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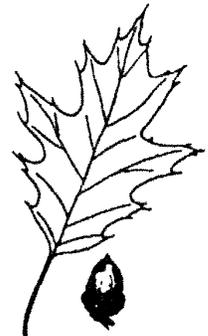
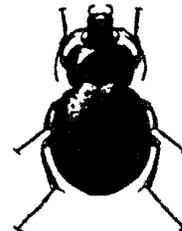
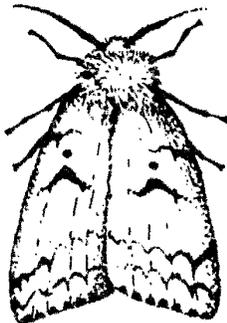
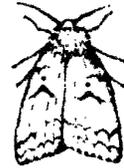
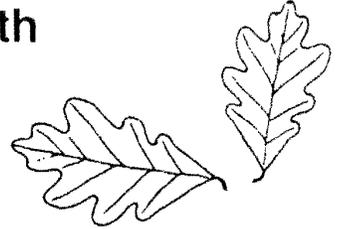
Forest Service

Northeastern Forest
Experiment Station

General Technical
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U.S. Department of Agriculture Interagency Gypsy Moth Research Review 1990



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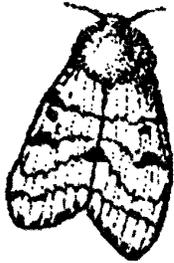
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FOREWORD

In July of 1989 representatives of Forest Service-Research (FS-R), Animal and Plant Health Inspection Service (APHIS), and Agricultural Research Service (ARS) began regular meetings to discuss opportunities for improving cooperation among the agencies conducting research on gypsy moth. Representatives from the Cooperative State Research Service (CSRS) and Forest Service-State & Private Forestry (FS-S&PF) were added over the next few months. The group is known as the USDA Gypsy Moth Research and Development Coordinating Group and has the following objectives:

- a. To monitor the progress of Service programs and any breakthroughs which may influence USDA policies;
- b. To keep the Services and the Gypsy Moth Working Group appraised of progress in research and methods development;
- c. To identify research and methods development issues and concerns;
- d. To set priorities;
- e. To maximize use of current resources as well as to provide appropriate rationale to justify increased resources.

The Coordinating Group resolved at its initial meeting that a combined interagency review of gypsy moth research and development activities would add immeasurably to better communication as well as provide a comprehensive overview of ongoing research. Members of the Coordinating Group also agreed that a proceedings should be published following the meeting.

These proceedings document the efforts of many individuals: those who made the meeting possible, those who made presentations, and those who compiled and edited the proceedings. But more than that, the proceedings illustrate the depth and breadth of studies being supported by the agencies and it is satisfying, indeed, that all of this can be accomplished in a cooperative spirit.

USDA Gypsy Moth Research and Development Coordinating Group
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M. McFadden, FS-R, Chairperson

USDA Interagency Gypsy Moth Research Review
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CONTENTS

INTRODUCTORY SESSION.....Moderator: Ralph Bram

Invited Papers:

M.E. Montgomery –
Variation in the suitability of tree species for the gypsy moth..... 1

J.S. Elkinton, J.P. Burand, K.D. Murray, and S.A. Woods –
Epizootiology of gypsy moth nuclear polyhedrosis virus 14

M.J. Twery –
Effects of defoliation by gypsy moth 27

POPULATION DYNAMICS.....Moderator: Kurt Gottschalk

Invited Paper:

W.E. Wallner, C.G. Jones, J.S. Elkinton, and B.L. Parker –
Sampling low-density gypsy moth populations 40

Abstracts:

A.E. Hajek and J.S. Elkinton –
Entomophaga maimaiga panzootic in Northeastern gypsy moth populations 45

R.M. Weseloh –
General and specific gypsy moth predators 46

J.S. Elkinton, H.R. Smith, and A.M. Liebhold –
Impact of small mammal predators on gypsy moth 46

J.A. Witter, M.E. Montgomery, C.A. Chilcote, and J.L. Stoyenoff –
The effects of tree species and site conditions on gypsy moth survival and growth in Michigan..... 47

C.W. Berisford and M.E. Montgomery –
Performance of gypsy moth larvae on hosts from the Deep South: Survival, development and host preferences..... 48

K.W. Thorpe, R.L. Ridgway, and R.E. Webb –
Development of appropriate methodologies for sampling gypsy moth populations in moderately-sized urban parks and other wooded public lands..... 48

M.R. Carter, F.W. Ravlin, and M.L. McManus –
Leading edge gypsy moth population dynamics..... 49

A.M. Liebhold and J.S. Elkinton – Analysis of spatial density dependence in gypsy moth mortality	50
---	----

BIOTECHNOLOGY Moderator: William Yendol

Abstracts:

K.S. Shields and T. Butt – Gypsy moth larval defense mechanisms against pathogenic microorganisms	51
J.M. Slavicek and N. Hayes-Plazolles – Temporal analysis and spatial mapping of <i>Lymantria dispar</i> nuclear polyhedrosis virus transcripts and <i>in vitro</i> translation products	52
S.T. Hiremath, M. Fikes, and A. Ichida – Construction of a transfer vector for a clonal isolate of LDNPV	53
J.M. Slavicek, C. Lanner-Herrera, N. Hayes-Plazolles, M.E. Kelly, and M. Fikes – Replication and inclusion body characteristics of two <i>Lymantria dispar</i> nuclear polyhedrosis virus plaque variants	54
E.M. Dougherty, D. Guzo, K.S. Shields, D.E. Lynn, and S.K. Braun – <i>Autographa californica</i> nuclear polyhedrosis virus replication in non-permissive <i>Lymantria dispar</i> cell lines	55
K.S. Shields and E.M. Dougherty – Response of gypsy moth larvae to homologous and heterologous nuclear polyhedrosis virus	56
J.P. Burand, S.T. Keating, and J.S. Elkinton Detection of <i>Lymantria dispar</i> nuclear polyhedrosis virus in infected larvae using a DNA hybridization assay	57
H.A. Wood and Yu Zailin – Genetically engineered baculovirus pesticides and their environmental safety	57

GYPSES SESSION..... Moderator: Sheila Andrus

Abstracts:

G.A. Elmes, C.B. Yuill, and T.L. Millette – Knowledge-based geographic information systems on the Macintosh computer: A component of the GypsES project.....	58
J.A. Logan, L.P. Schaub, and F.W. Ravlin – Phenology prediction component of GypsES.....	59
M.C. Saunders and M.A. Foster – The treatment implementation advisor: A component of the GypsES project	61
L.P. Schaub, F.W. Ravlin, J.A. Logan, and S.J. Fleischer – Monitoring components of GypsES	62

M.J. Twery and G.A. Elmes – Hazard rating for gypsy moth on a Macintosh computer: A component of the GypsES system	63
--	----

MICROBIAL CONTROL..... Moderator: Richard Ridgway

Invited Paper:

M.L. McManus – Microbial pesticides	64
--	----

Abstracts:

L.S. Bauer, M.L. McManus, and J.V. Maddox – Interactions between nuclear polyhedrosis virus and <i>Nosema</i> sp. infecting gypsy moth.....	76
R. E. Webb, M. Shapiro, J. D. Podgwaite, D. D. Cohen, and R. L. Ridgway – Evaluation of the Abington isolate of the gypsy moth nuclear polyhedrosis virus against a formulation of Gypchek® in small field plots	77
J. D. Podgwaite – Gypchek® use pattern realities.....	78
N.R. Dubois – Current research efforts with <i>Bacillus thuringiensis</i>	78
D.R. Miller, W.E. Yendol, M.L. McManus, D.E. Anderson, and K. Mierzejewski – Summary of the Blackmo 88 spray experiment	79
R.E. Webb, K.W. Thorpe, and R.L. Ridgway – Gypsy moth management program for moderately sized urban parks and other wooded public lands	79
J. Rosovsky, B.L. Parker, and L. Curtis – Vermont management in focal areas	80
J.V. Maddox, M. Jeffords, M.L. McManus, and R.E. Webb – Summary of experimental releases of exotic microsporidia: Conclusions and recommendations.....	81

GYPSY MOTH BIOLOGY..... Moderator: David Leonard

Abstracts:

J.M. Giebultowicz, A.K. Raina, and K.W. Thorpe – Regulation of disparlure titer in gypsy moth females: Effects of mating and senescence	81
A.P. Valaitis and J. Jolliff – Isolation and characterization of juvenile hormone esterase from gypsy moth (<i>Lymantria dispar</i>)	82

D.R. Gray, J.A. Logan, and F.W. Ravlin – Using respiration rates of single eggs to determine pre-diapause development rates.....	83
J. Werren and T. O'Dell – Use of molecular probes to detect parasites in gypsy moth	84
V.C. Mastro and A. Pellegrini-Toole – The backcross sterility technique	85
J.A. Tanner and C.P. Schwalbe – Outcrossing colonies of the Otis New Jersey gypsy moth strain and its effect on progeny development	86
R.W. Hansen – Pupal abnormalities among laboratory-reared gypsy moths.....	87
P.W. Schaefer – Variation in gypsy moth, with comparisons to other <i>Lymantria</i> spp.....	88

MONITORING / MODELING Moderator: Max McFadden

Invited Papers:

F.W. Ravlin, S.J. Fleischer, M.R. Carter, E.A. Roberts, and M.L. McManus – A monitoring system for gypsy moth management	89
---	----

J.J. Colbert – History of research on modelling gypsy moth population ecology.....	98
---	----

Abstracts:

B. A. Leonhardt, V.C. Mastro, C.P. Schwalbe, and R.L. Ridgway – Pheromone dispenser formulations for use in gypsy moth management programs	111
---	-----

J.S. Elkinton and M.L. McManus – Development of a pheromone-baited trap to monitor gypsy moth populations	111
--	-----

