

A model for testing hypotheses of gypsy moth, *Lymantria dispar* L., population dynamics

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Abstract

A model for simulating long-term gypsy moth (*Lymantria dispar* L.) population dynamics in North America has been developed. Simulated ecological processes include larval dispersal, foliage consumption on different host trees, reproduction, and mortality due to natural enemies (virus, 4 guilds of parasitoids, and 2 guilds of predators). Population dynamics in several forest stands can be simulated taking into account the migration of gypsy moth and its natural enemies. The model fits well to the following observations and data: (1) quasi-periodic outbreaks at approximately 10-year intervals, (2) life-tables in different outbreak phases, (3) increased parasitism in artificially augmented gypsy moth populations, and (4) phase plots of population dynamics. Simulated survival curves are intermediate between those reported by J.S. Elkinton et al. and by J.R. Gould et al. It is shown that low-density gypsy moth populations can be stabilized by immigration from high-density areas without any density-dependent local processes. The model supports the following hypotheses about gypsy moth population dynamics: (1) density fluctuations of small mammal predators is the most probable synchronization factor in gypsy moth populations; (2) the outbreak frequency depends on the proportion of susceptible tree species and the density of small mammal predators; (3) bacterial insecticide can be applied less frequently for gypsy moth control than can a chemical insecticide of the same killing power because the bacterial insecticide spares invertebrate natural enemies; (4) the success of gypsy moth eradication programs depends on the initial gypsy moth population density and on the type of functional response of predators. An alternative form of population bimodality hypothesis is suggested, according to which there are two types of gypsy moth population dynamics: eruptive in susceptible stands and stable in resistant stands.

Keywords: Population dynamics; Gypsy moth

1. Introduction

The gypsy moth (*Lymantria dispar* L.) is an important forest pest in the north-eastern USA

(Doane and McManus, 1981). Since its accidental introduction into North America it has spread to the west and south causing defoliation in an increasing area of forest. Factors in the population dynamics of this pest were reviewed by Elkinton and Liebhold (1990).

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Mathematical models of an insect's population dynamics are important for integration of knowledge about its life-system. Models can be used to test hypotheses regarding interactions between ecological processes and to link experimental data with management practices. Modelling of gypsy moth populations in North America has a long history (Sheehan, 1989; Elkinton and Liebhold, 1990). Regression-based empirical models are not discussed here, because they are primarily useful for short-term prediction of population density and do not represent the role of various ecological processes. The goal of the present work is to investigate the processes that determine long-term population dynamics patterns. Only simulation models can be used to reach this goal.

Gypsy moth simulation models range in complexity from several differential equations to complex cohort-based models (Sheehan, 1989). Simple models are oriented to only one ecological process, e.g., foliage consumption (Valentine, 1981), parasitism (Brown et al., 1983), or viral infection (Dwyer and Elkinton, 1993). Other life-cycle processes are either ignored or simulated in a simplified way in these models. For example, in a model simulating the potential gypsy moth impact on Michigan forests (Morse and Simmons, 1979) most ecological events, like triggering of an outbreak or activation of viral mortality, are simulated using random numbers without consideration of biological interactions that cause these events.

The most complex, the Gypsy Moth Life-System Model (McNamee et al., 1983; Sheehan, 1988; Colbert and Sharov, 1993), is primarily oriented to within-season population dynamics. It is unwieldy as a tool for the analysis of long-term population change. The model simulating the potential gypsy moth impact on North Carolina forests (Byrne et al., 1987), is simpler but contains a rather complex submodel of forest succession, while the role of natural enemies is poorly represented: predation and parasitism are ignored, and viral epizootics are triggered randomly when gypsy moth density is high. None of the existing simulation models handle spatial aspects of gypsy moth population dynamics, which may be important in extending regional outbreak

duration (Campbell, 1981) and in suppression of isolated infestations by parasitoids (Gould et al., 1990).

Our first objective was to develop a model of intermediate complexity with sufficient detail to represent biological reality in terms of the role of defoliation, reproduction, dispersion, natural enemies, and pest control options. The model is designed to predict patterns of population change rather than the exact density at specific time and space coordinates.

The second objective was to show that the model output corresponds to field data at least on the qualitative level. Several data sets were used for testing the model. These included: (1) historical defoliation record from USA (Anonymous, 1989, 1993), (2) life-tables (Campbell, 1981), (3) dynamics of parasitism (Williams et al., 1992), (4) survival curves (Elkinton et al., 1989; Gould et al., 1990), (5) parasitism in artificially augmented gypsy moth populations (Gould et al., 1990), and (6) phase plots of population change (Campbell and Sloan, 1978).

The third objective was to use the model for testing hypotheses about gypsy moth population dynamics. The following issues were addressed: (1) synchronization of population change over a large area, (2) factors affecting stand susceptibility to gypsy moth, (3) long-term consequences of application of chemical and bacterial insecticides, and (4) factors affecting the success of eradication programs.

2. Model description

The model simulates interactions between gypsy moth populations, host trees, and natural enemies, including nuclear polyhedrosis virus (NPV), 4 guilds of parasitoids, and 2 guilds of predators. We first consider ecological processes within one stand, and second, dispersion of organisms between stands. Thus, we distinguish two types of dispersion: local dispersion within a stand (e.g. selection of tree species) and global dispersion between stands.

2.1. Forest stand

The forest stand is represented in the model by 3 classes of trees: susceptible, resistant and immune to gypsy moth feeding (Twery, 1991). Each tree class is characterized by annual foliage production measured in grams of dry foliage biomass produced by all trees of this class per hectare. Natural stand dynamics (without defoliation) are simulated using a modified discrete-time analog of the Lotka–Volterra model. The general form of the Lotka–Volterra model has too many parameters and there is no direct way to measure them in each stand. In order to reduce the number of parameters and to simplify their estimation we assumed that (1) a stand has a single climax state with specific foliage production at climax FC_c for each tree class c , and (2) there are two components of tree growth: general growth and class-specific growth.

General growth rate GGR_t (proportion of growth per year) in year t is uniform for all tree classes and is equal to:

$$GGR_t = \alpha \cdot (1 - TFP_t/TFC), \quad (1)$$

where α is a constant, TFP_t is total foliage production (grams of dry foliage biomass per hectare) of trees of all classes in current year t , and TFC is total foliage production at climax. General growth rate is positive if stand density (measured by total foliage production) is less than at climax. General growth regulates total foliage production by the stand and draws it towards foliage production in the climax stand.

Class-specific growth rate $SGR_{c,t}$ of trees in class c in year t is equal to:

$$SGR_{c,t} = \beta \cdot (FC_c - FP_{c,t})/TFC, \quad (2)$$

where β is a constant, FC_c is foliage production at climax for trees in class c , $FP_{c,t}$ is foliage production of trees in class c in year t , and TFC is defined above. Specific growth rate is positive if trees of class c are underrepresented in the stand as compared to the climax stand. Specific growth regulates tree species composition in the stand and draws it towards the climax state.

Without defoliation, stand dynamics is simulated by the equation:

$$FP_{c,t+1} = FI_c + FP_{c,t} \cdot (1 + GGR_t + SGR_{c,t}), \quad (3)$$

where $FP_{c,t}$ is foliage production of trees in class c in year t , FI_c is foliage increment due to seed dispersion from other stands (this component is not present in Lotka–Volterra equations), GGR_t is general tree growth rate in year t (Eq. 1), and $SGR_{c,t}$ is class-specific tree growth rate of trees in class c in year t (Eq. 2).

The amount of foliage produced by trees is proportional to basal area (diameter²) (Botkin et al., 1972), and diameter increment of unshaded trees is about 1 cm/year for trees with diameter near 20 cm (Teck and Hilt, 1991). Hence, parameter α was estimated as $\alpha = (20 + 1)^2/20^2 - 1 = 0.1$. Parameter β was arbitrarily set 5 times smaller than α ($\beta = 0.02$) because it is assumed that the change in tree species composition is a much slower process than the increase of tree foliage biomass in regenerating stands. Parameter $TFC = 2000000$ g/ha was taken from the model of Valentine (1981); parameter FI_c was arbitrarily set to 2000 g/ha for all classes. The proportion of each tree class in a climax stand (FC_c/TFC) was arbitrarily set to 0.60, 0.25, and 0.15 for susceptible, resistant, and immune trees, respectively.

