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General Technical
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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
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March 1989

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

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PATHOGENIC VIRUSES AND BACTERIA
OF THE NUN MOTH (LYMANTRIA
MONACHA L.) DURING THE OUTBREAK
1978 - 1984 IN POLAND

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INTRODUCTION

The nun moth (Lymantria monacha L.), one of the most dangerous forest pests, is a polyphage feeding on pine, spruce and other coniferous trees, on deciduous trees and shrubs and on forest ground cover plants. Its outbreaks, being a mortal threat to the forest, are known in many countries in Europe. In Poland, in the years 1946-75, the nun moth was controlled 25 times, thus almost every year, on a total area of 113,000 ha. In the years 1978-84, during the greatest outbreak in the history of forestry, the total area where the nun moth was controlled reached more than 3 million ha.

Many factors contributed to the expansion of the pest on a scale now known to this time. Well developed in this species is its migration ability, high biological potential and reproductiveness of population. Lack of effective control in the first years of the outbreak resulted in the insect appearing from year to year in new locations, finally threatening stands on almost 40% of the total forest area in the country.

In the rich literature concerning mass appearances of the nun moth, especially in stands of central Europe, there are many descriptions of the nuclear polyhedrosis virus (Wipfelkrankheit, tree-top disease), causing rapid epizootics and considered in the 19th and the first half of the 20th century as the main factor limiting the pest outbreaks (Esherich & Miyajima, 1911; Komarek & Briendl, 1924; Tyniecki, 1891).

In Poland, the nuclear polyhedrosis virus of the nun moth was last observed in the years 1951-52. During later mass appearances of this pest (Fig. 1) in the years 1956-60, 1962-69 and 1970-75, no viral diseases were observed.

In the years 1970-72, Slizynski (1974), performed studies on activation of the latent form of virus in larvae from several outbreak centres. Use of chemical stressors, X-rays and ultraviolet radiation did not give positive effects. For unexplained reasons the tree-top disease stopped playing any role during outbreaks and one did not manage to find it in the period of 30 years. In the late seventies, at a very high population density where they never occurred before (reaching several dozen thousand larvae per tree), studies were started on epizootic diseases of the pest and on the influence of some factors on the induction of

Baculovirus efficiens. An evaluation was also made on possibilities of controlling the nun moth with the use of biological insecticides containing B. efficiens and Bacillus thuringiensis.

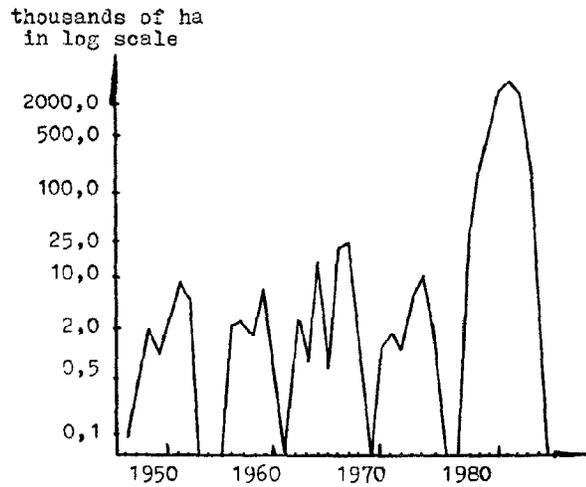


Fig.1 Area of the nun moth control in the years 1946 - 1984

Figure 1. Area of the nun moth control in the year 1946-1984.

METHODS

Viruses and bacteria evoking epizootic diseases of the nun moth were studied on:

- larvae hatched in laboratory and bred on culture medium
- diseased larvae sent to the laboratory from the forest districts
- larvae dying in stands in natural conditions

Possibility of the control of the nun moth with the use of B. efficiens and B. thuringiensis was studied on:

- larvae collected in pine stands and bred in the laboratory on medium or placed on 5-year-old pine trees
- larvae living in natural conditions in pine stands - Pinus

sylvestris L. or mixed pine-spruce stands; Pinus sylvestris + Picea abies Link.

V i r a l D i s e a s e s

In the years 1981-84, in June and July, trained workers of the forest administration noted the appearance of nuclear polyhedrosis virus in the nun moth populations.

In chosen stands where the virosis was occurring, we collected materials for microscopic analyses and observed in few day intervals the development of the disease and the rate of dying of the larvae.

The studies on the structure of polyhedra and measurement of virions were made by Dr. J. Ziemnicka from the Institute of Plant Protection in Poznan.

B a c t e r i a l D i s e a s e s

Pathogenic bacteria of the nun moth were studied in the years 1980-81. In July, materials were sent to the laboratory from forest districts where epizootics developed in late larval instars feeding on pine. After elimination of decaying material and parasitized larvae, we chose several live specimens from each sample and analyzed microscopically their hemolymph. In the case of finding bacteria in the body cavity of diseased larvae or pupae the bacteria were isolated from the hemolymph and identified by their morphological, cultural and physiological features, according to Bergey (1957) and Gibbs & Skinner (1966).

Mortality of Larvae and Induction of Latent B. efficiens in the Laboratory

In the years 1982-84, we studied the dependence of the total mortality of larvae and of the induction of the virus on three factors:

- density of larvae in laboratory breeding
- duration of the mass appearance in a given area
- population density of the pest in a stand expressed with the number of eggs found on one tree up to 2 m in height; the population density index was divided into three classes: 200-500 eggs in a sample; 501-1000 eggs, more than 1000 eggs.

In chosen stands with different stage of the outbreak and intensity of appearance of the pest, workers of forest districts searched out every year in January and February (using a uniform method) eggs on six trees and sent the eggs to the laboratory. From samples of eggs received from each forest district, we chose, if it was possible, three samples: from the trees on which 200-500 eggs were found, from trees on which 501-1000 eggs were found, and from trees on which more than 1000 eggs were found.

To eliminate vertical transmission of the virus on the surface of the chorion, the eggs were sterilized for 5 minutes in 6% formaldehyde and then washed five times in sterile water.

Hatched larvae were bred in three densities: 5, 25 and 50 specimens per glass flask of 100 ml volume, containing 20 ml of diet (Leonard & Doane, 1966). The percent mortality of the larvae and the frequency of *B. efficiens* were determined during the 3 weeks of breeding. To avoid transmission of the virus from flask to flask, the brushes used for taking out dead larvae were sterilized for 5-7 minutes in 3% chloramine after each use. If samples from one forest district contained similar numbers of eggs, two samples were taken for breeding and the larvae were bred in one density -- 50 specimens per flask.

Results were recorded taking into consideration the year of the outbreak. They were statistically evaluated with the use of three-factorial analysis of variance and by Tukey's test. The percentage distribution of the mortality was brought to the normal distribution through transformation $y' = 2 \text{ arc sin } \sqrt{y}$.

Control with the Use of *B. efficiens*

The evaluation of the virulence of *B. efficiens* to the larvae was made under laboratory and field conditions. The LT_{50} was calculated after the method of Litchfield and Wilcoxon (Slizynski & Lipa, 1973).

In the laboratory, the larvae were bred in flasks on diet mixed with standardized suspensions of polyhedra in order to get 5×10^4 , 5×10^5 , 5×10^6 , and 5×10^7 PIB/ml diet.

In field conditions, the larvae developed on 5-year-old pine trees which were sprayed (5 ml/tree) with polyhedra suspensions in concentrations of 5×10^5 , 5×10^6 , and 5×10^7 PIB/ml.

Moreover, we performed three trials of controlling larvae with the use of *B. efficiens* products prepared in the laboratory. The stands were sprayed by helicopters, at a volume of 100 l/ha. The reduction of the number of larvae was calculated according to Abbott's formula as modified by Schwerdtfeger (Glowacka-Pilot, 1986).

The first and second trials were performed in the years 1979-1980 in the Szczytno forest district. Five and 8 ha of 40-50 year-old pine stands were sprayed at 5×10^7 and 3×10^7 PIB/ml. The product was obtained from larvae bred on pine twigs sprayed with suspension of polyhedra (5×10^7 PIB/ml), kindly delivered by Dr. Edwin Donnabauer from the Federal Forest Research Institute in Vienna.

The third trial was carried out in 1983 in the Kudypy forest district. Mixed pine-spruce stand (4 ha, 60-year-old) was sprayed

with a product obtained from larvae collected in the Swidwin forest district, where the nun moth was dying as a result of endemic B. efficiens.

Control with the use of B. thuringiensis

In the years 1978-84 the microbial treatments were performed in pine or mixed (pine-spruce and pine-deciduous) stands where, because of environment protection, chemical insecticides were not applied. The stands were sprayed from helicopters and planes with imported and home B. thuringiensis products in doses of 0.75-2 kg in suspension quantities of 2-100 l/ha.

RESULTS AND DISCUSSION

Viral Diseases

In 1981, viroses were found in 32 forest districts. Observations of epizootics showed that the polyhedrosis was developing in third to fifth stage larvae, feeding mainly on spruce and larch. Numerous Sarcophagidae flying intensively among diseased and dying caterpillars were observed. Like in the observations made by Wellenstein (1942), warm and sunny weather contributed considerably to the development of epizootics.

The dead larvae were filled with triangular and hexagonal polyhedra. Bacilliform virions of 375-406 nm length and 36-48 nm diameter were immersed in the protein of polyhedra, in bunches of 1-15 pieces. On this basis, we acknowledged Baculovirus efficiens as the cause of viral diseases.

In 1982, viral epizootics were observed in 26 forest districts, in 1983 in 9 forest districts. Previous observations that the viral disease develops only in larvae feeding on spruce and larch have been confirmed. Besides typical cases of dying third to fifth stage larvae, dead first and second stage larvae were found. In 1984, the last year of outbreak, no viral diseases were observed in natural populations.

European forest literature concerning calamities of the nun moth in the 19th and first half of the 20th centuries contains many data giving evidence to an essential role of virus in suppression of the pest. The epizootics developed in cases of mass appearance of the nun moth on spruce, which was at that time the main food for larvae. Together with the reconstruction of stands and introduction of pine into larger and larger areas, the nun moth attacked the new host plant, but the larvae feeding on pine did not suffer viroses.

In the territory of Poland, the nun moth finally changed host plant in the fifties. Outbreaks that took place in the years 1946-52 in the pine-spruce stands were ended by viral epizootics in the northeastern part of the country. In the succeeding 30 years,

three outbreaks developed only in pine stands, and the larvae were free of polyhedrosis. However, *B. efficiens* survived in the nun moth and was observed during the last outbreak, when the insect occurred in immense quantities and came back to the spruce host. At first, in the years 1978-80, we observed cases when among pine trees with completely damaged needles, green intact spruce trees remained as "unsuitable" food for the pest. After that, in the years 1981-82, the nun moth partly damaged spruce in the northern part of Poland and in the same time viral epizootics commonly developed in spruce stands and on spruce undergrowth in pine stands.

Results suggest that *B. efficiens* is present in the latent form in the nun moth populations, but unknown components of pine needles protect the larvae against the induction of the virus into acute form. On other host plants (spruce, larch) latent *B. efficiens* becomes active in the larvae and, by horizontal transmissions, leads to the development of epizootics. When pine twigs were cut from a tree and kept for several days in water their needles lost the value as an inhibitor of virus induction. *B. efficiens* expresses itself in larvae bred on such twigs and acts similarly as on spruce.

