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PROCEEDINGS

Lymantriidae: A Comparison of Features of New and Old World Tussock Moths



FOREWORD

Tussock moths constitute the major forest pest throughout the world. While similarities in ecology, behavior, natural enemies, and means of control may be similar for different Lymantrid species, no previous effort had been made to synthesize this information.

These proceedings resulted from a five-day conference held in June 1988 at the Park Plaza Hotel in New Haven, CT. It offered scientists from Canada, the Soviet Union, the People's Republic of China, Great Britain, Switzerland, Japan, the Federal Republic of Germany, Denmark, Poland, the Netherlands, and the United States the unique opportunity to present research findings. Just as important, it provided a forum by which to discuss research issues and needs, clarify terminology and enhance international collaboration. The importance and timeliness of the conference was recognized by the USDA Forest Pest Sciences Competitive Grants Program, which provided funds for defraying travel expenses for invited foreign participants. The International Union of Forest Research Organizations (IUFRO) was the mechanism for identifying participants and, together with the Northeastern Forest Experiment Station which published these proceedings, co-sponsored the Conference.

The conference agenda allowed each participant 45 minutes for a presentation, followed by a 15-minute question and answer period. The comments that followed each presentation were recorded and are presented as a separate section at the end of the proceedings.

Most of the papers were submitted as camera ready copy. Some of the foreign authors requested that their papers be edited for clarity and retyped, and this has been done.

COVER

Elliptical projection of the world showing Lymantrid distribution, by Paul A. Godwin, USDA Forest Service, retired.

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Northeastern Forest Experiment Station
370 Reed Road, Broomall, PA 19008

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PROCEEDINGS

Lymantriidae: A comparison of features of New and Old World tussock moths

June 26-July 1, 1988, New Haven, Connecticut

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Sponsored jointly by the
Northeastern Forest Experiment Station and
The International Union of Forest Research Organizations

Welcoming Address

International cooperation on scientific issues
of common interest

*The Honorable Bruce A. Morrison, Representative in Congress,
Third Congressional District, Connecticut*

Contents

FAMILY CHARACTERISTICS

<i>P. W. Schaefer</i>	Diversity in form, function, behavior and ecology: An overview of the Lymantriidae (Lepidoptera) of the world	1
<i>P. J. Grijpma</i>	Overview of research on Lymantriids in Eastern and Western Europe	21
<i>X. Sun</i>	Lymantriid forest pests in China	51
<i>W. E. Wallner</i>	An overview of pest Lymantriids of North America	65
<i>I. Chaudhry</i> <i>W. Rahman</i>	Population studies on Lymantriid pests in Pakistan	81
<i>H. Bogenschütz</i> <i>K. Maier</i> <i>C. Trebitzky</i>	Gypsy moth outbreak and control in Southwest Germany, 1984-1986	89
<i>J. Novotny</i>	Natural disease of gypsy moth in various gradation phases	101
<i>R. T. Cardé</i> <i>M. A. Willis</i> <i>R. E. Charlton</i>	Mate-finding behaviors and chemical communication in the Lymantriidae	113
<i>N. J. Mills</i>	Life tables of the Lymantriidae with particular reference to <i>Lymantria obfusca</i> in Kashmir	143

POPULATION DYNAMICS

<i>T. S. Jensen</i>	Latency characteristics of tussock moths (Lepidoptera: Lymantriidae)	155
<i>J. Schönherr</i>	Outbreak characteristics of Lymantriids	171
<i>R. R. Mason</i>	Monitoring population change in the Lymantriidae	183

A. M. Liebhold J. S. Elkinton	Spatial aspects of gypsy moth population dynamics	203
K. W. Gottschalk	Impacts, silviculture and the gypsy moth	217
J. S. Elkinton J. R. Gould A. M. Liebhold H. R. Smith W. E. Wallner	Are gypsy moth populations in North America regulated at low density?	233

GENETICS AND BEHAVIOR

C. A. Clarke	The control of <i>Lymantria dispar</i> : Some genetic and behavioural considerations	251
R. G. Harrison T. M. Odell	Mitochondrial DNA as a tracer of gypsy moth origins	265
V. C. Mastro T. M. Odell C. P. Schwalbe	Genetic control of Lymantriidae: Prospects for gypsy moth management	275
Y. Higashiura	Oviposition site selection by Japanese Lymantriid moths	303

HOST AND SITE RELATIONSHIPS

Y. N. Baranchikov	Ecological basis of the evolution of host relationships in Eurasian gypsy moth populations	319
M. E. Montgomery	Relationship between foliar chemistry and susceptibility to <i>Lymantria dispar</i>	339
D. B. Lyons T. J. Lysyk	Development and phenology of eggs of gypsy moth, <i>Lymantria dispar</i> (Lepidoptera: Lymantriidae) in Ontario	351
D. E. Leonard J. G. Kunkel	Nutritional ecology: <i>Lymantria dispar</i> as a model system for study of serum storage proteins	367
R. F. Shepherd G. A. vanSickle D. H. L. Clarke	Spatial relationships of Douglas-fir tussock moth defoliation within habitat and climatic zones	381

BIOLOGICAL CONTROL AND POPULATION MANIPULATION

<i>B. Glowacka</i>	Pathogenic viruses and bacteria of the nun moth (<i>Lymantria monacha</i> L.) during the outbreak 1978-1984 in Poland	401
<i>E. A. Cameron</i>	<i>Bacillus thuringiensis</i> in the management of gypsy moth populations	417
<i>P. M. Kelly</i> <i>P. F. Entwistle</i> <i>P. H. Sterling</i> <i>M. M. Speight</i> <i>R. F. Laport</i>	Virus control of the brown-tail moth, <i>Euproctis chrysorrhoea</i>	427
<i>K. D. Murray</i> <i>J. S. Elkinton</i> <i>S. A. Woods</i> <i>J. D. Podgwaite</i>	Epizootiology of gypsy moth nucleopolyhedrosis virus	439
<i>M. L. McManus</i> <i>J. V. Maddox</i> <i>M. R. Jeffords</i> <i>R. E. Webb</i>	Evaluation and selection of candidate European microsporidia for introduction into U.S. gypsy moth populations	455
<i>H. R. Smith</i>	Predation: Its influence on population dynamics and adaptive changes in morphology and behavior of the Lymantriidae	469
<i>R. M. Weseloh</i>	Predation of Lymantriids by arthropods	489
<i>R. Fuester</i> <i>G. Ramaseshiah</i>	A comparison of the parasite complexes attacking two closely related Lymantriids	501
<i>J. R. Gould</i> <i>R. G. vanDriesche</i> <i>J. S. Elkinton</i> <i>T. M. Odell</i>	A review of techniques for measuring the impact of parasitoids of Lymantriids	517
<i>K. A. Sheehan</i>	Models for the population dynamics of <i>Lymantria dispar</i>	533
<i>P. S. Grinberg</i> <i>W. E. Wallner</i>	New and Old World Lymantriidae: Discussion and research issues	549

LATENCY CHARACTERISTICS OF
TUSSOCK MOTHS (LEPIDOPTERA:
LYMANTRIIDAE

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INTRODUCTION

Among the almost 2000 species of Lymantriidae, only a dozen or so are known to cause serious damage to plants in man-made or natural ecosystems to a degree that growers are concerned or the scientific community interested. Even these species remain below noticeable levels most of the time and such periods are termed latency periods, innocuous levels or low density periods. In the term latency is included the special characteristic of the species viz the ability at certain times to increase the population density rather steeply.

Thus, the most fascinating characteristic of these species is the ability to switch suddenly from low level density to high level density. However, most studies on these species have been performed at times when population levels are either close to outbreak (progradation), at outbreak levels (culmination) or on the decline (postgradation). In the past, very few studies have dealt with latency populations but, recently, several long term studies have been conducted.

In the present review an attempt is made to describe the characteristics pertaining to latency populations and to identify possible mechanisms that might operate when populations change from low density to high density levels. Data are mainly drawn from latency studies but occasionally only progradation data are available. The term 'characteristics' refers to a fan of quantitative and qualitative parameters, directly or indirectly influencing the population dynamics of a species. More specifically, we search for those characteristics that influence any of the parameters: initial population density, natality, mortality, immigration or emigration during the latency period.

Species

Lymantriids occur in the Old World and in the New World; in temperate regions and in the tropics. In Europe, a dozen species are of some economical importance, however only two are considered major pests (Lymantria dispar and Lymantria monacha). Similarly, in North America two species, Lymantria dispar and Orgyia pseudotsugata, are major pests, whereas in the tropical areas no species are major pests but several are minor pests. In the present context, it must be emphasized that although many species are of economical importance, almost all we know for most of them are characteristics that can be

attributed to outbreak situations. Not surprisingly, this is mainly the case when species from developing countries are considered. Generally, solid information about characteristics of latency populations is lacking and only in *L. dispar*, *L. monacha* and *Q. pseudotsugata* can bits and pieces be gathered.

INITIAL POPULATION DENSITY

It is obviously a tautology that the main characteristic of a latency population is that the population density of the species is low, but unfortunately the parameter is rarely measured due to sampling problems. Such problems arise when the density is extremely low and lymantriid latency densities sometimes reach very low numbers.

In the various lymantriid species densities are estimated by different means (Mason, 1988; Kolodny-Hirsch, 1986). In *L. dispar* the most common method is to count egg masses and eggs per hectare; in *Q. pseudotsugata* egg masses or larvae are counted per foliated branch area, and in *L. monacha* the number of adult females per tree is the most commonly used method.

In the three species the latency level varies considerably according to the literature. In *L. dispar*, egg mass numbers vary from 1 to 100 per hectare and 2-25,000 fourth instar larvae/ha (Campbell, 1981b), and figures as low as 39 larvae per 120 ha have been recorded (Sisojevic, 1960). In *Q. pseudotsugata* less than 1 larva/6452 sq cm of foliated branch is defined as latency levels (Williams et al., 1979), and figures from 0.01 to 2 larva/6452 sq cm are recorded (Mason, 1974; Mason & Luck, 1978; Dahlsten et al., 1985). The Arctic lymantriids *Gynaeophora rossii* and *Q. groenlandica* which never have been recorded as outbreak species reach pupal densities of 1-100/ha (Kukal & Kevan, 1987; Jensen & Maclean, unpubl.) In *L. monacha* the number of imagoes range from 0.04 to 190/ha (Wellenstein, 1942; Jensen & Nielsen, 1984) and the number of larvae from 0 to 4500/ha (Tinbergen, 1960; Jensen, 1985). Thus, latency density is a rather broadly defined term.

If we imagine so-called releasing factors suddenly acting on such different latency population densities, it is likely that only in the case of very high latency densities the final population might reach outbreak levels, otherwise it will not (e.g. Mason & Overton, 1983). If latency populations subjected to favourable releasing factors do not reach outbreak levels they will probably, due to density-dependent processes, return to a low-density stable equilibrium, whereas if they reach outbreak levels they will either attain a high-density equilibrium or the population will return to a low-density equilibrium, depending on the outbreak type (Berryman, et al., 1987).

Conversely, low and high initial population densities might lead to the same outbreak level if mortality rates or fertility rates are density-dependently regulated even at latency levels (Jensen, 1985).

Site characteristics

Outbreaks of, e.g. *L. monacha*, *Q. pseudotsugata* and European populations of *L. dispar*, often occur at the same locations (foci) at

years intervals (e.g. Wellenstein & Schwenke, 1978; Sliwa & Sierpinski, 1986). Such outbreak patterns could be established if multiplication factors were site specific, e.g., low mortality at certain sites under certain conditions, or if high latency population levels were related to site characteristics and influenced by the same amount of mortality release.

In *L. monacha*, evidence from pheromone traps and frass drop traps have revealed that during an outbreak the general population level was also high outside the outbreak areas, supporting the latter argument (Jensen, et al., 1981). However, this merely leads to another, yet unanswered question: Why, then, are the latency population levels consistently higher at particular sites?

Site characteristics have been described for a large number of lymantriid outbreaks. In a few species, certain common denominators seem to exist. *L. monacha* outbreaks occur mainly on poor sandy soils of fluvial or marine deposits and outbreaks are rarely met on the better soils although preferred host plants are also found in such sites (Wellenstein, 1942; Bejer, 1985). European populations of *L. dispar* also seem to perform outbreaks mainly on the poorer soils. In North America, old populations in the Northeast also seem to be adopting a similar pattern (Houston & Valentine, 1977). In *O. pseudotsugata* detailed analysis of a large number of outbreak sites have shown that foci could be characterised as multistoried older fir stands on poorer soil, ridge tops or upper slopes (Stoszek et al., 1981).

Weather

Climatic release mechanisms to explain widespread periodic outbreaks have been suggested for several lymantriid species. These climatic events are often coupled with site characteristics. However, hypotheses of forest insect outbreaks that involve climatic factors are difficult to test (Martinat 1987) and monthly weather summaries might be quite inadequate to describe real influential weather parameters.

Despite these arguments certain characteristics seem to be of general importance in some lymantriids. In *L. monacha* most major outbreaks have been preceded by several dry, warm summers; in the same years, springs have been rather cool (Bejer, 1985; Jensen, 1985). In the European populations of *L. dispar* Benkewich (1962) found the same characteristics. Outbreaks of *Dasychira pudibunda* and *Orgyia antiqua* might follow the same pattern although information here is more circumstantial (Sylvén, 1943; König, 1954; Pinder & Hayes, 1986).

In *O. pseudotsugata*, Watt (1968) found that the insect's abundance correlated with mean monthly temperatures in July-August, and Calluci et al. (unpubl., cited in Mason & Luck, 1978) suggested that outbreaks may be associated with warmer than average spring temperatures. However, studies using dendochronology (Brubaker, unpubl., cited in Mason & Luck, 1978) showed no relation between outbreaks and drought. This is not unexpected as *O. pseudotsugata* exhibits cyclical gradient outbreaks where climatic triggering would be unlikely, whereas the other species exhibit eruptive outbreaks (Berryman, 1987).

DISPERSAL AND MIGRATION

Generally, emigration and immigration are overlooked parameters in the population dynamics of insects as they are extremely difficult to quantify on a population basis. In Lymantriids, dispersal processes have received increasing interest mainly due to the expansion of the gypsy moth infested areas in North America.

In most insects, the dispersal unit is the same imago; however, in many Lymantriids, if not all, it is characteristic that the most important dispersal units are the first and second instar larvae as these larvae possess long, buoyant setae and are able to spin silken threads which can be caught by the wind even at moderate velocities. Dispersal distances of larvae are still a matter of controversy; no doubt most larvae only disperse very short distances, e.g., from one tree to its neighbour, and although repeated dispersal occurs the overall picture is that of dispersal within 1-2 km (Lance et al., 1986; Lance & Barbosa, 1979). If very special topographic conditions are present, e.g., in very turbulent terrain, long-range dispersal of up to 19 km can be found (Taylor & Relling, 1986).

Between-tree dispersal might constitute an important characteristic in certain Lymantriids as it is a means of redistribution if the synchrony between budburst and egg hatching is not perfect. In Norway spruce (*Picea abies*) there is considerable variation in the time of budburst, and dispersal of newly-hatched *L. monacha* larvae occurs from late bursting trees. Similarly, early-hatched *L. monacha* larvae might, in certain years, find trees with flowering buds, which burst 2-3 weeks earlier than the vegetative buds (Mors, 1942). As these male flowers are of excellent food quality (Jensen, 1985) they might even increase larval survival and, subsequently, female fecundity.

Certain aspects of dispersal seem to be density dependent (Lance et al., 1986), however, Capinera & Barbosa (1976) found that each *L. dispar* larva makes at least one dispersal movement irrespective of population densities. Therefore, we would always expect a redistribution of the larval population and even if it would be expected that such dispersal normally would lead to a less contagious distribution, under certain conditions local higher densities could build up. Such phenomena have probably occurred in *L. dispar* influenced by the Atlantic "sea breeze" which concentrates larval deposition in a band ca. 10-20 km inland. Another example includes the Pennsylvania "ridge and valley" systems where larvae are deposited in a band just short of the opposite ridge (Cameron et al., 1979).

Latency populations of *L. dispar* show a characteristic short-distance dispersal, viz the diel movements of older larvae from resting places in litter or under bark flaps and into the feeding places in the canopy (Campbell & Sloan, 1977b). During outbreaks, this behaviour disappears and larvae stay in the canopy (Lance & Barbosa, 1982).

In contrast to larval dispersal, imago dispersal is rarely encountered in Lymantriids and for obvious reasons not in the flightless *Orgyia* females. Similarly, *L. dispar* females, although winged, do not seem to disperse at all. In *L. monacha*, females often disperse after laying only a part of their egg-load, but normally only

short distances. Sometimes, however, L. monacha herds are formed and these herds can migrate several hundreds of km, i.e., across the Baltic Ocean from Poland to Denmark (Kaaber, 1982). Early 19th Century German reports speculated that L. monacha outbreaks could actually start from such herds (Wellenstein & Schwenke, 1978).

LIFE STAGE MORTALITY IN LATENCY POPULATIONS

Egg Mortality

Generally, lymantriids deposit their eggs in large batches some of which are rather visible on the surface of the female cocoon (O. antiqua, O. pseudotsugata, G. rossii), while others are hidden under bark flaps and twigs (L. monacha) or under a female excretion (L. dispar). Interestingly, in the four most serious defoliators (Orgyia and Lymantria species), eggs overwinter with a diapausing first instar larva inside, whereas in most other lymantriids, at least in Europe, the overwintering stage is either larvae or pupae. Lymantriid eggs seem to be rather cold-resistant and winter mortality due to low temperatures is minimal.

Despite the long time eggs are subjected to diseases, predators, and parasite attack, Wellenstein (1942) found that L. monacha egg mortality in the progradation phase was very low. Egg parasites are not known, unfertile eggs make up only 0.5%, arthropod egg predation 0.6%, and unknown deaths merely 3.9%. In this investigation, bird predation was not assessed. Later, Wellenstein (1973, 1974) found that in pine forests birds decimated egg numbers in latency populations up to 34% and in spruce stands 16-25%.

In L. dispar, egg parasites are present but the percentage of infested eggs is very low during latency. For example, Rynkin (1957) found rates of merely 1.3-1.9%.