S.J. Fleischer, E.A. Roberts, F. William Ravlin, and R.C. Reardon – Monitoring and mapping gypsy moth data in AIPM: The process and problems of implementation.....	112
---	-----

A.M. Liebhold, J. Halverson, G.A. Elmes, and J. Hutchinson – Landscape ecology of gypsy moth in the Northeastern U.S.....	113
--	-----

J.A. Logan and D.R. Gray – Modeling gypsy moth seasonality.....	114
--	-----

J.M. Russo, J.G.W. Kelly, and A.M. Liebhold – Mesoscale landscape model of gypsy moth phenology.....	115
---	-----

J.J. Colbert and Xu Rumei – Behavior of the gypsy moth life system model and development of synoptic model formulations.....	116
--	-----

IMPACTS Moderator: Robert Wolfe

Invited Paper:

R.R. Hicks, Jr. –
Hazard rating forest stands for gypsy moth..... 117

Abstracts:

C.G. Jones –
What causes the patterns of gypsy moth defoliation? 127

M.J. Twery and P.M. Wargo –
Development of a sampling system for *Armillaria* rhizomorphs in mixed oak stands:
a progress report 128

R.C. Whitmore and R.D. Greer –
Short term effects of gypsy moth defoliation on nongame birds 129

D. Samuel and R. Silvester –
The effects of gypsy moth infestation on gray squirrel habitat and populations 130

S.M. Brock, S. Hollenhorst, and W. Freimund –
Effects of gypsy moth infestation on aesthetic preferences and behavior intentions 131

K.W. Gottschalk –
Using silviculture to minimize gypsy moth impacts..... 132

R.D. Greer and R.C. Whitmore –
The effects of gypsy moth-oriented silvicultural treatments on vertebrate predator
communities..... 133

CLOSING COMMENTS USDA Gypsy Moth Co-ordinators

POSTER PRESENTATIONS:

Abstracts:

D. E. Anderson, D. R. Miller, and W. E. Wallner –
Demonstration of the gypsy moth energy budget microclimate model..... 134

D.E. Anderson, D.R. Miller, Y.S. Wang, W.E. Yendol, and M.L. McManus –
Micrometeorological measurements during the Blackmo 88 spray trials 135

J.P. Burand, H. Horton, J.S. Elkinton –
Detection of latent nuclear polyhedrosis virus in the gypsy moth 135

J. J. Colbert and G.E. Racin –
Gypsy moth life system model 136

J.R. Deans –
Modified lignin sulfonate formulation for the photo protection of GMNPV 137

B. Duan, K. Mierzejewski, and W.G. Yendol – Statistical comparison of AGDISP prediction with Mission III data	138
R.W. Fuester – A multiple regression model for parasitization of gypsy moths by the introduced larval parasite <i>Cotesia melanoscelus</i> (Hymenoptera: Braconidae)	139
K.W. Gottschalk – Does previous stand management influence gypsy moth-related mortality?.....	140
K.W. Gottschalk – Gypsy moth impacts on oak acorn production	141
R.R. Hicks, Jr., D.E. Fosbroke, S. Kosuri, and C.B. Yuill – The West Virginia University Forest hazard rating study: the hazards of hazard rating.....	142
J.B. McGraw and K.W. Gottschalk – Interactive effects of defoliation and low resource levels on photosynthesis, growth, and gypsy moth larval response to red oak seedlings	143
M.E. Montgomery – Predicting defoliation with egg mass counts and a "helper" variable.....	144
J.M. Slavicek and N. Hayes-Plazolles – Identification, cloning, and expression analysis of three putative <i>Lymantria dispar</i> nuclear polyhedrosis virus immediate early genes	145
H.R. Smith – Understanding predation: implications toward forest management.....	146
M.J. Twery – Changes in vertical distribution of wood production in hardwoods defoliated by gypsy moth	147
C.R. Vossbrinck, M. Baker, J.V. Maddox, M.R. Jeffords, and B.A. Debrunner- Vossbrinck – Using ribosomal RNA technology for classifying microsporidia	148
Y.S. Wang, J.Welles, D.R. Miller, D.E. Anderson, G. Heisler, and M.L. McManus – Architecture of the Black Moshannon forest canopy measured by hemispherical photographs and a Li-Cor LAI-2000 sensor	149
W.G. Yendol, K. Mierzejewski, D.R. Miller, D.E. Anderson, M.L. McManus, R.C. Reardon, and W. McLane – Aerial application of <i>Bacillus thuringiensis</i> to an oak forest: deposit analysis and predictions with FSCBG	150
LIST OF ATTENDEES.....	151

A MONITORING SYSTEM FOR GYPSY MOTH MANAGEMENT

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ABSTRACT

Within the last ten years considerable research has been directed toward the development of a gypsy moth monitoring system for project planning at a regional level and for making control decisions at a local level. Pheromones and pheromone-baited traps have been developed and widely used and several egg mass sampling techniques have also been developed. Recently these sampling techniques have been combined into a pheromone trap-based monitoring system which uses pheromone trap results to assist in prioritizing areas to receive egg mass samples. This approach has also made extensive use of graphical presentations using geographic information systems. This paper describes the status of monitoring tools and systems for determining gypsy moth densities for management purposes and areas in need of continued research.

INTRODUCTION

As late as 1984, major management units (states or areas of similar geographic scale) in the United States used a wide variety of methods for making gypsy moth control decisions. These methods focused primarily on egg mass sampling using an underlying assumption that egg mass density is related to defoliation in the subsequent larval generation (Ravlin et al. 1987). Several studies have found a significant relationship between egg mass density and defoliation (Gansner et al. 1985, Wilson and Talerico 1981, Montgomery in press). However, the question of how to arrive at precise and/or accurate estimates of egg mass density for management purposes within the constraints of pest management programs has only begun to be explored. Questions related to when in the gypsy moth population cycle to begin egg mass sampling, how many samples to collect, how to spatially distribute those samples, and how to present the results from these samples to determine treatment areas have also been only recently addressed. The objective of this paper is to present developments in sampling and monitoring technology and how they have or have not addressed these questions.

THE BASIS FOR MAKING CONTROL DECISIONS

The Relationship Between Egg Mass Density and Defoliation

The basis for control decisions in gypsy moth management programs is an assumed relationship between egg mass density and defoliation. The question is whether or not a given level of defoliation will occur as a result of the subsequent larval population. Consequently, it is necessary to only specify whether or not to treat based on a threshold egg mass density. The earliest thresholds mentioned in the literature were published in "The Comprehensive Gypsy Moth Management System" study where Etter discusses 250, and 1,000 egg masses per acre as possible action thresholds (Appendix K-9, National Gypsy Moth Management Board 1979). These thresholds have continued to be used by most gypsy moth management programs through the 1980's (Ravlin et al. 1987) even though there are no studies which provide economic or biological reasons for their use. Nevertheless, they have provided managers with a decision criterion.

Egg Mass Density Estimates

In 1981 the so-called "compendium" (Doane and McManus 1981) was produced and with it came a wealth of information for researchers and managers. The title "Research Toward Integrated Pest Management" was very appropriate because it was clear that many components of an IPM system were ready for implementation or were being used but a functional "system" had not been delivered to the manager community. Monitoring tools such as pheromone-baited traps, hazard rating models, knowledge of gypsy moth population cycles, and chemical and microbial controls were available for use on a day-to-day basis. The concept of how these components might be integrated was also presented but it was still clear that one of the weak links in the chain of management activities was an approach to predict the amount and spatial extent of defoliation based on egg mass density. Wilson and Fontaine (1978) developed the fixed- and variable-radius sampling method that could generate egg mass densities with any desired level of precision, given infinite resources, and this method was promoted throughout both the research and management communities. It became clear that the fixed- and variable-radius method was not suitable for most management situations because of their time-intensive nature and limited spatial coverage. In 1983 Eggen and Abrahamson devised a method which simply required field personnel to walk through areas of interest for five minutes, count all egg masses, and then relate the counts to absolute egg mass densities using regression models. However, Eggen and Abrahamson state that "More accurate surveys must be conducted when densities are at or near egg mass treatment thresholds". In other words, the technique is useful for gross categorization of populations and not a precise sampling tool. There are several variables that contribute to variability in density estimates based on five-minute walks. Bellinger et al. (1989) showed that the distribution of gypsy moth egg masses is affected by proximity to an "edge". Here edge is defined as the change from one habitat to another, such as where roads are cut through continuously forested areas or pastures. In the Bellinger et al. study an edge effect was so prevalent that significant differences occurred between the "edge side" of trees and the "forest side" of trees. Depending on the side of the tree that one walked by, different egg mass density estimates would be obtained using the timed walk method. In a study done by Fleischer et al. (unpublished manuscript) the timed walk method was compared to 1/40 acre fixed radius plots. Analysis of variance of these data showed that significant amounts of variability could be attributed to location, habitat, the agency responsible for taking the data, and the individual taking the samples. Thus, the five minute timed walk method does not produce consistent egg mass density estimates and cannot be relied upon for treatment decisions.

In an effort to simplify and reduce the time spent taking fixed- and variable-radius plot samples for the Maryland Gypsy Moth IPM Pilot Project Kolodny-Hirsch (1986) compared fixed- and variable-radius plot sampling (Wilson and Fontaine 1978) with fixed-radius plots. His findings were that 1/40 acre fixed-radius plots far exceeded the other methods tested in terms of relative net precision¹. Using 1/40 acre sampling as the sample unit, Kolodny-Hirsch developed a sequential egg mass sampling protocol for making treatment decisions, although implementation and validation data were not presented. Sequential sampling protocols are dependent on the underlying statistical distribution (e.g., poison, negative binomial) of data used to develop protocols and the amount of error that decision makers are willing to accept. Statistical distributions of gypsy moth egg mass samples are a result of the number and physical size of a sample unit and the spatial pattern of egg masses which, in turn, is dependent on habitat. Kolodny-Hirsch used randomly distributed 1/40 acre samples taken from 14 oak/sweetgum woodlots in urban/suburban Maryland. These woodlots were in flat terrain and had not experienced outbreak gypsy moth populations. Thus, it cannot be assumed that factors affecting the underlying egg mass distribution will stay constant for other types of populations, habitats, and terrain. Making this assumption, Fleischer et al. (unpublished manuscript) developed sequential sampling protocols from several data sets

¹Relative net precision (RNP) is defined by: $RNP = [1/(C_s)(RV)]100$ and relative variation (RV) is defined as $RV = (SE/x)100$ (Pedigo et al. 1972).

collected in northwestern Virginia in continuously wooded areas. This resulted in the development and validation of four sequential sampling protocols used in the Appalachian Gypsy Moth Integrated Pest Management demonstration project (AIPM).