It is difficult to say which group of components of pine needles is the factor inhibiting the induction of the virus. One of the differences between the pine needles and those of spruce is the quantitative content of volatile oils. Pine needles contain about 7 times more of them than spruce needles. To explain the inhibition of *B. efficiens* in larvae living on pine trees, special biochemical and physiological studies are required.

B a c t e r i a l D i s e a s e s

In the years 1980-81, we analysed 196 samples of diseased insects from heavy damaged pine stands. In June and July, in 51 forest districts, great quantities of diseased and dead larvae were present on the ground around the stems. Also, some larvae dying in the crown were observed. After the first evaluation of the material, 36 samples were rejected because they contained larvae and pupae attacked by *Tachinidae* or were in the state of decaying. In the other 160 samples mobile bacterial cells were observed in the hemolymph of examined insects. After identification, they appeared to belong to *Enterobacter cloacae*, *E. acrogenes*, *Proteus vulgaris* and *Pseudomonas fluorescens*.

Mentioned bacteria are the group of potential pathogens living in the environment and in the alimentary canal of insects (Bucher, 1960). In the case of excessive density of insects their defensive mechanisms can be weakened and the intestinal saprophytic bacteria becomes virulent. In most cases the food deficiency is the stressor that weakens the insects, although the death of the larvae was also observed in stands, where the crowns kept 40-50% of the needles, thus the insects had the possibility of feeding. Maybe, in partly damaged trees, the foliage changed the biochemical features unfavourably for the nun moth and that was the reason of

the reduction of resistance of caterpillars to intestinal microflora.

Bacterial epizootics observed in the years 1980-81 in several dozen forest districts had a small range, they occurred in patches of several hectares in pine stands. In 1982, when the efficacy of chemical control was in general high and in stands surrounding waters, *B. thuringiensis* products were applied; bacterioses were only sporadically observed. The practical importance of bacterial diseases was not great. One can consider them as an interesting example of the mechanism of restoration of balance in the forest environment. In case of food limitation, when number of insects excessively increased, they lose their resistance and die as a consequence of increased virulence of their own bacterial flora.

D i s e a s e s o f U n e x p l a i n e d E t i o l o g y

When larvae dying in natural conditions were observed, the occurrence of a disease was manifested by the lack of appetite, cessation of feeding, and drying up of the body. Analyses of internal organs did not reveal the presence of microorganisms distinguishable under the light microscope, but they showed changes in the alimentary canal and the presence of numerous brown melanin granulations in the cells of the mid-gut. When healthy larvae were infected with water filtrates of "drying up" individuals, experiments did not give positive results, which would suggest the non-infectious character of the disease.

The "drying-up" connected with the presence of melanin granulations in the mid-gut was also frequently observed in populations of larvae bred on diet in laboratory (Table 1). The analysis of variance (Table 2) and the Tukey's test showed a significant relation between that mortality and:

- the increase of density in breeding (Fig. 2)
- the duration of the mass appearance (Fig. 3)

In the literature, there are only mentions on the high mortality of insects caused by other factors than microorganisms. Campbell and Podgwaite (1971) published results of investigations on the complex of diseases of the gypsy moth. They suspected an unknown factor, physiological in nature, which was a frequent cause of the death of young caterpillars in oak stands in Connecticut. Physiological weakness of the larvae and decrease in number of the nun moth during an outbreak in Austria is described by Jahn (1968). An unexpected breakdown of an appearance of the nun moth in Holland in 1986 also was not connected with the occurrence of infectious diseases (Steijlen et al., 1987).

Most studies concerning diseases of insects deal with infections caused by microorganisms. These infections are easier to detect than disturbances in the functioning of organs. One estimates that about 30% of insects examined in laboratories of insect pathology die as a consequence of diseases not connected with the microorganism (Steinhaus, 1963). Because of insufficient knowledge of the physiology and biochemistry of insects which are

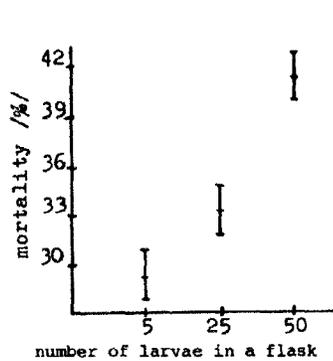
Table 1. Mortality of the nun moth and frequency of *B. efficiens* in the years 1982-84 (put together according to years of the outbreak)

Year of the outbreak	Larvae	Eggs in sample < 500			Eggs in sample 501-1000			Eggs in sample > 1000		
		5	25	50	5	25	50	5	25	50
I	Total	150	125	425	175	175	350	50	50	150
	% dead	21.3	24.8	33.65	21.71	26.28	26.85	18.0	22.0	24.66
	% <i>B. efficiens</i>	-	-	0.47	1.14	0.6	0.28	2.0	-	2.66
II	Total	300	300	2300	200	200	1850	250	250	2700
	% dead	20.0	22.66	25.56	27.0	22.5	34.0	21.2	25.6	31.18
	% <i>B. efficiens</i>	1.33	0.66	0.86	1.0	0.5	0.54	3.2	2.4	2.96
III	Total	400	400	4900	200	200	2150	600	600	3400
	% dead	19.75	24.5	40.08	29.5	35.0	41.53	26.66	23.5	45.14
	% <i>B. efficiens</i>	0.5	0.25	0.47	0.5	-	0.51	1.83	0.83	2.85
IV	Total	450	450	3050	50	50	750	200	200	800
	% dead	32.44	38.44	51.8	24.0	36.0	44.13	36.5	42.5	48.0
	% <i>B. efficiens</i>	0.22	-	0.36	-	-	0.4	2.5	1.5	3.12
V	Total	50	50	475	50	50	200	25	25	50
	% dead	56.0	42.0	55.79	42.0	60.0	63.0	48.0	64.0	62.0
	% <i>B. efficiens</i>	-	-	-	-	-	-	4.0	-	2.0

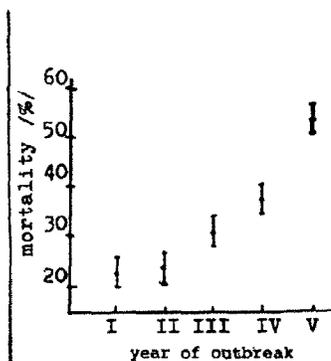
Table 2. Analysis of variance of total mortality of the nun moth in laboratory in the years 1982-84.

Source of variation	Degrees of freedom	Mean square	F theor. significance
a - density	2	574.9998	21.325xx
b - number of eggs	2	17.2377	0.639
c - year of mass appearance	4	1400.3549	51.935xx
Error	36	26.9638	-
Total	44	176.2857	-

xx = significance level $\alpha = 0.01$



5-25, 5-50, 25-50
significance of differences
at $\alpha = 0.05$



I-III I-IV I-V }
II-III II-IV II-V } significance
III-IV III-V IV-V } of differences
at $\alpha = 0.05$

Fig. 2. Total mortality of the nun moth in dependence on density.

Fig. 3. Total mortality of the nun moth in dependence on the year of outbreak.

necessary for the determination of the kinds of disturbances in normal metabolic processes, the non-infectious diseases are little known and studies on them are reluctantly undertaken.

Induction of Latent B. efficiens in the Laboratory

In 1982, we bred in flasks with diet 15,000 larvae originating from 152 samples of eggs collected in 50 forest districts. During 3 weeks of breeding, 4,753 (31.47%) of the larvae died. B. efficiens was observed in 260 cases; i.e., in 1.72%. In 1983, 13,625 larvae from 136 samples of eggs sent from 49 forest districts were bred. During 3 weeks, 5,944 (43.62%) larvae died; B. efficiens was observed in 103 (0.75%) cases. In 1984, the mass appearance of larvae was ending and from seven forest districts only small numbers of eggs were obtained. We bred 1,100 larvae, from which 500 (45.45%) died during 3 weeks, and viruses were found in 8 (0.72%) cases. Totally, from among 30,000 larvae bred on diet, the polyhedrosis developed in 371 larvae, amounting to 1.24%. Taking into account that the eggs for breeding were collected in pine stands, where the viruses did not occur in the previous generation of the insects and that the eggs were superficially sterilized, we can consider that the viral diseases in the first 3 weeks of breeding were caused by the induction of the latent form of B. efficiens.

The induction of B. efficiens proved to be significantly dependent on:

- the number of eggs on a tree; virus was most frequently revealed in larvae from samples containing more than 1000 eggs (Fig. 4);
- the year of duration of the mass appearance; the virus was most frequently found in the second year (Fig. 5);
- the breeding density; the virus was least frequently found in flasks containing 25 larvae (Table 3). Increased viral induction was connected with higher number of eggs in a sample, which suggests that the surpassing of a threshold population density causes an increase of the induction of latent B. efficiens in nature.

It is a characteristic fact that the highest frequency of B. efficiens occurred in 1982, when the mean number of eggs in samples was highest. In the later years, the induction decreased, which could be partly connected with the fact that the material for a breeding was collected in areas where the nun moth was controlled with insecticides, and each year a drastic intervention into the run of the outbreak took place.

Control with the use of B. efficiens

Evaluated virulence of the virus for nun moth bred on diet proved that the rate of disease development expressed in LT_{50} values amounted to 8-16 days depending on the concentration of the virus (Fig. 6). In a similar evaluation made in field conditions on pine trees sprayed with the same concentrations of polyhedra the

virus proved to be weaker than on the medium and the LT_{50} values oscillated from 12 to 31 days (Fig. 7).

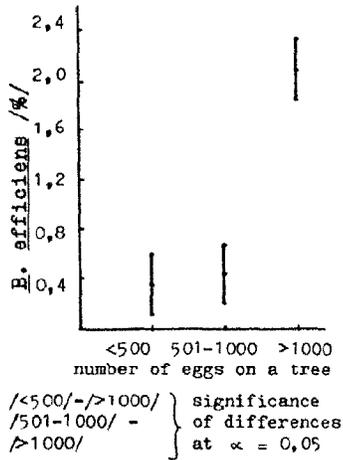


Fig. 4. Induction of *B. efficiens* in the nun moth depending on the number of eggs on a tree.

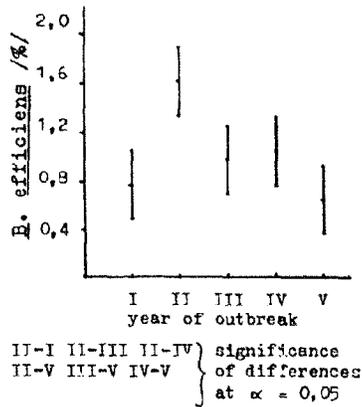


Fig. 5. Induction of *B. efficiens* in the nun moth depending on the year of outbreak.

Table 3. Analysis of variance of frequency of *B. efficiens* in laboratory in the years 1982-84.