Generally, Orgyia species show higher egg parasite infestation during latency or progradation. Skatulla (1974) and Wellenstein & Fabritius (1973) described egg parasitism of around 25% in O. antiqua, and Dahlsten et al. (1977, 1985) egg parasitism of 17-40% in O. pseudotsugata. In the latter investigation, egg predation made up 5.1-6.0% and unknown death causes 6.0-34.8%. In a thinned stand, egg masses were particularly heavily parasitized, averaging 61.9% in contrast to 48.9% in an unthinned stand (Wickman & Torgersen, 1987). Predation rate was approximately one-third higher in the thinned stand.

Host-Induced Larval Mortality

As stated above, the most important lymantriid defoliators overwinter as eggs, thus avoiding mortality factors acting on larvae or pupae for such an extended period as autumn-spring. Instead, they spend their whole larval period in late spring-early summer and the pupae period in mid-summer. An advantage of such a strategy is the presence of high-quality food; i.e., high water, nitrogen and carbohydrate and low tannin concentrations. A main disadvantage is the problems associated with synchronisation between egg hatch and budburst

as starving larvae only survive 5-7 days depending on temperature (Beckwith, 1983).

The phenological synchronisation between plant and defoliator has been little studied in lymantriids but is well documented in other major lepidopteran defoliators; e.g., the winter moth (*Operophtera brumata*). In *L. monacha*, newly hatched larvae confined to branches of different phenological stages suffered severe mortality in the first two instars on late-bursting trees, 37.1% vs 5.8% on early-bursting trees (Mitcherlich & Wellenstein, 1942). However, the effect of bud break on larval mortality may be blurred by larval between-tree dispersal and, in certain years, the presence of flowering buds, which in Norway spruce are associated with late-bursting trees (Mors, 1942).

The high mortality rate of early instar *L. monacha* can probably be related to the inability of young larvae to chew the hard old spruce needles. Similarly, in pines (*Pinus silvestris*, *P. mugo*) larval mortality, when confined on old needles, is 93-95% (Jensen, 1985). As young pine shoots develop much later than the eggs hatch and are heavily protected chemically the only chance of reasonable survival is to find branches that carry male inflorescences (Jensen, 1985).

In *Q. pseudotsugata* the only acceptable food for newly-hatched larvae on fir is current year's foliage freshly flushed from elongating shoots (Beckwith, 1976). The phenologies of both host and insect are primarily determined by accumulated spring temperatures and are apparently synchronous (Wickman & Torgersen, 1987).

Even in broadleaved trees, phenological synchrony seems important. By confining newly-hatched *L. dispar* larvae on leaves at different times, Hough & Pimentel (1978) showed that on one-month-old leaves 95-100% mortality occurred on all diets except white oak and in the few survivors fecundity dropped to ca. half its value on young leaves. Raupp et al. (1988) found significantly higher mortality in later hatched larvae on maple and hickory and in beech even a one week delay decreased survival from 78% to 0%.

Another black box at present is the effect of variable food quality on the growth and survival of early instar larvae. Current ecological theory states that the chemical composition of the leaves or needles (nutrients, secondary compounds, water) could be profoundly changed due to soil nutrients, soil moisture or air temperature, for example, and that this in turn would influence herbivore performance (see chapters in Denno & McClure, 1983).

Few studies quantify lymantriid performance parameters in such variable circumstances. Merker (1960) reported that the mortality of *L. dispar* larvae increased after fertilisation and, similarly in field and laboratory raised *L. monacha*, Jensen et al. (1981) found that early instar mortality increased 8-15% on fertilised plots.

Unfortunately, no experimental data are available for larvae raised on trees subjected to severe drought stress. Wallner & Walton (1979) found longer development time and increased larval-adult mortality when *L. dispar* larvae were reared on previously defoliated oak and birch trees.

Predation, Disease and Parasitism

In comparison with host-induced larval mortality, the mortality due to predation seems to be of considerably higher magnitude in most lymantriids. In *O. pseudotsugata* and *L. dispar* several studies on stocked and caged larvae have revealed that losses of larvae constitute a major factor in the generation mortality of the species at low densities (e.g. Mason et al., 1983), or postgraduation the major mortality factors are often diseases and parasitic dipterans and hymenopterans which, during latency, play a minor role in regulatory processes (Vezina & Peterman, 1985).

Disappearance of larval of course can be due to a number of factors; e.g., arthropod or vertebrate predation, or non-replaced dispersal. In *L. dispar*, it has been suggested for a long time that bird predation probably played the most important role in maintaining the populations at latency levels (Turcek, 1950). Similar proposals were made by Wellenstein (1942) in *L. monacha*. Later experimentation studies have largely supported these views; e.g., in *L. dispar* (Semevsky, 1973; Furuta, 1982; Campbell & Sloan, 1977a, b), and in *L. monacha* (Wellenstein, 1973; 1974).

In *O. pseudotsugata*, Mason & Torgersen (1983) found that actual or suspected predation accounted for 47.2% and dispersal for 40.5% of the total loss. Disappearance of early larvae was attributed primarily to predation by spiders and insects while disappearance of late larvae was suspected to be due mostly to bird predation. The loss rate/day of larvae was correlated with the number of high-potential bird predators and bird density accounted for 78% of the variation in larval loss rate; the highest losses occurred in larvae stage 4-5 (Torgersen et al., 1984).

The three major lymantriid pests are flush feeders and overwinter as eggs. In contrast, other lymantriids overwinter as larvae. Unfortunately, we know little about survival of these instars nor do we know much about survival or fecundity of those individuals feeding and pupating in the following spring. Winter mortality of *Euproctis chrysorrhoea*, however, are known to be very high due to bird predation (Auersch, 1955).

Pupal Mortality

Late larval instar mortality and pupal mortality during latency seem to be influenced by much the same factor; i.e., vertebrate predation. Only in medium increasing populations are invertebrate predators (Weseloh, 1985) or parasitoids of greater influence. This characteristic might, in part, be attributed to the large size of lymantriid late instar larvae and pupae.

Generally, pupal mortality in latency is not as high as late instar mortality. Torgersen et al. (1983) found in *O. pseudotsugata* that 13-47% of latency population pupae were eaten by predators, mainly by birds, but also by *Camponotus* ants. In this study, a negative correlation between pupal density and pupal mortality was described. In *L. monacha*, Wellenstein (1973, 1974) found mortality rates of 48-67%, also mainly due to bird predation.

In contrast, bird predation on *L. dispar* pupae does not seem to be as important as small mammal predation. *Peromyscus* species seem capable of a 47% contribution to total killing power during the

generation and a 60% contribution during the interval from instar 5 to adults (Campbell & Torgersen, 1983). Mammal predation on insects is a rather infrequent phenomenon but in the present case, the reason behind it can be sought in the sheltered pupation sites in the litter or under bark flaps on the tree trunk (Campbell, 1978; Campbell & Sloan, 1977a, b).

Mortality of Imagoes

Evidently, the ultimate mortality of imagoes is 100%. More interestingly in connection with adult mortality is the mortality of females before the whole egg load has been deposited. Mills (1988) found in stocked but high density populations of *Lymantria obfuscata* that the discrepancy between the number of females emerging and egg masses oviposited was a key factor. In Mill's study, there was a significant but very variable density dependence perhaps due to density related migration of females or density dependent mortality of females through vertebrate predation.

Such studies on adult female mortality is unfortunately rarely accomplished. Although Mill's study showed clear density dependency, density independent factors especially catastrophic weather conditions in the flight period might be equally important.

LATENCY FECUNDITY

Density-dependency

Most lymantriid species show dramatic changes in fecundity rate during the progression of an outbreak; often to such a degree that these parameters can be used to characterise the state of the outbreak and to predict population changes the following year (Schonherr, 1988). There seems to be clear inverse density dependent changes in fertility; in *L. dispar*, Campbell (1978) found that 71% of the variation in log(fertility) was due to variation in log(larval density). Other factors include food quality, available food biomass and stand composition.

However, although we know that these differences between progradation and outbreak populations exist, we know very little about differences in fertility rates between latency and progradation populations. What we do know seems to indicate that these differences are rather small and probably not sufficiently large to explain the release of an outbreak. Thus, fecundity rates in laboratory-reared *L. dispar* are generally in accordance with figures from progradation populations and much higher than fecundity rates of outbreak or postgradation populations. In *L. monacha*, pupal weights, which are closely correlated with fecundity rates, are rather similar in laboratory experiments and in progradation populations.

Sex Ratio

Sex ratios also change markedly through the outbreak phases from slightly female dominated to male-biased (Mauffette & Jobin, 1985). Generally, the sex ratios found in progradation, e.g., male:female ratios of 1:1.17 in *O. antiqua*, 1:0.65 in *O. pseudotsugata*, 1:1.27 in *L. monacha*, are similar to those found in latency populations (Skatulla, 1974; Dahlsten et al., 1985; Mors, 1942). Zwolfer (1935) found that the sex ratio of *L. monacha* was highly influenced by temperature during the larval period and the female percentage would change from 20 to 80 in the interval 12-26° C. In certain years, *L. monacha* female ratios of 0.8 have been recorded very early in outbreaks (Fischer, 1942). Dahlsten et al. (1985) in one locality also observed a ratio of 1:3.3. Thus, it is not unlikely that extremely female-biased sex ratios could exist in certain latency years, indicating very good survival of female larvae that particular year. Maybe such events could be important at the start of the release period (Campbell, 1981).

Number of Generations

A rather specific, but certainly very important source of increased fertility is the presence of a second generation. In the more important lymantriids no reports about second generations have been published; however, in the vapourer moth (*O. antiqua*), second generations have been observed in connection with outbreaks (Peterson, 1960; Wellenstein & Fabritius, 1973; Skatulla, 1974). In this species, second generations normally occur in more southern latitudes while only one generation normally is found in more northern latitudes. However, in the latter areas in summers with a long warm and dry period, a second generation may be found and lead to the start of an outbreak. It is unlikely that a second generation will be found in pure coniferous stands as the newly hatched larvae are unable to feed on old conifer needles, but in mixed forests and pure deciduous forests, larvae should be able to develop even in autumn (Skatulla, 1974). It is worth mentioning that a bivoltine *L. dispar* race should be present in Kaukasus.

Host Plant Relations

It seems to be a general trait that lymantriid larvae are highly polyphagous, and this includes the more than 2000 species that are not known to cause severe defoliations; i.e., are kept at a stable latency population level. In the more serious defoliators there seems to be a tendency that a larger number of plant species are consumed in the cause of an outbreak, probably related to increased density-dependent dispersal and starvation.

It is often observed that larvae may thrive on a non-preferred diet and that healthy adults develop although pupae are smaller and, subsequently, fecundity is lower. Laboratory tests even show that *L. dispar* which were first fed on a preferred deciduous tree diet and from the third instar on a nonpreferred conifer diet normally causing 100%

mortality, obtained 40% higher female pupal weights than individuals fed only on the preferred deciduous tree diet (Barbosa et al., 1986). The distribution of *L. dispar* among various tree species in a mixed wood actually changed markedly during the season (Barbosa, 1978) indicating that a change of diet could be a common phenomenon.

Previous host plant defoliation may also affect adult fecundity in the next generation. In *L. dispar*, repeated defoliation produced lighter females when larvae were reared on black oaks growing in a dry site, whereas no effect could be traced on gray birch growing in a mesic site (Valentine et al., 1983). In this study, pupal weights were directly related to the concentrations of total free sugars in the foliage. Unfortunately, very little is known about the long-term effect of defoliation on subsequent generations and hence the "induced response" effect (Haukioja & Neuvonen, 1987) is scarcely investigated in lymantriids.

RELEASE OF LATENCY POPULATIONS

In the preceding parts, the variability of different latency characteristics are described. In the following section, the main focus will be devoted to the question of whether changes in any of these characteristics could lead to a "release" of the latency populations and, subsequently, to an outbreak.

First, however, it seems necessary to make a distinction between the Douglas fir tussock moth, *Q. pseudotsugata*, and the *Lymantria* species, in as much as it makes rather little sense to talk about "release" in an apparently cyclic species like *Q. pseudotsugata*. However, it has not been documented that all *Q. pseudotsugata* populations are cyclic and for noncyclic species the concept of "release" might still be valid.

The change in population density from one generation to the next might, in the release phase (progradation), be quite substantial. In *L. monacha*, early forestry reports warned that the moth density could change "from one in ten trees to ten in one tree" over one generation; i.e., a hundred-fold increase. More precise counts made by Wellenstein (1942) demonstrated year-to-year increases of up to 28 times the numbers in the previous year. Similarly, in the release phase of *Q. pseudotsugata*, populations increased almost 10-fold per year (Mason & Luck, 1978). Yearly changes in stable *L. dispar* populations often amount to 10-100 fold (Campbell, 1981).

These dramatic changes lead us to a search for release factors that can produce such results. It is tempting to suggest that minor decreases in the key mortality factors, i.e., decreased bird predation, will lead to release conditions, whereas changes in rather insignificant mortality factors necessarily will have to be of relatively high magnitude.

We must, unfortunately, consider such simplistic reasoning unrealistic, in the light of a bewildering array of density-dependent and density-independent factors acting early or late in the life cycle of the lymantriids. Accordingly, although now we have insight into some of the key mortality factors, we know very little about if, when,

why and how much these factors vary in latency periods, or whether interact compensatorily (Campbell & Torgersen, 1983). Until we obtain such knowledge, by careful observations and experimentations, it is impossible to identify the release factor(s).

SUMMARY

Latency populations of lymantriids are characterised by low but variable population densities; the high density areas being most at risk if the populations over larger areas enter the release phase. Compared with outbreak populations, fecundity rates are high during latency. Mortality rates at all life stages seem mainly to be due to vertebrates. The major pest species overwinter as eggs and the precision of synchronisation between egg hatch and bud burst might be important during the latency phase. Between-tree and between-stand dispersal of first instar larvae is an important lymantriid characteristic and occurs even in the latency phase.

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O U T B R E A K C H A R A C T E R I S T I C S
O F L Y M A N T R I I D S

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INTRODUCTION

The Lymantriids, known as Tussock moths, are a small family of very destructive defoliators. They feed on conifers as well as broad-leaved trees (FURNISS and CAROLIN, 1977). The species shown in Table I have reached high economic importance.

Lymantriids normally occur in low densities in the forests. Sometimes, however, their number increases rapidly to extremely high population densities and they then cause immense damage to the forests. Heavy outbreaks happen only within the climatic optimum of the effective distribution of each insect species (CRAMER, 1962). Regions where mass reproduction of a species occurs in frequent intervals are called "gradation areas".

The variation in the population density from generation to generation is a result of interrelation between procreative power and detrimental influence of the environment. Procreative power is represented by the sex ratio (percentage of females) and number of eggs per female. Environmental resistance is the influence of climate (weather, temperature), food supply and natural enemies.

In this report I shall give a survey of the general concept of the population dynamics of the Lymantriids and investigate the causes of their outbreaks. Emphasis will be placed on the nun moth, *Lymantria monacha* L., which is the most important forest defoliator in Central-Europe.

PRINCIPLES of POPULATION DYNAMICS of LYMANTRIIDS

The population density of all Tussock moth species depends on endogenous and exogenous factors. Examples of endogenous factors are species specific constitution of the individuals, egg number per female, sex ratio, flight

		Common name	Distribution
<u>Lymantria</u> (Porthetria)	monacha	Nun moth	Europe/Asia
"	dispar	Gypsy moth	Europe/N-America
<u>Orgyia</u>	recens (=antiqua)	Rusty tussock moth	Europe/N-America
"	pseudotsugata	Douglas fir tussock moth	Europe/N-America
"	leucostigma	Whitemarked tussock moth	N-America
"	vetusta	Western tussock moth	
<u>Dasychira</u> (Parorgyia)	puvipunda	Buchenrotschwanz	Europe
"	griseifacta	Pine tussock moth	N-America
<u>Leucoma</u> (Stilpnotia)	salicis	Satin moth	Europe/N-America
<u>Euproctis</u>	chrysothoe	Brown-tail moth	Europe

behaviour. Exogenous factors are weather conditions (temperature, moisture, wind) food quality, predators, parasites, pathogens, inter- and intraspecific competition. Thus environment influences the reproduction, survival and movement of individual organisms. Favourable environments provide plentiful food of good quality, a low rate of mortality and good conditions for mating and fertility of the females. As a consequence insect populations increase. On the other hand bad environmental conditions delay or decrease population growth.

The simplest explanation of how a population of insects changes from year to year is that density is the result of birth, death and movement.

BERRYMAN (1986) formulates this as follows:

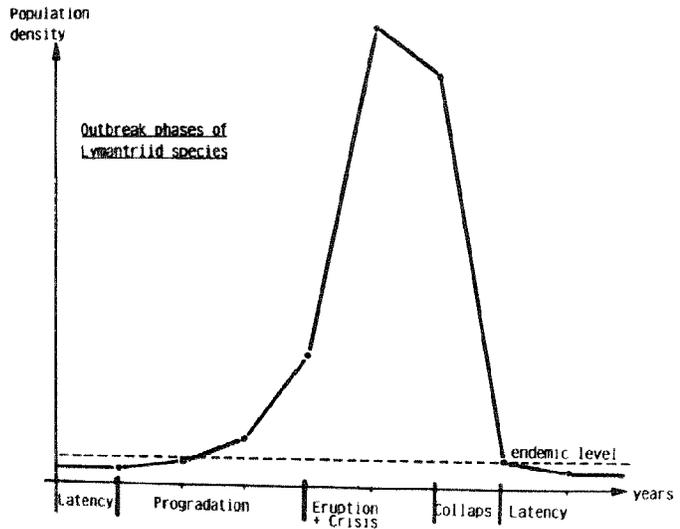
$$\text{Population change} = \text{birth rate} - \text{death rate} + \text{immigration rate} - \text{emigration rate}$$

Population density increases when individual births and immigrations exceed the loss owing to death and emigration, declines when births and immigrations are smaller than deaths and emigrations, and remains unchanged when births and immigrations are equal to deaths and emigrations. The forces affecting birth, death and emigration rate change from time to time and from place to place (BERRYMAN, 1986).

The Lymantriids belong to those forest insects which remain at very low density for long periods of time, but then suddenly explode to extremely high densities and spread over large areas causing severe damage to the forests and immense economical losses.

Outbreaks of the Lymantriids show characteristic phases: In Europe we use the terms latency, progradation, culmination and retrogradation to describe the phases of a gradation. These terms correspond to the American terms innocuous, increase, outbreak (including collapse) and postoutbreak phases (MONTGOMERY and WALLNER, *in press*).