USE OF PHEROMONE-BAITED TRAPS TO PRIORITIZE AREAS FOR EGG MASS SAMPLING

The Moths per Trap Model

Egg mass sampling is expensive and methods for prioritizing areas to receive egg mass samples are essential to working within budgetary constraints. There are no universal methods for prioritizing areas and research conducted during the last five years has sought to address this problem through the use of pheromone-baited traps for male gypsy moths. Pheromone-baited traps have been universally used in gypsy moth detection, eradication, and management programs in the United States (Ravlin et al. 1987). However, decision-makers have not had models that relate pheromone trap results (moths per trap) with the density of other gypsy moth life-stages, particularly egg masses. Thus, management programs are forced to expend more of their resources on expensive egg mass sampling without the benefit of using pheromone trap results to assist in the process of prioritizing areas to receive egg mass samples.

For gypsy moth management programs it would be useful if the number of pheromone trap-captured moths could be used to estimate one or more of the following parameters: egg mass density, egg density, the probability of occurrence of an unacceptably high population (i.e., exceeding a treatment threshold), or be used to trigger and target egg mass sampling for more precise population estimates. Regression techniques for determining if a relationship exists between moths per trap and egg mass density have been described for the Douglas-fir tussock moth (Daterman 1978, Shepherd et al. 1985) and the spruce budworm (Allen et al. 1986). Regressions have been performed on gypsy moth data taken from the Maryland Integrated Pest Management Pilot project, Shenandoah National Park, and plots distributed throughout Virginia. In all cases there are significant regressions between moths per trap and egg mass density. But, like the tussock moth and budworm, there were differences between locations and years with the proportion of variability explained ranging from 30 to 80%. While there is some utility in these relationships, data from Massachusetts do not always support them (Elkinton, 1987). Reasons for this are not known. Many factors affect the dynamics of pheromone trap/moth interactions and the relationship between trap catch and egg mass density. Male moth dispersal and behavior are particularly important. More importantly, because male moths move away from the location from which they emerged it is not reasonable to assume that there will always be a good relationship between moths and egg masses when data are taken from a single location. Developing relationships over larger areas (e.g., a radius 250-500 m) may provide more insight into this problem. Another approach to this problem is to stratify egg mass and moth data into density categories and determine the probability of exceeding different egg mass densities (Table 1). This approach has the advantage of providing managers with a measure of risk and alleviates the need to project egg mass densities given moth counts.

Table 1. Probability of exceeding a given egg mass density based on the number of moths captured in a pheromone-baited trap.

Egg Masses / Acre	Moths Captured per Trap		
	0 - 500	501 - 1000	>1000
0 - 250	0.88	0.40	0.10
251 - 500	0.00	0.20	0.05
501 - 1000	0.00	0.10	0.25
>1000	0.12	0.30	0.60

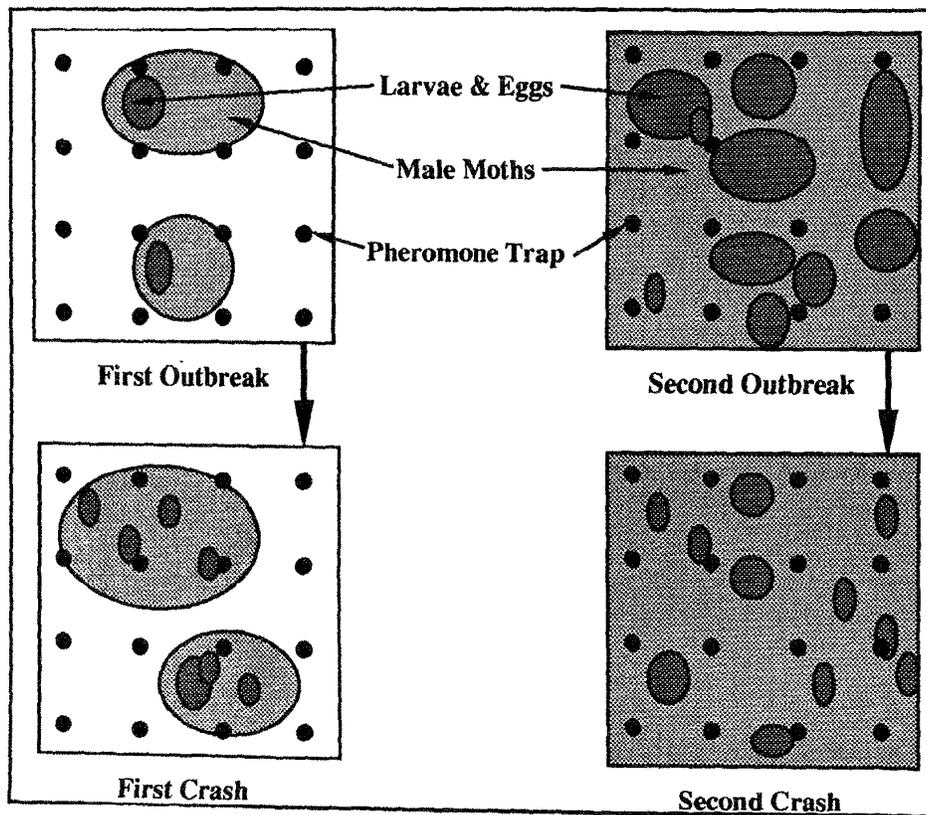


Figure 1. Hypothetical spatial pattern of eggs, larvae and male moths during and after the first two outbreak episodes in a leading edge area.

Other factors contribute to variability in the egg mass density-moths per trap relationship. Elkinton (1987) has shown that the standard gypsy moth milk carton-type pheromone trap decreases in efficiency after about 400 moths have been captured (i.e., increasing numbers of moths enter but subsequently leave traps). Also, traps that have accumulated water often contain rotten moths and presumably, volatiles from these rotting moths can decrease trap efficiency independent of the number of moths caught. Finally, it is not uncommon in the northeastern states (e.g., Massachusetts) to completely fill pheromone traps with male moths and yet fail to find egg masses or other life-stages in the immediate vicinity of the trap (Elkinton 1987). It may well be that the dynamics and/or spatial distribution of populations may contribute to this discrepancy. In theory, when populations first invade new areas their distribution tends to be highly aggregated (Fig. 1, top left) and it is not until after one or more outbreaks (defoliation episodes) that isolated populations begin to coalesce and become more generally distributed (Fig. 1, bottom left). The result would be male moths emanating from several sources creating a "cloud of moths" over the entire area even when other life-stages are highly aggregated and at low density (Fig. 1, right top and bottom).

The Male Wing Length Model

Use of a density index independent of the number of pheromone trap-captured moths would, in part, circumvent some of the problems listed above. Leonard (1968) reported that there was a relationship between body size and density of the gypsy moth and Hinckley (1970) suggested that male moth size, as measured by wing length, varied inversely with the level of defoliation. It follows that egg mass density should be directly related to larval density however, the relationship between defoliation and larval density is less direct. Wilson and Talerico (1981) and Gansner et al. (1985) found a relationship between egg mass density and defoliation, but there is significant variability in these relationships presumably due to population, site characteristics, and sample method. Despite the tenuous nature of these relationships we might expect to find a correlation between male moth size and population fecundity (eggs per unit area) based on the assumption that density dependent stress and defoliation will produce populations of smaller individuals. In 1984, field observations in the Shenandoah National Park indicated that the size of male gypsy moths and egg mass density were correlated and that some measurement of male moths might be used as an index of egg mass density and eggs per mass. We began a study to examine the relationship between male moth wing length and other population parameters. Data were collected in the Shenandoah National Park in Virginia and throughout Maryland. Male wing length and eggs per mass were correlated ($r = .70$) and wing length and egg mass density were also well correlated ($r = .72$) (Bellinger et al. in press). Additional research has found that moths falling into the smallest size classes may be produced only after larvae experience a defoliation episode ($> 40\%$ defoliation). The relative frequencies of small (< 19 mm) and large (> 19 mm) moths may then predict an egg mass density category but not necessarily an absolute density estimate (Carter et al. unpublished manuscript)

INTEGRATION OF PHEROMONE-BAITED TRAPS AND EGG MASS SAMPLING

Figure 2 describes how pheromone trap results and egg mass sampling can be combined with other variables to determine areas requiring more intensive sampling. The basis for this system is an area-wide grid of pheromone traps, the results of which, serve as a trigger for initiating egg mass sampling at the local level. Research into methods for delimiting egg mass sample blocks and treatment blocks has been conducted primarily through AIPM methods development and has been described by Fleischer et al. (these proceedings); Geographic information systems play an essential role in the spatial representation of male moth data, egg mass distributions, and subsequent treatment areas. Using the results of male moth surveys to determine egg mass sample

areas requires that point data from pheromone traps be converted to a continuous surface and lines of constant moth density (contours) determined. For the AIPM project, this was done using the ARC/INFO geographic information system. At this point a male moth threshold for egg mass sampling was determined by managers based on the probability of exceeding an egg mass treatment threshold (Table 1) and the risk associated with not sampling (treating) a location. Following the selection of a male moth threshold and generation of contours, a 1 km grid was overlaid on areas to be managed and all 1 km grid cells that were intersected by a contour line greater than or equal to the moth threshold were candidates for egg mass sampling. Other factors that influence the selection of areas for egg mass sampling are last year's egg mass density, population trend (previous moths/current moths), susceptibility, accessibility of sites for sampling, and political and economic considerations. All of these factors can be combined using a geographic information system to produce a composite map used in conjunction with USGS topographic maps and other relevant information (Fig. 3).