Source of variation	Degrees of freedom	Mean square	F _{theor.} significance
a - density	2	3.1566	9.110xx
b - number of eggs	2	15.7831	45.552xx
c - year of mass appearance	4	1.0509	3.033x
Error	36	0.3465	
Total	44	1.2399	

xx = significance level $\alpha = 0.01$
 x = significance level $\alpha = 0.05$

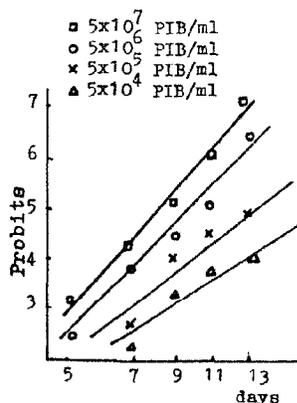


Fig. 6. Regressions of mortality of the nun moth at 4 concentrations of *B. efficiens* on diet.

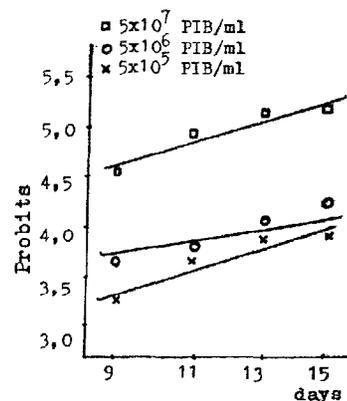


Fig. 7. Regressions of mortality of the nun moth at 3 concentrations of *B. efficiens* on pine trees.

LT_{50} values (8-16 days) obtained for the nun moth reared on diet with polyhedra of *B. efficiens* can be compared with LT_{50} (5-19 days) obtained for the gypsy moth (*L. dispar*) and *B. reprimens* (Doane, 1967) as well as LT_{50} (7.4-8.6 days) for the saw moth (*Leucoma salicis*) and *B. stlpanotiae* (Lameris et al., 1985). Such a comparison shows that *B. efficiens* is weaker than the viruses causing similar symptoms of nuclear polyhedrosis in other Lymantriidae.

In three aerial trials, performed in the years 1979-80 and 1983 to control the nun moth with the use of *B. efficiens*, the reduction of the population of caterpillars (after Abbots) reached up to 50%, 29-68%, and 32% for pine and to 82% for spruce.

In spite of the high doses of polyhedra ($1.5-3 \times 10^{12}$ PIB/ba), which were several times higher than doses used in control trials by other authors (Table 4), the reduction of the number of caterpillars was rather low.

Results obtained by Wellenstein (1973), Eidman (1976) and Zellner (1976) also show that the process of dying caused by *B. efficiens* in populations of larvae on pine is delayed or inhibited, whereas the mortality on spruce and larch appears earlier and reaches higher values.

In all described cases, the larvae fed intensively and caused visible damage in sprayed stands. No expansion of the virus in adjacent unsprayed stands was observed.

Because the virulence of B. efficiens is rather low and that the nun moth occurs now mainly on pine, which needles distinctly inhibit the development of polyhedrosis, one must state that the prospects of using the virus as a control product are little. B. efficiens can, however, regulate the number of the nun moth, inducing epizootics on spruce and larch.

Table 4. Aerial spray trials using B. efficiens to control the nun moth.

Country	Tree species	Dosage PIB/ha	Efficacy	Reference
West Germany	<u>Picea abies</u>	1.5 x 10 ¹²	1 week: mortality 84%	Wellenstein 1973
Sweden	<u>Pinus sylvestris Larix sp.</u>	6 x 10 ¹¹	2 weeks: epizootic on <u>Larix</u>	Eidman 1976
Denmark	<u>P. sylvestris Abies grandis P. abies</u>	8 x 10 ¹¹	2 weeks: epizootic on <u>Abies</u>	Zethner 1976
Denmark	<u>P. abies</u>	8 x 10 ¹⁰	4 weeks: epizootic on <u>Picea</u>	Zethner 1976

Control with the use of B. thuringiensis

In the years 1982-83, B. thuringiensis was applied in pine and mixed stands surrounding waters, recreation places and national parks, on a total area of about 46,000 ha. The mortality of larvae was differentiated and dependent on the insect density and on the species composition of the stands (Fig. 8). In pine stands, the efficacy of the treatments was as a rule higher than in mixed pine-spruce stands.

Different efficacy of control on pine and spruce resulted from varying crown coverage by the product. In the case of spruce trees with conical, long and dense crowns, even an increased dose of liquid up to 100 l/ha did not ensure sufficient coverage, and the efficacy of treatments often appeared to be unsatisfactory. In pine stands with umbrella-shaped tree crowns, good coverage was obtained at expenditure of 50 l liquid per ha.

SUMMARY

During the mass appearance of *Lymantria monacha* L. in Poland in the years 1978-84, studies on epizootic diseases of larvae and on the influence of some factors on the induction of the latent form of *Baculovirus efficiens* were conducted. Furthermore, possibilities of the pest control with the use of virus and *B. thuringiensis* were evaluated.

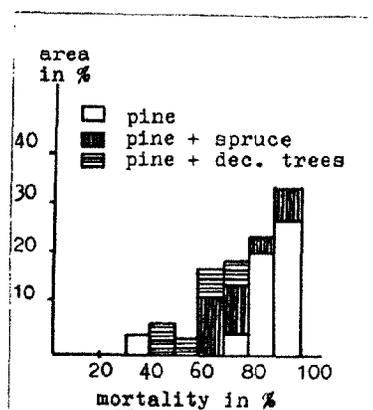


Fig. 8. Mortality of the nun moth after treatment with Bactospeine (1.2 kg/ha).

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**BACILLUS THURINGIENSIS IN THE MANAGEMENT
OF GYPSY MOTH POPULATION ERUPTIONS**

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INTRODUCTION

During the past 15-20 years the federal government of the United States, in a series of accelerated and expanded substantially-funded programs, has concentrated many scientist-years annually on efforts to improve our ability to manage the gypsy moth, *Lymantria dispar* (L). (Lepidoptera: Lymantriidae). Among the areas of investigation which have been pursued, research has attempted to expand the numbers of insecticides--both natural and synthetic--which are available for use, and to improve the technology associated with delivery of those pesticides. Success in these areas will permit us to protect our forests from damage and our people from excessive nuisance, to protect our environment from unnecessary insults, and to develop more effective and more efficient pest management capabilities. Many of these efforts are addressed in other contributions included in these *Proceedings*.

Two years ago in Ljubljana, Yugoslavia, I described the gypsy moth in the New World, briefly covering its history from its introduction into Medford, Massachusetts, in 1869 through its establishment and the expansion of its range to encompass northeastern, mid-Atlantic, and midwestern areas of the United States and adjacent parts of eastern Canada (Cameron, 1986). In that paper, I suggested that the geographic area infested by the gypsy moth would continue to expand (it has), that large-scale aerial spray programs would continue to be controversial (they are), and that such programs would become increasingly costly (that need not happen as quickly as I had feared only two years ago). I also reported, based on United States Department of Agriculture Forest Service figures, that the use of *Bacillus thuringiensis* (Bt) in cooperative suppression programs had decreased as a percentage of total hectares treated, from 79% in 1983 to only 38% in 1986. The preliminary figure for 1988 is 37% (personal communication, P. W. Orr, U.S. Dep. Agric., Forest Service, Broomall, PA), or essentially no change in the last two years; the total area treated in 1988, just over 300,000 hectares, was almost 30% more than in 1986. (The insect growth regulator, Dimilin[®], accounts for all but less than 1% of the remaining forested areas treated in these programs.) Bt is clearly the insecticide of choice in environmentally-sensitive situations, or areas such as National Parks or Monuments which are frequently used by people. The preference for Bt or Dimilin, or a combination of the two, for spraying large tracts of forest land varies from state to state, and undoubtedly reflects local political considerations as well as personal biases of those making decisions. Currently for the majority of such spraying, Dimilin is chosen more commonly than is Bt.

Studies conducted in 1987 and 1988, in both the United States and in Canada (Cameron and Fusco, 1987; van Frankenhuyzen *et al.*, 1988), give evidence that considerably smaller volumes of finished Bt spray per hectare than are normally used can be applied while still maintaining the efficacy of this insecticide. If spray volume can be reduced from what has been the practice in recent years, there are rather substantial economic implications. These would be expressed as reduced per-hectare costs of pesticide application if applicators can be persuaded to adopt technology which is already available.

Early attempts to control the gypsy moth through the application of insecticides relied on materials such as lead arsenate, a compound developed specifically for use against this forest defoliator (Burgess 1930) but later widely used against a number of agricultural pests. DDT was extensively used from the mid 1940's until environmental concerns about its persistence and its effects on non-target organisms arose in the 1960's; its registration was cancelled for most uses in the United States in 1972 (White *et al.*, 1981). During the 1960's and 1970's a number of new chemicals found their way into recommendations for control of *L. dispar*, including the carbamate Sevin® (carbaryl), the organophosphates Orthene® (acephate) and Dylox® (trichlorfon), and the insect growth regulator Dimilin® (diflubenzuron). A few other chemicals have been registered, but these were never widely used in pest control programs.

DEVELOPMENT OF BT FOR USE AGAINST THE GYPSY MOTH

It was not until the early 1960's that efforts began in earnest to develop Bt for use against this major forest defoliator, even though it had been known since 1929 that this pesticide kills the gypsy moth (Dubois, 1981). But field trials were characterized by erratic, inconsistent, and sometimes unpredictable results. Timing seemed to be critical, both as it related to the development of the larvae and to weather following application; if most larvae were beyond the second larval stadium, or if rainfall occurred within a day or two after application, results of spray programs were generally judged to be unsatisfactory. Early formulations were not as potent as those currently available, and in most cases two applications were needed if there was to be any hope at all of success. Needless to say, the logistics of repeated treatments, compounded by economic considerations, mitigated against enthusiastic acceptance of Bt as the pesticide of choice. Too often treatments 'failed'—they neither reduced the numbers of larvae adequately nor did they do it quickly enough; they did not protect foliage from further consumption; they did not reduce subsequent egg mass numbers to the (rather arbitrary) goal of 125 per hectare or fewer.

Early attempts to overcome the poor performance included increasing spray volume, if not dose; this was expected to improve coverage of foliage. Repeated applications were applied against successive cohorts of early instar larvae. Addition of selected adjuvants was expected to improve sticking to leaves, reduce evaporation during treatment, and extend the time during which

the insecticide was active after application (Lewis and Connola, 1965 (*in*: Dubois, 1981)). Feeding stimulants were added in later years.

New formulations, both water- and oil-based, continue to be developed and tested by commercial manufacturers of Bt in cooperation with researchers in universities and government laboratories, and private consultants. A new strain of Bt, NRD-12, has recently been identified and field-tested against the gypsy moth with promising results (Dubois *et al.*, 1988). Genetically-engineered Bt is receiving considerable interest in some quarters as attempts are made to exploit biotechnological advances to improve forest pest management capabilities. Available aerial spray technology offers improved delivery of Bt so that its efficacy is maximized while associated costs are minimized.

CHOICE OF BT FOR USE AGAINST THE GYPSY MOTH

For the balance of this paper, I will focus on the use of Bt in situations where management of gypsy moth in forested situations is the primary goal. Once a decision to treat has been made, the choice of Bt as the insecticide to be applied in situations which are especially sensitive environmentally, or where human exposure to pesticide applications is of particular concern, generally is not controversial. I shall not discuss those situations further.