Outbreaks of the Lymantriids show following phases (Fig. 1). After many years at low density, endemic levels, the population increases and reaches outbreak thresholds in a short time. The nun moth population, for instance, reaches epidemic level after 2-3 years. At outbreak levels crowding and malnutrition of the individuals causes the birth rate of the pest population to decline while death rates rise. As a consequence of starvation and lower food quality caused by defoliation and increase of mortality by density-dependent factors (e.g. natural enemies), the population rapidly collapses to its endemic equilibrium again. Outbreaks of all Lymantriid species show the same general sequence. There are however differences owing to



species specific conditions (e.g. fertility) and differences in response to density-independent factors, such as site characteristics (elevation, aspect, slope) and weather (wind, temperature, precipitation) and biotic factors (food supply). (SCHWERDTFEGER, 1963 and 1981; MORS, 1942).

DENSITY-DEPENDENT and INDEPENDENT FACTORS

Fertility

The fertility or procreative power of an insect population is a function of

- female rate and
- number of eggs per female

The female rate (percentage of females of a population) is not constant within Lymantriids. At the beginning of an outbreak (progradation), the percentage of females is much higher than 50 %; in the course of time the female rate diminishes and the sex ratio changes in favour of the male

rate. The female's egg number also diminishes during an outbreak and furthermore the mortality of the pest population rises (Tab. 2).

Table 2: Investigations of pupae of Lymantria monacha
(WELLENSTEIN, 1942)

Year of gradation	Mortality	Female rate	Average number of eggs (per female)
1 st year	5 %	60 - 70 %	220
2 nd "	10 - 20 %	50 - 60 %	150
3 rd "	50 - 80 %	20 - 40 %	80
4 th "	100 %	0	--

The product of female rate and average egg number is an indicator (index) for the procreative power; for example:

$$\begin{array}{ll} \text{for the 1st year} & \text{for the 3rd year} \\ F = 0.65 \times 220 = \underline{143} & F = 0.3 \times 80 = \underline{24} \end{array}$$

This shows that in the third year of a nun moth outbreak reproduction is 6 times lower and a mortality is 13 times higher than in the first year. This illustrates the extent that fertility of a pest population decreases during the progress of an outbreak.

Mortality

The mortality is influenced by different factors and variable from time to time and from place to place. Fertility and mortality together yield the population density at a certain time and place and this is influenced by several "abundance-dynamical factors", namely:

- constitution
- food supply
- abiotic influences of environment (e.g. weather)
- biotic environmental factors (antagonists)

Constitution

The constitution of insects depends on the local circumstances of nourishment and development of the individual organisms. Consequently the constitution of an insect population can change. Young larvae, for instance, are more susceptible to bad weather conditions and diseases than older ones. Also the decrease of female-rate and egg production result from change of the constitution.

Food supply

Food quality and quantity influence sex ratio, egg production and mortality of pest populations. During outbreak conditions caterpillars starve and surviving individuals produce less offspring (WELLENSTEIN, 1942). Since female larvae need more food than males, they are more likely to starve and the sex ratio changes in favour of the males.

As caterpillars are forced to feed on unfavourable food (hard needles, sun needles) their rate of development is decreased (e.g. *Lymantria dispar* 13 days more; KURIR, 1952). Thus, caterpillars on unfavourable food will be exposed to parasites and predators for a longer time and mortality is higher than under normal conditions.

Abiotic influences of environment

Temperature

Temperature is absolutely decisive for duration of insect development, especially during egg and larval stages. Slow development prolongs the influence of unfavourable weather or site conditions; on the other hand faster development will give a better chance of survival. Temperature can affect fertility by influencing the sex ratio and egg production. Caterpillars reared at different temperatures showed a significant dependency on their female rate and egg production of adults (WELLENSTEIN, 1942; ZWÖLFER 1934).

Humidity

Humidity also influences the sex ratio. When eggs of nun moth and gypsy moth were reared at 32 - 50 % relative humidity, more male larvae hatched whereas at 100 % relative humidity more female larvae hatched (SKUHRAVY, 1952).

Climate

Climate is decisive for the geographical distribution of the several tussock moth species and for the regions where they remain in latency or where they build up outbreaks frequently.

Weather

Weather, however, has local influence and affects the pest population in time and place. Outbreaks of the nun moth often happen after warm, dry summers. Furthermore, weather influences insect mortality by unfavourable events such as storm, heavy rain fall, cold weather fronts etc. and can affect the antagonists as well as the pest insects. Also, the coincidence between flushing of buds of the trees and the hatching of the first instar larvae is affected by weather conditions.

Biotic environmental factors

Natural enemies or antagonists are predators, parasites and pathogens. Their action is not only mortality but they also influence the fertility of a population by changing the female rate and egg production. For example: Female caterpillars of all Lymantriids have one more larval stage than males and for that reason are exposed for a longer time to predators (e.g. birds) and parasites. Thus natural enemies diminish the female rate.

Ichneumonids prefer female over male nun moth pupae which causes higher female mortality (NICKLAS, 1942). As a rule, predators and parasites increase during an outbreak with a temporal lag of 1 or 2 years.

Pathogens, particularly nuclear polyhedrosis viruses (NPV), play an important role among all Lymantriid species. Nun moth outbreaks always end by NPV epizootics. During the large nun moth outbreak in Poland 1978-1984, the virus disease occurred in spruce and larch stands but never in pine forests (SCHÖNHERR, 1985). Cytoplasmic polyhedrosis virus, microsporidia and fungal diseases are generally unimportant in the decline nun moth outbreaks.

DEVELOPMENT and DURATION of NUN MOTH OUTBREAKS

The natural distribution of the nun moth extends from western Europe (Spain, Ireland) through the Soviet Union to China (WELLENSTEIN and SCHWENKE, 1978). The northern limit of distribution is near the 60th degree of latitude, the southern border reaches to the Mediterranean area and the Caucasus mountains. The nun moth does not exist on the North American continent.

Lymantria monacha is the most important forest defoliator of Europe. The species caused the heaviest outbreaks and largest forest destructions of the past. There were many nun moth outbreaks during the last century in Europe (see Fig. 187 in WELLENSTEIN and SCHWENKE, 1978, p. 356).

Lymantria monacha is polyphagous like other Lymantriid species but reaches epidemic levels only in spruce and pine forests. Spruce forests are generally more susceptible than pine, but the last outbreak in Poland occurred in pine forests.

The most severe nun moth outbreaks occur in Central Europe. Most outbreaks happen in areas of low precipitation (400 - 700 mm annual rain fall) and monthly temperatures of 11.5 - 13.3°C in May, 15 - 17°C in June, 16.5 - 19°C in July and 16 - 18°C in August (LEUTHOLD, 1931). This shows that nun moth prefers warm and dry regions.

Nun moth outbreaks usually begin after a period of one or more of the following favourable weather conditions:

- Coincidence of flushing of trees and hatch of the larvae which diminishes larval mortality
- Warm, dry summer months (June/July) which reduces mortality and enhances weight gain of the caterpillars
- Warm dry weather during the flight period (August) which facilitates mating of the adults.

Under favorable weather and nutrition conditions a nun moth population can increase 50 to 100 times. Nun moth gradation proceed from initial stage of high potency of reproduction because of high female rates and large egg numbers. With increasing population density, the constitution of the individuals gets worse and the female rate and egg production declines. Finally the outbreak collapses, owing to the influence of density-dependent environmental factors, such as starvation, natural enemies and diseases.

In detail, a nun moth outbreak shows the following development:

First year: The pest population exceeds the endemic level, but the augmentation is restricted to small areas of infestation. Defoliation is not yet visible; thus, the beginning of the outbreak is not noticeable.

Second year: Defoliation of the forest amounts to around 10 percent, but the damage is not perceptible. During the flight period, however, many moths are seen sitting on the stems. Large numbers of healthy eggs are found on the tree trunks. These are indications of mass attack for the following year.

Third year: In spring of the third year a very high number of first-instar larvae are conspicuous. Several thousands of young caterpillars may be on each tree. In June/July suddenly heavy frass occur and defoliation reaches 50 - 90% loss of needles. Infestation centers are clearly discernible. In these centers the number of eggs diminishes.

Fourth year: Inside of the infestation centers of previous year many caterpillars still occur. However they are weak, often sick, feed little and only a few of them pupate. The majority of the caterpillars die from NPV disease and other antagonists. Very few moths complete development and these are weak and not very fertile. The pest population remains healthy in the border zones, where the population density is lower.

The outbreak continues and spreads out from the border area of the infestation centers. Drifting of the first instar larvae by wind and moths flying is not very important in spreading the outbreak. The many new infestation centers result from augmentation of the endemic population on each place.

Duration of nun moth outbreaks in conifer depends on the host species:

<u>Population Phase</u>	<u>Number of Years</u>	
	<u>Pine Forest</u>	<u>Spruce Forest</u>
progradation (increase)	2	4
eruption } (outbreak)	1	2
collaps }	1	1

Thus, the total outbreak gradation usually lasts 4 years in pine forests and 7 years in spruce forests.

Reasons for the different development in pine, spruce and broadleaf tree forests are following:

The open pine forests are moderately favourable for nun moth larvae. The abiotic conditions are suitable and bird predation is relatively low. Larvae however suffer starvation owing to late flushing of the trees. Pine trees also provide less food than spruce trees. For that reason, outbreaks are of short duration.

Result: In pine forests nun moth outbreaks occur more often but are shorter in duration than those occurring in spruce stands (on average four years).

In old spruce stands, the even temperatures, calm winds and high humidity are favourable environmental conditions for nun moth reproduction. Also favourable are the rough bark of the trunks, the temporarily wide spread flushing of the spruce trees, and the high biomass of foliage on spruce trees. Egg and first larval stage mortality is low under such conditions. The lower temperatures of spruce forests however retard the increase of the population. Also the natural enemies increase slower than in broadleaf forests. Therefore, the gradation starts and develops slower and the outbreak lasts longer because of

larger, more predictable supply in spruce stands.

Result: In spruce forests the outbreaks of the nun moth lasts longer than in pine forests (on average seven years).

Broadleaf-tree forests are not favourable for nun moth development. The smooth bark of the beech trees result in high egg mortality by predators. Also in hardwood forests are more parasites and predators (esp. birds) than in conifer forests. The deciduous leaves toughen too fast and become unfavourable food for young larval stages.

Result: Since nun moth does not reach high population densities in broadleaf-tree forests, there is little opportunity for outbreaks in such forests.

CONCLUSIONS

The nun moth provides a prototype of the principle pattern of outbreaks of the tussock moth species shown in Table I. Differences among the Lymantriids result essentially from species specific behaviour, such as host tree preference and climatic requirements and on the volume and effectiveness of their antagonists. Gypsy moth, for instance, prefers warmer and dryer habitats than nun moth. For that reason, the traditional European outbreak areas of the gypsy moth are in southern and southeastern Europe.

In summary, I have tried to draw a general picture of the outbreak characteristics of the Lymantriids and I would like to restrict my considerations to these general statements. In my opinion more details about other tussock moth species might be the subject of some of the other speakers.

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MONITORING POPULATION CHANGE
IN THE LYMANTRIIDAE

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INTRODUCTION

Monitoring is specifically defined in this paper as the procedures used to generate insect census data. Its principal purpose in modern pest management is to detect spatial and intergenerational changes in the densities of problem species. Of the worldwide number of lymantriids, monitoring systems have been developed for only a few of the most economically important species. Regular monitoring of populations over successive generations has been concentrated on even fewer species: Lymantria dispar (L.) (the gypsy moth) in the new and old world; Lymantria monacha L. (the nun moth) in Europe; and Orgyia pseudotsugata (McDunnough) (the Douglas-fir tussock moth) in western North America. Although some attention has been given to the sampling of other pest species of the Lymantriidae, consistent monitoring of their numbers over extensive areas has been the exception rather than the rule. This is unfortunate because much can be learned about the numerical behavior of pest populations from an analysis of their long-term census data (Berryman, 1987).

Populations of univoltine species, like most of the Lymantriidae, need to be monitored annually to capture changes in abundance from one generation to the next. There is no universal sampling method for doing this (Graham and Stark, 1954). Types of monitoring differ with each species depending on its life cycle, spatial distribution, and behavioral characteristics. Annual censuses are based on either direct counts of the insect in one of its developmental stages, or on a measurable indicator of the species' abundance such as the extent of defoliation of its principal hosts or the production of excrement or other residues. Direct counts are interpreted as absolute density when numbers are expressed in terms of a fixed unit of space like a hectare, and as relative density when the unit of expression is variable like a trap or volume of foliage. Indirect measures, such as defoliation or frass, are only indices of insect abundance, but they can be as useful for censuses as direct counts.

COMMON TECHNIQUES OF MONITORING

Defoliation

Visual reconnaissance of defoliation is one of the oldest techniques for monitoring the major problem species of the Lymantriidae. Aerial detection surveys and the sketch-mapping of infestations are annual events in most pest management programs. Infestations are ultimately reported as the number of acres or hectares defoliated by a species, which in turn reflects year to year changes in its abundance. The record of *O. pseudotsugata* defoliation in northern Idaho over the last 58 years is a good example of the usefulness of such data. The plotting of defoliated hectares over time shows the six peak fluctuations in abundance that have occurred in northern Idaho since 1930 (Fig. 1). The last recorded defoliation in 1986 was only 1371 ha (Stipe et al., 1987); this was small compared to the size of previous outbreaks, yet it followed the previous pattern of periodic eruptions. Periodicity of major fluctuations of *L. dispar* in coastal forests of Morocco and *L. monacha* in southern Germany has also been determined indirectly by long-term records of their defoliation (Fraval, 1986; Klimetzek, 1971). An obvious weakness of such surveillance methods is that population changes cannot be estimated at low densities when defoliation is undetectable. This results in a data gap between outbreaks, seen in Figure 1, that could be important in the long-term analysis of serial data.

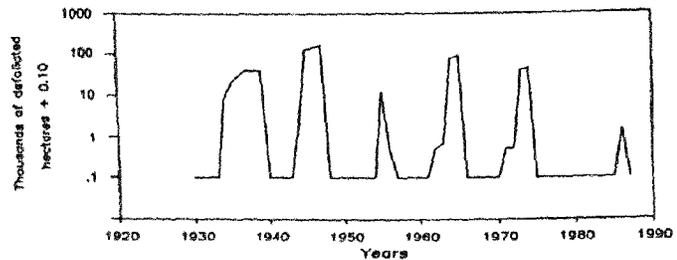


Figure 1. Trend of visible defoliation by *Orgyia pseudotsugata* in northern Idaho, 1930-87 (modified from Livingston, 1984).

E g g s

Eggs of many of the lymantriids, especially of *Lymantria* and *Orgyia* species, are deposited in a large mass. Egg masses are relatively easy to see and, because they are the overwintering stage for many species, they can be sampled through the fall and winter months with less concern about critical timing. Eggs have unquestionably been the favored stage for monitoring populations of *L. dispar* in Europe and North America (Maksimović and Sivčev, 1984; Semevsky, 1973; Wilson et al., 1981). Densities of egg masses are usually estimated directly by counting all the masses on trees and shrubs in small sample plots and summarizing the results in absolute terms as the number per hectare. Plots may be a fixed size or a combination of fixed and variable size, with the variable radius determined by prism selection of live trees on which to observe masses (Wilson and Fontaine, 1978). In comparative studies a fixed plot size of 0.01 ha has proved to be superior to other methods over a wide range of densities (Kolodny-Hirsch, 1986).

The longest series of direct counts for any lymantriid are of *L. dispar* egg masses in eastern New England (Fig. 2). These

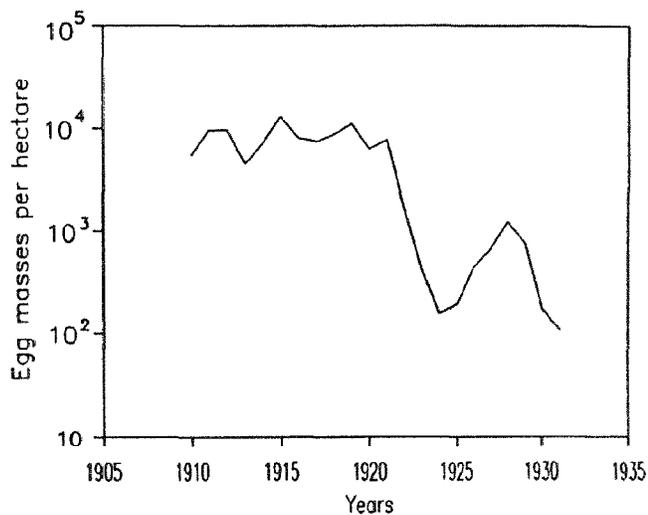


Figure 2. Trend of egg mass densities of *Lymantria dispar* in eastern New England, 1911-31 (modified from Campbell, 1967).

densities were estimated over 21 consecutive years on permanent 0.18-acre (0.073-ha) plots (Campbell, 1967, 1973). Because of its duration the data set is unique and was the basis for recognizing numerical bimodality as well as other population behavior of the species (Berryman, 1987; Campbell and Sloane, 1978). Egg mass density expressed in absolute terms has also been used in numerous studies of *L. dispar* in Yugoslavia (Maksimović, 1953; Maksimović et al., 1970). Figure 3 shows the results of monitoring egg masses for six years to evaluate the effect of artificially stocking *L. dispar* in forest stands to maintain natural enemies during periods of low natural density (Maksimović and Sivčev, 1984).

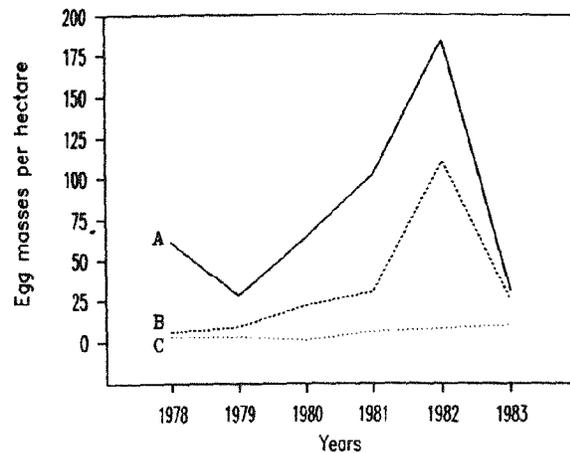


Figure 3. Trend of egg mass densities of *Lymantria dispar* in three study areas in Yugoslavia: A. Check area, B. Egg masses added, and C. Egg masses added (from Maksimović and Sivčev, 1984).