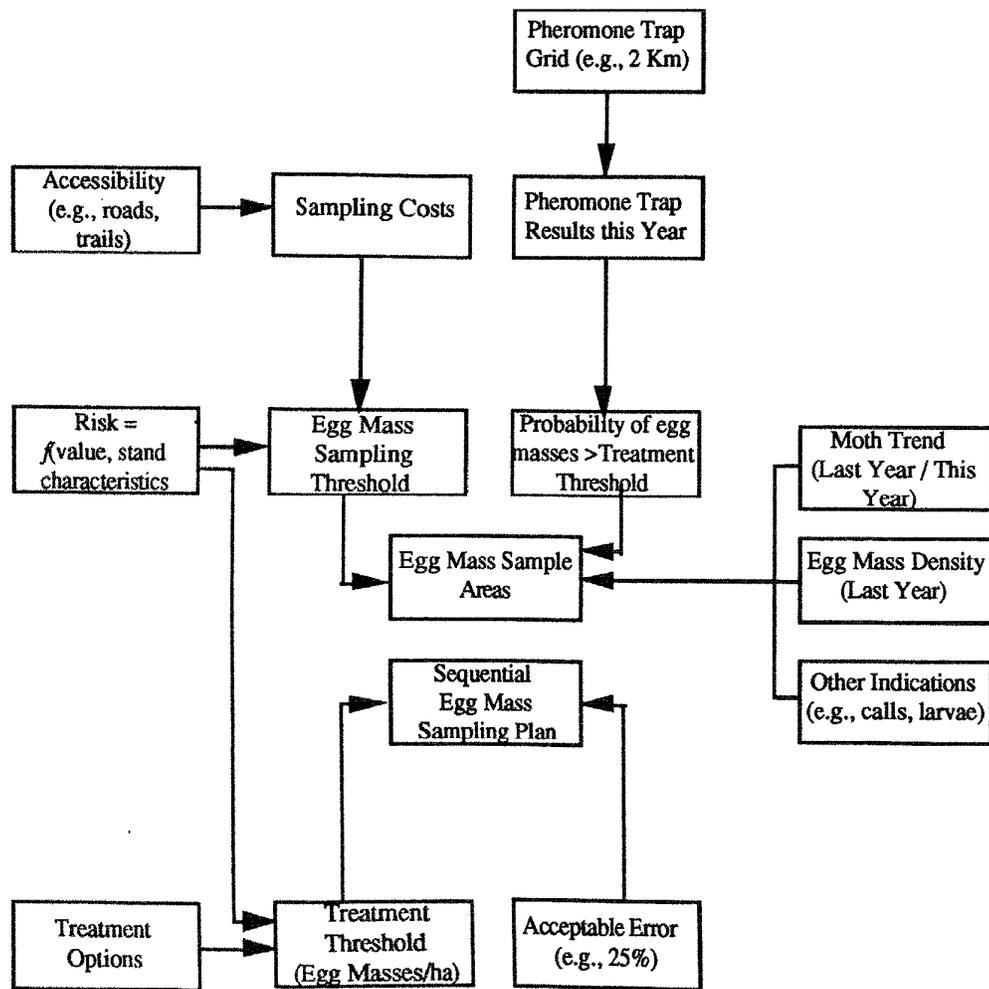


Figure 2. Sequence of events and flow of information to determine the location and number of egg mass samples to be taken for a given geographic area (figure by L. Schaub).

Once an area has been targeted for sampling, sequential egg mass sampling schemes can be generated based on treatment thresholds and sampling error selected by managers. Treatment thresholds should be determined on the basis of expected levels of defoliation (e.g., Montgomery in press) and the efficacy and cost of treatment options (e.g., diflubenzuron vs *Bacillus thuringiensis* (Berliner)). Methods for implementation of sequential egg mass sampling schemes are described in Rutherford and Fleischer (1989). Treatment blocks can then be delimited based on egg mass density, landscape features, and management objectives. For AIPM this threshold was 200 moths in 1988 and 500 in 1989. Results of egg mass surveys can be analyzed similar to pheromone trap results to produce treatment blocks.

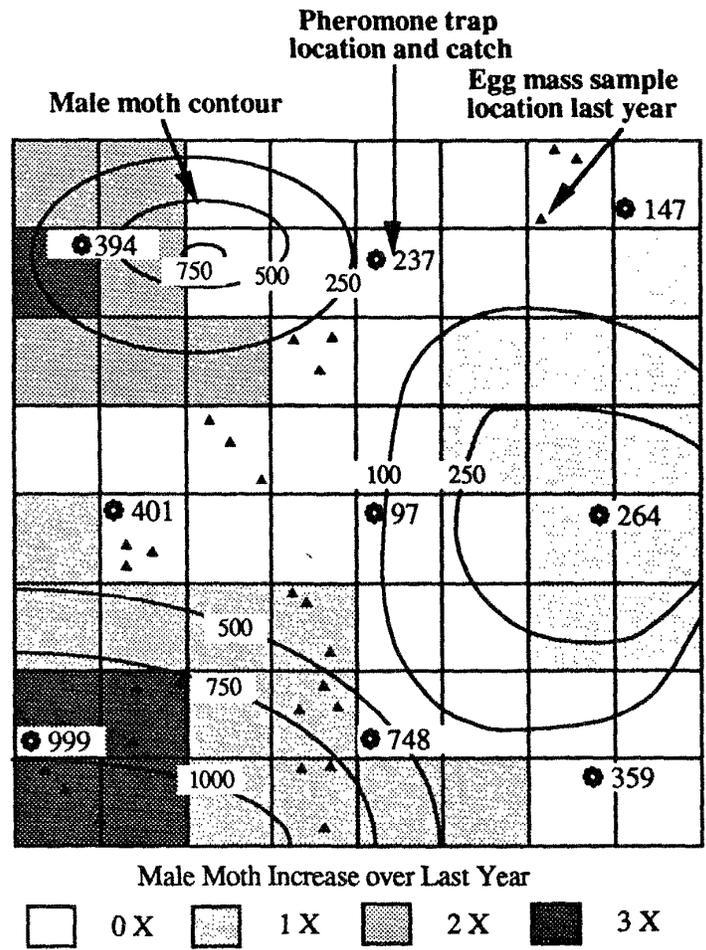


Figure 3. Map used for determining egg mass sample areas in the Appalachian Gypsy Moth Integrated Pest Management demonstration project.

SUMMARY AND CONCLUSIONS

Several problems remain in the development of gypsy moth monitoring systems. As yet, the pheromone trap-based system described above can be used only in areas which are not generally infested (i.e., at or in front of the leading edge). Problems with trap saturation and lack of a reliable moth-to-egg mass relationship prohibits its use in northern Virginia and areas to the north and east. We now have a sequential egg mass sampling scheme that has been field tested and appears to produce the best results to date, but cost remains a constraint to sampling large geographic areas. Systems to access land-use and habitat-related variables could reduce the number and size of areas requiring egg mass sampling. Thus, the cost of this approach would also be reduced. Alternative egg mass sampling approaches need to be developed. These approaches may include stem counts which relate the proportion of stems with egg masses to the probability of exceeding treatment thresholds. This approach would satisfy the need to cover large areas of land and provide decision makers with an estimate of the risk associated with not treating a given area. Stratified sampling in residential situations may also provide risk and density estimates while reducing the cost of intensive searches around houses and man made objects. Burlap bands placed around trees to collect larvae, pupae, and egg masses may also generate useful information.

No matter what type of systems are developed, they must be evaluated in a variety of management situations including leading edge populations and generally infested areas with endemic and increasing populations. The idea that only one monitoring system needs to be developed must be challenged. Yet, standardized protocols need to be put in place to allow good interpretation of data and a wide area perspective of data collected from adjoining geographic regions. One approach may be useful in generally infested areas but may not be appropriate for leading edge populations or data may not lend themselves to spatial presentations essential to making good treatment decisions over large land areas. Evaluation criteria for monitoring systems must include accuracy and precision of population estimates, ease of use, and cost effectiveness. The entire process of data collection, data base management, and data presentation must also be considered before making global sampling recommendations to the gypsy moth manager community.

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HISTORY OF RESEARCH ON MODELLING GYPSY MOTH POPULATION ECOLOGY

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ABSTRACT

History of research to develop models of gypsy moth population dynamics and some related studies are described. Empirical regression-based models are reviewed, and then the more comprehensive process models are discussed. Current model-related research efforts are introduced.

Software that models the life system of gypsy moth (*Lymantria dispar* L.) is described. The gypsy moth life system model (GMLSM) is designed to simulate the dynamics and interactions of gypsy moth, its hosts and natural enemies, in a forest stand over a number of years, with or without human intervention. Working hypotheses of gypsy moth researchers can be synthesized. The purpose and objectives of model construction, the history of model development, model structure and subsystems, and plans for testing and additional developments are described.

INTRODUCTION

The range and extent of damage by gypsy moth, *Lymantria dispar* L., in North America have been increasing since 1869 when it was imported and inadvertently released in the Boston area. The gypsy moth has nearly reached its northern limits but is continuing to spread west and south. It has been suggested that the gypsy moth may find suitable habitat farther north as it continues to move west. The insect is a naturally occurring pest in Eurasia. With its spread in North America, research and attempts to control the gypsy moth have expanded and intensified, and more recently, increased emphasis has been placed on mitigating the effects of this pest.

The U.S. Department of Agriculture initiated accelerated and expanded funding of gypsy moth research in the 1970's. Much of this work is summarized in *The gypsy moth: research toward integrated pest management* (Doane and McManus 1981). Since that time, the Gypsy Moth Research and Development Program in the Northeastern Forest Experiment Station has been one of the leaders in organizing and supporting research on this insect.