Tree mortality due to defoliation by gypsy moth is expressed as a reduction of annually produced foliage. Actual tree mortality $ATM_{c,t}$ in class c in year t is estimated as a weighted sum of defoliation effects in previous years:

$$ATM_{c,t} = TM_0 \cdot \sum_{\tau=0}^{\infty} DCR^{\tau} \cdot \max\left\{0, \frac{PD_{c,t-\tau} - DT}{1 - DT}\right\}, \quad (4)$$

where TM_0 is tree mortality immediately after 1 year of total defoliation, τ is time lag since defoliation, DCR is the annual reduction in the effect of previous defoliation on tree mortality, $PD_{c,t-\tau}$ is the proportion of defoliation in class c in year $t - \tau$ (foliage actually consumed (8) divided by foliage production), and DT is defoliation threshold which is defined as the maximum proportion

of defoliation that causes no tree mortality. According to Houston (1981), tree mortality after 1 year of heavy defoliation is 7.2%, 17.1% and 33.3% for trees in good, fair and poor condition, respectively. Parameter TM_0 was set to 0.10 (10% mortality) assuming that almost all trees were in good condition. Parameter $DCR = 0.5$ was estimated as a ratio of tree mortality in the second year after single defoliation to tree mortality in the first year after defoliation; data on tree mortality was taken from Houston (1981). As a rule, defoliation causes tree mortality when it exceeds 60% (Gansner et al., 1985). However, defoliation is not uniform in the stand, and some trees in the same class may be more defoliated than others. Thus, we suggest a defoliation threshold of $DT = 0.5$. At this average defoliation level some trees will be defoliated by more than 60%.

In the model, it is inconvenient to keep information about defoliation in all previous years, and thus, Eq. 4 was substituted by an equivalent recurrent equation:

$$ATM_{c,t} = ATM_{c,t-1} \cdot DCR + TM_0 \cdot \max\left\{0, \frac{PD_{c,t} - DT}{1 - DT}\right\}. \quad (5)$$

To account for tree mortality, foliage produced in year $t + 1$, $FP_{c,t+1}$, is multiplied by $(1 - ATM_{c,t})$.

2.2. Gypsy moth

The gypsy moth life-cycle is divided into five stages: eggs, small larvae (I–III instars), large larvae (IV–VI instars), pupae and adults. Ecological processes involving the gypsy moth (Fig. 1) are simulated sequentially. We use the term ‘background mortality’ for mortality which cannot be attributed to gypsy moth interaction with natural enemies or host plants. In this section we discuss ecological processes related to a gypsy moth population itself and to its interaction with host plants. Gypsy moth interactions with natural enemies will be considered below.

At the beginning of each year, a gypsy moth population is characterized by the density of egg masses per hectare and average number of eggs per egg mass. Egg viability decreases after years

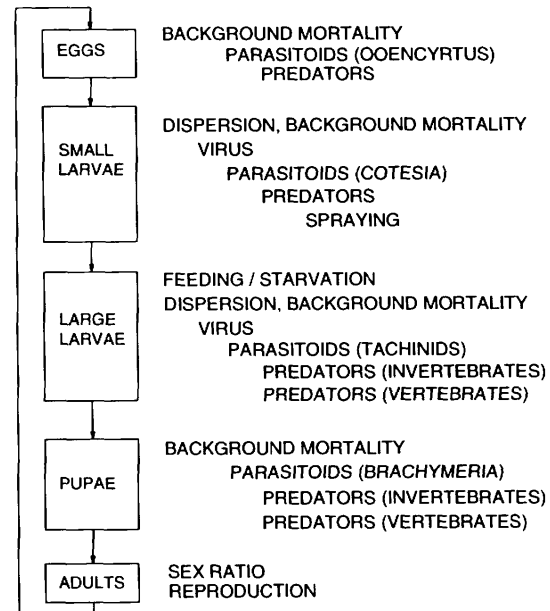


Fig. 1. Ecological processes considered in the model of gypsy moth population dynamics.

of defoliation (Williams et al., 1990). Thus, we assumed that egg background mortality was a linear function of average tree defoliation in the previous year. The intercept for this linear function, 0.15, was taken from Campbell (1981), and the slope, -0.437 , was taken from Williams et al. (1990).

In the model, first-instar larvae are allocated to different tree classes in quantities proportional to the product of the amount of foliage produced by tree class and foliage preference coefficient of the class (Table 1). Preference coefficients are equal to the relative probability of a larva not

Table 1
Parameters of gypsy moth interaction with different tree classes

Tree class	Mortality due to food		Foliage preference coefficient	Relative consumption rate
	Small larvae	Large larvae		
Susceptible	0.00	0.00	1.00	1.00
Resistant	0.75	0.10	0.74	0.49
Immune	1.00	0.30	0.59	0.35

dispersing. Lance and Barbosa (1981) estimated that 35.9%, 52.7%, and 61.7% of small larvae attempt to disperse from susceptible hosts (oak), resistant hosts (red maple), and immune hosts (hemlock), respectively. Therefore we set preference coefficients equal to 1, 0.74 and 0.59 for susceptible, resistant and immune classes, respectively.

Background mortality of small larvae which is associated with unsuccessful dispersion of first instars and physiological mortality, was arbitrarily set to 50%. Additional mortality of small larvae due to poor foliage quality is zero for susceptible host species, 75% for resistant species (mean value of 60% for red maple and 90% for loblolly pine; Barbosa et al., 1983), and 100% for immune host trees (Table 1).

Local dispersion of large larvae is simulated as follows. The proportion of larvae dispersing from host tree class c , PLD_c , is a linear function of the ratio of foliage potentially consumed FPC_c to the amount of foliage produced by trees FP_c :

$$PLD_c = \min\{1, a + b \cdot (FPC_c/FP_c)\}, \quad (6)$$

where a and b are intercept and slope which were arbitrarily set to 0.10 and 0.6, respectively.

Foliage potentially consumed is estimated using:

$$FPC_c = ILLD_c \cdot FCN \cdot RCR_c \quad (7)$$

where $ILLD_c$ is initial density of large larvae in tree class c , FCN is food consumption on susceptible trees (grams of foliage consumed by one larva), and RCR_c is relative consumption rate on tree class c . Relative consumption rate is equal to 1 for susceptible species. It was set to the average suitability index (0.49) for resistant species (Montgomery, 1991); and it was arbitrarily set to 0.35 for immune species (Table 1). According to Miller et al. (1991), food consumption FCN is equal to 4.664–5.380 g/larva (dry wt) for females and 1.591–2.008 g/larva for males. Averaging these values for both sexes yields 3.411 g/larva. Actual foliage loss is greater because larvae start feeding on small leaves and the reduction in final leaf area is greater than the area removed by feeding (Valentine, 1983). Foliage growth is not considered in this model. Instead, we adjusted

the food consumption. We simulated defoliation in stands with 100% susceptible trees, and compared it with empirical relationships between gypsy moth egg mass density and subsequent defoliation (Gansner et al., 1985, Liebhold et al., 1993). Good fit was obtained with a food consumption of $FCN = 4$ g/larva.

Dispersing large larvae are pooled together from all tree classes and redistributed proportionally to the product of amount of foliage on each tree class (FP_c) and foliage preference coefficient (Table 1).

Background mortality of large larvae was set to 0.10. This value is close to experimental results of Barbosa and Capinera (1977). Additional mortality of large larvae due to poor food quality was arbitrarily set to 0, 0.1 and 0.3 for susceptible, resistant and immune species, respectively. These values are lower than for small larvae because large larvae are less sensitive to food quality (Barbosa et al., 1983).

Defoliation is simulated using the model of Semevskii (1971) where it is assumed that larvae have a log-normal distribution on foliage (Fig. 2). Because of their arbitrary nature, foliage units may be interpreted as locations in the stand, as

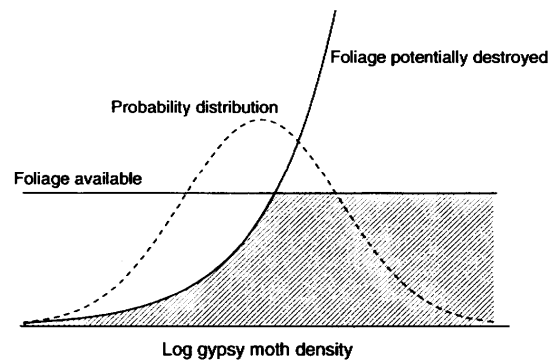


Fig. 2. The submodel of foliage consumption by gypsy moth. Gypsy moth larvae are considered to have a log-normal distribution on foliage; the initial amount of foliage is uniform and independent of gypsy moth density; foliage potentially destroyed is proportional to gypsy moth density; foliage actually destroyed (shaded area) is a minimum of two functions: the amount of foliage available and foliage potentially destroyed. The weighted integral of foliage actually destroyed (probability used as weight) gives the average amount of foliage actually destroyed.