Eggs of other lymantriid species like *L. monacha* and *Q. pseudosugata* are likewise sampled to predict population trends, particularly during outbreaks, but have not been preferred for longer term monitoring (Mason, 1969; Schönherr, 1985; Shepherd et al., 1984). Egg masses of *Q. pseudosugata* are counted only on branches and are usually expressed as relative densities per whole branch or specific area of the branch (Luck and Dahlsten, 1967; Mason, 1970; Shepherd et al., 1984). One of the problems with using eggs for monitoring trends of *Q. pseudosugata* is that at low densities, masses are often concentrated with a high variance in the

tops of trees where they are difficult to sample without examining an excessive number of trees (Mason, 1970).

Another technique for monitoring species with conspicuous masses is the so-called five-minute walk. This procedure, which has been successful for *L. dispar*, involves observing and counting egg masses while walking through the stand (Wilson et al., 1981). After five minutes have elapsed, the total count is translated into absolute density by a regression relation developed previously. Variations of the walk technique have also been used for *Q. pseudotsugata* eggs in scouting infestation centers (Shepherd and Otvos, 1986; Sower et al., 1983) and in predicting the relative density of first instars of the next generation (Mason and Torgersen, 1977). These time-search methods are relatively low cost and may be practical for generating long-term census data of some species.

L a r v a e

Many lymantriids have been sampled at one time or another as larvae, partly because damage by defoliation focuses more attention on the feeding period than on other metamorphic stages. Also, larvae are often sampled to evaluate the early effects of chemical or microbial controls or to monitor intrageneration survivorship in ecological studies. Larval numbers are most frequently given as relative densities per branch or foliage unit, or sometimes the whole tree, but a variety of expressions have been used. For example, densities of *L. dispar* and *Euproctis chrysorrhoea* L. (the brown-tailed moth) larvae have been evaluated in chemically treated and untreated stands in Rumania by their number per hundred leaves; *E. chrysorrhoea* has also been monitored annually by the number of hibernating caterpillars per tree (Scutăreanu, 1986a, 1986b). In Poland, the severity of a *L. monacha* outbreak was characterized by the total number of larvae per tree (Schönherr, 1985); in Japan, larval survivorship was estimated for *L. dispar* by sampling one-meter long branches (Furuta, 1982) and for *Dasychira argentata* Butler (the Sugi tussock moth) by total counts on small trees (Shibata, 1981). In North America, densities of *Dasychira plagiata* (Walker) (the pine tussock moth) and *Q. pseudotsugata* larvae are estimated for life tables by sampling 38- to 46-cm branch tips in the tree crown (Dahlsten et al., 1977; Mason 1976; Sreenivasam et al., 1972). Relative numbers of *L. dispar* larvae have also been determined in New England by counting all visible larvae during a 10-minute walk (Connola et al., 1966). The monitoring of larvae of some species, especially those feeding on broad-leaved trees like *L. dispar*, can be difficult because of unpredictable aggregation and the diurnal movement of older instars (Higashiura, 1987; Liebhold and Elkinton, 1988a; Wilson et al., 1981).

The most continuous direct monitoring of lymantriid larvae has been conducted in Canada by the Forest Insect and Disease Survey of the Canadian Forestry Service (Richmond, 1954). In this survey,

defoliator data are collected annually from permanent sampling locations by systematically beating three-tree samples with a 3.7-meter pole and counting all the larvae that fall onto a ground cloth (Harris et al., 1972). Sample plots were originally selected to be broadly representative of an entire forest area. An equal emphasis was placed on collected insects whether they were of major or minor economic importance (Richmond, 1954). Data from the early years of monitoring are published (Prentice, 1962), and the average number of larvae per collection is easily calculated each year for several species of the Lymantriidae (= Liparidae). An example of the long-term trends of *Orgyia leucostigma* (J.F. Smith) (the white-marked tussock moth) over a large area of eastern Canada are shown in Figure 4. Numbers are also summarized in Table 1 for species represented by at least 10 years of consecutive entries. In general, these illustrate the stability (i.e., small variance-mean ratio) at low densities of three *Dasychira* species compared to the other more outbreak-prone species. *Leucoma salicis* (L.) (the satin moth), a severe pest of *Populus* spp. introduced from Europe in 1918, occurred at especially high densities during the 12 years that it was monitored. The data also confirm the extreme volatility of *O. pseudotsugata* populations, already well-known in British Columbia for their periodic outbreak behavior (Harris et al., 1985).

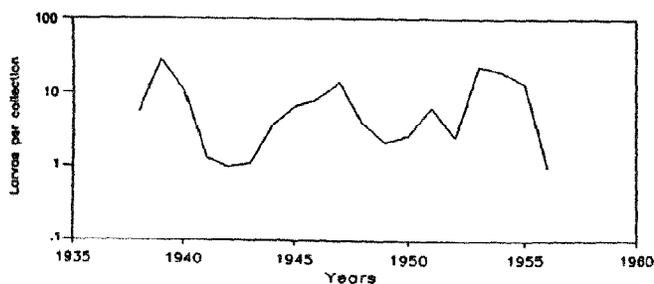


Figure 4. Trend of larval collections of *Orgyia leucostigma* in Canada, 1938-56. Data collected by the Forest Insect and Disease Survey of the Canadian Forestry Service (calculated from Prentice, 1962).

Larval monitoring techniques are probably more advanced for *O. pseudotsugata* than any other species in the family Lymantriidae. Populations are sampled by counting larvae on three 45-cm branches from each tree in a tree-cluster and relating their number to a

Table 1. Summary of monitoring statistics for 7 species of Lymantriidae (= Liparidae) reported by the Forest Insect and Disease Survey of the Canadian Forestry Service (calculated from Prentice, 1962).

Species	Number of consecutive years	Mean larvae per sample	Var-iance of mean	Var-iance/mean ratio
<u>Dasychira</u> (= <u>Parorgyia</u>) <u>grisefacta</u> (Dyar)	11	1.22	0.10	0.08
<u>Dasychira</u> (= <u>Parorgyia</u>) <u>plagiata</u> (Walker)	17	1.25	0.06	0.05
<u>Dasychira</u> (= <u>Parorgyia</u>) <u>vagans</u> (B. and McD.)	10	1.36	0.23	0.17
<u>Leucma</u> (= <u>Stilpnotia</u>) <u>salicis</u> (Linnaeus)	12	43.19	577.15	13.36
<u>Orgyia</u> <u>antiqua</u> (Linnaeus)	19	3.27	12.99	3.97
<u>Orgyia</u> <u>leucostigma</u> (J. E. Smith)	19	8.23	66.08	8.03
<u>Orgyia</u> <u>pseudotsugata</u> (McDunnough)	12	16.04	290.87	18.13

standard unit of branch area (Mason, 1979). In outbreaks the sample branches are clipped from the middle one-third of the tree crown by using a pole pruner with an attached basket. To prevent the escape of larvae the clipped branches drop into the basket, which is lowered to the ground where the samples are removed and beaten over a cloth to dislodge the larvae. In sparse populations, a nondestructive technique is used where lower branches are beaten over a hand-held drop-cloth without cutting them off the tree. This way more foliage can be easily sampled when larvae are scarce. Density in the midcrown is indirectly estimated simply by the frequency of occurrence of larvae on the lower branches (Mason, 1977, 1987) using the equation,

$$M = -17.75d^{-0.598} \ln(1-p), \quad (1)$$

where M is midcrown density per m² of branch area, d is the average number of days since egg hatch, and p is the proportion of sample units with larvae. Because of the cost efficiency of the method we have been able to monitor low-density populations of O. pseudotsugata continuously over a longer period of time than would be possible by other more expensive methods (Fig. 5). Lower crown

sampling has also been used effectively in the pest management of *Q. pseudotsugata* as a followup to other detection methods to evaluate the status of rising populations (Mason, 1978; Shepherd, 1985; Shepherd and Otvos, 1986).

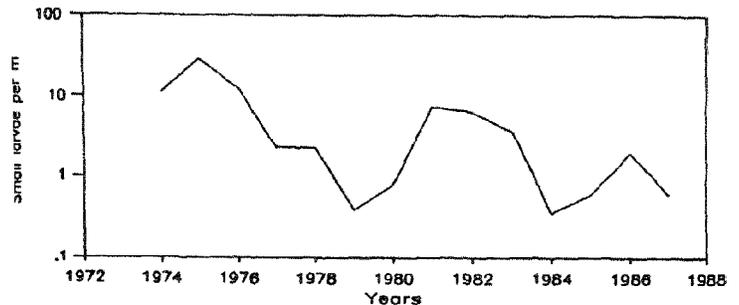


Figure 5. Trend of larval densities of *Q. pseudotsugata* in a nonoutbreak population in southern Oregon, 1974-87. Plotted data are means of eight sample plots (from Mason and Torgersen, 1987).

Although fluctuations in numbers of lymantriid larvae are usually given in relative terms, an indirect technique taking advantage of the movement of older *L. dispar* instars to and from the crown could lead to an expression of absolute density for this species (McManus and Smith, 1984). Recent findings of a relation between the total number of *L. dispar* larvae on trees and the number resting during the day on burlap bands attached to the main stem will make estimates of absolute density more practical (Liebhold et al., 1986; Wallner et al., manuscript in review).

P u p a e

Lymantriids are rarely monitored in the pupal stage, probably because pupae are temporally close to the egg stage which is more representative of the surviving generation. When pupae are sampled it has usually been for life table studies or for specifically valuating mortality (Dahlsten et al., 1977; Luck and Dahlsten, 1980; Mason et al., 1983; and Sreenivasam et al., 1972). Estimates of the relative density of *Q. pseudotsugata* and *D. plagiata* pupae have been made by sampling whole branches or 38-cm branch tips.

There is no reason why some of these techniques could not be used equally well for intergeneration monitoring. Pupae of Q. pseudotsugata, for example, can be easily sampled on lower branches by observation and converted into midcrown densities by the same function (equation 1) used for larvae (Mason, 1987). We have also sampled Q. pseudotsugata cocoons at very low densities using the time-search technique. The rate that cocoons were collected per person hour of foliage searching was closely related to relative density in the midcrown (Mason and Torgersen, 1977).

Providing artificial habitats for pupation is another method with promise for monitoring populations of L. dispar and Q. pseudotsugata. The procedure involves fastening shelters to the main stem of trees in the form of plastic flaps for L. dispar (Reardon et al., 1986; USDA Forest Service, 1986) or small wooden blocks with four 2.5-cm diameter holes for Q. pseudotsugata (Dahlsten et al., 1978). Larvae pupate on or near the devices where their cocoons are collected and counted. These data can be interpreted as relative indices or converted to absolute densities by regression techniques. The method also has the advantage of providing additional information on sex ratio, parasitization, and egg mass size.

A d u l t s

Natural lures for trapping male moths have long been used for detecting presence or forecasting trends of L. dispar populations (Collins and Potts, 1932; Maksimović, 1965, 1969). The sex pheromones of L. dispar and Q. pseudotsugata have now been synthesized (Bierl et al., 1970; Smith et al., 1975) and are effective adult attractants at extremely low concentrations (Livingston and Daterman, 1977). Disparlure, the pheromone of L. dispar, also attracts L. monacha adults and the pheromone of Q. pseudotsugata is similarly attractive to several other lymantriid species (Brewer et al., 1985; Daterman et al., 1976, 1977; Grant, 1977; and Schönherr, 1972). The availability of these synthetic compounds has stimulated considerable research on environmental factors affecting the use and reliability of baited sticky traps as a relative index of population abundance (Cameron, 1979; Daterman, 1982; Hochmut et al., 1977; Jensen and Nielsen, 1984; Shepherd et al., 1985; Skuhřavý and Zúmr, 1981). Computer-operated information systems that analyze and display annual trapping data for large geographical areas are also being developed (Reardon et al., 1986).

Pheromone-baited traps have not been used long enough to have generated extended data sets. However, the ability of traps to monitor short-term trends is illustrated for an endemic population of L. monacha in southwestern Germany (Fig. 6). Tree defoliation did not occur at any of the locations during the years they were monitored. On the other hand, significant defoliation did develop at another site in 1978 where the number of moths caught was much higher than that recorded at these locations (Bogenschütz, 1979).

Such results indicate that detecting critical thresholds in population density may be the most important product of monitoring adults.

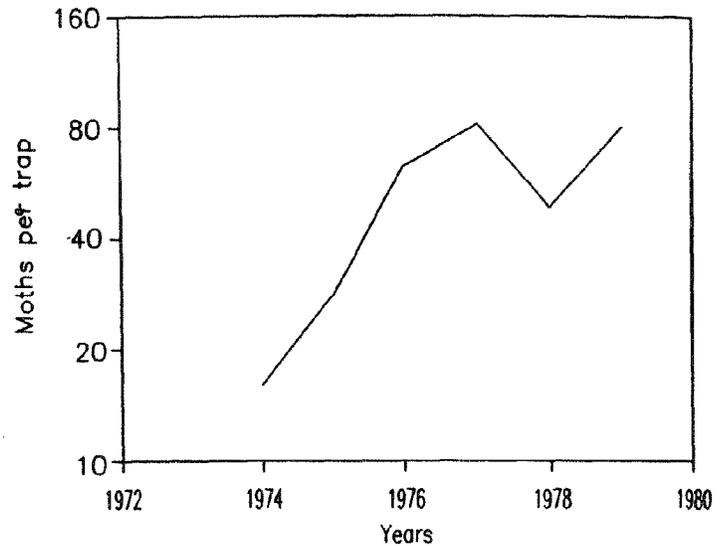


Figure 6. Trend of trapped adults of *Lymantria monacha* in a nonoutbreak population in southwest Germany, 1974-79. Plotted data are means of 130 traps in four forest districts (modified from Bogenschütz, 1979).

Similar findings have come from the annual monitoring of *Q. pseudotsugata* where the number of trapped adults may not always correlate well with local densities of eggs or larvae, but it does accurately indicate general abundance and critical changes in the population (Daterman et al., 1979; Shepherd et al., 1985). An example is the 1986 cyclic peak of *Q. pseudotsugata* that occurred in northern Idaho (Fig. 1). Average moth densities trapped at permanent monitoring sites from 1978 to 1987 clearly tracked the buildup and decline of this population. Although the outbreak

caused only minimal defoliation in 1986, it was accurately forecast by the peak moth catch in the fall of 1985 (Stipe et al., 1987). The annual monitoring of adults with pheromone-baited traps is today an important phase in the pest management of *Q. pseudotsugata* in the Pacific Northwest and British Columbia (Daterman, 1979; Daterman et al., 1979; and Shepherd and Otvos, 1986).

F r a s s a n d E x u v i a e

Measurements of the quantity and quality of frass produced by larvae has occasionally been used as an index for evaluating populations of *L. dispar*, *L. monacha*, and *D. argentata* (Connola et al., 1966; Liebhold and Elkinton, 1988a, 1988b; Maksimović, 1953; Shibata and Nishiguchi, 1980; Zethner, 1976). Frass droppings are collected in various kinds of suspended cloths and containers or on sticky boards, sorted by size, and weighed or counted. Corrections may need to be made for the effects of temperature on production. The weight and number of droppings is well correlated with larval abundance, and pellet size is a good indicator of instar number (Higashiura, 1987; Liebhold and Elkinton, 1988a; Zethner, 1976). A novel technique has also been tried in Japan for estimating the absolute density of *L. dispar* larvae by the number of head-capsules falling into traps (Higashiura, 1987). The density of larvae determined by this method was almost identical to that estimated by frass collection. Although these techniques have been used mostly for determining intrageneration changes in outbreaks, they may have potential for the annual monitoring of absolute numbers.

DISCUSSION

Selecting a permanent monitoring system depends on many considerations that are only partly biological. Statistical and economic concerns also need to be addressed. The ideal scheme should provide annual estimates of a species' abundance with a small variance at a low cost. Expensive methods that require excessive sampling are less likely to be sustained through many consecutive generations of monitoring. Unfortunately, except for *L. dispar* egg masses (Kolodny-Hirsch, 1986), there are few published studies comparing relative efficiencies of the monitoring techniques that I have described.

A final caveat for all monitoring schemes is to keep them as simple as possible. The collection of continuous data, so vital for understanding the long-term dynamics of defoliators, demands consistency that can only be accomplished by a commitment over many successive years. Idealistic systems that are impractical and expensive to use in the field are less likely to survive tight budgets in the real world. It sometimes becomes more important to maintain completeness of the data set, even if at the expense of having to sacrifice statistical rigor for practicality. There are

probably many examples in forest entomology where the collection of important census data was suspended simply because of the unnecessarily high cost of the monitoring system.

SUMMARY

Many techniques have been used to estimate insect abundance in the Lymantriidae. Except for the general defoliator collections made annually by survey groups, the systematic monitoring of single-species populations in successive generations has been limited mostly to three economically important species: Lymantria dispar (L.) (the gypsy moth), Lymantria monacha L. (the nun moth), and Orgyia pseudotsugata (McD.) (the Douglas-fir tussock moth). Defoliation recorded in annual surveys is a valuable index of abundance at high densities, but such records alone are inadequate for detecting critical population changes at low densities or making analyses of long-term population behavior. Instead, sampling by direct counts of the insect to estimate either absolute or relative densities is the most successful method of monitoring change over a wide range of natural population densities. Traditionally, populations of L. dispar have been monitored in Europe and the United States by counting egg masses on small sample plots and expressing their numbers as absolute density per hectare. Other methods like baited-traps for adults, artificial habitats for larvae or pupae, and frass-drop measurements also have potential for monitoring. Relative densities of L. monacha in Europe are monitored primarily by the number of moths caught annually in pheromone-baited traps. Population trends of O. pseudotsugata in western North America can be followed successfully by either the relative density of moths in pheromone traps or small larvae counted annually on foliage samples. To ensure perpetuity during periods of austerity, the best monitoring systems should be statistically efficient and relatively simple and cheap to use.

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SPATIAL ASPECTS OF GYPSY MOTH POPULATION DYNAMICS

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INTRODUCTION

Like many other insect species, the dynamics of gypsy moth, *Lymantria dispar* L., is difficult to predict. Populations often exist at very low densities for many years and then, for unknown reasons, densities increase several orders of magnitude to defoliating levels. Despite many years of study, the mechanisms by which low densities are maintained and, conversely, the mechanism by which outbreaks develop are largely unknown.