Researchers have applied the modelling approach to understand many facets or components of the gypsy moth-mixed hardwood ecosystem. Here, I review the history of gypsy moth population modelling research; describe the gypsy moth life system model (GMLSM), and discuss plans for development and testing of the GMLSM and related models.

HISTORY OF MODELLING RESEARCH

Sheehan (1989) published a review of most of the currently available literature on models dealing with gypsy moth in North America. In a recent article, Elkinton and Liebhold (1990) described a few of these models and discussed factors that should be considered in models of specific portions of the life system, such as phenology.

Sheehan (1989) partitioned her review into two major sections: the first covers models dealing with specific components such as fecundity or mortality sources, and the second covers those whole-population models that deal with year-to-year changes in population numbers, and primary factors that determine density or trend. She further partitioned her review of population models into the regression-based empirical models and process-based system models. I will concentrate on whole-population models and discuss some of the work on component models that I believe to be particularly significant to overall population ecology.

Regression-based empirical models

These models predict the number or proportional change in number of gypsy moth from year to year based on statistical methods such as correlation or regression. They are used to ascertain the relationship between population parameters and other relevant factors, but not necessarily in ways that directly describe the biological processes that give rise to the relationships. Such models specify independent variables such as past temperature or precipitation regimes, previous gypsy moth density, forest type or forest condition. These models assume that all remaining influences on the dependent variable can be and are absorbed into a normally distributed error term about the model.

There have been a number of models developed that predict trend, egg density, or egg-mass density. Using data from the Melrose Highlands and the Forest Service's Intensive Plot System, Campbell and Sloan (1978a) used multiple regression to fit log transforms of annual trend to a polynomial of log transforms of prior egg density and the coefficient of variation of the log transform of egg density. In a second regression model they fit log transform of egg-mass density to precipitation in June, log transform of prior year's egg-mass density, and the square of the coefficient of variation of the log transform of prior egg-mass density. Later they published (Campbell and Sloan 1978b) additional linear regression models fitting log(annual trend) to the cube of the log transform of egg-mass density.

Earlier, Campbell (1967, 1973a) produced three equally complex polynomial models for predicting trend or density. Biging et al. (1980) developed a regression model using log transformed data from the Melrose Highlands (Campbell 1973b), predicting plot egg-mass density from 3 prior year's egg-mass density and 2 prior year's temperature and precipitation. They applied the model to Wisconsin forests using weather data from that state and found that there is potential for maintaining gypsy moth populations throughout the entire state for protracted periods of time. To predict egg density, Znamienski and Liamcev (1983) used the proportion of oaks in the stand; average temperatures for May-August and July-August, minimum temperature for May and its departure from an average for the prior 10 years; egg-mass density, eggs/mass, and egg weight for the previous generation. Three sets of stand data were tested separately and a final model, where egg weight was not included in the model, was developed using all stands.

Only one developed by Campbell and Sloan (1978b) and those developed by Znamienski and Liamcev (1983) have been tested, and only the latter was tested successfully on independent data.

There are generally three problems with models such as these that are based on correlation rather than on the underlying biological principles or mechanisms that give rise to the behavior that is exhibited. First, to provide confidence in predictions, large data sets are required to build such models; second, models of this type rarely apply well outside the range of data on which they were built; and third, indicator variables chosen as independent variables for analyses may not always correlate with processes that give rise to the variability being analyzed. Campbell and Sloan (1978a) describe one such problem as follows: "...intrapopulation influences on the dynamics of gypsy moth populations probably include occasional switches in key factors over time...Specifically, we infer from these results that neither multiple regression models such as those in Campbell (1973a) nor any other models can possibly provide accurate projections of the

natural maintenance of area wide gypsy moth outbreaks unless these intrapopulation phenomena are accounted for."

Problems can be overcome and additional valuable information can result from follow-up studies. For example, existing relations can be tested or strengthened by collecting additional data in other years or at new sites. Models can be extended to include additional variables. This often requires recollecting initial data and can be expensive. Again, Campbell and Sloan (1978b) state: "We infer from these differences [between areas] that one or more of the truly major mortality (or natality) factors that govern this life system may differ substantially from one area to another or from one time to the next." While Campbell and his coauthors have provided many extremely valuable results, too often people attempt to apply such results without heeding the caveats.

It should be noted that many of the same procedures that produce empirical models are used in the development of process models.

Process simulation models

Process models are designed to synthesize biological hypotheses and to provide a means to understand their interactions. Such models are not meant to predict exact futures, but may elucidate relationships and provide a holistic understanding by integrating many hypotheses. I will briefly review six published process models.

Picardi's (1973) model was designed to investigate management policy associated with gypsy moth population dynamics. Pheromone control and pheromone in combination with insecticide at high densities were proposed. He did not specify a particular spatial resolution and no stand model was developed BUT the basis for population density was on a "per available oak leaf surface area" that included production and death rates for this substrate. It did have a well-developed population dynamics section that included stage specific mortality from predators, parasites, and disease, as well as the effects of management actions.

Morse and Simmons (1979) developed a model to examine possible results of management actions taken against colonizing populations in Michigan forest. The purpose of this model was to describe year-to-year forest/gypsy moth interactions and the effect of gypsy moth on forest growth and mortality, and to examine control policies and propose alternatives to an eradication policy. Large tracts of land are represented by average units of 1 square mile. Each unit is simulated as a product of terms: number stems/unit, average tree diameter, ratio of host/non-host, average foliage per tree of the given diameter. A single tree growth equation was combined with mortality based on three site classes and three classes of defoliation. Gypsy moth population dynamics were constructed from three life stage mortality rates with three additional random number multipliers. Additional virus mortality resulted when population density was sufficiently high for 2 or more years. No results of inter-site spatial patterns or interactions were reported.

Valentine (1981) designed a model to assess the influence of gypsy moth on an even-aged oak forest stand. The dynamics of a number of individual trees were simulated through difference and differential equations. Gypsy moth and foliage dynamics were built in continuous, differential equation models within each year on each tree. This model was given the most thorough sensitivity analysis but only limited calibration tests. Only one host species, red oak, was used in the sensitivity analysis.

Etter (1981) developed simulation models for use in development and analysis of a comprehensive gypsy moth management system. Two differential equation models were designed to show interactions of gypsy moth density with NPV in a policy analysis setting. He does not include stand or natural enemies except for a uniform foliage growth equation and fixed mortality rates for all factors other than NPV. In the discussion of the more complex model that is not actually

presented, he describes expanding the 15 equation model to 130 equations by partitioning a population by sex and life stage, and by adding more detailed accounting of NPV and non-NPV mortality rates and feedbacks.

Brown et al. (1983) used two simulation models to examine the effects of *Ooencyrtus kuvanae* (Howard) parasitism on gypsy moth populations. A discrete model of gypsy moth populations and an extension of Picardi's model with modifications were developed. They analyzed simulation results and compared outputs to field data. The study is the most comprehensive in terms of modelling the biological processes of the gypsy moth life system. They include mortality factor formulations, using functional, numerical, and density dependent relationships. They compared simulation results to two field data sets using ANOVA to obtain measures of effectiveness of *Ooencyrtus* mortality. No foliage or stand interactions were modeled or discussed in this publication.

Byrne et al. (1987) developed a model that was built around Johnson's (1977) model of forest succession in the North Carolina Piedmont. The objective was to determine the effects of gypsy moth outbreaks on forest succession and to evaluate the sensitivity of forest management practices. Their conclusions were made relative to managed or natural succession on the Piedmont. Using the distribution of 12 forest types described by Johnson, Byrne et al. refined the stand development stage distribution of each type. The 12 forest types were then grouped into three food preference categories. Gypsy moth larvae were classified as either small (L₁-L₃) or large (L₄-L₆) with no distinction of sex until pupation. Feeding was considered only for large larvae; daily mortality rates were fixed along with dispersal mortality rates. They did not model any spatial or multi-year temporal dynamics but uniformly projected a single outbreak population pattern for each food preference group for the entire Piedmont.

CURRENT POPULATION MODELING RESEARCH

There are a number of model-related studies being pursued at present. Mike Foster at The Pennsylvania State University is working on the NPV virus-pathogenicity-interactions with host foliage phenolics as exhibited in gypsy moth feeding, infection, and mortality rates. The landscape ecology of gypsy moth in the northeastern United States and southeastern Canada is being studied by Andrew Liebhold and Joel Halverson of the USDA Forest Service, in cooperation with Gregory Elmes and Jay Hutchinson of West Virginia University, in an attempt to understand the large-scale spatial and temporal dynamics of gypsy moth populations. Jesse Logan and David Gray of Virginia Polytechnic Institute and State University are developing a three-phase temperature-dependent model of gypsy moth egg phenology that utilizes temperature thresholds and thermal requirements specific for each of the three phases, and includes possible developmental constraints imposed by a preceding phase. Joseph Russo and John Kelly of Zedx Inc. and Andrew Liebhold of the Forest Service are developing a mesoscale landscape model of gypsy moth phenology by using high-resolution climatological data and the Gypsy Moth Phenology Model (GMPHEN) (Sheehan¹) within a geographic information system to produce high spatial resolution of the average gypsy moth development for selected days in the northeastern United States.

Modelling of a very different sort is being done by Mark Twery of the USDA Forest Service, Mike Saunders and Mike Foster of The Pennsylvania State University, Bill Ravlin and Jesse Logan of

¹Sheehan, Katharine A. GMPHEN: a gypsy moth phenology model. 52 p. Unpublished manuscript.
Sheehan, Katharine A. User's guide for GMPHEN: a gypsy moth phenology model. 38 p. Unpublished manuscript.

Virginia Polytechnic Institute and State University, and Gregory Elmes and Charles Yuill of West Virginia University. They are developing the Gypsy Moth Expert System (GypsES). A full section of these proceedings is devoted to this topic. This system will have models imbedded within it and there are plans to allow communication between the expert system and other models, particularly the GMLSM and the Stand Damage component of the GMLSM.