Does Bt have a role in the management of gypsy moth population eruptions? Most managers responsible for protection of forests from insects today have at least a familiarity with terms such as 'environmental impact', 'integrated pest management', 'population regulation', and 'foliage protection'. But what these terms mean to individuals often varies from person to person even among entomologists; when we expand our pool of specialists to include foresters, environmentalists, bureaucrats, legislators, and others who may be involved either directly or indirectly in decision-making, we have communication problems! Let me present a few biases.

I believe that those who ultimately make the decisions which determine which of the available tools will be used in various programs to combat the ravages of the gypsy moth are seldom as knowledgeable of the alternatives as they ought to be. Even if they were sufficiently knowledgeable, political and economic constraints as well as personal preferences play far too important a role in final decisions and choices.

A forest is a valuable resource, renewable but only over a long period of time. There is little room for, nor tolerance of, error. Those charged with pest control responsibilities tend to be conservative, and want to use a material in which they have a high degree of confidence so the end result will be 'successful'. Success normally is defined within narrow limits which relate almost solely to the insect and the alleviation of its nuisance, prevention of losses above often artificial or unrealistically low thresholds, or reduction of

residual populations to levels which, in the context of management, may be unnecessarily low. Under such conditions, it is easy to appreciate how there is a tendency to choose chemical insecticides as the agent through which protection is to be effected. After all, a large proportion of today's senior decision-makers were in some of their most impressionable years in school, or in entry level positions in their profession, during a time when chemical insecticides (specifically DDT) were widely used, considered to be very effective, and were relatively inexpensive. Except for a few lonely voices in the wilderness, no one then was openly talking about, investigating, or apparently even concerned about things such as effects of pesticides on non-target organisms, development of resistance, food-chain magnification of toxicants, or pollution of aquatic systems. The simple answer was to spray, and often the attitude was 'the more the better'. Having seen--and often been a part of--programs which, by standards then used, were clearly successful, adopting new methods and materials is understandably difficult.

Environmental concerns

Conditions have changed. Environmental issues now are very much a part of the public consciousness. But understanding of these issues often leaves much to be desired. Demands for unrealistic restrictions on pest control programs too often result from naive hopes for or premature expectations of developing technologies or control alternatives, and exaggerated fears--often based on legitimate concerns--of the use of chemical insecticides. When these run headlong into traditional attitudes of pest management decision-makers, and too often a lack of confidence by decision-makers in new technologies, conflict ensues. It is in precisely this available middle ground that I see a major role for Bt in management of gypsy moth population eruptions.

There has been considerable research time and money devoted to understanding Bt and its role in gypsy moth management over the last 25 years or so. A standard for assessing potency of Bt formulations has been developed; mode of action studies have been undertaken; feeding behavior of larvae has been investigated; production of Bt is possible on a commercial scale; both oil-based and water-based formulations continue to be tested; methods of spray delivery to maximize efficacy and minimize costs are under investigation.

Certainly not all of the goals and expectations of the perfect insecticide have been achieved. But it is unlikely that any single material will ever be found that is our long-sought but elusive panacea--silver bullets and magic cures do not exist. Therefore, we must consider a series of compromises. Once we enter this area, there are legitimate differences of opinion over just which individual factors are most important and which are of lesser importance.

I suggest that environmental concerns must be near the top of the list of important concerns. Forests are complex ecosystems in which the dynamics of gypsy moth populations are played out annually. Man has the ability to introduce disruptive elements into these systems in the form of broad-spectrum

pesticides, pollutants of aquatic systems, or toxicants with long-lasting residual activity. At the same time, Man can employ materials which have a much narrower activity spectrum, have minimal or no adverse effects on aquatic systems, and which disappear either completely or as harmless breakdown products in a relatively short time after application. Bt stands up well to these latter criteria.

Protection goals

Regardless of how 'safe' a material is, it must also be expected to achieve the goals of the protection program before it will be considered for use. This is one area where the use of Bt is often questioned. On the other hand, the criteria used to set program goals may be inappropriate, arbitrary, or otherwise open to question.

There is continuing debate about just what the goal(s) of gypsy moth pest management programs are or ought to be. Many would agree that intervention with pesticides occurs primarily to suppress populations which otherwise might precipitate unacceptable tree mortality as a consequence of defoliation by the current generation of insects, and/or to abate a nuisance to people. In the former case, this is closer to handling of a minor or major crisis than it is to pest management; in the latter, non-biological factors, for example, political and emotional factors, play an important role in reaching decisions.

Given suitable growing conditions--adequate moisture, for example (and we haven't yet learned to manipulate rainfall)--following gypsy moth larval defoliation, trees have a much better chance of survival if they do not have to re-foliate in the same year in which heavy defoliation has occurred. Situations in which successive years of heavy defoliation are followed by re-foliation the same season increase the likelihood of tree mortality. While with any pesticide application program we normally want to achieve all possible objectives, it would seem that the objective of primary importance would be to maintain enough of the original foliage on the tree that re-foliation would not occur. That is, defoliation should be held to less than 60%. (See: *Impacts, Silviculture, and the Gypsy Moth*, by K. W. Gottschalk, these *Proceedings*, for a more detailed discussion of defoliation and stand vulnerability.) If this argument is accepted, it matters little whether defoliation is in fact 15% or 50%. Certainly higher levels of defoliation will likely contribute to a smaller annual increment of volume on a given site; depending on the stage in the rotation, this may or may not be of any important consequence. I would submit, however, that our ability critically and precisely to evaluate growth loss leaves much to be desired.

Normal practice in pesticide application programs targeted against the gypsy moth is to treat many smaller blocks, rather than vast unbroken acreages as has been done in other forest defoliator spray programs, for example, spruce budworms in Canada. Economics dictates this strategy in part, but citizen opposition to massive spray programs, sometimes regardless of the material being used, colors decisions as well. Pesticide applications are almost always

restricted to situations where the insect is expected to cause at least moderate (30-60%) defoliation in the absence of treatment, and often heavy defoliation (>60%) is expected. Given this reality, along with the ability of first stadium larvae of the gypsy moth to undergo airborne dispersal over considerable distances, site protection only in the year of pesticide application is the reality that we must accept. Truly it matters little whether new egg masses are deposited at a rate of 50 per hectare or 500 per hectare, or perhaps even as many as 1000 or more per hectare. A large enough source population will exist in the forest surrounding the area treated that, in the succeeding year, it will be virtually impossible to identify differences in larval population density within the previously treated block and the area outside of it. It is quite likely that, if populations are again heavy, the naturally-occurring nucleopolyhedrosis virus, if it has not previously become epizootic, will appear and cause the entire population to collapse. Tree mortality in that portion of the forest not treated the previous year may well be higher than in the blocks that were treated, but this would occur regardless of which insecticide was used for treatment; those areas not treated received no protection in any case.

Host reservoir for natural enemies

I said earlier that environmental concerns ought to be among the most important in the selection of a pesticide for aerial application. Compared to most of the available chemical insecticides, Bt has a much narrower non-target organism activity spectrum even though it has broad toxicity against Lepidoptera; it tends to act more slowly, at least in terms of dramatically reducing numbers of larvae visible in treated areas; it often allows larger numbers of gypsy moth larvae to complete their development with consequent higher numbers of egg masses subsequently deposited. On the other hand, avoiding drastic decimation of larval populations may aid in the buildup or maintenance of parasite populations, or keep predators in the area since their entire food supply isn't eliminated. If these natural enemies have any real effect on the site dynamics of this pest (see other papers in these *Proceedings* for more detailed discussions of the role of natural enemies), the use of Bt could well have substantial advantages over the choice of an insecticide which would virtually eliminate all hosts within treated blocks.

Timing

It has long been believed that Bt must be applied when gypsy moth larvae are in the first or second larval stadium. In mixed oak hardwood forests which occur throughout much of the northeastern United States, leaf expansion on overstory trees may barely be underway at this stage of insect development. White oak, *Quercus alba* L., a common species in our forests, typically flushes its leaves relatively late. Decision-makers then get nervous that Bt will not work because application must be delayed until adequate leaf expansion (a minimum of 35%; 50% or more is preferable) has taken place. There is at least one suggestion in the literature, based on a modeling exercise, that application

of Bt to late instars of gypsy moth will be effective under some circumstances (Valentine *et al.*, 1986).

Whether it is improvement in formulations, increased numbers of BIU's being applied per unit area, or some other reason, the first-or-second-larval-stadium requirement at the time of application does not hold up. Since 1984, we have been evaluating various Bt formulations (Cameron, unpublished). Rarely have we applied sprays before we had numbers of third stadium larvae present in the field; in one year we had approximately 60% fourth stadium larvae, 40% third stadium larvae, and small numbers of fifth stadium larvae present at the time of treatment. Subsequent monitoring of pesticide efficacy, using a modification of the techniques described by Cameron *et al.* (1983), allowed us to conclude that numbers of larvae observed during the post-spray period, as well as numbers of egg masses deposited, were not statistically separable from numbers in other Bt-treated plots where larval development was not as advanced at the time of treatment. Reductions in numbers of egg masses from one generation to the next ranged from almost 85% to over 96% in the various Bt treatments. Foliage protection in the blocks with larger larvae present at the time of treatment was intermediate between other Bt treatments and the untreated check plots, being separable from neither, and in this one case certainly not satisfactory. However, it should be noted that, at the time of pesticide application, defoliation had already exceeded acceptable levels in some of the test areas.

It has been the norm rather than the exception that numbers of third stadium larvae were present at the time of treatment during the last five field seasons. In spite of this, we have consistently achieved acceptable foliage protection in treated areas, with estimated final defoliation amounting to about 15-35%. Numbers of egg masses, while higher than what one would expect following a treatment with most chemical insecticides, have in all cases been reduced to levels which are acceptable.

Gypsy moth population density

Another prevalent belief has been that Bt will not give adequate protection in areas supporting 'heavy' populations. Ideally we would prefer to conduct our efficacy trials in forests with 2500-4000 egg masses per hectare, i.e., in populations that are in early outbreak phase, where there is a high probability of at least moderate or even heavy defoliation, and where the chances of a virus-induced collapse are minimized. The ideal seldom is manifested in reality, and numbers of trials have been conducted in forests with entering egg mass populations of up to 10,000-12,000 per hectare. On occasion compensation has had to be made during data analysis for virus-induced mortality occurring in the untreated checks. In trials where mortality in untreated plots was not common, satisfactory larval mortality has been obtained in treated areas, populations have been reduced, foliage has been protected, and reduction in numbers of subsequent egg masses has been adequate.

