult to explain the effect of elevation on moth counts. Thus, we feel that the weak vegetation effect is not likely to be explained by moth dispersal.

Local factors had a stronger effect on male moth populations in the transition zone than in the infested and uninfested zones. We assume that in the uninfested zone, moth counts are mainly affected by colony establishment (*c*-effect). In the transition zone, colonies have been growing for a relatively long time, and thus, population densities should be determined by differential population growth in different habitats (*r*-effect). In the infested zone, colonies coalesce and population dynamics become stationary. Thus, the differences in population numbers should be interpreted as the difference in carrying capacity (*K*-effect). Thus, our results indicate that local factors have a much stronger *r*-effect than *K*-effect or *c*-effect. The *c*-effect of elevation was found to be opposite to *r*- and *K*-effects. However, moth counts are of limited value for the analysis of *K*-effects because pheromone traps often become saturated in the infested zone (Elkinton 1987). Additional analysis of egg mass populations will be helpful to clarify *K*-effects.

The results of this study have several implications for population monitoring and management. First, gypsy moth populations in the transition and infested zones build up faster at high elevations than at low elevations. Thus they require more intensive monitoring and population management than populations at low elevation. In contrast, it may be better to put more traps at low elevations in the uninfested zone, especially at locations with a high probability of egg mass transportation on motor vehicles (e.g., residential areas,

nurseries, timber mills). Elevation might be used as a secondary variable in certain geostatistical procedures, such as co-kriging, to increase the accuracy of interpolated moth counts at unsampled locations. Other landscape characteristics that were used in this study are not likely to increase the accuracy of interpolation.

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