The stand damage subsystem can be executed independent of the rest of the GMLSM when defoliation in a stand is known or assumed. In Morgantown, we are also working on development of synoptic models that will capture the major features of the gypsy moth life system in a compact form that can be more readily explored for asymptotic behavior and stability. This work is being carried out in cooperation with Dr. Xu Rumei of Beijing Normal University, Peoples Republic of China (currently a visiting scientist at West Virginia University).

GYPSY MOTH LIFE SYSTEM MODEL

As discussed above, a number of models have been constructed to simulate various aspects of the population dynamics of the gypsy moth in North America (Elkinton and Liebhold 1990, Sheehan 1989). Each of the simulation models described by Sheehan was designed to investigate a specific set of circumstances and specific management implications. The gypsy GMLSM was designed to capture, as much as possible, all of the current hypotheses related to gypsy moth population dynamics, its natural enemies, and its host trees, representing a gypsy moth susceptible stand as the basic ecological unit. As a stand-based model, there are phenomena that will not be addressable using this model.

In 1983, the Gypsy Moth Research and Development Program sponsored a series of workshops to begin development of a model system that would provide a comprehensive framework for research development, synthesis, and testing. This initial development relied heavily on prior research (Doane and McManus 1981, Campbell et al. 1978). The GMLSM development was initiated under contract with ESSA Adaptive Environmental Assessments Inc.¹ Three workshops were scheduled to gather a variety of experts on the gypsy moth and related topics and to gather advice on the ecological system. This version of the model was turned over to the Forest Service late in 1983. Between then and now the model has undergone extensive revisions and considerable extensions in complexity and scope. We are now completing the final revisions and initial tests of the model.

Recent work has relied heavily on published literature (e.g., Elkinton and Liebhold 1990, Fosbroke and Hicks 1987) and on the cooperation of many individual researchers of state and federal agencies in and near currently infested areas (e.g., Smith 1989). Agencies and institutions cooperating in the construction of the Gypsy Moth Life System Model are:

United States Department of Agriculture
Forest Service
Northeastern Forest Experiment Station
Appalachian IPM Gypsy Moth Demonstration Project
Northeastern Area Forest Pest Management

Agricultural Research Service
Beneficial Insects Research Laboratory

¹McNamee, P.J.; Bunnell, P.; Jones, M.L.; Marmorek, D.R. 1983. Final report of a project to identify and evaluate important research questions for the gypsy moth life system, August, 1983. Unpublished report on file at USDA Forest Service, RWU-4507, PO Box 4360, Morgantown, WV 26505. 182 p.

Animal and Plant Health Inspection Service
Otis Methods Development Center

Institutions

Connecticut Agriculture Experiment Station
Dartmouth College
Hammermill Paper Company
Illinois Department of Energy & Natural Resources
New Jersey Department of Agriculture
North Carolina Department of Agriculture
Pennsylvania Bureau of Forestry
Pennsylvania State University
State University of New York
University of Connecticut
University of Massachusetts
University of Rhode Island
University of New Hampshire
West Virginia Department of Agriculture
West Virginia University

Background

Initially, the purpose of this modeling effort was to serve as a research planning tool that could later be extended and expanded into a facility for research entomologists, foresters, and economists. With the model, investigators could test and develop working hypotheses, and evaluate means for developing management-oriented tools. It was envisioned that the model would: integrate existing research information and understanding of the gypsy moth life system, identify areas where information was incomplete, identify research needs, and provide a vehicle for evaluating alternate hypotheses. The modelling exercise integrates existing information, understanding, and hypotheses; the model provides a means to view working hypotheses within the framework of the stand. In this context, hypothesis testing and sensitivity analysis provide mechanisms for identifying needs and setting priorities, including impacts on human use and management objectives. Dynamics that might be very impractical or impossible to capture in field studies may be simulated, providing a means to explore and develop understandings of the gypsy moth/forest ecosystem. It has already served as a research evaluation and planning tool and will, in the future, serve to analyze factors or relationships that might show promise as management tools, that is, to evaluate relative consequences of alternate scenarios.

Between 1984 and 1988, Sheehan and others did considerable work to develop and expand the model (Sheehan 1988). The first version was near completion when Sheehan left the project at the end of 1988. Documentation of the model structure and formulation was drafted except for one subsystem. Considerable work was required during the 1984-88 period to transform the code from a nonstandard FORTRAN to ANSI-77 Standard FORTRAN and complete additions and enhancements proposed by researchers.

Model Design

General structure.--The current model is composed of four major subsystems that are driven by weather. The stand subsystem incorporates the effects of damage by the gypsy moth into annual tree diameter and height growth as well as tree mortality. These calculations are modified by ambient heat (degree-days) accumulated each calendar year. The stand subsystem can be run

independently as a stand-alone model. Gypsy moth growth and portions of the predator-parasite subsystems are driven by accumulated ambient heat (degree-days) on a much finer scale.

The gypsy moth subsystem follows insect growth in each cohort, partitioned into a number of insects per cell (host species and canopy strata), and larval movements between cells. The predator and parasite subsystem follows several natural enemy guilds and species that have been determined to be significant mortality agents of the gypsy moth; detailed feedback relationships are provided for natural enemy populations where sufficient information is available. The pathogen subsystem follows naturally occurring nucleopolyhedrosis virus (NPV), and introductions of both NPV and *Bacillus thuringiensis* (Bt) as insecticides. The pathogen subsystem operates from initial conditions and feedback from infected gypsy moths. This subsystem models distribution of NPV in the environment and in infected gypsy moth.

Scope and Scale.--The spatial scope of the model is a single forest stand. No spatial coordinates of trees are needed, but the model does use vertical stratification of the tree canopies. The stand is partitioned by tree species and diameter class for calculation of tree growth, tree mortality, and foliage biomass. Stand variables are updated once each year; these updates include stand management prescriptions imposed by the user.

Foliage, gypsy moth, and natural enemies are followed on a finer time scale within each calendar year. After sufficient degree-day accumulation, foliage begins to grow and gypsy moth eggs begin to hatch. As long as the current generation of gypsy moth exists, each accumulated 30 degree-days produces another simulation step. Following the completion of an insect-generation cycle, annual summary accounts and links to the stand model are completed for a year, and another year produces another generation. These routines operate on a spatial scale that aggregates among the diameter classes for each tree species present. Four strata are distinguished: (1) overstory trees, (2) understory trees, (3) boles of overstory trees, and (4) a shrub and ground layer.

Weather Subsystem

Both the stand and gypsy moth are affected by ambient temperature and the gypsy moth model by rain (rain data are not required); such physical parameters in turn affect gypsy moth development rates and foliage growth rates. Daily maximum and minimum temperatures are required to derive degree-day accumulation for each Julian day. The average of the daily minimum and maximum temperatures, less the lower threshold, are accumulated into 30 degree-day steps; or the sine wave method (Allen 1976) is available. The user can alter the number of degree-days that are accumulated each cycle or step. The stand model uses only annual total accumulated degree-days. The user can provide known or expected daily temperature regimes. Weather data can be introduced in any of three formats. A stochastic weather generator is available as is default weather data for several years at a few sites.

Stand Subsystem

The stand model is fashioned after JABOWA (Botkin et al. 1972) and the FORET model (Shugart and West 1977). There are parameters for 20 tree species (Table 1); up to 6 species can be included in a single simulation. Tree establishment, growth, and mortality are simulated. This is a distance-independent diameter class model. Thus, a stand is assumed to be spatially homogeneous. The user can stipulate the number and size of diameter classes.

To describe a stand, the user specifies tree counts by species and diameter class and provides one of three soil-moisture categories for the stand. Annual ambient heat accumulation (day-degrees) is required for each year. An average for the site may be used in place of annual data.

Table 1. Tree species that can be simulated in the Stand Model.

Tree species Common Name	Species	Host food preference ^a
white oak	<i>Quercus alba</i>	1
scarlet oak	<i>Quercus coccinea</i>	1
chestnut oak	<i>Quercus prinus</i>	1
northern red oak	<i>Quercus rubra</i>	1
black oak	<i>Quercus velutina</i>	1
eastern white pine	<i>Pinus strobus</i>	1
quaking aspen	<i>Populus tremuloides</i>	1
basswood	<i>Tilia americana</i>	1
paper birch	<i>Betula papyrifera</i>	1
sweet birch	<i>Betula lenta</i>	2
yellow birch	<i>Betula alleghaniensis</i>	2
American beech	<i>Fagus grandifolia</i>	2
black cherry	<i>Prunus serotina</i>	2
hickory spp.	<i>Carya</i> spp.	2
red maple	<i>Acer rubrum</i>	2
sugar maple	<i>Acer saccharum</i>	2
striped maple	<i>Acer pensylvanicum</i>	3
yellow-poplar	<i>Liriodendron tulipifera</i>	3
white ash	<i>Fraxinus americana</i>	3
flowering dogwood	<i>Cornus florida</i>	3

^a Host food preference:

1 = most preferred food for gypsy moth larvae;

2 = not particularly favored but upon which a small portion may develop;

3 = unfavored as food of gypsy moth, larvae are not able to complete development.

Each year, tree height is used to calculate potential resting sites for gypsy moths. Potential foliage biomass is calculated as a sum, over species and diameter class counts, of species-specific allometric functions of class midpoint diameters. Diameter growth of trees is calculated as a reduction from maximum potential growth. Reductions due to relative stocking (a measure of tree crowding), shading, temperature, and defoliation are calculated. Base tree mortality rate is altered according to reduced growth, gypsy moth defoliation, and other stresses. Following mortality calculations, tree growth is updated for the residual stems by moving trees between diameter classes; new stems are recruited to the smallest class for each species that has been included in a particular simulation. Recruitment is species specific and decreases as stocking increases.