Costs of application

The costs of insecticide application are always of concern. In recent years, the cost of Bt has steadily declined in comparison with chemical insecticides, and it is now competitive. This is in situations that call for 7.0, 9.4, or as much as 14.0 l/ha (96, 128, or 192 oz/ac) of finished spray to be delivered. In 1987, both van Frankenhuyzen *et al.* (1988) and Cameron and Fusco (1987), in independent tests, showed that Bt could be applied in as little as 1.75 - 2.3 l/ha (24 - 32 oz/ac) of finished spray while maintaining efficacy. Preliminary results from experiments I am conducting during 1988 suggest that the 1987 results will be confirmed. In addition, leaf bioassays (van Frankenhuyzen *et al.* 1988) or direct counting of fluorescent spots from a dye added to the formulation (Cameron and Fusco, 1987; van Frankenhuyzen *et al.*, 1988) gave evidence that droplets of spray were well-distributed throughout the canopy of mature oak trees, with impingement on both upper and lower leaf surfaces. It would appear that, rather than the early emphasis on larger volumes of spray (Lewis and Connola, 1965, (*in*: Dubois, 1981)), we ought now to change to nozzles, such as those under the trade name of Micronair®, which can create very large numbers of very fine droplets and reduce the total volume of material applied. With continuing improvements in Bt formulations, and the ability to achieve potencies of at least 64 BIU's per US gallon of neat material, we are in position to exploit economies that can be realized in application costs. With smaller payloads required to cover similar areas of forested land, spray aircraft would require fewer ferrying trips to airports or helicopter operations pads; on larger jobs, it is likely that fewer aircraft would be required. A spray window which is already none too wide, and which frequently narrows with typical weather not conducive to spraying at the time when spraying must be done, could more efficiently be exploited.

Eradication of isolated infestations

This discussion has focused on the use of Bt primarily in forested situations where the gypsy moth is a recurrent pest. It should be noted at least in passing that Bt was used from 1984-1986 by the state of Oregon in the western United States in a massive eradication effort. Up to 100,000 hectares of forest were to be treated three times each year. I was among those initially who gave that program virtually no chance of success, especially since gypsy moth adults had been trapped over a very large area. Much to my astonishment, that program, although costly in dollars, has to be classified as successful by many standards. I don't think it is fully understood just why success was achieved. There is no way to report, except through speculation, what would have happened had either nothing been done or alternative methods been employed in the eradication effort. The fact is that locally heavy and widely scattered sparse populations of the gypsy moth have been drastically reduced following three successive years of multiple applications of Bt, even though eradication has not yet been achieved.

In 1987, the state of California, also in the western United States, used four aerial applications of Bt in combination with narrowly targeted ground applications of Dimilin to attempt to eradicate an established but local infestation of the gypsy moth before the pest became established and spread to surrounding areas. Even though egg masses were located within an area of less than one hectare in size, 16 hectares were treated by air in an effort to kill any larvae that might have dispersed during the first larval stadium. No adults were trapped in pheromone traps during the summer of 1987, nor were any new egg masses found. Eradication of gypsy moth from that spot may well have been accomplished in a single season; monitoring will continue through 1988 and 1989 before such a claim will be made, however.

CONCLUSIONS

We have by no means reached the end of the line in improving either Bt formulations or our ability to deliver them efficiently, effectively, and economically. Open questions remain concerning the relative merits of oil- vs. water-based formulations, helicopters vs. fixed-wing aircraft, flat fan vs. Micronair vs. Beecomist® or other nozzles, volumes of spray to deliver, amounts of toxicant to deliver, timing of applications, and other factors. But Bt has given evidence during the last few years that it has a much wider potential role in management of gypsy moth population eruptions in forested areas than has generally been considered. It need not be restricted to areas which are especially sensitive either ecologically or politically. It is also cost competitive with chemical insecticides.

Bt is unlikely completely to displace materials such as Dimilin unless currently unrecognized adverse environmental impacts of that material are identified, or non-biological considerations dictate pest management decisions. Nor is Bt likely to cause reductions of populations to the same low levels that Dimilin or other chemicals frequently achieve. But it must seriously be asked, 'Are such reductions necessary given the conditions under which pesticides are used in contemporary gypsy moth management programs?' By the same token, does leaving a small residual population of gypsy moth confer a benefit in conservation or perpetuation of natural enemy populations that would be lost if pest populations were more drastically reduced? Perhaps those who work with the computer models can conduct the pertinent simulations to shed light on these questions.

Does Bt have a place in management of gypsy moth population eruptions in forested land? Yes, I believe it does. I also believe that its role is likely to increase at the expense of the use of chemical insecticides as both forest managers and other decision makers are persuaded by the accumulating evidence that Bt does, indeed 'work'. Its environmental advantages are considerable; its relative cost is continually declining when compared to alternatives; its reliability is improving all the time; exploitation of available application technology is only just beginning and can be expected to increase

in the next few years. Add all these factors together, and the place of Bt looks secure.

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VIRUS CONTROL OF THE BROWN-TAIL MOTH, *EUPROCTIS* *CHRYSORRHOEA*.

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INTRODUCTION

Infestations of the brown-tail moth, *Euproctis chrysorrhoea* (L.) (Lepidoptera: Lymantriidae) in the United Kingdom (UK) and in many other parts of its geographical range present an unusual pest control problem. It is principally a defoliator of woody Rosaceae, including ornamental and fruit trees and is, therefore, often a common insect in urban and suburban areas. The larvae have highly irritant hairs to which human allergic reactions can be strong (Blair, 1979). Symptoms vary from mild urticaria to temporary blindness and, amongst those disposed to respiratory problems, to asthma and even death. *E. chrysorrhoea* is, therefore, a plant pest and a public health problem.

Throughout its range, Europe (including south-east England), North Africa and, by accidental introduction, some eastern parts of the U.S.A., it is univoltine. Eggs are laid in the summer. The larvae live and feed gregariously through the autumn and overwinter as second or third instars inside silken nests. In the spring they emerge and, in the UK, complete their development by June. The adult female flies feebly so that dispersal tends to be very local (Sterling, 1983).

In the UK practical pest control at present tends to be by spraying chemical insecticides, especially synthetic pyrethroids, an activity which is unpopular in built-up areas and unsuitable for use in nature reserves. An alternative strategy is to cut out and destroy overwintering nests, but this is a labour intensive and, therefore, expensive option; it is also difficult where trees are tall. Consequently, there is much interest in the development of a cheap and strongly species-directed control method which would be compatible with both human and conservation interests.

The main mortality factors operating in UK populations were examined by Sterling and Speight (1988). Their analysis suggests that the most appropriate potential

biological control agents are microbial pathogens, one of which is a naturally occurring baculovirus. The Baculoviridae is a family of viruses whose infections are restricted to Arthropoda, and particularly to insects where they are often major natural population regulatory agents. Members of two major subgroups, the nuclear polyhedrosis viruses (NPV) and the granulosis viruses, have been used widely as sprayable pest control agents especially against larval Lepidoptera and dipteroid sawflies (Entwistle and Evans, 1985). After extensive safety testing of over a dozen types it is widely accepted that the baculoviruses are detrimental neither to human welfare nor the environment.

An NPV of *E. chrysorrhoea* (EcNPV) has been isolated from larvae in the wild in the UK and in Yugoslavia. In the latter country infection levels were at times very high (60%; Sidor, 1975), but in the UK they have always been observed to be low.

This paper describes the quantitative and qualitative relationships of *E. chrysorrhoea* larvae with the NPV's, preliminary trials in the use of EcNPV as a sprayable control agent and studies on the possible development of more than one infection cycle within single host generations and the import of this for practical suppression.

METHODS

Rearing *E. chrysorrhoea*. Larvae were obtained either from the field or were reared from eggs surface sterilised to minimise the persistence of transovum passed pathogens in culture. Most larval rearing was on leaves of bramble (*Rubus fruticosus* L.) but a low nutrient semi-synthetic diet was also found to adequately support development (Kelly, in preparation).

EcNPV production. The NPV isolate used as seed stock to produce bulk NPV for spray trials was originally collected in the Isle of Grain, Kent, UK, in 1978. A virus suspension of 2.5×10^8 polyhedral inclusion bodies (PIB)/ml was painted onto the surface of *Crataegus monogyna* Jacq. leaves which were fed to fourth instar larvae. The infected larvae were maintained at room temperature and fed further *C. monogyna* leaves *ad libitum*. Larvae began to die of NPV infections 15 days later when they were harvested and stored frozen pending full purification for use in bioassay and DNA work or semi-purification prior to formulation for spraying in control trials. The virus particles of NPV's are bound up in small crystals of virus-coded protein which confers considerable environmental stability (Kelly, 1985). These crystals, which are of various polyhedral forms generally range in size from 1-5 μ m in diameter and are commonly known as polyhedral inclusion bodies (PIB). The PIB is easily visible with the compound microscope and is the usual calibratory unit of NPV preparations. The PIB content of our preparations was counted using the dry film method of Wigley (1980a).

Infectivity testing. LD₅₀ tests on large larvae (3rd instar and older) were conducted by feeding measured volumes of PIB suspensions dried on *C. monogyna* leaf fragments of a size which is rapidly and totally consumed by an individual larva. For smaller larvae

the droplet feeding method of Hughes *et al.* (1986) was successful. This method was also tried using fourth instar larvae, but they refused to imbibe an aqueous PIB suspension; however, they did so readily when a leaf extract of *C. monogyna* was added.

EcNPV formulation. Following maceration and crude filtration of infected larvae, NPV was prepared for spray trials by semi-purification, involving a single cycle of low speed centrifugation to remove host body debris. The subsequent NPV concentrate was formulated to suppress secondary replication of any contaminant microorganisms (formulation details are currently confidential).

EcNPV spray application. Immediately prior to spraying, the formulated PIB suspension was diluted with water and mixed with an emulsifiable adjuvant oil (Actipron; British Petroleum) in the proportion of PIB suspension:Actipron of 4:1. This fluid was sprayed using a hand held, fan assisted, spinning disc ULV sprayer, the Turbair Fox (Pan Britannica Industries), producing a fixed flow rate of 1.3ml/second. This machine produces droplets with a volume median diameter in the size range 70 to 100µm.

Assessment of NPV infection. Larvae from spray samples were individually smeared on microscope slides and the smears stained by the simple Giemsa method of Wigley (1980b). PIB's could easily be detected under oil immersion at x900 magnification.

Spray trials: (i) post-hibernation trial. This was conducted on third instar larvae emerging from overwintering nests previously stored at 4°C. Potted *C. monogyna* plants (two/pot), *circa* 1m tall, were infested with 250 larvae per pot. A sample of these larvae was individually weighed and allocated to instar. Five trees were apportioned to each treatment and the spraying conducted inside a large draught free building, the Turbair Fox being held 2m from the line of trees and moved along the line at approximately 1.3m/sec. Five dosages were used ranging from 2×10^7 to 2×10^9 PIB/m of spray lane. After spraying the trees were placed in a greenhouse; due to high levels of defoliation by 6 days post spray the larvae were then transferred to large plastic boxes, kept at room temperature and fed fresh foliage *ad libitum*. Ten days post spraying samples of 50 larvae were taken and placed in smaller boxes. These were checked daily until 27 days post spraying and any dead larvae removed and diagnosed for NPV infection. Further details of this experiment can be found in Kelly *et al.* (1988).