The traditional approach to understanding and predicting the dynamics of insect populations is to quantify natural population processes averaged across a given location. In the past, spatial processes have been considered too complex to quantify in detail. We have attempted to characterize spatial patterns and processes that may be important to the dynamics of gypsy moth populations. This analysis was undertaken at two levels of resolution: the within-stand and regional levels.

WITHIN-STAND PROCESSES

The collection of life-table data at one or more sites over several years has proven to be a useful method for studying insect population dynamics (Varley et al. 1973). Using the classic approach, data are collected on animal density and mortality for successive stages within a generation. These data are used to quantify mortality over specific age intervals and mortality attributable to specific agents. K-factor analysis (Varley and Gradwell 1960, 1968) is one of several techniques used to evaluate the importance of various mortality sources and intervals to total generation mortality. These data are also used to evaluate which, if any, periods or specific sources of mortality act in a density-dependent fashion. Positive density-dependence is thought to contribute to population stability (Varley et al. 1973).

Hassell (1985, 1986) pointed out that the classic life table approach may be inadequate because it fails to recognize spatial variation in prey densities. Often, insect populations are patchy, in part due to the spatial variation of host plants. Hassell (1985, 1986) postulated that natural enemies may respond in a density-dependent fashion to this spatial variation in density and that by averaging across an area, as is done in most life-table studies, one may fail to detect density-dependence.

Hassell (1985) described a need to collect life-table information from a sampling design that is stratified in space as well as time. Typically, quantification of spatial heterogeneity in density and mortality often requires intensive sampling. Partly for this reason, few studies have attempted to quantify these relationships. The holly leaf-miner (Heads and Lawton 1983) and viburnum whitefly (Hassell et al. 1987) are perhaps the

only insects that have been systematically analyzed in this manner. These studies showed that patterns of spatial density-dependence may vary considerably at different spatial resolutions and that these patterns are often quite different from patterns of temporal density-dependence.

In this study of gypsy moth population dynamics, as an alternative to the classic collection of series of life tables, we collected matrices of life tables stratified by two (horizontal) dimensions in space within a generation (Liebhold and Elkinton 1988c). Densities were estimated for a matrix of cells throughout a plot. We also attempted to account for causes of larval mortality occurring in spatial subplots.

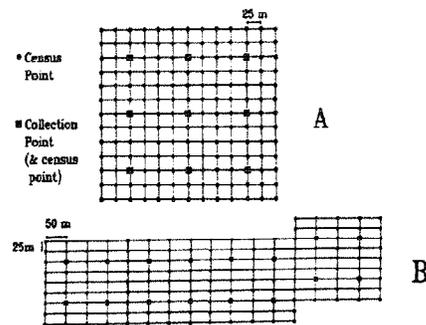


Figure 1. Location of density estimation census points and larval collection points. A. 9-ha site (site 1). B. 16-ha site (site 2).

Sampling Methodology

A 16-ha and a 9-ha study site were located on Otis Airbase, Cape Cod, Massachusetts. At the 9-ha site a 13 x 13 grid (25 m between each point) was established and a 9 x 17 grid (50 m between points on the x axis, 25 m between points on the y axis) was located at the 16-ha site (Fig. 1). Densities of successive gypsy moth life stages were estimated at each grid point.

Egg-mass densities were estimated by counting all new egg masses within 5 m of each point. The density of larvae hatching from each mass was estimated as the product of egg mass density and first instars (L_1) per egg mass (estimated from 40 field-collected masses [Buonaccorsi and Liebhold 1988]). Fourth instar (L_4) densities were estimated at each point as the ratio of frass drop and frass yield (rate of frass production per insect) estimates (Liebhold and Elkinton 1988a,b,c; Buonaccorsi and Liebhold 1988). Frass drop was measured by placing a frass trap at each grid point. Frass yield was measured by individually caging a cohort of 40 larvae from the site on host foliage over the same period as frass drop measurement. Pupal, adult, and adult female densities were estimated by locating all pupae in 2 x 5 m quadrats, marking them with acrylic paint, and recording their positions. Pupae were marked once a week during the period that larvae were entering the pupal stage. When all adults had eclosed, the quadrats were revisited and the condition of pupal remains (i.e., missing, preyed upon, parasitized, or successfully emerged) was recorded.

Counts from adjoining census points were averaged for 1-ha subplots (9 subplots at site 1; 16 subplots at site 2) to form estimates of density and mortality (expressed as k values [Varley and Gradwell, 1960, 1968]). k_1 corresponded to the difference between expected predispersal L_1 density and L_4 density. Since most dispersal occurs during the first instar, k_1 represented the change in density due to both mortality and dispersal. k_2 was the mortality between the L_4 and pupal periods. k_3 was the difference between the pupal and adult densities. k_4 was the difference between adult density and adult female density (sex ratio effect).

Within-plot variation in larval parasitism and disease incidence were measured by making collections of larvae from the center of the 1-ha subplots (Fig. 1). Either weekly or semi-weekly, 50-100 larvae were collected in each subplot. These larvae were placed on artificial diet (Bell et al. 1981) and were checked for parasitism and mortality biweekly. Mortality occurring between collections was totaled for each agent and expressed as k values (Varley and Gradwell 1960, 1968). Marginal mortality probabilities were calculated to account for simultaneously acting mortality agents (Royama 1981; Elkinton, unpublished).

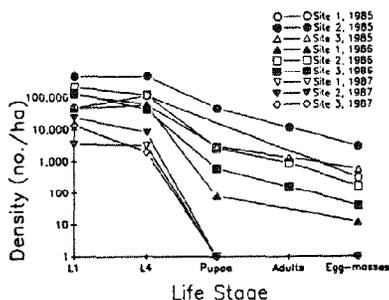
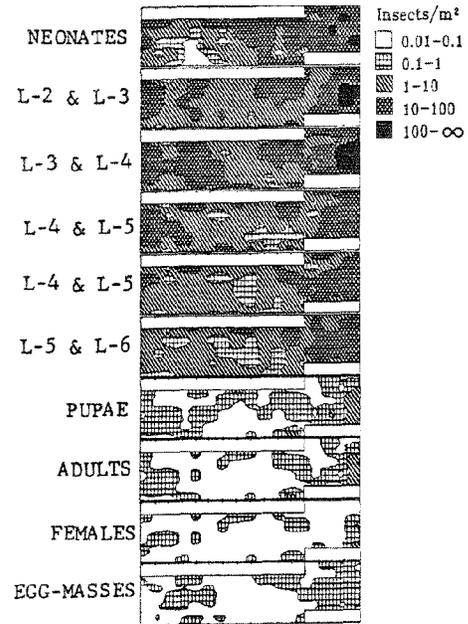


Figure 2. Densities of successive gypsy moth life stages at each site from 1985-1987. Site 3 was an additional 9 ha plot at which detailed spatial data was not collected.

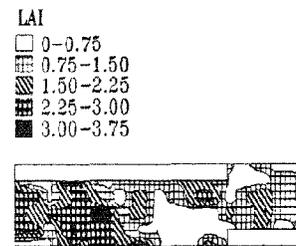
Results

The general pattern of within-generation survival was similar among years and sites (Fig. 2). k_2 - k_4 generally were greater than k_1 . During the course of the 3 years, densities declined at all sites. The major sources of mortality in larvae were NPV, parasitism by *Parasetigena sylvestris*, parasitism by *Cotesia melanoscelus*, and mortality due to unknown causes. Elkinton et al. (this proceedings) discuss a preliminary application of classical life-table analysis to these across-plot averages.

Considerable within-plot variability in density was observed frequently. For example, at site 2 in 1985, one end of the plot had distinctly higher densities through all life stage (Fig. 3). Liebhold et al. (1988) showed that some of the variation in gypsy moth density within a plot can be explained by differences in host-foilage density. However, the difference seen in Figure 3 clearly is not explained only on the basis of host-foilage density (Fig. 4).



3. Spatial distribution of successive gypsy moth life stages at site 2, 1985. Data interpolated from 86 point estimates using a Bessel interpolation.



4. Spatial distribution of oak leaf-area (expressed as leaf area index [LAI]) at site 2. Data from 86 photographs (Liebhold et al. 1988).

Table 1. Significance of regressions of mortality to initial density at two study sites for 2 years ("/" indicates significant positive slope; "\" indicates significant negative slope; "." indicates no significance).

Mortality	-----Site 1-----		-----Site 2-----	
	1985	1986	1985	1986
k ₁	/	.	/	/
<i>C. melanoscelus</i>	\	.	.	.
Unknown
NPV	.	.	/	.
k ₂
<i>C. melanoscelus</i>	\	.	\	.
<i>P. sylvestris</i>	.	.	/	.
Unknown
NPV
k ₃	.	.	/	.
k ₄	\	.	/	/

K₁ was the most consistently density-dependent mortality (Table 1). Rearing of larval samples indicated relatively little mortality due to parasitoids and disease during this period. Thus, it is likely that the density-dependence observed during this period is due to predation or dispersal. The finding that mortality due to parasitization by *C. melanoscelus* tended to be inversely density-dependent is in agreement with findings from a similar study (Weseloh 1973). In general, specific density-dependent relationships did not remain constant across all plots and years. Hassell et al. (1987) found this to be true in their study of the spatial density-dependence of viburnum whitefly mortality. Thus, conclusions about density-dependence derived from spatial data are unique to the generation under observation.

Spatial life tables may detect density-dependence occurring on a finer spatial scale than would be detected using the classic time-series. For example, the fine scale, aggregative response of a parasitoid to host densities could be detected only from spatially stratified data. By contrast, the classic approach to life-tables will detect any numerical response (in the sense of reproduction rather than dispersal) of mortality agents. Thus, the classic approach has an advantage in that it can be used to detect delayed density-dependent relations. Because of the different nature of information derived from the two types of studies, spatial life tables may complement, but not replace classic life-table studies.

REGIONAL PROCESSES

We now consider spatial processes on a much larger scale: the regional level. Little is known about spatial patterns of gypsy moth outbreak development. Valentine and Houston (1979) and Campbell (1976) hypothesized that outbreaks may be initiated by immigration of larvae from nearby outbreak areas. Campbell (1973, 1976) and Campbell and Sloan (1978) concluded that outbreaks are likely to persist from one year to the next when insect densities range widely among subpopulations in a region and, conversely, outbreaks are likely to decline when numerical variability is minimal among subpopulations.

At the core of modern integrated pest management systems for gypsy moth are geographically based monitoring systems (Ravlin et al. 1987; Reardon et al. 1987). The objective of this approach is to use spatially stratified monitoring (typically a grid of stations separated by 1-3 km) to detect new, rising populations and then treat these rising populations in order to prevent regional outbreaks. To evaluate treatment decisions, there is a need for models that predict the large-scale spatial dynamics of gypsy moth populations. In this study we applied several statistical methods to characterize historical spatial patterns of defoliation in Massachusetts.

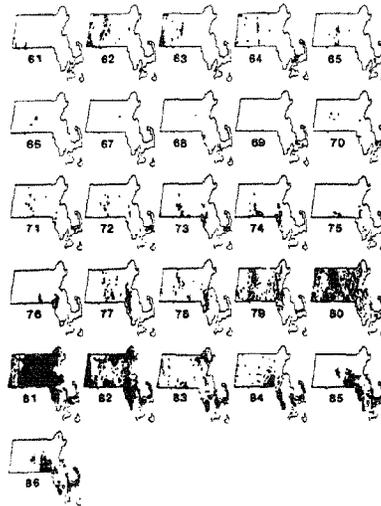


Figure 5. Defoliation incidence for each 1.9 x 1.9 km cell in Massachusetts, 1961-86.

Description of the Data

The Massachusetts Department of Environmental Management monitors gypsy moth defoliation annually in all parts of the state using aerial sketch maps. Maps are sketched during a series of flights over the state in late July when defoliation is at its peak. Composite 1:760,320 maps covering the entire state from the years 1961-86 were digitized into a 65 x 101 matrix of cells (Fig. 5). Each cell represented a 1.9 x 1.9 km area. Each cell was coded as either 1: containing defoliation, 2: undefoliated, 3: not part of the state.

Defoliation frequencies for each cell were summed from 1961-86. From the original 65 x 101 matrix of defoliation frequencies, a 25 x 25 matrix was interpolated using a modified inverse-distance weighting function (Sampson 1975). This new grid matrix was then used in a piecewise Bessel interpolation algorithm to generate defoliation frequency contour intervals (Fig. 6). Portions of Cape Cod and an area near the northeastern border of Rhode Island exhibited the greatest numbers of years of defoliation.

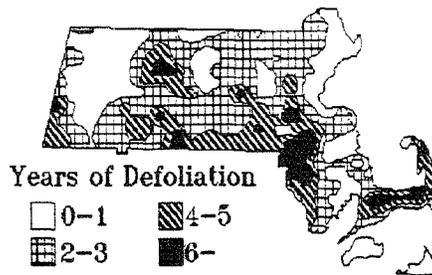


Figure 6. Spatial contour of defoliation frequency in Massachusetts from 1961-86.

Cluster Analysis

The outbreak that occurred in 1981 was an unprecedented phenomenon in terms of the overall quantity of defoliated cells and in terms of the high synchrony of most regions during this period. Except for the 1981 outbreak, defoliation timing was not synchronous among all portions of the state (Fig. 5). We used cluster analysis in an attempt to categorize similar regions according to synchrony of defoliation.

All map cells were assigned to one of 30 regions, which consisted of 10 x 10 submatrices of adjoining cells. For each region, yearly defoliation magnitude was calculated as a proportion of the maximum observed defoliation for the region from all years. This relative magnitude was used to eliminate the effect of areas that were incapable of supporting defoliating populations (e.g., agricultural land and resistant stands). Ward's cluster algorithm (Hair et al. 1987) was then used to separate regions according to their squared Euclidean distance in the 26 variables (years).

The first cluster to be identified (i.e., most distinctive defoliation pattern in terms of outbreak synchrony) from the body of other regions consisted of Cape Cod and the southeastern portion of the state (Fig. 7). In this cluster, regions characteristically experienced high defoliation from 1980-86 and had other more minor eruptions from 1963-78 (Fig. 8). The cluster algorithm identified several other clusters of regions having similar defoliation frequencies though they were not as distinct as cluster 1.

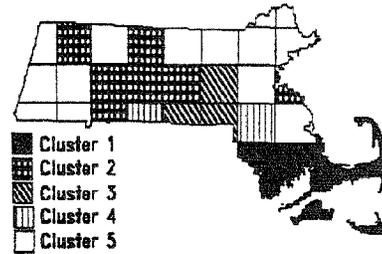


Figure 7. Map of clusters generated using Ward's algorithm.

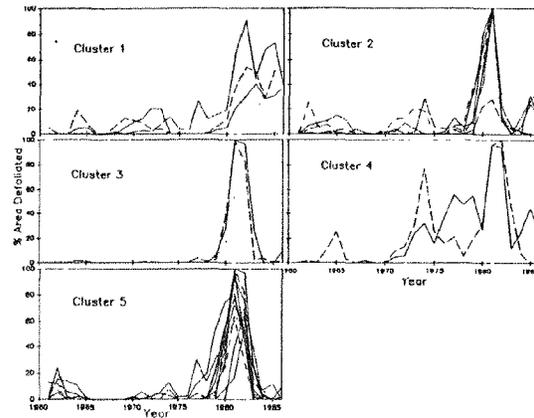


Figure 8. Yearly defoliation frequencies in each of 30 regions.

Transition Models

In this study we used a two-state transition model (Parzen 1962) to describe the transition of cells from 0 (undefoliated) to 1 (defoliated) and from 1 to 0. Separate transition probabilities were calculated to compare cells in different clusters (previously identified using cluster analysis). We performed this analysis taking into account the state of adjacent cells (using a Queen's move definition of adjacency [Cliff and Ord 1973]).

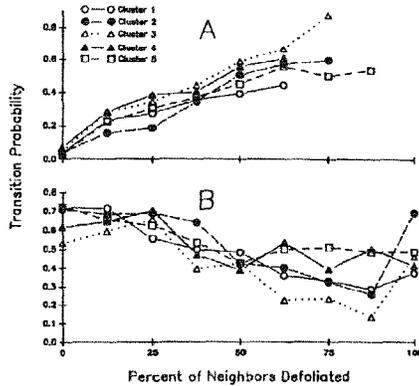


Figure 9. Probabilities of transition to a different defoliation state with varying numbers of defoliated neighbors: A. Transition from nondefoliated to defoliated; B. Transition from defoliated to nondefoliated.

All clusters exhibited similar trends in defoliation transition frequencies with respect to the defoliation status of adjoining cells. Probabilities of defoliation initiation increased as the proportion of defoliated neighbors increased (Fig. 9a). This represents what is referred to as the "focal area phenomenon" where visible defoliation begins at some localized area and then that area grows larger through time (Chugunin 1949; Valentine and Houston 1979; Wallner 1987). These results confirm this pattern; however, it provides no evidence of a causal connection between defoliation in the localized area and subsequent defoliation in surrounding areas.

The probability of defoliation termination decreased as the proportion of defoliated neighbors increased (Fig. 9b). This relationship does not conflict with Campbell and Sloan's (1978) theory that outbreaks often are maintained by a redistribution of insects from neighboring outbreak areas.

Autocorrelation Analysis

Spatial autocorrelation is a method of describing spatial patterns by quantifying the correlation between spatially adjacent points (Cliff and Ord 1973; Sokal and Oden 1978). We applied spatio-temporal autocorrelation analysis (STAA) to the defoliation data. STAA is used to evaluate the relationship between adjacent points, where adjacency is described in both space and time. Results from STAA can be useful for understanding the spread of epidemics through space (Cliff and Ord 1978; Reynolds et al. 1988). We restricted adjacency definitions to separate cardinal directions (Oden and Sokal 1986). This directional STAA was used to statistically evaluate the extent to which defoliation spread in one cardinal direction. Qualitative analysis of other gypsy moth defoliation maps suggested that changes in the spatial distribution of defoliation between years is often unidirectional due to the wind-borne dispersal of first instars (Anderson and Gould 1974).

Directional STAA yielded nearly identical correlograms in all four cardinal directions (Fig. 10). Cells which were within six time-space cells were significantly autocorrelated. These results suggest that defoliation in a given cell may have had an effect on the condition of spatially adjacent cells in the future. However, it does not indicate that there was a unifying directional component to the spread of gypsy moth defoliation. Instead, the lack of a significant effect of cardinal direction on directional STAA suggests that, at least in Massachusetts, outbreaks radiate outward in all directions.