The stand is stratified by tree species and size to provide foliage and resting site information to the gypsy moth subsystem. Defoliation is returned by the gypsy moth subsystem or entered by the user when the stand subsystem is run as an independent model to assess growth and mortality losses.

Gypsy Moth Subsystem

The egg population starts the cycle. Egg parasitoids and other mortality agents that affect eggs between the time they are laid in late summer of the previous year and they hatch in late spring are taken into account. Once sufficient heat has accumulated, eggs begin to hatch. As many as 10 cohorts result from eclosions; the user can stipulate what portion of the population hatches at each step. Within each cohort, each sex is followed separately. Larvae go through five or six instars and then pupate. This period of growth and feeding is modelled in detail.

During each 30 degree-day step: foliage grows; eggs hatch (first 10 steps); larvae age; larvae move to feeding sites between hosts and canopy strata; nocturnal foliage consumption and destruction or dispersal occurs if no food available; larvae grow (both biomass accumulation and stage transition); if appropriate, suppression mortality is accounted for; natural enemies attack; move to resting sites to spend the daylight hours (large larvae only); natural enemies attack; and gypsy moth survivorship is tallied.

When all gypsy moth have reached the adult stage, the population cohort vector is collapsed to a single variable. Mating and egg laying take place to complete the generation. Larval stages can be affected by chemical or microbial pesticides; adult mating and reproduction can be disrupted by pheromone trapping, confusion (pheromone disruption), or release of sterile eggs. Indirect effects on gypsy moth may be simulated through stand management such as removal of preferred hosts.

Natural Enemies

There are a number of naturally occurring factors that keep the gypsy moth in check. Besides the natural factors that exist in North America, researchers are looking for natural enemies in Europe and Asia where the gypsy moth occurs naturally. Promising natural enemies might be introduced into North America. At present, we are modelling all natural enemies that are thought to play significant roles in the gypsy moth's population ecology in North America. Those natural enemies that are currently incorporated or under consideration for incorporation are:

PREDATORS:

- Insects
- *+¹ *Calosoma sycophanta*, *C. spp.*
- * Birds
- Small mammals
- * white footed mouse *Peromyscus leucopus*
- shrews *Sorex spp.*, *Blarina brevicauda*

PATHOGENS:

- Virus
- * nucleopolyhedrosis virus
- Bacteria
- Streptococcus faecalis*
- Serratia marcescens*
- *+ *Bacillus thuringiensis*
- Fungi

- Beauveria bassiana*
- Paecilomyces farinosus*
- + Microsporidia spp.
- PARASITES:
- Diptera (flies)
- *+ *Parasetigena silvestris*
- *+ *Compsilura concinnata*
- *+ *Blepharipa pratensis*
- + *Exorista larvarum*
- Hymenoptera (wasps)
- *+ *Cotesia melanoscelus*
- + *Phobocampe dispar*
- *+ *Brachymeria intermedia*
- + *Monodontomerus aureus*
- *+ *Ooencyrtus kuvanae*
- + *Anastatus dispar*
- Itoplectes conquisitor*

¹ * = modeled now, + = introduced species

Predator and Parasite Subsystem.--Arthropod, avian, and mammalian predators and a number of insect parasitoids are simulated. Where sufficient information is available, functional or numerical responses to gypsy moth numbers are simulated by density-dependent recruitment of predators and parasitoids to gypsy moth prey. Probabilities of encounter, and of successful and unsuccessful attacks, are included. When parasitized, gypsy moth populations are followed until the parasitoids emerge and the gypsy moths die. Parasitized gypsy moth progeny continue to be at risk to superparasitism, predation, disease, or starvation. Inter- and intra-specific competition of parasitoids within gypsy moth can be determined by the sequence of attacks. It is possible to simulate the probability of a predator or parasitoid actively avoiding previously parasitized individuals, because the parasitized proportion of each cohort is known.

Pathogen Subsystem.--The pathogen subsystem follows polyhedral inclusion bodies of NPV and infectious particles of Bt on the foliage and in other strata. The probability that gypsy moth larvae will encounter sufficient quantities to become infected is used to predict viral or bacterial infections in the population. Virus propagation through the gypsy moth population is modelled; that portion of each cohort that becomes infected with lethal concentrations of the virus is followed and the virus polyhedral inclusion bodies produced become available to other gypsy moths through cadaver ruptures. Both virus and Bt must be ingested to affect the gypsy moth. The half-lives of NPV and Bt are used to simulate the degradation rates of these pathogens under ultraviolet light exposure or other causes of deactivation.

Input Data Files and Output Tables and Files

There are default inputs for all required data, and minimal outputs are generated under the default inputs. Four input data files are required and three others are optional. These provide the users with maximum flexibility in controlling the model. There are a number of tables and plain ASCII text files that can be generated upon request; the latter are designed for use as input to graphic packages or for use in statistical analyses.

Inputs.--The first required file is used for general information and includes controls for further input or output. The second contains all of the data for the stand subsystem, and provides a vehicle for the user to manipulate many of the growth parameters and to assign the initial stand tree counts by species and diameter class. An optional data file can be used with the stand model to provide defoliation data when the stand subsystem is run separately, without the detailed gypsy moth and natural enemy subsystems. This independent version of the stand model has been referred to as the Damage Model. The weather data file can be provided in any of three formats. An optional file of precipitation data can be included. A large portion of the parameters (for example, rates and coefficients) and all of the initial conditions for the gypsy moth subsystem are located in the third required data file. Finally, a natural enemies file containing all parameters and initial conditions for these mortality agents can be manipulated by the user. Default files are provided for all required data.

Outputs.--There are 10 different output tables describing the gypsy moth and its natural enemies that users may request; parallel to 9 of these are summaries as formatted ASCII data files. There are 2 stand summary tables for viewing and 4 ASCII data files. These 13 data files are designed for use in other software packages such as graphics or statistical analysis programs.

The life table is the basic output of the gypsy moth subsystem. It provides the breakdown of mortality source for each life-stage age interval through each year. Annual summary tables of gypsy moth population attributes or mortality sources can be requested; these can also be broken out by host species. A direct control summary provides information on timing and efficacy of NPV, Bt, or chemical applications. Population attributes can further be broken out by degree-day

interval. There is a phenology summary. Finally, mortality information can be summarized annually or be requested in detail for each 30 degree-day interval.

The stand table gives summary input and parameter information as well as annual summaries of tree growth, mortality, and stand volume. A separate defoliation summary can be requested for review of data inputs or transferred from the gypsy moth subsystem. Stem counts, basal area, volume, and diameters for each simulated year also can be output in ASCII text file format.

Current Status and Future Plans

The model is running on MS-DOS® and Apple® Macintosh™ microcomputers and on Data General® minicomputers. Coding of the model is complete, and analysis and testing of the model have been initiated. Only cursory examinations of state variables and intermediate calculations have been made. We are reviewing and structuring the code and beginning detailed analyses, including comparisons with field data. We are using USDA Forest Service watershed growth and yield research plots to examine stand growth and tree mortality in the absence of gypsy moth. Plots throughout Pennsylvania, designed to assess damage, will be used to assess the effects of defoliation on growth and tree mortality, within stands of various age, structure, and defoliation histories. Additionally, we are in the process of completing user-oriented documentation for the model and a design for a user-friendly input/output control system to be written in C. These will provide access for researchers and other potential users who are not computer specialists.

CONCLUSIONS

Empirical statistical models and process oriented simulation models have been shown to provide insights into the dynamics of the gypsy moth life system. However, to date, none of these models have been shown to be useful as predictive tools. Researchers have suggested that models might be useful for predictive purposes and, too often, people have come to expect more than can be delivered. I strongly doubt that models will ever be able to answer questions such as "When will gypsy moth become a problem here?" or "When will this outbreak subside?" with any fine degree of accuracy.

Just as we cannot predict the weather total accuracy, we cannot expect to make exact predictions about the gypsy moth. That does not mean that there are not significant gains to be made from the use of models. Models have been able to assist us in organizing and analyzing available information. The use of GIS to obtain long-term trends for spread and expert systems surely will play a positive role in answering questions that are appropriate to their design. We have been able to elucidate significant biological processes and relationships in useful contexts. Models have been shown to provide useful information to both researchers and managers.

Process models usually require that a number of empirical relationships be fitted, that is, the same statistical procedures that are used to develop empirical models are used to develop relationships within process models. Thus, process models can contain all the drawbacks of empirical models and more, because of their complex design. By watching our own development process carefully and involving sufficient biological review on a continuing basis, we hope to avoid this. Any model is only as good as the basis on which it is built. As mentioned above, we are in the process of extensively testing the models we are developing. This testing should provide us with information on model applicability. We will develop documentation that describes what we think will be appropriate and inappropriate uses of the models. We will be working with many of you to find concerns and ways to improve the system as it is being further developed.

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PHEROMONE DISPENSER FORMULATIONS FOR USE IN GYPSY MOTH MANAGEMENT PROGRAMS

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ABSTRACT

The sex attractant pheromone, disparlure, is utilized in several aspects of gypsy moth (*Lymantria dispar* L.) management programs. These include detection of new infestations, assessment of population levels of existing infestations, and disruption of mating communication in control efforts. Each of these applications requires the development of an effective and commercially feasible dispensing system. In 1989 efforts were undertaken to biologically and chemically evaluate 11 different controlled-release pheromone dispensers from 7 commercial firms for use in the detection traps deployed by the Animal and Plant Health Inspection Service. In addition, results were obtained on dose/response in 3 population levels using a new PVC dispenser containing 1 ng to 10 mg of disparlure. A new ARS dispenser was found to be equal to the preferred commercial dispenser for detection. A 1 µg PVC dispenser was selected for additional study in monitoring established populations.