Spray trials: (ii) pre-hibernation trial. A field trial of the virus was conducted in an area of infested *R. fruticosus* at Portsmouth. Twenty four 3m sections, each separated by a buffer zone of at least 3.5m, were marked out in a hedgerow 200m long. Existing nests were redistributed to produce 12 nests per plot. Because of variation in bush size, a stratified random allocation of treatments was employed in which each treatment group of three had one 'small', one 'medium' and one 'large' bush replicate. A series of five doses from 2×10^7 to 1×10^9 PIB/m, was applied plus a further treatment of 1×10^8 PIB/m applied with the others on 18:9:87 and again one week later. Two control treatments were included, one unsprayed and one sprayed with the 20% Actipron carrier fluid. No dead

larvae were found on foliage during visits to the site shortly after spraying. Samples of larvae were collected on 23:10:87 (at the onset of diapause) by removing three nests from each plot and dissecting them open to reveal both dead and live larvae. Samples of both were smeared and diagnosed for the presence of NPV.

EcNPV infection cycling and disease dispersal. In two field experiments, one in the autumn and one in the spring, live laboratory infected larvae were introduced into natural larval populations (Sterling *et al.*, 1988). Introduction sites were large discrete *R. fruticosa* bushes where larval densities had been estimated from nest counting and sizing, employing a linear relationship between nest volume and number of resident larvae (Sterling, in preparation). Since data involving proportions has a binomial distribution, it is more essential to detect small differences in response towards the extremes of the distribution than at the centre. The proportions introduced were, therefore, varied linearly along an angularly transformed scale (Little & Hills, 1978). Infected larvae were thus introduced in the proportions 0.024, 0.206, 0.500, 0.794 and 0.976. Subsequently, disease incidence was measured both over time and at a series of distances from introduction centres. The five introduction treatments were each replicated three times (in low, medium and high natural infestations) in both the spring and autumn experiments.

RESULTS

Quantitative host-EcNPV relationships. The LD₅₀ was measured in four larval instars (Table 1). These values were plotted logarithmically against larval weight (Figure 1) where it can be seen that for Lepidoptera the apparently linear relationship is

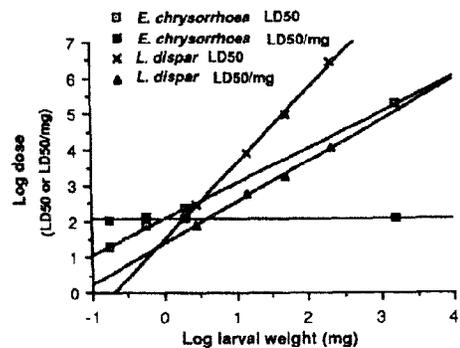


Figure 1. Relationships of log LD₅₀ and LD₅₀/mg with log initial body weight for *Euproctis chrysorrhoea* and *Lymantria dispar* (data for *L. dispar* from Burgerjon *et al.*, 1981).

not abnormally steep. Dividing the LD₅₀ by larvae weight produced a linear relationship of zero slope against larvae weight.

EcNPV and heterologous 'hosts'. Using challenging doses of 1×10^3 and 1×10^6 PIB to individual second instar larvae, no EcNPV replication was detected in any of 66 other species of Lepidoptera (in 11 families, including Lymantriidae) tested. Cross-infection was also absent in the honey bee, *Apis mellifera* L., and two species of sawfly.

Heterologous NPV's in *E. chrysorrhoea*. In addition to EcNPV, nine other NPV's from eight different lymantriid host species were fed to *E. chrysorrhoea* larvae. Four proved to be cross-infective (see Discussion).

Spray trials: (i) post-hibernation trial. The larvae in this trial were third instars with a mean weight of 3.2mg at the time of spraying. The development of virus-related mortality over time is shown in Figure 2 (the top dose shown is 1×10^9 PIB/m; the highest dose of 2×10^9 PIB/m gave similar results to this dose). The two top doses delivered distinct sigmoid responses of mortality against time, starting 11 days post spraying and reaching *circa* 90% by 17 days. Deaths in other doses began later and largely levelled off by 20 days. Application of probit analysis to the final virus mortality:dose relationship (up to 1×10^9 PIB/m) gave a spray LD₅₀ of 1.3×10^8 PIB/m and an LD₉₀ of 8.5×10^8 PIB/m.

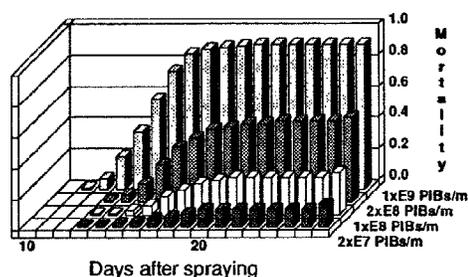


Figure 2. Virus mortality in *E. chrysorrhoea* populations on potted *C. monogyna* bushes sprayed with a series of doses in the post-hibernation trial.

The large majority of the deaths were in the instar (fourth) following that predominant at spraying, with some mortality delayed until the fifth instar, particularly in the low dose treatments.

Spray trials: (ii) pre-hibernation trial. The larvae in this trial were also mainly in the third instar, with a mean weight of 2.6mg at the time of spraying. The extensive samples taken on 23:10:87 showed that infection had entered nests in all treatment plots. However, no relationship could be discerned between dose and infection levels. Bush dimensions also had no effect.

Treatment	Bush category		
	Small	Medium	Large
Control	0.0	0.0	0.0
Actipron control	1.7	0.0	0.0
2x10 ⁷ PIB/m	11.5	36.4	8.3
1x10 ⁸ PIB/m	5.0	84.1	24.2
1x10 ⁸ PIB/m x2	4.8	9.4	25.0
2x10 ⁸ PIB/m	15.0	25.0	47.5
5x10 ⁸ PIB/m	40.3	16.1	41.9
1x10 ⁹ PIB/m	29.4	55.3	46.8

Table 1. Mean percentage NPV infection in larvae in nests in the pre-hibernation spray trial on 23:10:87.

During the winter the site suffered very heavy damage and loss of nests due to an exceptional storm (the worst in the UK for 200 years). In addition there was severe predation on nests, presumably by flocks of birds. Consequently, very few larvae could be found post-hibernation. In these an appreciable level of apparently non-virus related, idiopathic, mortality was observed, even in the controls. However, in the remaining larvae substantial levels of NPV infection were found in the spring.

EcNPV infection cycling and disease dispersal. Rapid defoliation of bushes in the spring led to large scale emigration of larvae. Initial densities had ranged from 332-6500 larvae/m², but, at ten days post introduction of infected larvae density had fallen to about 50 larvae/m². No relationship was found between initial density and subsequent levels of infection. Whilst larval infection, almost certainly laboratory derived, was found at ten days none was detectable after this date until 52 days after introduction when a significant second peak of infection began. However, not all bushes developed this second peak, and Figure 3 illustrates infection levels in two plots in which the peak was present. No relationship was found between the size of this second peak and the proportion of infected larvae introduced.

In the autumn experiment differences between bushes were again extremely variable. Although a second peak of infection was not as clearly pronounced as in the spring experiment, its presence was suggested by greater levels of infection being found 40 days after introduction than were present at 24 days. Figure 3 illustrates two plots which showed this response.

At 64 days significant proportions of infected larvae were found at all distances from the introduction centre in the spring experiment (Figure 3). However, in the

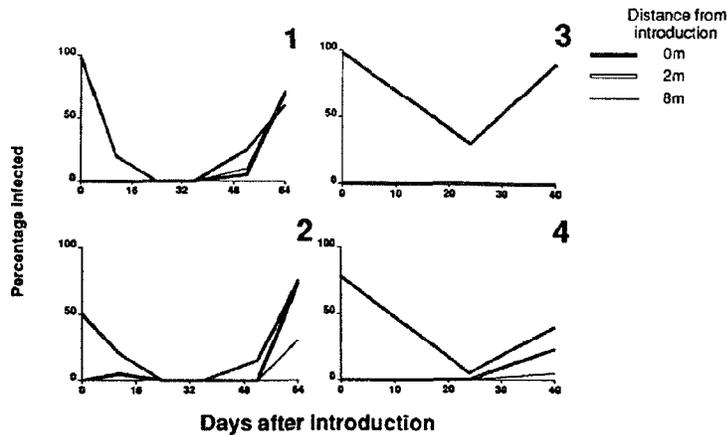


Figure 3. Examples of bushes which showed secondary infection cycles following primary introduction of laboratory infected larvae in the spring (1 & 2) and in the autumn (3 & 4).

autumn experiment there were few examples of disease beyond 2 metres from the introduction.

DISCUSSION

A highly infectious NPV isolate (i.e. low LD₅₀) is essential for good insecticidal effect, since as susceptibility decreases the quantities of virus required to establish control rapidly become uneconomic. To fully assess the infectivity of an NPV, and contrast it with others, it is necessary to study its impact throughout the host larval period. The susceptibility of lepidopterous larvae to infection is known to decline strongly with increasing weight (e.g. Entwistle & Evans, 1985). However, the degree to which this occurs appears to vary greatly with different NPV-host species systems. There seems to be a generally good linear relationship between log larval weight at inoculation and log LD₅₀/unit weight (mg). The gradient of this regression and the LD₅₀ *per se* of very early instar larvae (i.e. during the ideal period when NPV spraying would be conducted) provide two valuable parameters for contrast. In estimating the

effect of the virus it is, however, important to take larval feeding rate, and hence the rate at which larvae acquire virus from plant tissue, into account; larger species may well feed faster and thus compensate for an inately higher LD50.

In Figure 1 the responses of EcNPV and *Lymantria dispar* (L.) NPV (LdNPV; the use of this virus is very well documented) are contrasted in terms of the mutual relationships of log LD50 and log LD50/mg to log body weight. It is evident that, although the LD50 values for the various instars of *L. dispar* are much higher than for *E. chrysorrhoea*, the values of LD50/mg are most favourable for the former species (data from Burgerjon *et al.*, 1981, and interpreted by Briese, 1986).

EcNPV is unusual amongst NPV's in general in that taxonomically broad tests indicate a very high level of host specificity. None of the species of Lepidoptera tested became infected.

This is not, however, a two-way phenomenon since, in testing a quite limited number of NPV's of other Lymantriidae, and characterising both the inoculum and the progeny viruses by restriction endonuclease analysis Laport (1987) was able to demonstrate true cross-infection in *E. chrysorrhoea* of the NPV's of *Euproctis similis* (Fssl.), *L. dispar* and of two geographical isolates of NPV from *Leucoma salicis* (L.). Some information is available on the susceptibility of *E. chrysorrhoea* to the Polish isolate of *Leucoma salicis* NPV (LsNPV). Skatulla (1985) contrasted the susceptibility of five European Lymantriidae to their homologous NPV's with that to LsNPV employing fourth instar larvae (weights not declared). Unfortunately he was not able to report on the susceptibility of fourth instar larvae of *E. chrysorrhoea* to its own NPV and no direct information on this appears to exist elsewhere. Employing weights for UK *E. chrysorrhoea* instars (1,2,3, early 5 and 6) it can be seen that the relationship of instar to log weight is close to linear, suggesting a weight range for 4th instars of 15-40mg and, therefore, (interpolating from Fig. 1) an LD50 of 1580-3980 PIB. This last value is not strikingly different than that for LsNPV in *E. chrysorrhoea*, 5140 PIB, quoted by Skatulla (1985). However, this information is too sketchy for conclusions about the relative worth of the two viruses for use in controlling *E. chrysorrhoea*.