trees, or as branches. The initial amount of foliage is uniform in all foliage units. Potentially consumed foliage is proportional to the number of larvae in the foliage unit. In a foliage unit, foliage actually consumed is equal to the minimum of two values: potentially consumed foliage and the amount of foliage available (Fig. 2, shaded). The average amount of consumed foliage is estimated as an integral of foliage actually consumed weighted by a log-normal distribution. The following equation is derived in the Appendix:

$$\text{FAC}_c = \text{AFPC}_c \cdot \Phi(G_c - \sigma/2) + \text{FP}_c \cdot [1 - \Phi(G_c + \sigma/2)], \quad (8)$$

where FAC_c is foliage actually consumed on tree class c , AFPC_c is adjusted foliage potentially consumed, FP_c is initial amount of foliage, σ is a standard deviation of log-transformed larval density among foliage units, Φ is the cumulative function of normal distribution, and G_c is an auxiliary variable:

$$G_c = -(1/\sigma) \cdot \ln(\text{AFPC}_c/\text{FP}_c). \quad (9)$$

Parameter σ can be estimated from the coefficient of variation, CV , of larval density among foliage units: $\sigma = [\ln(\text{CV}^2 + 1)]^{1/2}$. Parameter CV was arbitrarily set to 0.3.

Adjusted foliage potentially consumed AFPC_c accounts for the effect of large larval mortality on reducing the amount of foliage potentially consumed, and is estimated as:

$$\text{AFPC}_c = \text{MLLD}_c \cdot \text{FCN} \cdot \text{RCR}_c \quad (10)$$

where MLLD_c is mean density of large larvae in tree class c (mean density is equal to the sum of initial and terminate densities divided by 2), and FCN and RCR_c are as defined above. Larval mortality is accounted here by using average larval density, MLLD_c , instead of initial density.

Larval mortality due to starvation is assumed to be a monotonically increasing function of tree defoliation. The function was arbitrarily defined by straight line segments which connect points with coordinates (0,0), (0.4,0), (0.9,0.9), and (1,0.99). This kind of mortality includes both physiological reaction of larvae to food deficit and ecological consequences of food shortage,

e.g. increased predation rate on larvae while they are searching for food.

Pupal background mortality was set to 0.15 in accordance with Campbell (1981).

The proportion of adult females in the subpopulation emerged in tree class c , PAF_c , is a linear function of larval mortality due to NPV (Campbell, 1981): $\text{PAF}_c = 0.664 - 0.58 \cdot \text{MV}_c$, where MV_c is the mortality of large larvae due to NPV in tree class c . The virus kills more females than males because female larvae have an additional instar and are exposed to the pathogen for longer.

The fecundity of gypsy moth females FEC_c depends on two factors: foliage quality, represented in the model by relative consumption rate, and tree defoliation:

$$\text{FEC}_c = F_0 \cdot \text{RCR}_c \cdot (1 - \text{DFC} \cdot \text{FAC}_c/\text{FP}_c), \quad (11)$$

where F_0 is maximum fecundity (fecundity on susceptible non-defoliated trees), RCR_c is relative consumption rate on foliage of tree class c (see Table 1), DFC is a constant, and FAC_c/FP_c is the proportion of defoliation. Maximum fecundity (540 eggs) was estimated using female pupal weight (Montgomery, 1991) and a relationship between pupal weight and fecundity (Hough and Pimentel, 1978). Parameter $\text{DFC} = 0.7$ was estimated by combining linear relationships between defoliation and pupal biomass (Rossiter et al., 1988) and between pupal biomass and fecundity (Hough and Pimentel, 1978).

The proportion of mated females PMF depends on density of both sexes. We assume that all males hatch simultaneously, while females hatch with a constant rate during male flight period. In this case the proportion of mated females and, respectively, the proportion of fertilized eggs can be estimated using a modified disc equation:

$$\text{PMF} = 1 - \exp[-\text{MSR} \cdot \text{MD}] / (1.0 + \text{MSR} \cdot \text{FD}/\text{MM}) \quad (12)$$

where MSR is male search rate (hectares per adult female lifetime), MD is male density per hectare, FD is female density per hectare and

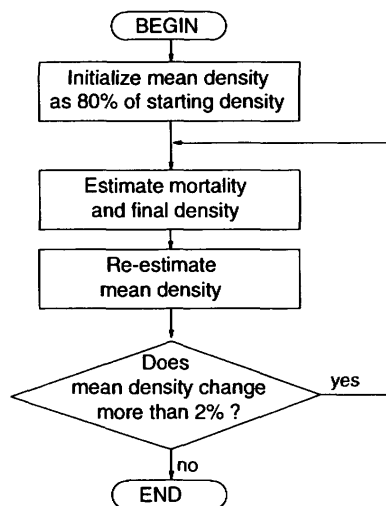


Fig. 3. Algorithm to account for simultaneous density-dependent mortality of large larvae and pupae: mean density (initial plus final density divided by 2) is used as input for density-dependent processes; this density is set equal to 80% of initial density, then it is re-estimated in a cycle of simulations until the desired accuracy (here 2%) has been reached.

MM is the maximum number of matings per one male. Parameters were set arbitrarily: MSR = 0.2 ha, MM = 20.

In the model, ecological processes related to the same stage of gypsy moth are simulated sequentially while in reality they are simultaneous. An algorithm was designed to circumvent the effect of the order of density-dependent processes on stages of large larvae and pupae. Ecological processes are assumed to depend on mean gypsy moth density (sum of initial and terminal density divided by 2), which is estimated with increasing precision in a sequence of iterations (Fig. 3). Mean gypsy moth density is first set to 80% of initial density, then ecological processes are simulated using this mean density. At the end of the stage, the mean density is updated and simulation is repeated until the desired precision (2%) is reached.

2.3. NPV infection

Larval mortality due to NPV is bimodal (Woods and Elkinton, 1987). Larvae that become infected

at hatch time by consuming NPV-contaminated egg shells die in the first wave. The second wave may result from two (or more) generations of NPV infections in large larvae.

In the model, three cycles of viral infection are considered: one in small larvae, and two in large larvae. Infection rate is simulated using a logistic dose-effect function with log-transformed doses (Valentine and Podgwaite, 1982). We added a multiplier to the equation which is interpreted as maximum infection rate. All infected individuals are assumed to die, thus mortality rate is equal to infection rate. The proportion of infected small larvae PISL is a logistic function of the logarithm of viral polyhedral inclusion bodies (PIBs) produced by large larvae in the previous year (NPB). It is estimated by the equation

$$\text{PISL} = \frac{\text{MISL} \cdot (\text{NPB}/\text{LC1})^{\text{SL1}}}{1 + (\text{NPB}/\text{LC1})^{\text{SL1}}}, \quad (13)$$

where MISL is the maximum proportion of infected small larvae, LC1 is the density of viral PIBs per hectare in the previous year that causes 50% of maximum mortality of small larvae, SL1 is a slope parameter of dose-effect curve. Parameter values (MISL = 0.2, LC1 = 1.0×10^{15} , and SL1 = 1.0) were set arbitrarily. To prevent extinction of viral population at low gypsy moth density we assume a lower limit for NPV numbers of 1.0×10^8 PIBs per hectare.

The proportion of large larvae infected by NPV (PILL) is modelled using a similar dose-effect equation:

$$\text{PILL}_c = \frac{\text{MILL} \cdot (\text{PBD}_c/\text{LC2})^{\text{SL2}}}{1 + (\text{PBD}_c/\text{LC2})^{\text{SL2}}}, \quad (14)$$

where MILL is maximum proportion of infected large larvae, PBD_c is viral PIB's density per gram of dry foliage biomass in tree class c , LC2 is the NPV density that causes 50% of maximum infection, and SL2 is the slope of the dose-effect curve. Parameters LC2 = 52000 and SL2 = 0.77 were estimated using results of laboratory experiments with 4th instar larvae (Shields, 1984). Maximum NPV-caused mortality of large larvae was set to MILL = 0.99.

Simulation of NPV-caused mortality of large larvae is complex because (1) infected larvae may move from one tree class to another and (2) there are two generations of NPV infection in large larvae. It is assumed that larvae become infected before their dispersion and die after dispersion. Thus, infection may be transferred from one tree class to another. Then large larvae become infected in the second generation of NPV infection. Total mortality of large larvae due to viral infection (TMV) is estimated using:

$$TMV = 1 - (1 - MV1) \cdot (1 - MV2), \quad (15)$$

where MV1 and MV2 are mortalities in the first and second generations of NPV infection in large larvae.