DEVELOPMENT OF A PHEROMONE-BAITED TRAP TO MONITOR GYPSY MOTH POPULATIONS

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ABSTRACT

The standard milk carton trap baited with 500 µg of (+) disparlure has worked very well in detecting populations of gypsy moth in regions where it is just becoming established. However, it has not been useful in New England or anywhere within the area generally infested by gypsy moth. In such areas, the traps fill up with males even in populations of extremely low density. Repeated sampling of such traps during the flight season is neither practical nor advisable. We have explored several strategies for modifying the trap to reduce the number of males captured. These are: 1) baiting the trap with racemic disparlure, 2) baiting with a low release rate (+) disparlure dispenser and 3) modifying the trap so that it is difficult for males to get into. We have explored whether traps based on any of these modifications would be correlated with other estimates of local population density (egg mass counts or pupal counts under burlap). Other experiments and behavioral observations have aimed at elucidating the factors which influence trap catch.

MONITORING, AND MAPPING GYPSY MOTH DATA IN AIPM: THE PROCESS AND PROBLEMS OF IMPLEMENTATION

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ABSTRACT

The Appalachian IPM program (AIPM), due to its size (12.8 million acres), location along the leading edge, and use of new technology, will influence the development of gypsy moth management programs. This paper reviews the data collection, management and mapped display of the adult male and egg mass life stages in the AIPM project. Data are field-collected using optically-scanned forms and managed using database management and geographic information systems. Maps showing population density, trend in density, extent of infestation and proximity to other infestations are delivered to land managers.

Male moth data are collected from ca. 9,000 pheromone traps in a 2 or 3 K systematic survey. Sentinel traps (ca. 3% of the traps) are checked weekly towards the end of the season to establish the end of moth flight and initiate egg mass surveys. A small proportion of traps along the northern edge of the project have been filling and this problem is projected to increase. Progress of trap placement and service visits are mapped weekly to aid in personnel management. Moth catch and trend in moth catch are modelled into surfaces. Male moth maps at the same scale and size as USGS 7.5 minute topographic maps display male moth trend as shaded polygons, moth catch as contours and postings, and last year's egg mass point data. Computer programs which automate this procedure are in place. About 100 minutes of computer time is currently necessary to produce and plot each map, and ca. 130 quads were produced in 1989 by the USFS in Atlanta.

Egg mass data (1/40th acre fixed-radius plots) are collected where male moth data suggest positive counts are likely. The number of egg mass samples between the two years is increasing dramatically. A sequential sampling plan was established in 1989 to help increase precision in the face constrained sampling resources. This problem is projected to continue, and additional sampling plans are needed. Due to the resolution, spatial distribution, and spatial dependence of the egg mass data, surface models easily produce artifacts at locations distal to collection sites. To prevent this, mapped displays are restricted to within 250 m of collected data by creating a polygon that defines the area within 250 m of any sample, and restricting the display of all surfaces to fall within this polygon. Defoliation data are also included on egg mass maps.

LANDSCAPE ECOLOGY OF GYPSY MOTH IN THE NORTHEASTERN UNITED STATES

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ABSTRACT

The gypsy moth was accidentally introduced to North America near Boston by E. Leopold Trouvelot in 1869. Since that time, the range of the gypsy moth has slowly spread and the generally infested region presently extends as far as Ohio, West Virginia, Virginia and North Carolina. A separate isolated but expanding population exists in Michigan. The goal of this study was to quantify the process of gypsy moth spread through North America and relate the process to other landscape features. The ultimate purpose of this research is the development of sound predictions of future gypsy moth spread.

The past spread of the gypsy moth in North America was quantified from historical quarantine records. Since the enactment of the Domestic Plant Quarantine Act of 1912, the federal government has designated certain parts of the United States as officially "infested" by the gypsy moth. Though there has been some variation in detection methods used to make this designation, it is the only record we have of past gypsy moth spread. We compiled these historical records to designate the yearly infestation status of each county in the United States and similar records that designate the status of each census district in Canada. We used the IDRISI geographical information system (GIS) to manage these data. County and census district coordinates were imported from the SAS system and were used to define the geographical boundaries of historical infested areas.

We used the historical spread data from 1966 to 1986 to model a county's time to infestation as a function of its minimum distance from the generally infested region and the county's mean minimum January temperature. The minimum distance was calculated using the GIS and minimum temperatures were interpolated from 30 year historical weather station data collected through out the area. Both distance and temperature contributed statistically significantly to the model. Extremely cold winter temperatures can kill overwintering gypsy moth egg masses and this is the most likely explanation of the effect of January temperatures on spread. When we applied the spread model that was developed from 1966-1986 data to the 1900 data, it greatly over-estimated the rate of spread from 1900-1950. This indicated that the rate of spread over the last 20 years has been much greater than it was during the earlier part of the century. There are many possible reasons for this change and we are currently attempting to incorporate this process in an improved model.

MODELING GYPSY MOTH SEASONALITY

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ABSTRACT

Maintaining an appropriate seasonality is perhaps the most basic ecological requisite for insects living in temperate environments. The basic ecological importance of seasonality is enough to justify expending considerable effort to accurately model the processes involved. For insects of significant economic consequence, seasonality assumes additional importance because management decisions are often based on seasonal timing. In gypsy moth management, timing of BT applications and determining an efficient sampling interval for placement of pheromone traps are two such applications. We are, therefore, in the process of developing models required for representation of gypsy moth seasonality. Model representations currently under consideration are those for egg diapause and embryogenesis, and larval phenology.

The conceptual basis for our diapause model is founded in two generally accepted first principles. These are (1) there are two important temperature dependent rate related processes that define diapause, that of diapause development and that of embryogenesis, (2) the relationship between these two temperature dependent rate processes results in arrested development that is the outward manifestation of diapause. We differ from traditional interpretations, however, in that we conceptually allow the relationship between these two phases to be more flexible than conventional models. In particular, we acknowledge that the relationship may allow concurrent phase development as well as the more traditional strictly sequential progression through phases. Larval phenology is modeled by a flexible modeling paradigm developed by Logan (1988). The empirical foundation for this model resulted from a reevaluation of data published by Casagrande *et al.* (1987).

Linking the models of egg diapause with that of within season dynamics results in a composite representation of seasonality. The resulting model allows long-term representation and analysis of gypsy moth seasonality. In this paper, we discuss: (1) the structural detail of the two modeling approaches (2) coupling of the models to produce a composite model that links one year to the next, and (3) implications, both basic ecological and applied, of long-term simulation experiments with the seasonality model.

MESOSCALE LANDSCAPE MODEL OF GYPSY MOTH PHENOLOGY

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ABSTRACT

A recently-developed high resolution climatological temperature data base was input into a gypsy moth phenology model. The high resolution data were created from a coupling of 30-year averages of station observations and digital elevation data. The resultant maximum and minimum temperatures have about a 1 km resolution which represents meteorologically the mesoscale.

The GMPHEN phenology model was used to simulate the seasonal development of gypsy moth. The model predicts the timing of male and female gypsy moth stages based on degree-day thresholds. As daily maximum and minimum temperatures are input into the GMPHEN model, the simulated insect population passes through a succession of phenological stages according to accumulated degree days.

Weekly averages of daily high resolution climatological maximum and minimum temperatures for two areas, one in western Pennsylvania and the other centered on West Virginia, were input into the GMPHEN model. The resulting model output were displayed as landscape maps overlaid with county boundaries. Beginning with January 1, the weekly landscape maps depict the average seasonal development of gypsy moth starting with egg and ending with the adult stage. By viewing the succession of maps, one can follow the progression of gypsy moth development both temporally and spatially. The series of maps provide a strategic tool for anticipating the seasonal date of a particular gypsy moth stage at a given location.

BEHAVIOR OF THE GYPSY MOTH LIFE SYSTEM MODEL AND DEVELOPMENT OF SYNOPTIC MODEL FORMULATIONS

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Aims of the research. The Gypsy moth life system model (GMLSM) is a complex model which incorporates numerous components (both biotic and abiotic) and ecological processes. It is a detailed simulation model which has much biological reality. However, it has not yet been tested with life system data. For such complex models, evaluation and testing cannot be adequately accomplished comparing the outputs with life systems data. Our strategy is to combine structural and functional analysis of the ecological processes within the GMLSM with development of synoptic models that incorporate the fundamental ecological processes, gradually increasing their complexity and reality.

Ultimately, we hope to achieve the following results: A. for the GMLSM: 1. Improve our knowledge of the life system, discover the weak points of present hypotheses and their linkages via parameter sensitivity and structural analysis, and thus direct further experimentation and modelling; 2. By evaluating and improving the GMLSM, we hope to provide a standard and clearly documented model which can be widely used, providing means to investigate optimal strategies for gypsy moth management under specific local conditions. B. for the simplified models: 1. Understand mathematical behavior and stability of models with regard for formulations, parameter values, and initial conditions; 2. Understand biological and ecological processes and parameters and how they should be most appropriately incorporated in models, i.e., how they should best be expressed in model formulations; 3. Understand how the mathematical characteristics of simpler models compared with the more detailed GMLSM and help us understand what in the GMLSM gives rise to the major stability and behavioral characteristics of the GMLSM.

Scheme of the research. The general scheme of our research is to parallel the work on the analysis of the GMLSM with construction of simple model formulations that provide means to explore major components of the ecosystem. These two approaches can be very complementary.

For structural analysis of the GMLSM, we have constructed flow charts to elucidate the basic components and interactions of the system model and each submodel. Computer diagnostic tools have a mechanism for step-by-step examination of calculations being performed. This process has already allowed us to uncover obscure behavioral problems and to correct inappropriate component interactions.

But is it structured on a sound biological basis, and is it interpreted correctly in mathematical terms and computer program representation? The most fundamental procedure is to evaluate the functional behavior of the basic ecological processes. This approach can be very helpful for constructing simple model systems. On the other hand, constructing and operating simple model systems in correspondence with the GMLSM can very efficiently detect errors in the GMLSM.

³Due to personal problems, Dr. Xu had to return to China; with the time required for international communication and the need to balance this work against other obligation, we do not expect this work to progress as fast as originally scheduled.