The application of EcNPV as an insecticidal spray using the Turbair Fox machine was an efficient method of control for the spring emergent larvae under the specific conditions of the trial described here (notably the lack of wind). It appears unlikely that 100% primary mortality can be achieved since a dose increase from 1×10^9 to 2×10^9 PIB/m resulted in no increase in mortality. Spray coverage is never likely to be totally uniform, and a proportion of larvae must escape ingestion of a lethal dose.

A serious divergence between this trial and a field application was the reduction in exposure to solar ultra violet (UV) radiation, to which NPV's are very susceptible. However, in a commercial formulation UV screening agents could be used.

In the autumn trial, carried out on slightly smaller larvae using the same equipment in the open air, the results up to the onset of hibernation were very uneven.

Post-hibernation, for reasons explained above, it was not possible to continue quantitative assessments. However, the data indicated strongly that in at least on of the replicat plots of each treatment a high level of infection had been achieved. This was particularly apparent in the next to lowest dose, 1×10^8 PIB/m, suggesting that control in the autumn could be achieved using lower doses than in the spring. It seems likely that the wide variation in the results achieved in this trial was due largely to poor spray coverage achieved on the leaves in some replicates, due to prevalent wind conditions and the orientation of the leaves. Good coverage is of particular importance in the autumn given the limited feeding area of the larvae.

Neither of these trials was able to clearly demonstrate the effects of additional infection cycles generated by virus produced in the primary spray induced infection. However, the introduction of pre-infected larvae to healthy populations in both the spring and autumn showed that such cycles can be generated in *E. chrysorrhoea*, thus enhancing the potential efficacy of the virus as a control agent.

It is a common observation that NPV infected larvae of Lepidoptera die of disease in the following instar, as was the case in the spring trial described here. It thus appears possible that, if virus was applied in the autumn, several cycles of infection might occur following the initial response. The gregarious habit of the larvae is likely to facilitate this process. It is well documented that NPV can persist overwinter on trees (e.g. Doane, 1975; Evans & Entwistle, 1982) and that NPV's may be dispersed widely by predatory and scavenging organisms (Entwistle, 1982). Consequently, pools of inoculum created at the death of host larvae can not only persist but can also be dispersed. Whatever the mechanisms involved, it is clear that transmission of virus is possible within a single generation of *E. chrysorrhoea*.

It is apparent from this data that EcNPV has considerable potential as a bioinsecticide. It not only seems possible that satisfactory primary control can be achieved, but there may well be valuable persistence giving rise to prolonged cycles of mortality and host suppression. Environmentally it is unusually well suited for use in nature conservancy and urban contexts, since it has an exceptional level of specificity of action.

On the debit side, this host specificity means that EcNPV must be produced in the homologous host, which poses severe problems for safeguarding the health of staff working on the production system. The use of LsNPV as an alternative would facilitate virus production, but much further work would be required to assess its relative efficacy and environmental impact. The spray technology used to date has proved incompatible with the need to achieve good coverage on discrete vegetation units in urban areas and further work on alternatives, such as knapsack mistblowers, will have to be carried out.

SUMMARY

Larvae of the univoltine lymantriid *Euproctis chrysorrhoea* (L.), which overwinters gregariously in tents in the second or third instar, have intensely urticating hairs. They feed preferentially on woody rosaceous plants and, because of the damage inflicted and public health problem presented, are a notable pest in urban areas. In such a situation, and in nature reserves, chemical insecticidal control is unacceptable and a more specific biological approach seems appropriate. A nuclear polyhedrosis virus of *E. chrysorrhoea* (EcNPV), isolated in Britain, has an exceptional degree of host specificity and, by LD₅₀ tests, seems highly infective to host larvae. Therefore, post- and pre-hibernation EcNPV spray application trials were conducted. The results demonstrated a strong primary mortality response to the virus. The nature of these trials precluded demonstration of the possibility of secondary infection cycles developing in surviving larvae of the sprayed generation. This question was separately investigated. Introduction of pre-infected larvae into the autumn and spring stages of a single generation resulted in secondary infection cycles. Collectively the data acquired will be employed to conduct control trials designed to assess the comprehensive effect of virus sprays in controlling *E. chrysorrhoea* larval infestations. EcNPV is potentially the most acceptable and practicable means of controlling this pest, especially in environmentally sensitive areas.

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EPIZOOTIOLOGY OF GYPSY MOTH
NUCLEOPOLYHEDROSIS VIRUS

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INTRODUCTION

Nucleopolyhedrosis viruses (NPV) are frequently associated with the collapse of high density populations of many of the lymantriids including the gypsy moth (Lymantria dispar L.) (Bess, 1961; Doane, 1970; Woods and Elkinton, 1987), the nun moth (L. monacha) (Komarek and Breindl, 1924), the Douglas-fir tussock moth (Orgyia pseudotsugata) (Torgerson and Dahlsten, 1978), and the red-bellied tussock moth (L. fumida) (Katagiri, 1977 cited in Evans and Harrap, 1982). Lethal infections result in destruction of most internal tissues and larvae killed by NPV have a characteristically flaccid appearance. The cuticle is fragile and ruptures easily, releasing the liquified remains of the destroyed tissues and massive numbers of virus particles occluded within crystalline protein structures (occlusion bodies, or OBs). These OBs are resistant to environmental degradation and can persist outside of the host for several years if protected from sunlight. Larvae become infected primarily through ingestion of the occluded virus, which is digested in the alkaline gut, thereby releasing virions which enter the host tissues via the midgut.

The gypsy moth, the Douglas-fir tussock moth and other lymantriids are of economic and esthetic importance in North America, Europe and Asia. Because the NPVs appear to play a significant role in the dynamics of their host populations, information concerning the epizootiology of NPV diseases is potentially very valuable in management and research of these pests. Unfortunately there are still many gaps in our understanding of the causes and patterns of expression of these diseases. Although viruses have been formulated and applied as control agents for several of these insects, the results have often been disappointing (Yendol et al., 1977; Lewis and Yendol, 1981; Podgwaite, 1985). Therefore, it is clear that we need a better picture of the processes by which naturally-occurring NPVs act in order to successfully utilize viruses as

control agents. Knowledge of the factors that affect expression and transmission of the disease might be used to improve efficacy of augmentative NPV releases through genetic selection of more effective strains, or through genetic engineering to produce new, more virulent strains. Management of pest populations by manipulation of the habitat to enhance effectiveness of naturally-occurring NPV may be another approach.

This review includes what is presently known concerning the epizootiology of NPV of lymantrilids with emphasis on the gypsy moth. This includes important factors influencing host susceptibility and disease transmission as well as various environmental factors which affect both the pathogen and its host.

FACTORS AFFECTING PATHOGENICITY AND PERSISTENCE OF NPV

Genetic Variability

Different strains of NPV differ in their pathogenicity. When isolates from Europe, North America, and Asia were tested against a laboratory strain of gypsy moth, the LD₅₀s ranged from 1.7×10^3 to 5×10^6 OB/ml (Shapiro et al., 1984). The results of several studies in which potencies of viruses from various sources were compared were reviewed by Lewis et al. (1981).

Persistence and Plant/Pathogen Interactions

The occlusion body in which NPVs are embedded affords a great deal of protection to the virions which allows the virus to maintain viability for several years in certain habitats (David and Gardiner, 1967; Thompson et al., 1981). Soil is well known as an important reservoir for many insect viruses (Jaques, 1970). Soil pH can significantly affect persistence of viruses (Thomas et al., 1973). Podgwaite et al. (1979) found high concentrations of gypsy moth NPV persisting in soil, litter, and on bark for at least one year following epizootics. Newly-hatched larvae can become infected upon contacting bark, pupal exuviae, and soil collected from a forested site following an epizootic (Doane, 1975; Weseloh and Andreadis, 1986; Woods et al., in press).

Persistence of virus on plant foliage is limited, primarily due to inactivation by ultraviolet radiation of sunlight (David, 1969; Smirnov, 1972). Virus survival may also be affected by physical and chemical features characteristic of the plant. NPV may persist longer on the underside of leaves (Stacey et al., 1977) or in stomates (Reed, 1971). Leaf exudates can also affect the

survival of viruses (McLeod et al., 1977; Young et al., 1974) as has been demonstrated on cotton. Virus survives longer on some plant species than on others (Young and Yearian, 1974), due to structural or chemical differences, but also because of differences in growth characteristics or phenology. For instance, persistence of NPV on the deciduous foliage of the gypsy moth's preferred host is limited to one season, since oak leaves are dropped each autumn.

Plant/pathogen interactions may affect the impact that a viral pathogen has on its insect host. The work of Rossiter (1987) and Keating and Yendol (1987) suggest that NPV pathogenicity may be different for gypsy moth larvae feeding on oaks compared with larvae feeding on other tree species. However, studies with Douglas-fir tussock moth NPV indicate that the pathogen is equally effective on Douglas-fir, grand fir, and white fir (Thompson et al., 1978; Stelzer et al., 1977).

FACTORS INFLUENCING HOST SUSCEPTIBILITY TO NPV

Variation in susceptibility or resistance to viral pathogens both within and between populations has been shown for several lepidopterous hosts, including the gypsy moth (Briese and Podgwaite, 1985). For example, Rollinson and Lewis (1973, cited in Lewis, 1981) compared the response of different gypsy moth populations to a single NPV isolate and found that the LC_{50} of the most resistant strain was more than 100 times higher than that of the most susceptible strain. That these differences represent a real shift in the level of resistance between the different populations is indicated by a comparison of the regression slopes (Briese, 1987). A genetic basis for the variation in response to NPV challenge has been demonstrated for *Spodoptera frugiperda* (Reichelderfer and Benton, 1974) and *Epiphyas postvittana* (Briese et al., 1980) and in response to a cytoplasmic polyhedrosis virus for the silkworm, *Bombyx mori* (Watanabe, 1987). Such susceptibility can be controlled by a single autosomal gene or by complex genetic mechanisms (Briese, 1987). A gradual, but significant increase in LD_{50} was shown for a laboratory gypsy moth strain exposed to NPV for 11 generations, suggesting that shifts in susceptibility of this population to NPV are also heritable (W. D. Rollinson, unpublished data cited in Briese and Podgwaite, 1985). However, as Briese (1987) points out, these results are weakened by the fact that some of the early observations were based on single-dose comparisons. Viruses have evolved with their hosts, therefore, some degree of host resistance to these pathogens is likely to have arisen independently among different geographically isolated populations. Some of the variability between

gypsy moth populations is likely to be genetically based, however, a heritable component for host susceptibility to NPV has yet to be conclusively demonstrated for this insect.

Developmental factors can also influence host susceptibility to viral pathogens. In general, resistance increases with the age of the host (Briese, 1987). The LC₅₀ for second-instar gypsy moths tested with the Hamden Standard NPV was about 200 times lower than the LC₅₀ for fourth instars (Lewis et al., 1981). This age-related increase in resistance is largely accounted for by the increase in body weight in gypsy moth, however, an additional age-related factor also appears to be involved (Briese, 1987). Briese (1987) suggests that the development of specific defense mechanisms against viral infection in older insects could be involved. Other developmental factors such as growth rate, hormonal levels, metamorphosis, diapause, and stage of development may also affect host susceptibility (Briese and Podgwaite, 1985; Watanabe, 1987). Shapiro and Robertson (1987) reported that the number of OBs in infected gypsy moths was reduced 12-fold during the transformation from larva to pupa and 115-fold during the metamorphosis from pupa to adult. This suggests that metamorphosis is deleterious to virus or that adult and pupal tissues are less favorable for viral growth than are larval tissues.