The number of NPV PIBs per gypsy moth cadaver is 4.0×10^8 per small larva and 3.0×10^9 per large larva (Shapiro, 1981). We assume that only a small portion (2%) of these PIBs are deposited on the foliage. The density of viral PIBs on the foliage declines with time. We assumed that only 1.5% of PIBs survive between successive generations of NPV infection.

2.4. Predation

Two guilds of predators are considered in the model: invertebrates, including ants and ground beetles; and vertebrates, including birds and small mammals. Mortality of small larvae due to predation is assumed to be constant (15%). In life tables this mortality is attributed to invertebrate predators. Density-dependent predation occurs on large larvae and pupae.

In the model, the density of invertebrate predators is constant and equal to 44 100 individ-

uals/ha, the density of ants reported by Weseloh (1989). The number of vertebrate predators changes independently from gypsy moth density because gypsy moth is not their main food source (Smith, 1989). The population dynamics of vertebrate predators are simulated using:

$$VD_t = VD_{t-1} \cdot \exp[VDD \cdot ((1 - DEL) \cdot (1 - VD_{t-1}/VE) + DEL \cdot (1 - VD_{t-2}/VE)) + \xi_t], \quad (16)$$

where VD_t is vertebrate density in year t , $VDD = 1.4$ is the coefficient of density dependence, $DEL = 0.7$ is delay in density-dependence, VE is equilibrium vertebrate density, and ξ_t is a random normally distributed variable with mean zero and standard deviation 0.05. The number of white-footed mice (*Peromyscus leucopus*), which are the most efficient vertebrate predators, usually fluctuates from 10 to 120 per hectare (Smith and Lautenschlager, 1981; Krohne et al., 1988). Also, there are up to 20 individuals of shorttail shrew and 5–10 pairs of birds per hectare. As a default, equilibrium density of all vertebrate predators was set to $VE = 50$ individuals per hectare.

The functional response of predators is described by a modified model of random predation (Rogers, 1972):

$$N_a = PYD \cdot [1 - \exp(-PSR \cdot (PRD - N_a/MC))], \quad (17)$$

where N_a is the density of gypsy moths killed by predators, PRD and PYD are predator and prey densities per square meter of ground surface, respectively, PSR is predator search rate (square meters per year), and MC is maximum number of prey consumed per predator. This equation was derived by assuming total search time $T = 1$ (predation is considered in one time step), and handling time $T_h = T/MC$. The value of N_a is estimated as a numerical solution of Eq. 17, and prey mortality is equal to N_a/PYD . Parameter values are listed in Table 2. Search rates were adjusted in order to get reasonable prey mortality.

Both guilds of predators were assumed to have type II of functional response (Holling, 1959),

Table 2
Parameters of gypsy moth predators

Predator guild	Search rate (m ² /prey stage) for:		Maximum consumption (prey/predator/prey stage) of:	
	Large larvae	Pupae	Large larvae	Pupae
Invertebrates	0.10	0.05	10.0	10.0
Vertebrates	150.00	300.00	300.0	300.0

with a constant search rate. But in several simulation experiments we changed predator functional response to type III, assuming that search rate depends on prey density:

$$PSR = PSR_{\max} \cdot [RSZD + (1 - RSZD) \cdot PYD / (RFR + PYD)], \quad (18)$$

where PSR_{\max} is maximum search rate, $RSZD$ is relative search rate at zero prey density, and RFR is range of functional response – prey density at which search rate increases by half of the possible increment.

The maximum consumption rate of vertebrate predators was estimated as follows. In captivity, white-footed mice consumed 20 gypsy moth pupae per day when alternate food was available (Smith and Lautenschlager, 1981). Pupae are available to predators for about 15 days. Thus, maximum consumption was set to 300 gypsy moth pupae per year. The same value is used for gypsy moth larvae as prey.

2.5. Parasitism

Gypsy moth eggs are attacked by the parasitoid *Ooencyrtus kuvanae* (Howard). Percent parasitism correlates with host density and egg mass size (Williams et al., 1990). We selected host density as a predictor of parasitism because egg mass size is not simulated with necessary accuracy in the model. The relationship was taken from Williams et al. (1990):

$$EMP = 0.1272 + 0.05742 \cdot \log_{10}(EMD), \quad (19)$$

where EMP is egg mortality due to parasitism and EMD is egg mass density per hectare.

Other parasitoid guilds include *Cotesia melanoscela* (Ratz.) (a parasitoid of small larvae),

tachinids (parasitoids of large larvae), and pupal parasitoids. These are all simulated in the same manner with the parameters of Table 3.

The density of parasitoid females in spring is estimated on the basis of overwintering parasitoid density, overwinter survival and sex ratio. Overwinter survival of *C. melanoscela* is relatively low (Table 3) because of: (1) high percent of hyperparasitism (Griffiths, 1976; Weseloh, 1981), and (2) low synchronization of the parasitoid's second generation with the host (Weseloh, 1976). In this model we simulate only one generation of *C. melanoscela*, and lack of synchronization is accounted for by decreasing overwinter survival.

The functional response of parasitoids is simulated as follows. The average number of parasite eggs AE laid on 1 host is equal to:

$$AE = \frac{PSD \cdot PSSR}{1 + PSSR \cdot HD_c / PSF}, \quad (20)$$

where PSD and HD are parasite and host densities per square meter of ground surface, respectively, $PSSR$ is parasite search rate (square meters per lifetime), and PSF is average parasite fecundity. This equation was derived from the disc equation from Holling (1959) by assuming total search time $T = 1$ (parasitism is considered in one time step), and handling time $T_h = T / PSF$. All parasitoids are assumed to have a type II functional response. Thus, the search rate ($PSSR$) is constant. Average parasitoid fecundity PSF was estimated as one-half of recorded maximum fecundity. Maximum fecundity of parasitoids is 500 eggs for *C. melanoscela* (Weseloh, 1981); 300 eggs for the pupal parasitoid *Brachymeria intermedia* (Nees) (Leonard, 1981); tachinid species have varying maximum fecundities ranging from 120

Table 3
Parameters of gypsy moth parasitoids

Parasitoid guild	Overwinter survival	Proportion of females	Fecundity	Maximum search rate (m ² /year)	Parameter k of egg distribution on hosts	Parasitoids from alternate hosts (per ha)
<i>Cotesia melanoscela</i>	0.2	0.5	250	3	2.00	30.0
Tachinids	0.6	0.5	150	3	2.00	1500.0
Pupal parasitoids	0.6	0.5	150	3	2.00	500.0

for *Compsilura concinnata* (Meigen) to 5000 for *Blepharipa pratensis* (Meigen) (Griffiths, 1976). *B. pratensis* lays its eggs on the foliage, and thus, its fecundity is not comparable with that of other tachinids. In the model, average fecundity of tachinids was arbitrarily set to 150 eggs. Search rate of parasitoids (Table 3) was adjusted in order to get parasitism-related mortality approximately in the same range as in nature (Williams et al., 1992).

Superparasitism is simulated by a negative binomial distribution of parasitoid eggs on hosts (May, 1978) with parameter k arbitrarily set to 2.0. Host survival is equal to the zero term of the distribution with mean value equal to AE (Eq. 20). Only one parasitoid survives if more than one egg is laid on a host.

At the end of each year, parasitoid density is increased by the density of individuals that developed in alternate hosts. We assume that tachinids (especially the polyphagous *C. concinnata*) have many more alternate hosts than *C. melanoscela*

and pupal parasitoids (see Table 3). In reality some tachinid species (e.g. *Parasetigena silvestris* (R.-D.)) are oligophagous, but in the model we aggregate all tachinid species and average their biological characteristics.

2.6. Spatially-distributed version of the model

Space is considered as a set of sites with no distance relations between them. Sites have different tree class composition (FC_c) and different equilibrium density of vertebrate predators (VE). These parameters are set for all sites using random numbers: total foliage production at climax has a normal distribution, proportion of each tree class has a normal distribution constrained to a simplex plane, and vertebrate predators have a log-normal distribution.