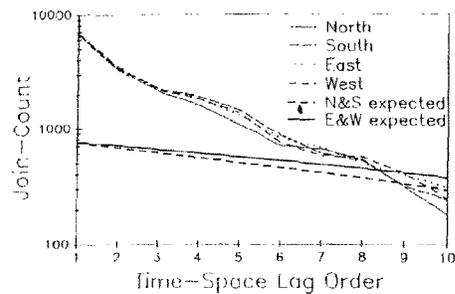


Figure 10. Directional spatio-temporal autocorrelation correlograms (Reynolds 1988; Oden and Sokal 1986) based on defoliation join-counts from 1961-86. Join-counts expected under a random distribution through time and space were the same for both North-South and East-West adjacency definitions.

SUMMARY

Spatial processes affecting gypsy moth population dynamics were examined at two levels: within-stand and regional levels. A spatially stratified sampling scheme was used to measure within-stand spatial variation in gypsy moth density and mortality. This method was used to quantify the extent to which various types of mortality operated in a spatially density-dependent fashion. This information supplements analyses of space-averaged density and mortality.

Regional spatial processes were studied by digitizing 26 consecutive annual defoliation maps from the state of Massachusetts. Analysis of these maps showed that outbreaks in different regions of the state did not arise simultaneously. Cluster analysis was used to categorize the regions according to their outbreak synchrony. Transition models and spatial autocorrelation analysis were used to quantify the spatio-temporal distribution of defoliation. The probability of defoliation in a given area was dependent on the defoliation status of adjoining areas.

ACKNOWLEDGMENTS

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IMPAIRMENTS, SILVICULTURE, AND THE GYPSY MOTH

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INTRODUCTION

An integrated pest management process for forest managers to deal with potential defoliation by and catastrophic losses from the gypsy moth, *Lymantria dispar* L., is described. The process outlines how to: (1) assess stand susceptibility, (2) rate stand vulnerability and project potential losses, (3) consider impacts on management objectives, (4) monitor gypsy moth populations, and (5) select action alternatives (Fig. 1). It is hard to find two forest managers who share identical concerns about the gypsy moth. The district forester in Pennsylvania worries about how, where, and when to salvage dead timber after an outbreak. In Virginia, the supervisor of a park frets over potential effects on a delicate plant community. And a municipal watershed manager in New York wonders about possible consequences to water yields and quality. Problems in areas threatened by gypsy moth are as varied as the owners and managers of the millions of acres of hardwood forest in the East. But no matter what your perspective, your course of action for coping with gypsy moth will be guided by your understanding of how much defoliation may occur, the resulting mortality, the impact on management objectives, and the action alternatives available.

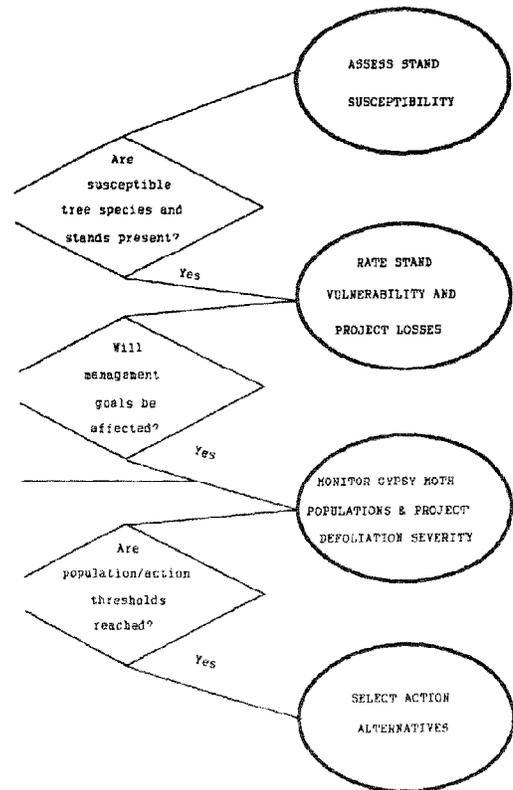
Infestations in the 1970's and 1980's were monitored closely in several areas that are fairly typical of millions of acres of susceptible forest in the Eastern United States. Information about the impacts of gypsy moth has been assembled, and "rule-of-thumb" guides for predicting tree defoliation and subsequent mortality have been developed.

The rule-of-thumb label is appropriate for the guides since they by no means account for all of the variation in damage caused by gypsy moth. What actually happens in the forest will be affected by many interrelated factors (for example, defoliation frequency and intensity, tree stress, action of secondary organisms such as shoestring root rot and the two-lined chestnut borer, influence of gypsy moth parasites and predators, effectiveness of control measures, and weather conditions). Most of these factors are in themselves difficult to predict. Although not perfect, the following information gives managers an indication of what to expect from gypsy moth infestations, removes some uncertainty, and leads to improved management decisions.

ASSESSING POTENTIAL STAND DEFOLIATION (SUSCEPTIBILITY)

Gypsy moths attack trees or stands by defoliating their leaves. All tree species and forest stands are not equally susceptible. Feeding preferences of gypsy moth are a key indicator of potential defoliation (Fig. 2, Gansner and Herrick 1985). Vegetation can be sorted into four food-preference classes, ranging from Class I—species that are favored as food by gypsy moth larvae (including oaks, aspen, birch, basswood, and sweetgum) through Class IV—unfavored species that are rarely fed upon (including ash, cedar, dogwood, locust, and yellow-poplar) (Mosher 1915 and Table 1).

DECISION PROCESS FOR GYPSY MOTH



Forest management (IPM) decision chart to help forest managers manage gypsy moth.

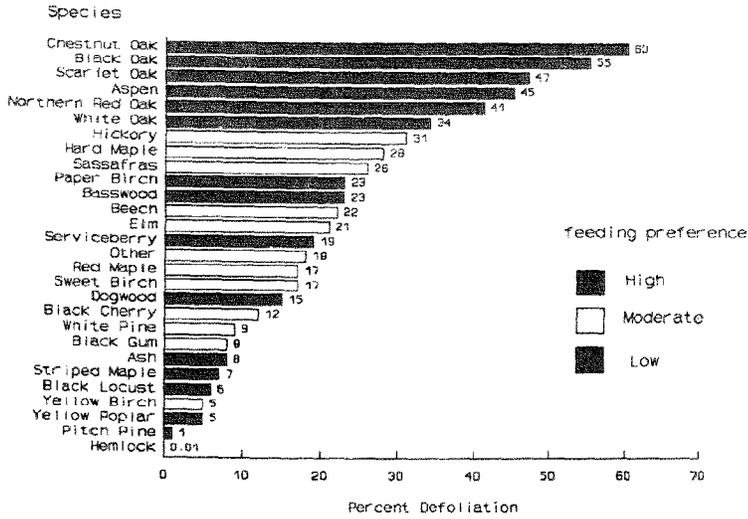


Figure 2. Average species defoliation on 600 plots in central Pennsylvania in 1981 (Gansner and Herrick 1985).

Rating Stand Susceptibility

Herrick and Gansner (1986) developed a procedure that uses species composition, tree size, and crown condition to rate the susceptibility of forest stands in a newly infested area. With this model, stands at risk of heavy defoliation can be separated from those where defoliation is likely to be light. For example, stands with high basal area in oak species, especially black and

Table 1. Host preferences of the gypsy moth.

Preference level	Species
High	oaks, aspens, basswood, birches, larch, willows, apple, sweetgum
Moderate	beech, butternut, cherry, hickories, hemlock, cottonwood, pines, maples, yellow birch, chestnut, spruces, walnut
Low	ashes, cedars, locusts, junipers, sycamore, yellow-poplar, balsam fir

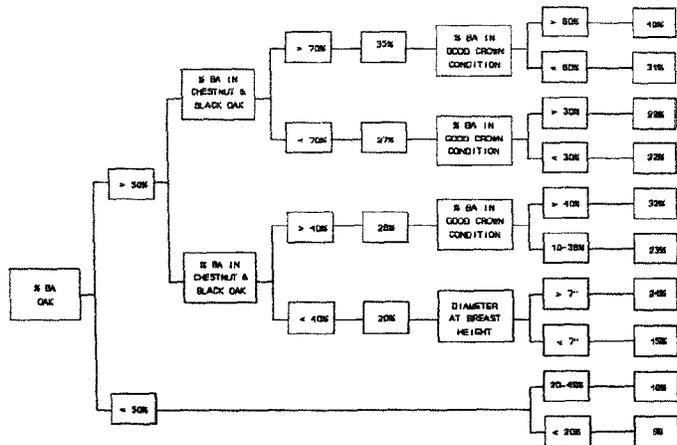


Figure 3. Guide for estimating gypsy moth defoliation potential in newly infested areas (Herrick and Gansner 1986).

chestnut oaks, have potential for heavy defoliation (Fig. 3). Houston and Valentine (1977) have developed a susceptibility rating system for use in the New England area where gypsy moth has been present for decades.

ASSESSING POTENTIAL TREE MORTALITY (VULNERABILITY)

In general, gypsy moth infestations result in mortality losses of less than 15 percent of total basal area. Losses of 15 to 35 percent are not uncommon, and occasionally levels greater than 50 percent are reported. The survival of host trees depends on the interaction between: intensity, distribution and frequency of defoliation; whether trees refoliate; tree condition before defoliation; site factors; environmental conditions immediately before and after defoliation; and extent of disease or other insect invasions.

Defoliation Intensity, Distribution, and Frequency

Gypsy moth defoliation intensity is commonly classed as light, moderate, or heavy. The term "light defoliation" describes conditions where less than 30 percent of the foliage has been removed. Stand defoliation in this class cannot ordinarily be detected during routine aerial surveys. A single light defoliation usually causes little damage to trees. Stands where 30 to 60 percent of the foliage is removed fall within the "moderate defoliation" class. Damage to these trees will depend primarily on the specific amount of defoliation, and tree vigor before defoliation and during the recovery period.

Removal of more than 60 percent of the foliage places a stand in the "heavy defoliation" class. When this occurs, refoliation places a heavy demand on the tree's food reserves. Thus, a tree that refoliates can remain under considerable stress during the following weeks and become vulnerable to other mortality agents (Table 2).

Table 2. Effect of defoliation intensity on mortality of 600 plots in central Pennsylvania between 1978 and 1985 (Gansner and Herrick 1987).

3-year average defoliation (%)	Mortality (%)
<10	13
10-19	15
20-29	16
30-39	17
>40	28

Gypsy moths begin feeding on preferred host species within a stand before moving on to less preferred tree species. For example, a "light defoliation" (averaging less than 30 percent) in a stand composed entirely of preferred species usually means that less than 30 percent of the foliage was removed from all crowns in the stand; and all trees are subjected to roughly the same amount of stress. In a mixed-species stand, "light defoliation" could include moderate to heavy defoliation on many preferred trees, resulting in stress and death, while less preferred trees would be affected only slightly (Table 3). This differential distribution of defoliation in mixed stands might cause a significant shift in species composition.

Table 3. Differential mortality by species groups in 600 central Pennsylvania plots (Herrick and Gansner 1987b).

Species Group	Mortality (%)
Black & chestnut oak	25
Other oaks	19
Other species	14

Under "normal" environmental conditions, a single (even heavy) defoliation does not result in heavy tree mortality (Campbell and Valentine 1972). However, the stress from this defoliation usually weakens a tree and lowers its resistance to mortality in subsequent defoliations. Multiple defoliations (increasing frequency) have an additive effect and can result in significant loss in timber value.

Tree Condition

Tree vigor before defoliation (sometimes expressed in terms of crown condition) has been shown to be significantly related to tree mortality (Table 4). Low vigor can result from a number of environmental factors; previous attacks

Table 4. Mortality in 600 central Pennsylvania plots as influenced by crown condition (Herrick and Gansner 1987b).

Crown Condition	Mortality (%)
Poor	49
Fair	21
Good	10

from insects and diseases can cause stress, as can prolonged drought or excessive moisture. Suppressed trees are especially vulnerable (Table 5).

Table 5. Mortality of 600 central Pennsylvania plots as influenced by crown class (Herrick and Gansner 1987b).

Crown Position	Mortality (%)
Dominant & codominant	14
Intermediate	18
Suppressed	28

Site and Stand Conditions

Gypsy moth defoliation is more frequent and severe on poorer sites. However, when defoliation occurs on moister, mesic sites with higher site indices, mortality is higher than on poor sites (Table 6, Gansner 1987). Aspect,

Table 6. Mortality of 600 central Pennsylvania plots as influenced by site quality (Gansner 1987).

Site Class	Mortality (%)	
	Oaks	Others
Poor (site index <55)	13	9
Medium (site index 55-74)	23	11
Good (site index >75)	24	12

slope position, site index, crown class, and species all affect stand mortality (Fosbroke and others 1985).

Rating Stand Vulnerability

Gansner and Herrick (1984) examined a number of stand and tree characteristics associated with gypsy moth infestation in Pennsylvania, and developed a stand vulnerability rating system. The system is based on the

percentage of trees in the white oak group (found to be particularly vulnerable) and the percentage of trees with poor crowns (more than 5 dead branches, very thin foliage, reduced leaf size, poor color, or heavy

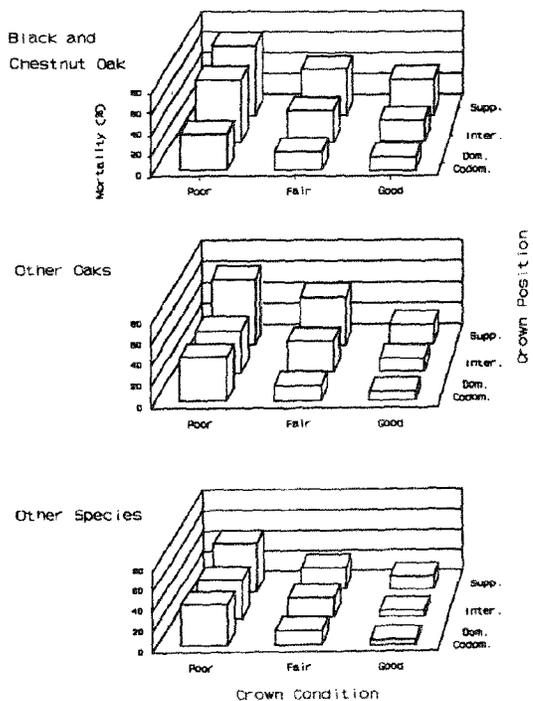


Figure 4. Individual tree mortality probabilities based on 600 central Pennsylvania plots (Herrick and Gansner 1987b).

sprouting) (Fig. 4). Stands with a large percentage of trees with poor crowns and in the white oak species group have a potential for high mortality. This guide was used to predict losses in central Pennsylvania. Predicted values were within 2% of actual average loss. Still, these projections are rule-of-thumb estimates; actual average mortality in a given situation will depend on the influence of local site and environmental conditions.

Individual tree mortality can be predicted from the combination of crown condition (tree vigor), crown class, and species group (Herrick and Gansner 1987b). For example, a suppressed black oak tree in poor crown condition has a 67 percent probability of mortality, while a good crown condition, dominant black oak tree has a probability of only 13 percent, and a good crown condition, dominant red maple has a 5 percent probability of mortality (Fig. 5). Using the probabilities based on these three factors with

Change in Stocking After Gypsy Moth Infestation Poconos 1971-1979

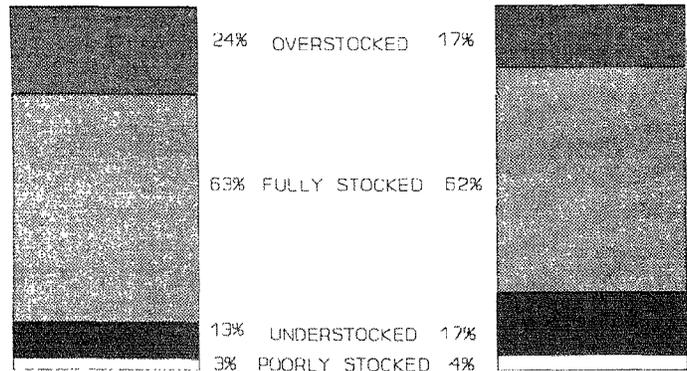


Figure 5. Change in stand stocking in Poconos Mountains region of Pennsylvania following gypsy moth related mortality (Gansner and Herrick 1984).

stand inventory data can provide stand-level estimates of mortality. Also, they can be used to determine which trees to cut and which ones to leave when conducting silvicultural treatments.

CONSIDERING IMPACT ON MANAGEMENT OBJECTIVES

Decisions about specific preventive or remedial actions will depend on individual land management objectives. A timber manager may not care about the expected loss of a few trees in an overstocked stand that would provide a natural thinning (Fig. 6). But the recreation manager may have a very low tolerance for any mortality in an historic or scenic area. Wildlife managers might welcome small openings created by tree mortality, but would

Percentage of trees in white oak species group	Percentage of trees with poor crowns						
	0	5	10	15	20	25	30+
0	L	L	M	M	M	M	H
10	L	L	M	M	M	M	H
20	L	L	M	M	M	H	H
30	L	L	M	M	M	H	H
40	L	L	M	M	M	H	H
50	L	L	M	M	M	H	H
60	L	M	M	M	M	H	H
70	L	M	M	M	M	H	H
80	L	M	M	M	H	H	H
90	L	M	M	M	H	H	H
100	M	M	M	M	H	H	H

STAND MORTALITY: L = < 10% M = 10-25% H = > 25%

Figure 6. Expected mortality in forest stands based on proportion of trees in the white oak group and tree crown condition (Gansner and Herrick 1984).

be concerned if too many mast-producing tree species were killed or defoliation resulted in a mast failure. The manager of wilderness lands might be indifferent to any natural tree mortality.

By rating the forest stands' susceptibility to gypsy moth defoliation and vulnerability to tree mortality, managers can determine if impacts on their objectives are acceptable. If acceptable, then he or she might allow the infestation to develop. If not acceptable, some preattack action such as silvicultural cutting or enhancement of biological controls might be considered. Table 7 shows the total impact of gypsy moth in the state of Pennsylvania from

Table 7. Cumulative defoliation and timber losses in Pennsylvania from 1968 to 1987 (Quimby, personal communication).

Area defoliated (without counting repeated defoliations)--6,901,500 acres
Total timber value loss--\$310 million
Average loss per acre--\$45.00

the time of its first outbreak to 1987. As the outbreak continues to develop, insect populations can be monitored to estimate when infestation is likely and what the severity of defoliation might be. If warranted, foliage protection with insecticides can be considered.