Gypsy moth and its natural enemies, vertebrate predators and three guilds of parasitoids, can migrate from one site to another. Migration of egg parasitoids is not considered. The default

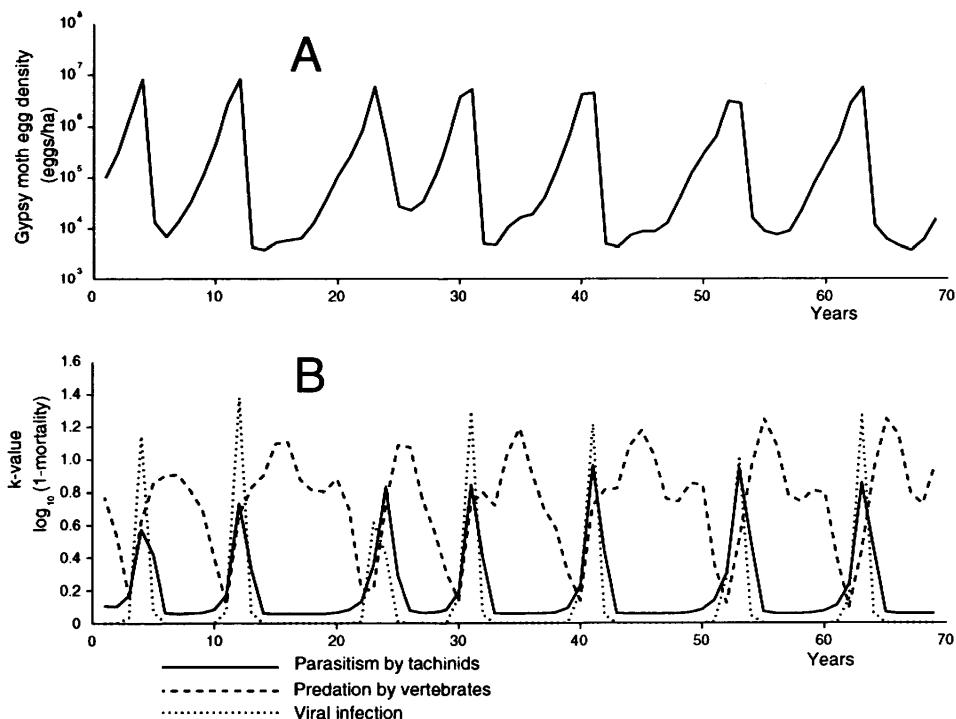


Fig. 4. Simulated gypsy moth population dynamics (A) and principal mortality factors that affect population change (B).

proportion of gypsy moth small larvae that emigrate is set equal to 0.02 (egg masses transferred by humans can be considered as a part of this dispersion). Migrants from all sites are pooled together and then redistributed to sites according to the log-normal distribution with coefficient of variation equal to 0.5. Gypsy moth females in North America do not fly and in the model they remain in the same site. However, males can fly, and in the model their dispersion is simulated in the same way as the dispersion of small larvae. The proportion of emigrating males is arbitrarily set to 0.5.

The proportion of emigrating vertebrate predators is constant and equal to 0.1. Migrants from all sites are pooled together and then redistributed to sites uniformly.

The proportion of emigrating parasitoids is constant and equal to 0.7 for tachinids and 0.4 for other parasite guilds. It is greater for tachinids because they are assumed to be better flyers than other parasitoids. Migrants from all sites are pooled together and then some proportion of them is redistributed to sites uniformly while the other portion of parasitoids is redistributed to sites proportional to gypsy moth density. The proportion of migrating parasitoids that are distributed according to host density is set to 0.7 for tachinids and 0.4 for other parasitoid guilds. We assume that tachinids, due to their high flight ability, have more chances to find patches of increased host density than other parasitoids.

3. Comparison with field data

Our simulated gypsy moth population has regular outbreaks with peaks about 7–12 years apart (Fig. 4A). Historical defoliation records in the United States are also characterized by quasi-periodic oscillations with similar frequency (Fig. 5). The same frequency of gypsy moth outbreaks was observed in Yugoslavia (Sisojevic, 1979).

In the model, gypsy moth mortality between outbreaks is caused mainly by vertebrate predators (Fig. 4B). Mortality due to predation declines when prey density increases, and this may lead to an outbreak. At high population density, mortal-

ity due to viral infection becomes most important, and parasitism causes additional mortality in declining gypsy moth populations. The simulated density-related shift in mortality factors corresponds well to the life tables obtained by Campbell (1981). According to Williams et al. (1992), in New Jersey, maximum parasitism by the tachinid *C. concinnata* was recorded at the end of gypsy moth outbreaks, similar to our simulation. However, the pattern of parasitism by other species was different in New Jersey (Williams et al., 1992): maximum parasitism by *C. melanoscela* coincided with the peak of gypsy moth density and then declined, parasitism by tachinids *P. silvestris* and *B. pratensis* was highest at the start of host outbreak. Ecological mechanisms that determine population trends of these parasitoid species in New Jersey are not known. However, in Yugoslavia, parasitism of *P. silvestris* was highest at the end of outbreaks (Sisojevic, 1979) as it is in our model.

In simulated forest stands, the proportion of susceptible tree species decreased due to defoliation caused by gypsy moth (Fig. 6). Resistant and immune tree species gradually replaced susceptible trees that were killed. These results are consistent with Melrose data (Campbell, 1981) and with other simulation models (McNamee et al., 1983; Byrne et al., 1987). The proportion of susceptible tree species stabilized at about 40–45%.

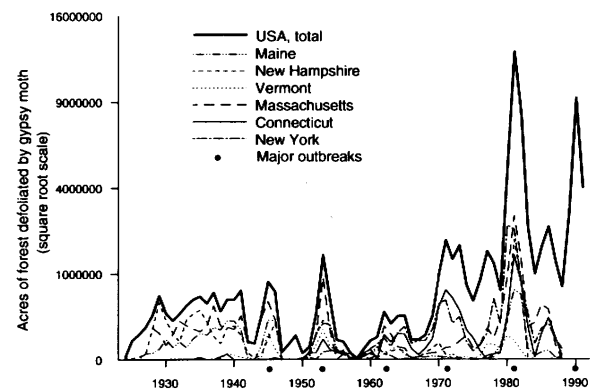


Fig. 5. Gypsy moth-caused defoliation in the USA and in selected states (data from Anonymous, 1989,1993); circles correspond to years with large-scale defoliation.

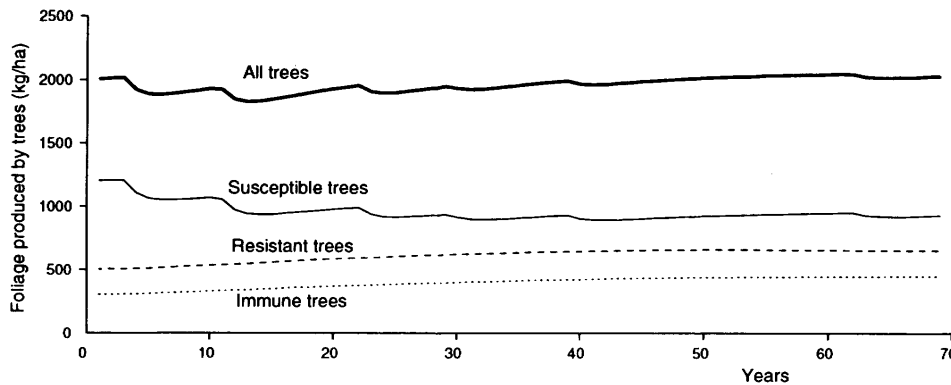


Fig. 6. Simulated stand succession in the course of gypsy moth defoliation (gypsy moth population dynamics is shown in Fig. 4).

For sites with a higher density of vertebrate predators, this level may be higher.

Simulated gypsy moth survival curves for a series of 8 years are shown in Fig. 7. Only one curve has a pronounced density drop during the stage of large larvae. This curve corresponds to a population collapse due to an NPV epizootic. In several field studies, mortality of large larvae was significantly higher than mortality in other stages (Bess, 1961; Campbell, 1981; Elkinton et al., 1989). Large larvae die due to predation, parasitism and disease, but these known factors account for only a small portion of gypsy moth mortality in this stage (Campbell, 1981). Only during viral epizootics can the majority of this

high mortality be reasonably attributed. The major source of larval mortality in non-outbreak years is unknown. According to Gould et al. (1990), mortality was moderate in larval stages and high in pupae and adults. Simulated survival curves (Fig. 7) are intermediate between those reported by Elkinton et al. (1989) and by Gould et al. (1990). Additional information is needed about gypsy moth survival during different stages.

In several experiments, the density of gypsy moth was artificially increased by the release of eggs on 1-ha plots (Liebhold and Elkinton, 1989; Gould et al., 1990). It was shown that parasitoids were attracted to these artificially augmented host populations, causing unusually high rates of parasitism. Our model was used to simulate this aggregational response of parasitoids. One hundred 1-ha stands were simulated. In one stand, the density of gypsy moth was increased to the same level (from 43 538 to 1 144 325 eggs/ha) as in experiments of Gould et al. (1990). Our simulation was replicated for each of eight experimental plots. Parasitoids were allowed to migrate to the experimental stand from other stands. Simulated mortality caused by tachinids exhibits the same density-dependent pattern as in the experiment (Fig. 8). However, the total k -value for the generation was significantly higher in the experiment than in the model. The main difference was in the extremely high gypsy moth mortality during pupal and adult stages in the experiment (Gould et al., 1990). The cause of this mortality is not known.

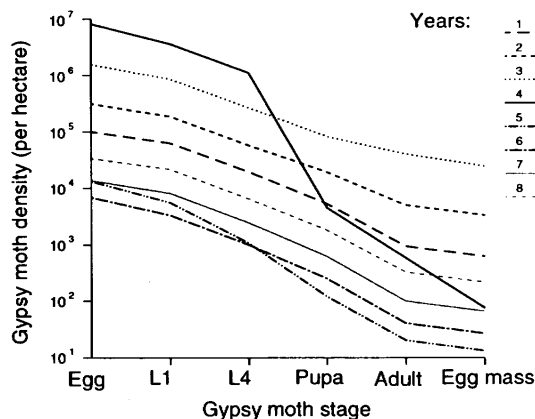


Fig. 7. Survival curves in simulated gypsy moth populations in 8 subsequent years.

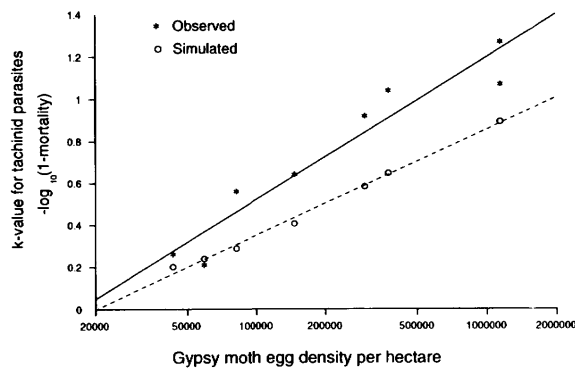


Fig. 8. Actual (data from Gould et al., 1990) and simulated gypsy moth mortality (expressed in k -values) due to the parasitoid *Compsilura concinnata* in artificially augmented populations; in the model, density of gypsy moths was increased in one stand (1 ha) surrounded by 99 stands with low population density (10000 eggs per ha); solid line corresponds to asterisks and dashed line corresponds to circles.

Campbell and Sloan (1978) studied the density-dependence in gypsy moth populations by plotting the rate of population growth against log-transformed population density. These plots are often called “phase plots”. The simulated rate of population growth decreased with gypsy moth density in the same way as in Glenville (NY) in 1958–1963 (Campbell and Sloan, 1978), where defoliation was generally high (Fig. 9A). In the model, density-dependence was caused mainly by viral epizootics and starvation in dense populations.

Besides high-density populations in Glenville, Campbell and Sloan (1978) studied low-density populations in Eastford (CT) and showed that phase plots in these two locations were qualitatively different. Campbell (1981) suggested that Eastford gypsy moth populations were controlled by predation. When the average density of vertebrate predators in the model was increased from 50 to 80 ha^{-1} , then there was no density-dependence in the phase plot (Fig. 9B) and finally the population become extinct. To get more points on the graph we simulated 5 populations with different initial egg mass densities. We found two possible mechanisms which can produce phase plots similar to that in Eastford: (1) the type III functional response of vertebrate predators (Fig.

9C) and (2) gypsy moth immigration from high-density populations (Fig. 9D). The type III functional response was simulated using Eq. 18 with parameters $\text{RSZD} = 0$ and $\text{RFR} = 100$ prey/ha. The average density of vertebrate predators was set to 100 individuals/ha. Immigration was simulated using 10 sites with different average densities of vertebrate predators (global mean = 80 predators/ha, coefficient of variation = 0.5). Data in Fig. 9D correspond to the site with the highest density of vertebrate predators (143 ha^{-1}). Gypsy moth immigration gives a much stronger negative

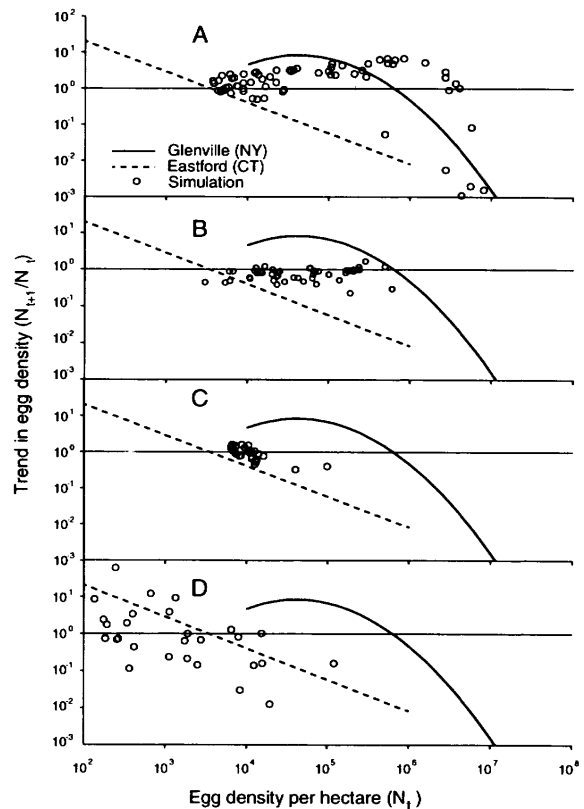


Fig. 9. Simulated and actual relationship between the trend in egg density and population density at the start of the generation; actual data, represented by regression lines, taken from Campbell and Sloan (1978). A: simulation with default parameters; B: vertebrate predator density is 80 individuals/ha, 5 sites; C: vertebrate predator density is 100 individuals/ha, their functional response is changed to the III type, 1 site; D: one of 10 sites with the highest density of vertebrate predators, emigration rate of gypsy moth small larvae is 10%.

relation between population trend and population density than predation. However, there is no density-dependence in the strict sense. An illusion of density-dependence results from the fact that relative increase in population density due to immigration decreases with initial density which is a denominator.

4. Testing hypothesis about gypsy moth population dynamics

4.1. Synchronization of outbreaks

We used the spatial version of the model to address the key question of synchronization of gypsy moth population dynamics over large areas. In the majority of states infested by the gypsy moth, synchronous outbreaks were recorded in 1944–1946, 1953–1954, 1981–1982 (Fig. 5). In several states high defoliation was observed in 1970–1974. Average correlation between log-transformed defoliated areas in Maine, New Hampshire, Vermont, Massachusetts, Connecticut, and New York in 1944–1988 was 0.25 (S.E. = 0.06, $P < 0.01$). Earlier years were not used for analysis because gypsy moth was not present in all of these states.

Synchronization mechanisms tested were: (1) migration of gypsy moth first instar larvae, (2) migration of parasitoids, (3) direct weather effects on gypsy moth, and (4) synchronous population dynamics of vertebrate predators.

Only one synchronization mechanism was studied at a time. For example, when the effect of weather was analyzed, there was no migration of parasitoids, the number of vertebrate predators changed independently in different sites, and migration of gypsy moth larvae was very low (2%). This level of gypsy moth migration does not cause synchronization, and it was allowed in all simulations to prevent extinction of local populations. Average correlation between log density of gypsy moth eggs in 20 simulated sites was used as a synchronization index. Synchronization was apparent when this index was about 0.25 or greater.

According to Fig. 10, migration of gypsy moth larvae may synchronize population dynamics if

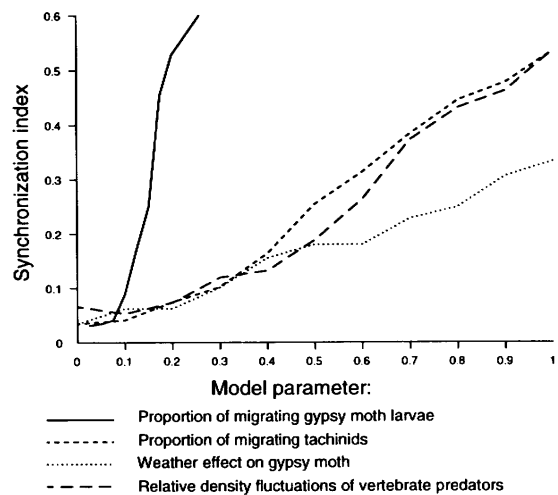


Fig. 10. Simulated synchronization of local gypsy moth population dynamics by different mechanisms. Synchronization index is the average correlation between log-transformed gypsy moth densities in 20 sites.

the percent of emigrating larvae is more than 15%. Migration rates reported by Mason and McManus (1981) are high enough to reach the threshold of 15% emigration from a 1-ha stand. Thus, migration of gypsy moth larvae may play an important role in synchronization of population dynamics at least at short distances (within 1 or 2 km²). The proportion of larvae that move further than 2 km is definitely low. Taylor and Reling (1986) evaluated the proportion of airborne larvae as 0.3%. Thus, larval dispersion cannot be considered as a mechanism of synchronization of population dynamics over large areas.