MONITORING GYPSY MOTH POPULATIONS

As gypsy moth invades new areas, managers will want to keep close track of its location and abundance. Information on the location and spread of gypsy moth infestations is collected by USDA Animal and Plant Health Inspection Services (APHIS), by state forest pest management agencies, and by the Forest Pest Management group within the USDA Forest Service. These specialists can provide the best early information on the extent of the infested areas, population areas, population levels, trends, direction, and rate of movement.

Once gypsy moths have been confirmed in an area, the most useful measure for determining potential populations and suppression needs is the number of gypsy moth egg masses per acre. Egg masses are visible on trees and ground litter for 7 to 8 months before spring defoliation. Early assessment of expected populations provides lead time for planning and organizing treatments. Several egg-mass sampling techniques are used. These include "5-minute walks," fixed-radius plots, variable-radius plots, and combined fixed- and variable-radius plots. The "best" technique depends on population size and the availability of time, personnel, and money. The 5-minute walk is popular because of its simplicity. It is most applicable in areas with high egg-mass densities when a quick population estimate is needed to determine spray threshold conditions (Eggen and Abrahamson 1983).

A method for predicting potential gypsy moth defoliation percentage based on the number of egg masses per acre has been developed (Fig. 7, Gansner et al. 1985). The model works well given all the factors that can influence defoliation (e.g., host species, larval dispersion, weather).

Tolerance levels of gypsy moth population vary with particular management goals and specific landowner objectives. Urban and state

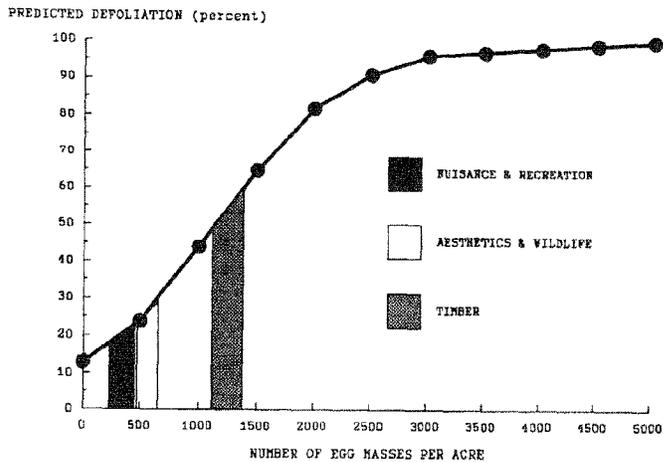


Figure 7. Egg-mass to defoliation prediction curve and thresholds for gypsy moth control treatments for different management objectives (altered from Gansner et al. 1985).

programs for aerial spraying are often aimed at preventing nuisance caused by caterpillars, or unsightliness of defoliated trees at homesites and recreation areas. A common threshold for nuisance prevention is 250 to 500 egg masses per acre. The threshold for foliage protection to minimize tree mortality and growth loss in forest stands would be much higher, about 60% potential defoliation. This level is an egg-mass density threshold of approximately 1,400 per acre. For wildlife mast-production, a threshold of 500 egg masses per acre would be appropriate.

SELECTING ACTION ALTERNATIVES

Action alternatives available to the resource manager faced with gypsy moth-caused damage include silvicultural treatments, insecticide application, enhancement of natural control agents, or just letting nature take its course. The appropriate action depends on projected losses and their impact on management objectives. Silvicultural prescriptions are determined by the proximity of infestation, coupled with timber stand characteristics and maturity.

The development of a computer simulation model (Gypsy Moth Life Systems Model, GMLSM) provides forest and pest managers with a tool for long-term projections of gypsy moth impacts and testing of management actions. These long-term trends would not be evident from examining single-outbreak situations (Sheehan 1984).

Silvicultural Treatments

Silvicultural treatments have potential for reducing both susceptibility and vulnerability of forest stands (Table 8 and Gottschalk 1987). The use of

Table 8. Strategies and techniques for silvicultural treatments to minimize gypsy moth impacts.

Alteration of stand susceptibility:

- Maximizing tree growth and vigor
- Manipulating gypsy moth habitat
- Increasing forest diversity

Alteration of stand vulnerability:

- Maximizing tree growth and vigor
- Removing high risk trees and stands
- Manipulating secondary organism habitat

silvicultural treatments is very recent with most forest managers just accepting them as management philosophy (Trew 1987). Despite this recent interest, silviculture will only be able to treat a small portion of the total area needing treatment within any given outbreak interval. Treatments need to be prioritized so that the most vulnerable and valuable stands are treated first.

If defoliation is not expected within the next 5 years, there is adequate lead time for taking preventive action. Seven silvicultural prescriptions have been described that may aid in reducing timber losses. If the stand is poorly stocked (less than C level; 35%), or if the stand is adequately stocked (C level or better; > 35%) but is within 5 years of maturity, stand regeneration may be considered. Shortening the rotation will allow marketing of the current stand, avoiding lost value in the salvage of dead material, and assuring adequate regeneration through seed production and sprouting from live stumps. If advanced regeneration stocking and stump sprouting potential are adequate, the stand can be regenerated with a harvest. For stands where sources of regeneration are not adequate, a shelterwood or conversion cutting may be considered. If susceptibility or vulnerability of the stand is high, then conversion to nonpreferred host species will help reduce the establishment and spread of gypsy moth. On lower quality sites, conversion usually will be to a pine species, while higher quality sites can be converted naturally to mixed hardwoods by shelterwood or selection cutting. When susceptibility and vulnerability are low, shelterwood cutting can develop adequate advance regeneration; a drastic change in species composition is not needed.

If the stand is fully stocked but will not reach maturity for another 6 to 15 years, it is advisable to defer cutting for 6 to 15 years, and re-examine for possible protection, early harvest, or salvage if mortality has occurred. Younger fully stocked stands (16 or more years from maturity) with less than 80% stand density may best be handled by deferred cutting for 10 to 15 years and re-examining their status as defoliation becomes an immediate threat. Experience suggests that stresses created by thinning or cutting can remain for 3 to 5 years after treatment. Reduced vigor resulting from this stress, coupled with defoliation stress, could result in high mortality. High-value, highly stressed stands should be observed closely and are good candidates for chemical spray protection if an outbreak is expected during the recovery period.

For younger, fully stocked stands with more than 80% stand density, sanitation thinning or presalvage thinning may be considered, depending on the percentage of the basal area that is in preferred food species. Sanitation thinning is best applied in stands where less than 50% of stand basal area is in preferred food species, and where other management objectives make it appropriate. This treatment is designed to reduce the spread and establishment of gypsy moth by removing trees that are refuges and preferred food species. Presalvage thinning is best suited for stands with more than 50% of the basal area in preferred food species. This treatment reduces defoliation-caused losses by removing the most vulnerable trees before they are defoliated and die. Trees considered most vulnerable are oaks in poor crown condition, other species in poor crown condition, then trees with fair crowns. Trees with good crowns are less likely to die (Herrick 1982).

If defoliation is currently taking place or expected within the next 5 years, the appropriate actions are to protect with insecticide application, closely monitor and evaluate through stand examinations, or move ahead with stand regeneration plans. Priorities for chemical application can be based on stand maturity, condition, and value; gypsy moth population densities; and management objectives. Under conditions of low stand value or low risk, the best course of action may be to delay treatment and re-examine the stand after defoliation to assess extent of damage, and salvage potential.

If defoliation has recently occurred, wait 1 to 3 years for any subsequent mortality. At that time, the stand can be re-evaluated to consider regeneration cutting (based on damage level and stocking condition); deferred cutting (as determined by stocking level, amount of damage, and stand maturity); and salvage cutting or thinning (again determined by stocking, stand condition, and damage level). A more complete guide for silvicultural treatment has been developed by Gottschalk.¹ A computerized, decisionmaking expert system is under development that will automate the selection of the proper silvicultural treatment based on the stand and insect conditions present.

Pesticide Applications

Seven approved insecticides, both synthetic and biological, are used as aerial sprays to control gypsy moth populations. These products give adequate control when used properly. Most are applied when larvae are in very early developmental stages and when leaves are about one-third expanded. Pesticide and application costs vary by size of project, type of equipment, materials used, and terrain of the treated area. Total costs in 1985-86 ranged from \$4 to \$12 per acre for large areas. Additional information and assistance in planning spray projects can be obtained from local forest pest management offices.

No Action

Taking no action is sometimes the best choice. If projected effects of gypsy moth are not expected to affect management goals significantly, prudent managers may elect to take no action and "take their chances." Under these circumstances, no action probably is the most cost-effective option.

¹Gottschalk, Kurt W. Silvicultural guidelines for forest stands threatened by the gypsy moth. USDA For. Serv., Northeast. For. Exp. Stn., Gen. Tech. Rep. In preparation.

SUMMARY

The gypsy moth has moved south and west from its original confines in New England and has spread out to infest a large portion of the Nation's hardwood forests. Repeated outbreaks have left its impact on all sections of the forest community. The pest has affected recreation, wildlife habitat, water yield and quality, and local timber markets. As the gypsy moth continues its invasion of new areas, new questions and concerns will arise. Information and guidelines presented here will provide forest managers with a better understanding of what to expect and serve as a basis for improved decisions for coping with the pest. One finding that deserves special mention is the great amount of variability in loss attributed to the insect. It follows that planning for cost-effective gypsy moth control programs should aim at forest stands most sensitive to heavy damage, with efforts made to identify such areas and hold damage to acceptable levels.

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A R E G Y P S Y M O T H P O P U L A T I O N S
I N N O R T H A M E R I C A R E G U L A T E D
A T L O W D E N S I T Y ?

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I N T R O D U C T I O N

Campbell and Sloan (1978a, Campbell 1975) theorized that gypsy moth populations in North America exhibit bimodal stability. By this they meant that increases in gypsy moth density are compensated by increases in mortality at two levels of density (Fig. 1). At high density, increases in mortality from disease, particularly from nuclear polyhedrosis virus (NPV), along with starvation prevent further increases in gypsy moth density. At low density, populations are stabilized primarily by avian and small mammal predation. Campbell believed that the white footed mouse, Peromyscus leucopus, was the major gypsy moth predator among a community of small mammals that included several species of shrews (Smith and Lautenslager 1974, 1981). Parasitism in this scheme played a minor role.

Campbell's model has been cited (Berryman et al. 1987) as an example of a similar general model proposed by Southwood and Comins (1976) who believed it was characteristic of many insect species. According to the model, outbreaks occur when, for one reason or another, the population rises above a threshold level above which the predominant low density mortality agent (in this case small mammal predation) is inversely density dependent. In this intermediate range of density the populations grow exponentially into outbreak phase.

Campbell and Sloan (1978b, Campbell 1975) added a spatial component to this model to explain why high density gypsy moth populations may persist for many years. They suggested that individual populations, on the scale of a few ha, may collapse to low densities within one or two generations after attaining outbreak phase. On a regional scale (many 100 ha), however, populations rise and collapse asynchronously, and first instar larvae

dispersing from high density populations elicit outbreaks in surrounding stands. High density populations across the region are thus maintained for ca. one decade.

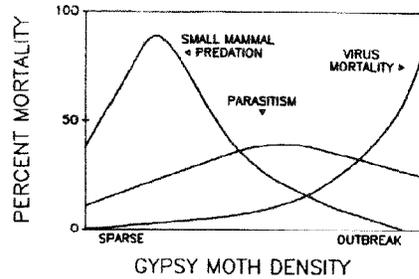


Fig. 1. Hypothetical percent mortality caused by the principal mortality agents maintaining bimodal stability in gypsy moth populations in North America (redrawn from Campbell 1975, Berryman et al. 1987)

Since 1984, we have conducted field studies aimed at testing various aspects of this model. We have followed gypsy moth populations on three permanent plots on Cape Cod, Massachusetts. Each year we monitored changes in gypsy moth density throughout its life cycle. Measuring gypsy moth larval density is difficult because the larvae are highly mobile and a variable proportion of them seek daytime resting locations in the litter. After evaluating several approaches, we settled on density estimates based on counts of frass particles (Liebhold and Eikinton 1988a,b). The method entails making counts of the number of frass particles falling per m^2 into large plastic funnels during an overnight sampling period while simultaneously measuring the number of particles produced per individual larva over the same interval. The ratio of these two measures constitutes an estimate of the number of larvae per m^2 . Pupal and egg mass counts are made within and above fixed-radius sample plots. Neonates per egg mass are determined by collection and rearing. With these techniques, we have been able to generate survivorship curves (Fig. 2.) which illustrate that the predominant mortality occurs during the late larval and pupal stages on these sites. These findings are entirely consistent with those of Campbell and Sloan (1977, Campbell et al. 1977).

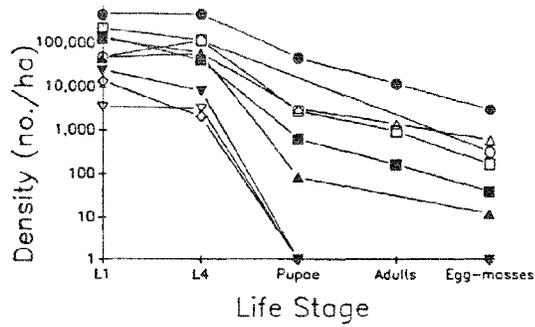


Figure 2. Survivorship curves for gypsy moth at three sites on Cape Cod, MA 1985-1987.

In order to estimate the impact of parasitism and disease, we made weekly collections of larvae and pupae from these plots and reared them individually in 30 ml cups on artificial diet in an outdoor insectary. We determined the proportion of these larvae that died from different sources of mortality over the subsequent week. Because the temperature conditions in the insectary approximated those that were experienced by the field populations, we believe that the mortality observed constitutes a reasonable estimate of the mortality caused by these agents in the field population during the same interval.

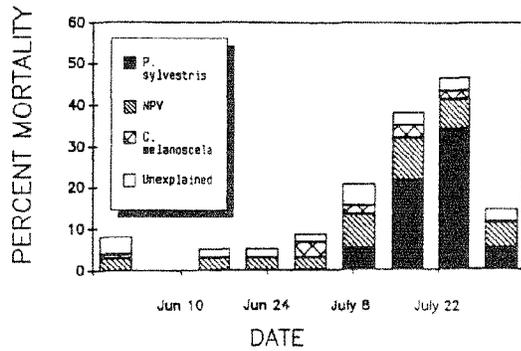


Figure 3. Proportion of gypsy moth larvae dying each week from various parasitoid spp. and disease in a low density population on Cape Cod, 1985.

Figure 3. Illustrates the temporal pattern of mortality from different agents that are characteristic of low density gypsy moth populations on these sites. Our results indicate that *Parasetigena sylvestris* always caused higher mortality than any other parasitoid when gypsy moth densities were low. *P. sylvestris* emerges from the late larval and pupal stages and accounts for part of the large drop in density that invariably occurs during this period (Fig. 2.). At high densities, other parasitoids become dominant, especially *Brachymeria intermedia* and *Blepharipa pratensis*. Of course, such rearings detect mortality from parasitism and disease but not from other agents, notably predators. The total mortality caused by these other agents is estimated from the fraction of the total decline in density which remained unaccounted for after measuring mortality due to disease and parasitoid emergence. This residual mortality is usually larger in magnitude than the total mortality caused by disease and parasitism during the late larval and pupal periods (Fig. 4).

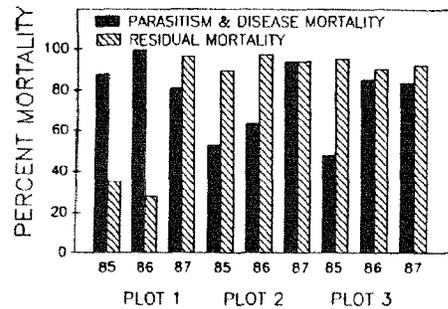


Fig. 4 Comparison of mortality of gypsy moths occurring between the fourth instar larva and pupal stages caused by parasitism plus disease versus residual mortality (which includes predation) at 3 sites on Cape Cod 1984 - 1987.

Because predation was obviously a major mortality factor, we initiated separate studies of the impact of avian and small mammal predation on these populations. Avian predation was studied in collaboration with T. Lloyd-Evans of Manomet Bird Observatory and R. Holmes of Dartmouth College. We obtained a detailed census of the density of the various breeding birds on our plots. We also determined what proportion were feeding on gypsy moth by examining gut contents from emetic treated birds captured in mist nets and by making direct field observations of bird feeding activity. The results of

these studies will be presented elsewhere (Elkinton et al. in prep.) but the conclusions were that, while many bird species fed on gypsy moth larvae to a small extent, they were not a major component of the diet of any of the common species on our plots. We suspect that the impact of avian predation on gypsy moth dynamics is minor.

Small mammal predation was studied by deploying pupae on burlap covered boards (Smith and Lautenschlager 1981) which were placed in the litter on our plots on Cape Cod and in western Massachusetts. In low density populations in North America, most gypsy moth pupae are found in the litter. We measured the daily rate of predation on these pupae by small mammals and by invertebrates, which were distinguished by the kind of feeding damage that we observed. We view the predation rates that we measure with this technique as an index of predation and not a direct measure of the predation on naturally occurring pupae because the latter would depend in part on the proportion of pupae that were located in protected sites above the litter. We also measured small mammal population density using mark recapture techniques and Sherman live traps. As Smith and Lautenschlager (1981) discovered, small mammal predation was much greater than invertebrate predation and *P. leucopus* was usually the most abundant insectivorous small mammal in our live traps. Furthermore, there was a strong positive correlation between total predation on these pupae and *P. leucopus* population density both on the Cape (Fig. 5A.) and western Massachusetts (Fig 5B.).

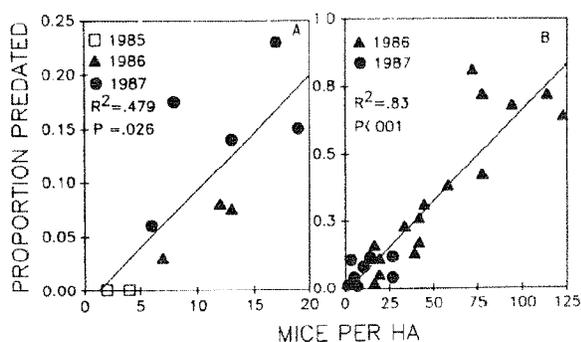


Fig. 5. Daily proportion of gypsy moth pupae consumed by vertebrate predators versus density of *P. leucopus* on A) 3 sites on Cape Cod and B) 16 sites in western Massachusetts.