Migration of tachinid parasitoids has a strong synchronization effect on gypsy moth population dynamics (Fig. 10). However, this mechanism is effective only within the migration range of parasitoids, which is expected to be not more than 10–20 km.

The effect of weather was simulated using the hypothesis of Campbell (1967) that gypsy moth population growth is negatively correlated to precipitation in June. Average precipitation in June in four Connecticut locations (Falls Village, Hartford, Norfolk, and Storrs) in 1921–1989 was used as input. Weather can change both survival and

fecundity, but for simplicity we checked its effect on fecundity only. Weather effect on survival can be substituted by equivalent effect on fecundity. Gypsy moth fecundity was multiplied by:

$$\exp[-WE \cdot (PRC - MPRC)/SDPRC], \quad (21)$$

where WE is weather effect (parameter), PRC is precipitation, MPRC is mean value of PRC in 1921–1989, and SDPRC is standard deviation of PRC. Synchronization of gypsy moth populations was achieved only at WE = 0.8 (Fig. 10), but simulated peaks of gypsy moth density did not coincide with real outbreaks. The range (maximum/minimum) of fecundity variation due to weather can be approximately estimated as $\exp(4 \cdot WE) = 24.5$. This value is too high to be realistic. The equivalent change of survival can be achieved if gypsy moth mortality due to unfavourable weather is equal to $1 - 1/24.5 = 0.96$. This value is also too high. We tried to use other weather parameters (temperature and precipitation in April, May, and June) but the results were similar. Thus, the model does not support the hypothesis that direct weather effect can cause synchronous outbreaks of gypsy moth.

In order to analyze the synchronizing effect of predation, we modified the model, assuming that vertebrate predators had sine-wave dynamics:

$$VD_t = VE \cdot [1 + RDF \cdot \sin(2 \cdot \pi \cdot t / PER)], \quad (22)$$

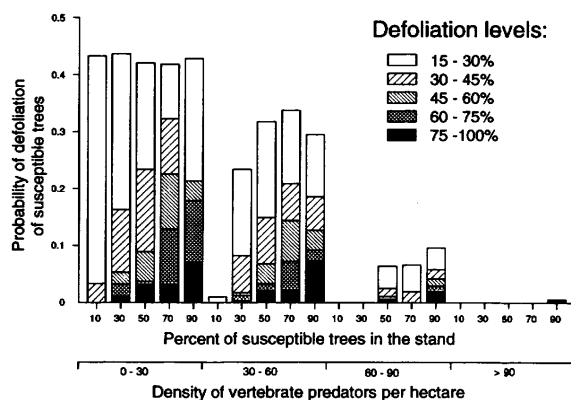


Fig. 11. Simulated frequency of defoliation of susceptible trees as a function of the proportion of susceptible trees in the stand and of the vertebrate predator density.

where VD_t is vertebrate density in year t , VE is the equilibrium density of vertebrates, RDF is relative density fluctuations of vertebrates, and PER is the period of fluctuations (we used the value PER = 5 years). Synchronous fluctuations in the density of vertebrate predators can synchronize gypsy moth population dynamics if RDF is near 0.6 or greater (Fig. 10).

4.2. Factors of stand susceptibility to gypsy moth

The probability of stand defoliation was simulated using 100 stands with different tree species composition and different densities of vertebrate predators. Site conditions were generated randomly. Five defoliation levels were used: 15, 30, 45, 60, and 75%. The probability of defoliation of susceptible trees increased with their proportion in the stand, and decreased with density of vertebrate predators (Fig. 11). Probability of light defoliation primarily depended on predator density, while the probability of heavy defoliation primarily depended on the proportion of susceptible trees. Simulation results qualitatively correspond to studies of forest stand susceptibility to gypsy moth defoliation (Bess et al., 1947; Gottschalk, 1989). Susceptible stands were characterized as having a high proportion of susceptible tree species and low mortality of gypsy moths due to predation.

4.3. Population management

The effect of pesticides is usually tested on the basis of induced mortality of a target species. However, a pesticide application may change the number and efficacy of natural enemies either directly (lethal effect) or indirectly (by reducing the number of prey). Indirect effects are exhibited in the target population with considerably greater delay than direct effects. It is difficult to test delayed effects of pest management in field experiments because external influences (weather and other factors) mask the differences, and many replications would be required to test for such confounded effects. Thus, we think that the simulation model is a useful tool for preliminary evaluation of indirect effects. Two management ob-

jectives were considered: suppression of high-density gypsy moth populations and eradication of low-density populations.

We tested the application of dimilin and *Bacillus thuringiensis* (Bt) against high-density gypsy moth populations. We assumed that Bt, in contrast to dimilin, does not kill invertebrate natural enemies, and we hypothesized that Bt treatments can be applied less often because natural enemies would decrease gypsy moth population growth rate. Reduction of egg masses due to dimilin aerial treatments varied from 20 to 98% (White et al., 1981). Spray with Bt resulted in 57–98% reduction of egg masses (Dubois et al., 1988; Webb et al., 1991). We decided to use an equal mortality rate 90% for both treatments in order to reveal their net indirect effect related to differences in mortality of natural enemies. For the dimilin treatment, we assumed that the mortality rate of parasitoid adults and invertebrate predators was 90% (the same as for gypsy moth).

Pesticides are generally applied when gypsy moth density is greater than 250 egg masses per acre (Anonymous, 1989). This is equal to 334 000 eggs/ha, assuming that the average egg mass contains 540 eggs. This was used in the model as a decision threshold on whether or not to treat the stand. Using this threshold, maximum defoliation was about 10%. During 70 simulated years, dimilin was applied 56 times, compared to 28 times for Bt. This threshold (250 egg masses per acre) appears to be too low. If it is increased 3 times, the maximum proportion of defoliation is still acceptable, about 30%. Using this higher threshold (750 egg masses per acre), dimilin was applied 26 times, Bt 14 times. For timber-production areas, an even higher threshold is recommended: 1400 egg masses per acre (Gottschalk, 1989). Using this threshold in the model, dimilin was applied 10 times, Bt 9 times. Thus, the model suggests that Bt can be applied less often than dimilin because it does not reduce the number of invertebrate natural enemies; but there is no difference at high treatment threshold density.

Eradication of isolated populations was simulated using a Bt treatment every year. We studied the effect of initial gypsy moth density and the functional response of vertebrate predators on

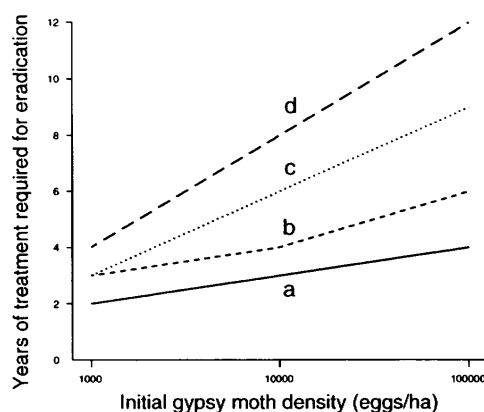


Fig. 12. Years of continuous Bt application resulting in eradication of an isolated gypsy moth population. RSZD = 1.0 (a), 0.5 (b), 0.2 (c), 0.1 (d).

the number of years required to eradicate the population. Functional response is characterized by relative predator search rate at zero prey density (RSZD). When RSZD = 1.0 the functional response is of the type II. As RSZD decreases, the functional response is transformed to type III, and it takes more time to eradicate gypsy moth population (Fig. 12). Low-density populations can be eradicated faster than high-density populations.

5. Discussion

The model generates a pattern of population dynamics similar to that observed in nature. It simulates well the aggregational response of parasitoids to increased gypsy moth density. Some differences between simulation and actual data have been found in the parasitism trends during an outbreak and in gypsy moth survival curves. Currently, there is no rational explanation of these differences and additional model simulations and field studies may be necessary to determine the cause. The model helps to find the problem, it shows that we do not have complete understanding of some ecological processes like parasitism and survival of large larvae.