EXPERIMENTAL MANIPULATION OF POPULATIONS

Thus far, the analyses of our life table data from Cape Cod support the conclusions of Campbell and Sloan (1977, Campbell et al. 1977). More detailed analyses will be presented elsewhere (Elkinton et al., in prep.). However, there has been much discussion in the recent ecological literature about the shortcomings of traditional studies of this type in which life tables are collected over a long series of generations and analyses such as those of Varley and Gradwell (1960, 1968) are applied. Acquisition of such data requires a substantial and long-term commitment of resources. Even so, selection of an inappropriate spatial scale on which to conduct the study (Heads and Lawton 1983, Hassell 1987) and a variety of statistical problems (e.g. Kuno 1971, Royama 1977) may obscure the identification of key factors and the operation of density dependent mortality. Several of these authors have advocated experimental manipulation of populations as an alternative or supplement to such life table studies. For this reason we have conducted a series of experiments which involve deploying different densities of gypsy moth egg masses on experimental plots and then collecting data on survivorship and sources of mortality. These studies have been conducted in western Massachusetts and on Cape Cod.

In 1987 we released field-collected gypsy moth egg masses onto eight 1 ha plots in western Massachusetts that had < 10 naturally occurring gypsy moth egg masses per ha. The plots were located in a region that had experienced extremely sparse populations for the previous five years. The eggs were released just before hatch which was timed to coincide with the hatch of naturally occurring egg masses and with bud break of the oak species on the sites. In this manner we created larval gypsy moth populations in four density categories, ranging from ca. 43,000 to 1,140,000 neonates per ha. The highest densities would be characteristic of outbreak populations, whereas the lower densities would be characteristic of non-defoliating, moderately low density populations. We monitored the change in larval density on these plots as the season progressed, using frass traps and counts under burlap bands and we collected larvae weekly from these plots and reared them on diet.

The resulting survivorship curves (Fig. 6) indicate that the populations on all sites collapsed to a very low level, especially in the highest density plots. Converting the total mortality to a k -value (Varley & Gradwell 1960) and regressing against LOG_{10} (neonate density) proved that the total mortality was density dependent (slope = 1.87 p = .004). Further details are provided in Gould et al. (1989). The principal agent responsible for this dramatic decline in density was the Tachinid parasitoid Comptosia concinnata. During the

late larval period, it caused more mortality than any other agent including residual mortality (i.e. predation). Of all the parasitoids it was the only one exhibiting significantly density dependent mortality. Unlike the other dominant larval parasitoids common on gypsy moth in North America, *C. concinnata* has many alternate hosts. This fact may explain why it was present in large numbers in the experimental region even though gypsy moth populations in the area had been very sparse for many years.

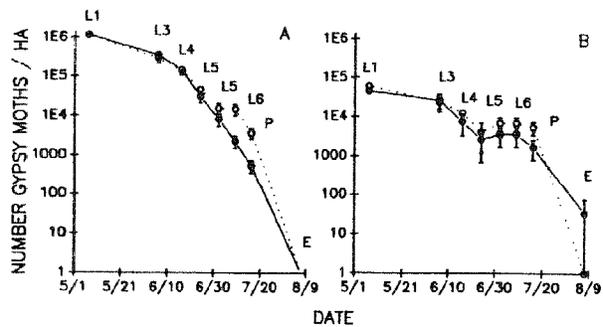


Figure 6. Survivorship curves obtained from A) two high density and B) two low density gypsy moth populations created on 1 ha plots in western Massachusetts by releasing field collected egg masses. Four other plots of intermediate initial densities showed similar patterns of survivorship that were intermediate between those shown here. For details see Gould et al. 1989.

In contrast, *Parasetigena sylvestris*, a gypsy moth specialist, showed inversely density dependent attack rates (based on the proportion of larvae bearing the large macrotype eggs of this Tachinid) during mid-larval instars but this pattern switched to positive density dependence during late larval instars. We think that the most likely explanation for this result is that more *P. sylvestris* aggregated in the high density plots compared to the low density plots but initially the numbers of larvae in the high density plots was so much higher that percent mortality was inversely density dependent. However, as larval density declined markedly during the late larval stages, the higher number of *P. sylvestris* females in the high density plots were able to cause density dependent mortality. The mortality caused by *Cotesia melanoscela* was density independent and whereas *Phobocampe disparis* mortality was inversely density dependent. Despite the large amount of mortality observed

from parasitoids during the larval stages, the largest rate of mortality (hence k values, illustrated by the slope of the survivorship curve in Figure 6) occurred between the late larval and adult stages (based on subsequent egg mass counts). We found no evidence of pupal parasitism and the results of experiments involving deployed pupae in these plots (Gould et al. 1989) suggest that small mammal predation was the principal source of mortality during this period. This finding was consistent with our results on Cape Cod (Fig. 2) and the earlier conclusions of Campbell and Sloan (1977, Campbell et al. 1977).

In 1987 we performed similar experiments on Cape Cod, Massachusetts. The results of these trials are presented in Liebhold and Elkinton (1989). The findings were much the same as those from western Massachusetts. We witnessed the same elevated levels of parasitism in the 1 ha plots in which we had released large numbers of neonate gypsy moths compared to plots which were not manipulated and which contained much lower gypsy moth densities. Sandra Wilmot and collaborators (Tom O'Dell, personal communication) have obtained similar results in Vermont. All of these studies indicate that parasitoids, particularly *C. concinnata*, can respond to local increases in gypsy moth density in a strongly density dependent fashion and may play a role in suppressing incipient outbreaks.

With these experiments we have demonstrated strong spatially density dependent responses. Whether spatially density dependent responses translate into temporal density dependence and can stabilize a host population is matter of debate in the recent ecological literature (Hassell 1985, 1986, Dempster and Pollard 1986). Temporal density dependent parasitism occurs when percentage parasitism increases with increasing host density in a single population over a series of host generations. Typically this occurs because the number of parasitoids surviving to the next generation increases with increasing host density. In systems with discrete generations it is usually expressed as delayed density dependence in which highest values of percent parasitism occur one or two generations after the host population densities have declined from peak levels. At present we have little evidence for such a response for gypsy moth parasitoids in North America. Several of the dominant species face severe constraints that would limit between-generational increases. For instance, *C. concinnata* has obligate alternate hosts whose abundance may limit any such response to changes in gypsy moth density (Culver 1919). *C. melanoscela* is severely limited by hyper-parasitoids (Weseloh 1978). Other species only become a significant source of mortality in high density gypsy moth populations, for example *B. pratensis* and *B. intermedia*, and are therefore unlikely to play an

important role in maintaining the apparent stability of low density gypsy moth populations. Of the major gypsy moth parasitoids that are abundant at low density, only *P. sylvestris* appears to be a major candidate for unconstrained generation to generation numerical response to gypsy moth. At present, we have insufficient information to say whether this parasitoid shows such delayed density dependent responses in North American gypsy moth populations. Evidence from European populations suggest, however, that this parasitoid may play an important regulatory role in European gypsy moth populations (Montgomery and Wallner 1989).

The importance to gypsy moth population dynamics of the strong spatially density dependent parasitism that we have demonstrated remains to be determined. The levels of parasitism by *C. concinnata* that we observed in the artificially elevated populations on Cape Cod far exceeded the levels we have ever observed in any of the naturally occurring populations over a large range of gypsy moth densities in our nearby, permanent life-table plots. We suspect that the most likely explanation of this result is that a high density population on a small spatial scale (1 ha) surrounded by a large region in which gypsy moth densities are very low, elicits aggregation by large numbers of *C. concinnata*. In contrast, when gypsy moth populations increase over a much larger area, the aggregation of *C. concinnata* into any one stand would be much less pronounced. Consequently, we think that the ability of spatially density dependent parasitism to regulate low density gypsy moth populations and to decimate incipient outbreaks probably depends on the spatial scale on which such populations are synchronized. If gypsy moth densities increase simultaneously over a large region, parasitoid aggregation is probably of little consequence. If, on the other hand, gypsy moth populations increase on the scale of an individual stand, spatially density dependent parasitism may play a very important regulatory role.

IS SMALL MAMMAL PREDATION DENSITY DEPENDENT?

We have demonstrated experimentally that parasitoids can exert strong spatially density dependent mortality on gypsy moth populations. What about small mammal predation? The model of Campbell (1975, Fig.1) requires that small mammal predation show positive density dependence in low density gypsy moth populations.

Let us consider the manner in which a generalist predator such as *Peromyscus leucopus* could regulate a prey population (i.e. cause density dependent mortality). A very basic idea in population ecology is

that density dependent predation (or parasitism) can arise from two sources: the numerical and functional responses. (Solomon 1949, Holling 1959, 1965). The numerical response is an increase in the density of the predator or parasitoid in response to the increasing prey density. It may arise from an increase in fecundity or survival of predators or parasitoids due to increasing prey density or it may arise from aggregation of predators or parasitoids into a region of high host density. The functional response is an increase in the number of prey consumed or parasitized by each individual predator or parasitoid due to an increase in prey density. We believe that it is unlikely that a long lived generalist predator such as *P. leucopus* will show much if any numerical response to increases in gypsy moth density. There is considerable evidence that increases in food supply can have an effect on *P. leucopus* density, but usually it includes overwintering food supply (Smith and Lautenschlager 1981). Late instar gypsy moth larvae and pupae represent an ephemeral food resource that occurs when other food supplies are plentiful. We therefore believe that increases in gypsy moth density will have little impact on *P. leucopus* survival or reproduction. Furthermore, previous work has shown that gypsy moth pupae are not highly preferred over other common food sources (Smith and Lautenschlager 1974). Because *P. leucopus* occupies specific home ranges of limited size (ca. 0.1 ha, Sticker 1968) we think there will be little if any aggregation of this small mammal into areas of high gypsy moth density.

Density dependent small mammal predation, if it occurs at all, probably arises from a functional response. As intelligent predators with a high capacity for learning, they are likely to exhibit a type III functional response (Holling 1959, 1965) caused by switching to gypsy moth from other food sources or by learning to forage specifically for gypsy moth in response to an increase in gypsy moth density (Fig. 7C,D). This change in foraging activity may include aggregation to clumps of high host density within the home range of the small mammal. Thus, aggregation (but on different spatial scales) may contribute to both the functional and numerical response. In the absence of such learning or changes in foraging activity, we would expect the functional response to be type II, in which the number of prey consumed per predator increases with prey density at a steadily decreasing rate (Fig. 7A,B). The importance of type II versus type III responses is that the functional response is density dependent only during the accelerating, low density phase of the type III response. Ultimately, all predators have a limited capacity for consumption, so both type II and type III functional responses approach an upper asymptote. In other words, even the type III functional response is

ultimately inversely density dependent and therefore destabilizing at densities above the threshold defined by the point of inflection in the type III sigmoid curve. This fact explains the central feature of the Campbell model: at some low - intermediate density, there exists a threshold above which total mortality is inversely density dependent and gypsy moth populations grow without check into outbreak phase. Note the similarity between percent predation indicated in Fig. 7D and that due to small mammal predation in Fig. 1.

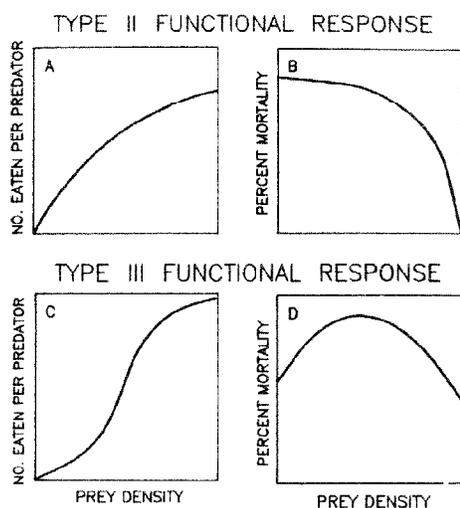


Figure 7. Hypothetical number and corresponding percentage of prey consumed as a function of prey density in Holling's (1959) Type II (A,B) and Type III (C,D) functional responses.

In our studies of predation rates on pupae on Cape Cod (Fig. 8A) we deployed pupae in populations with naturally occurring populations of different densities. The results of these and similar experiments in the artificially created populations in Western Massachusetts (Fig. 8B), indicate inverse density dependent predation. Similarly total mortality during the period from fourth instar to pupae in the populations on Cape Cod was also inversely density dependent (Fig. 2). These findings are consistent Campbell's model which predicts inverse density dependence in the range of densities above the low density equilibrium point.

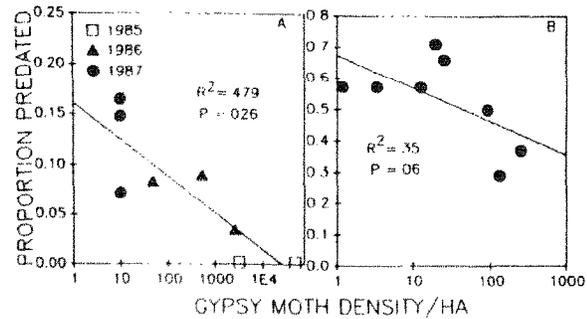


Figure 8. Proportion of pupae predated by vertebrate predators versus density of naturally occurring pupae on A) 3 sites on Cape Cod 1985-1987 and B) on the eight experimentally created populations in western Massachusetts, 1987.

To examine the relation between pupal density and predation more closely we conducted the following experiment. Along a 5 km transect in oak forests near the Quabbin Reservoir in western Massachusetts we deployed laboratory reared pupae in 1 m x 1 m and 20 m x 20 m plots. Plots were located at intervals of ca. 100 m. Gypsy moth pupae attached to small squares of burlap were placed in the litter in these plots. Each plot was stocked with a number of gypsy moth pupae ranging from 3 - 400 per plot. We compared the predation rates by small mammals on these pupae to that experienced by single pupae deployed at least 50 m from the nearest plot with multiple pupae. We ran this experiment 3 times in late summer after any naturally occurring pupae had enclosed in a region that had had extremely sparse gypsy moth populations for the previous 5 years. The results (Fig. 9) indicate no evidence for positive density dependent predation at any level of density and the expected inverse density dependence at higher densities presumably due to predator satiation. We have conducted similar experiments involving pupae deployed over longer time periods and on larger spatial scales. The results of these experiments will be presented elsewhere but the conclusions were the same. We found no evidence for positive density dependent predation by small mammals. On the other hand, Smith (1985, this volume) deployed pupae in replicated plots in three 2 ha sites at densities of 237, 712 and 2491 pupae per ha. He found a significantly higher rate of predation at the two high density sites compared to the low density site. Whether this result was due to the differences in gypsy moth density between the sites or other factors we do not know. Obviously, more

work needs to be done to determine whether or not small mammal predation is positively density dependent over the lower range of gypsy moth density.

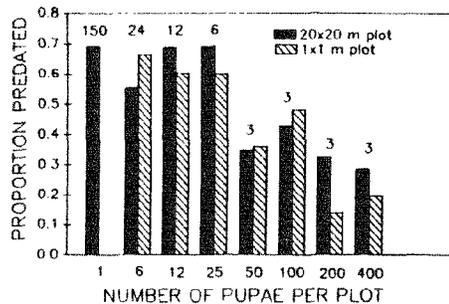


Figure 9. Proportion of gypsy moth pupae deployed in 1 X 1 m and 20 X 20 m plots that were consumed by vertebrate predators over three day test periods. Numbers above each bar indicate number of replicates conducted at each density.

In conclusion, our studies indicate that small mammal predation is probably the key mortality factor in the populations we have studied. It causes greater stage specific mortality than any other source of mortality and it varies greatly from year to year and place to place. The variation in predation could easily cause variation in the number of female pupae surviving to the next generation by several orders of magnitude.

Our results provide strong support for the notion that small mammal predation is inversely density dependent at higher levels of gypsy moth density as Campbell's model suggests (Fig. 1). However, we do not have firm evidence that small mammal predation is positively density dependent at lower levels of gypsy moth density. We would not be surprised if future research demonstrates some level of type III functional response to gypsy moth pupae in these predators. However, we believe that such a response, if it occurs, will probably be small in comparison to the many things that cause variability in small mammal predation. Examine, for instance, the enormous changes in small mammal density and predation that we observed between 1986 and 1987 at our sites in western Massachusetts (Fig. 5B). Not only does small mammal population density vary greatly, but so does the availability of alternate foods which can also have a dramatic impact on predation rates, as the research of H.R. Smith (this volume) clearly

indicates. At best, small mammal predation on low density populations is extremely density vague (sensu Strong 1984); so vague in fact that it may be essentially indistinguishable from density independent predation. Indeed, we think it is entirely possible that low density gypsy moth populations may not be regulated at all. At low densities, mortality from small mammal predators is extremely high so that most populations experience little net growth. We agree with the arguments of Morrison and Barbosa (1987), Murdoch et al. (1985), and others, that such populations, fluctuating asynchronously and coupled by dispersal, may show apparent stability on a regional scale. These arguments constitute a low density analogue to the spatial model of Campbell and Sloan (1978b) for high density gypsy moth populations.

SUMMARY

Gypsy moth life table studies conducted on Cape Cod, Massachusetts, supported the conclusions of Campbell and Sloan (1977, Campbell et al. 1977) that the predominant mortality in gypsy moth populations was predation occurring during late larval and pupal stages. P. leucopus appeared to be the dominant source of predation and predation rates were highly correlated with P. leucopus density. However, predation by P. leucopus was inversely density dependent. We saw no evidence for a type III functional response or for positive density dependence at low gypsy moth density as predicted by the model of bimodal stability in gypsy moth populations proposed by Campbell and Sloan (1978a).

In additional experiments, we created artificial populations of gypsy moth on 1 ha plots on Cape Cod and in western Massachusetts by releasing different densities of field collected egg masses. We observed a dramatic collapse of all these populations caused primarily by density dependent parasitism from C. concinnata. These findings suggest that spatially density dependent parasitism by this species (and perhaps P. sylvestris) may play an important role in regulating low density populations. The importance of this phenomenon to gypsy moth population dynamics remains to be determined and we believe that it depends on the degree to which changes in gypsy moth population density are synchronized over a large area. We think it is possible that low density gypsy moth populations are not regulated but fluctuate asynchronously which, coupled with dispersal, leads to apparent stability on a regional scale.

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