It is unrealistic to expect that a complicated model will fit all available data sets. We feel that validation procedure for simulation models should

be different from validation of regression models which is based on a pass-fail rule. A simulation model represents the current knowledge of insect life-systems and there is no reason to reject all the knowledge if there are some gaps in it. However, if gaps are present, it is necessary to be cautious in interpreting model results. We think that our model can be considered valid on a qualitative level. Direct quantitative validation of the model is currently impossible because there are no experimental data sets with information about the density of all guilds of natural enemies.

One of the problems in simulation of gypsy moth populations is the functional response of vertebrate predators. Campbell and Sloan (1978) suggested that low-density gypsy moth populations are regulated by mammal predators due to their type III functional response. As a result, populations exhibit bimodal stability: at low density they are regulated by predation, while at high density they are regulated by diseases and starvation (Campbell and Sloan, 1978). Our model indicates that the type III functional response is a possible stabilizing mechanism in low-density gypsy moth populations. However, a stabilization effect may result from migration of gypsy moth larvae from high-density populations.

Elkinton et al. (1989) argued that there is no good evidence that small mammal predators have a type III functional response. In their experiments, mortality of artificially deployed gypsy moth pupae was always a monotonically decreasing function of their density. We think that this evidence is not sufficient because Elkinton et al. (1989) used unprotected pupae to test their hypothesis, but natural gypsy moth pupae are often located in safe refuges like bark flaps where their survival rate is higher (Campbell et al., 1975; Smith, 1989). The number of such refugia is limited and gypsy moth larvae were shown to be attracted to refugia like burlap bands (Liebhold et al., 1986). Thus, the proportion of gypsy moths outside these refugia may increase with population density. Data obtained by Campbell et al. (1975) support this hypothesis. Additional information is necessary to specify the type of small mammals' functional response.

The hypothesis of bimodality of gypsy moth

populations, proposed by Campbell and Sloan (1978), suggests that two stable equilibria at high and low density are present in the same environment so that population can be instantly transferred from one equilibrium to another one. However, there is no evidence of that in nature. Examples of low- and high-density populations were taken from different geographical locations (Campbell and Sloan, 1978). We agree with Liebhold (1992) that differences in phase plots among populations separated by space or time does not necessarily imply an inherent numerical bimodality.

As an alternative to the original bimodality hypothesis, we suggest that there are two types of gypsy moth population dynamics: eruptive in susceptible stands and stable in resistant stands. Eruptive dynamics is quasi-periodic and is driven by a combination of non-delayed (pathogens, vertebrate predators) and delayed (parasitoids) density-dependent processes. Stable populations exhibit moderate fluctuations in density, and are apparently stabilized by immigration of gypsy moth and its natural enemies from high-density populations. Predation and parasitism may have an additional stabilizing effect, but this is not yet proved. Immigration is not a density-dependent process but it stabilizes low-density populations because of the persistence of high-density populations around. However, the phase plot makes an illusion of density-dependence.

Our hypothesis is supported by the existence of susceptible and resistant stands which are characterized by different ecological features and different average gypsy moth densities (Bess et al., 1947; Gottschalk, 1989). The original bimodality hypothesis ignores local conditions. Unfortunately, there are not enough data on the dynamics of low-density gypsy moth populations and thus, it is impossible to test our hypothesis numerically.

Simulation results (Fig. 12) suggest that the functional response of vertebrate predators is an important factor in determining the success of gypsy moth eradication programs. In the case of the type III functional response, mortality due to predation decreases at low prey density and makes population extinctions less probable. Successful

eradication of gypsy moth in Oregon after three years (1984–1986) of intensive Bt spraying (Cameron, 1989) indicates that vertebrate predators apparently have the type II functional response.

Simultaneous fluctuation of small mammal populations is probably the major synchronization factor in gypsy moth dynamics. The most important species, the white-footed mouse, exhibits great changes in population density: the ratio of maximum to minimum density in the same location reaches 5 in Ohio (Vessey, 1987), 10 in Quebec (Grant, 1976), and 13 in Michigan (Sexton et al., 1982). According to Fig. 10, these fluctuations are large enough to cause gypsy moth synchronization. Population fluctuations of different small mammal species in different eastern regions of North America seem to be more or less synchronous (Smith et al., 1974). Krohne et al. (1988) found a significant difference of population density ranks among years, which indicates synchrony. Summarizing data from Smith et al. (1974), Grant (1976), Sexton et al. (1982), Vessey (1987), Krohne et al. (1988), and Linzey and Kesner (1991), it is possible to pin-point the years of maximum small mammal densities: 1967–1968, 1972–1973, 1979–1980, and 1984–1986. The interval between maximums is about 5–7 years. It is possible to hypothesize that gypsy moth outbreaks in 1971–1973 and 1980–1983 were induced by declines in small mammal population in 1969–1970 and 1976–1978, respectively. But there are insufficient data to reach a conclusion.

In nature, the frequency of gypsy moth density fluctuation is different from that of white-footed mice. In the model these frequencies are equal when vertebrate predators have a synchronization effect on gypsy moth. But two additional facts keep us from rejecting the hypothesis of small mammal synchronization effect. First, there seem to be second order peaks in gypsy moth defoliation (in 1949, 1977, and 1986) between major peaks (Fig. 5). These peaks may be caused by intermediate predator cycles. Second, if in the model parasitoids are allowed to migrate, then their synchronization effect may be stronger than that of predators, and the frequency of gypsy moth outbreaks will decrease.

Acknowledgements

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Appendix 1

Equation of foliage consumption

Eq. 8 is derived as follows. Foliage actually consumed FAC_c of tree class c is equal to the sum of two integrals:

$$FAC_c = \int_{-\infty}^{x_1} AFPC(x) \cdot \phi((x - M)/\sigma) \cdot dx + FP_c \cdot \int_{x_1}^{\infty} \phi((x - M)/\sigma) \cdot dx \quad (A1)$$

where x is the logarithm of gypsy moth density in tree class c , $AFPC(x)$ is adjusted foliage potentially consumed if log mean density of gypsy moth large larvae is equal to x , M and σ are the mean and standard deviation of x , ϕ is the normal distribution function (density of probability), FP_c is initial amount of foliage, and x_1 is a root of equation $AFPC(x) = FP_c$. Index c is omitted for x and M for simplicity. According to Eq. 10,

$$AFPC(x) = \exp(x) \cdot FCN \cdot RCR_c, \quad (A2)$$

where FCN is food consumption on susceptible trees and RCR_c is relative consumption rate on tree class c as compared with susceptible class. Combining Eqs. A1 and A2 yields:

$$FAC_c = FCN \cdot RCR_c \cdot \exp(M + \sigma^2/2) \cdot \Phi((x_1 - M)/\sigma - \sigma) + FP_c \cdot [1 - \Phi((x_1 - M)/\sigma)], \quad (A3)$$

where Φ is cumulative function of normal distribution. Using Eq. A2 we can estimate x_1 :

$$x_1 = \ln(FP_c / (FCN \cdot RCR_c)). \quad (A4)$$

Mean value of log-transformed gypsy moth density M is related to mean density of large larvae $MLLD_c$:

$$M = \ln(MLLD_c) - \sigma^2/2. \quad (A5)$$

Combining Eqs. A3, A4, and A5 we get Eq. 8.

Appendix 2

Glossary

Adjusted foliage potentially consumed. Foliage biomass that can be consumed by gypsy moth larvae without food limitation, adjusted to larval mortality during the feeding period.

Background mortality. Gypsy moth mortality which cannot be attributed to interaction with natural enemies or host plants.

Class-specific tree growth. A component of total tree growth rate (proportion of growth per year) which is specific to a tree class and which depends only on the amount of foliage produced by trees in this class.

Foliage potentially consumed. Maximum foliage biomass that can be consumed by a given number of gypsy moth larvae.

Foliage preference coefficient. Relative foliage preference by gypsy moth larvae. It is equal to 1 for susceptible trees, and is less than 1 for resistant and immune trees.

Foliage production. Dry foliage biomass (grams/ha) produced by trees in one year.

General tree growth rate. A component of total tree growth rate (proportion of growth per year) which is uniform in all tree classes and which depends only on the total amount of foliage produced by all trees.

Large larvae. Gypsy moth larval instars 4–6.

Life-system. A system that includes a population and its effective environment, i.e. all major factors and processes directly or indirectly affecting population dynamics.

PIB. Viral polyhedral inclusion body.

Relative consumption rate. Relative rate of foliage consumption on different tree classes. It is

equal to 1 for susceptible trees, and is less than 1 for resistant and immune trees.

Small larvae. Gypsy moth larval instars 1–3.

Tree class. Class of tree species that are similar in their interaction with gypsy moth. Three classes are considered: susceptible, resistant, and immune.

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