The host's nutritional state is also an important factor influencing susceptibility or resistance. Levels of sucrose, protein, cellulose, tannins and other chemical and physical characteristics of the insect's food plants can affect susceptibility to NPV. Keating and Yendol (1987) showed that mortality among gypsy moth larvae which were fed NPV on oak leaves was significantly lower than among larvae fed NPV on aspen leaves. These differences were shown to be related to leaf pH and tannin content (Keating et al., 1988). In another study, NPV-dosed larvae reared on pitch pine foliage survived longer than dosed larvae feeding on oak foliage (Rossiter, 1987). Such host-mediated effects could be important in the development of gypsy moth NPV epizootics as has been suggested for some lepidopteran defoliators (White, 1974).

Evidence that parasitism affects susceptibility to virus was presented by Godwin and Shields (1984). These workers showed that parasitism by Blepharipa pratensis increased the pathogenicity of NPV in gypsy moth larvae.

Population density may affect insect susceptibility to virus, either directly, or indirectly through changes in host plant foliar chemistry. Foliar chemical changes associated with defoliation have been shown to affect gypsy moth development time, pupal weight and survival (Waliner and Walton, 1979; Valentine et al., 1983; Rossiter et al., 1988). Density also affects

physiological and behavioral changes in high-density gypsy moth populations (Capinera and Barbosa, 1976; Leonard, 1970; Lance et al., 1986, 1987). It is likely that such density-related changes may also affect gypsy moth susceptibility to pathogens, however this has not been examined.

Steinhaus (1958) suggested that crowding acts as a stress factor capable of inducing latent virus to an active state or of lowering resistance to infection. Although the idea that latent infections can be induced by various stress factors is somewhat controversial, some experiments have been cited as evidence supporting that hypothesis. For example, gypsy moth larvae fed the heterologous NPV of another insect, *Aglais urticae*, died from gypsy moth NPV infection (Longworth and Cunningham, 1968), not from infection of the *A. urticae* NPV. Introduction of chemical agents have also resulted in mortality due to NPV (Yadava, 1971). However, it is possible that treatment with heterologous virus or chemical stressors reduced resistance to low levels of gypsy moth NPV contamination in the environment, rather than inducing a latent NPV infection. Additional research will be needed to conclusively demonstrate the phenomena of latency and activation of NPV in gypsy moth hosts.

Various models, but notably those of Anderson and May (1980) are based on the notion that populations consist of susceptible and resistant individuals. Obviously more research to identify and elucidate the factors which influence susceptibility and resistance to NPVs is needed in order to utilize similar models to describe the epizootiology of these pathogens and to use such information in gypsy moth population management.

FACTORS AFFECTING TRANSMISSION AND DISSEMINATION OF NPV

Transmission in Space

Factors determining the extent to which insects transmit and acquire virus within a spatial context are crucial aspects of epizootiology. Altered behavior, increased activity level, greater amounts of inoculum present in the environment, or increased gypsy moth population density may serve to increase the probability of larvae encountering and acquiring virus. Population density can directly or indirectly affect behavior, inoculum quantities and activity level.

NPV appears to be spread through a gypsy moth population in a density-dependent manner, modified by environmental persistence of the pathogen after an epizootic (Campbell, 1963; Doane, 1969, 1970, 1975, 1976;

among larvae hatched from the eggs from 80% to 0.1%, indicating that virus is carried on the surface of the egg rather than internally. He suggested that infected female moths transmit NPV transovum to the surface of the egg.

Shapiro and Robertson (1987) concluded from their laboratory study, that females fed sublethal doses of NPV transmitted virus to their offspring. These workers did not examine whether the inoculum was transmitted transovarially or transovum. In a similar study, we were unable to show transmission from NPV-fed parents to progeny when egg masses were oviposited and overwintered on forest oak trees (Murray and Eikinton, in press). However, mortality rates among our dosed parental stock were somewhat lower than those in the earlier study.

We also compared environmental versus maternal factors in vertical transmission of NPV (Murray and Eikinton, in press). We examined the role of precipitation in leaching NPV from the environment to contaminate gypsy moth egg masses as has been shown to occur with the Douglas-fir tussock moth (Thompson, 1978). We found that egg masses acquire most NPV at the time of oviposition and subsequent precipitation was not an important factor. When we switched females between high density, high-infection rate and low-density, low-infection rate populations, for oviposition in the opposite site, we found that the site in which the eggs were oviposited was the most important factor influencing the incidence of NPV infection among progeny. Because progeny of females from the epizootic population suffered very little mortality when oviposited in the low-density site, we concluded that transovum transmission may not be as important a factor as environmental contamination of eggs in transmission of NPV from one generation to the next. We suggest that NPV is incorporated from the substrate into the egg mass during oviposition (Murray and Eikinton, in press).

Although transmission across and within generations may occur by a number of routes, and various factors appear to have an influence, the relative importance of the various routes and each influencing factor are not well understood. It is likely that the importance of different transmission mechanisms varies with environmental conditions such as host plant chemistry, population density, or the amount of inoculum present in the environment.

SUMMARY

Epizootiology attempts to describe and explain the causes and patterns of disease. Complex interactions between the insect, its host plants, the pathogen, and

the environment, influence the expression and spread of nucleopolyhedrosis viruses in lymantriid populations. Factors affecting the susceptibility of the insect to viral infection, as well as transmission, dissemination and environmental persistence of the pathogen are all important in the development of epizootics. Recent studies have shown that gypsy moth NPV is transmitted in a density dependent manner and have elucidated some of the mechanisms by which NPV is transmitted. Other studies have shown that insect/plant interactions are important in expression of NPV infection. But many questions remain unanswered. For instance, there is circumstantial evidence that NPV can occur in a latent state and may be activated by environmental stress, but such a phenomenon has not yet been conclusively demonstrated. Transovarial transmission, which occurs in other host/pathogen systems has also yet to be conclusively shown. The effects of many environmental variables on expression, transmission, dissemination and persistence of NPV are not clear. A better understanding of these influences is needed in order to effectively utilize these viruses in the management of pest lymantriid populations.

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EVALUATION AND SELECTION OF CANDIDATE
EUROPEAN MICROSPORIDIA FOR INTRODUCTION
INTO U.S. GYPSY MOTH POPULATIONS

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IMPORTANCE OF MICROSPORIDIA IN INSECT POPULATIONS

The Phylum Microsporida is a group of obligately parasitic eukaryotes many species of which are parasites of insects. Unlike many viral and fungal diseases of insects, Microsporidia do not typically cause dramatic epizootics during which large numbers of insects die over a short period of time. Most microsporidia are insidious in that they cause some mortality in all life stages of the insect; more important, they cause many sublethal effects such as reduced fecundity, slower developmental rates, and detrimental behavioral changes. For this reason microsporidian infections often go unnoticed in insect populations. Different species of microsporidia affect their hosts in a variety of ways depending on the tissues infected, the modes of transmission, the virulence of the microsporidium, and the initial spore dose.

As insect pathologists have become more involved in studies on the population dynamics of insects, they have begun to recognize that microsporidia are often important naturally occurring biological control agents affecting insects (Maddox, 1987; Canning, 1982) and that they influence the population cycles of many insect species. Microsporidia that affect the dynamics of insect pests have several similar characteristics: they have a relatively low IC-50; they are transmitted efficiently, both horizontally and vertically; they are moderately pathogenic; and much of the mortality caused by microsporidia occurs in the vertically infected progeny of infected females.

MICROSPORIDIA OF GYPSY MOTHS

Several species of microsporidia have been described and/or reported from European gypsy moths (Table 1). There are additional reports, both published and unpublished, of unidentified microsporidia infecting gypsy moths collected in Poland, Bulgaria and Iran. Thus, it is

likely that microsporidia are widespread in European gypsy moth populations.

Table 1. Microsporidia described or reported from European gypsy moths.

Microsporidian species	Location	Reference
<i>Nosema lymantriae</i>	Czechoslovakia	Weiser, 1957a *
<i>Nosema lymantriae</i>	Yugoslavia	Sidor, 1979
<i>Nosema muscularis</i>	Czechoslovakia	Weiser, 1957 *
<i>Nosema muscularis</i>	Spain	Romanyk, 1966
<i>Nosema muscularis</i>	USSR, Ukraine	Zelinskaya, 1981
<i>Nosema serbica</i>	Yugoslavia	Weiser, 1964 *
<i>Nosema serbica</i>	USSR, Ukraine	Zelinskaya, 1981
<i>Thelohania disparis</i>	Not given	Timofejeva, 1956 *
<i>Thelohania similis</i>	Czechoslovakia	Weiser, 1957a *
<i>Vavrata schubergi</i>	Czechoslovakia	Weiser, 1964
<i>Vavrata schubergi</i>	USSR, Ukraine	Zelinskaya, 1981
<i>Nosema</i> sp.	Portugal	Cabral, 1977

* Species description.

There are major taxonomic problems associated with differentiating the microsporidia of gypsy moths. The original descriptions of these species of microsporidia contain no ultrastructural details and very little information on life cycle. Thus, it is difficult to compare current isolates with the originally described species. These problems are not unique to gypsy moth microsporidia because ultrastructural observations have only recently become a necessary part of the procedure used to describe microsporidian species. The lack of ultrastructural and life cycle details is especially critical in identifying the microsporidia isolated from Lepidoptera because many species are dimorphic (Maddox and Sprengel, 1978). These dimorphic species, most of which are in the genus *Vairimorpha*, produce two types of spores. Unfortunately, the microsporidia described from the gypsy moth in Europe were described before the occurrence of dimorphism was recognized (see Table 1). Consequently, many of these species that were described earlier as mixed infections of *Thelohania* sp. and *Nosema* sp. may represent a single dimorphic species in the genus *Vairimorpha*. Therefore, it is essential that the microsporidia from gypsy moths be characterized ultrastructurally and, if appropriate, transferred to the appropriate genera.

The importance of microsporidia in the population dynamics of the gypsy moth in Europe is not clearly defined; however, there are several references suggesting that they can cause significant mortality and

contribute to the demise of populations in regions where the period between outbreaks is shorter, i. e., the Mediterranean Region, the Balkans, and Crimea (Weiser and Novotny, 1987). Unlike the nucleopolyhedrosis virus (NPV) of the gypsy moth, which kills massive numbers of larvae outright and frequently decimates high-density populations, microsporidia were found to infect only 30-40% of the individuals at the peak of the outbreak but had an insidious effect on the surviving population (Zelinskaya, 1980). Infected larvae developed at a slower rate and were subject to increased parasitization, the fecundity of surviving females was reduced from 2 - 9 times, and eggs produced by infected females incurred higher overwintering mortality. Further, the incidence of infection by microsporidia and its synchrony with gypsy moth outbreaks in Slovakia (Weiser, 1987) suggests that microsporidian infections precede the buildup of NPV during the progradation phase and may act as a precursor to the development of viral epizootics.

Although microsporidia have been recovered from gypsy moth larvae collected throughout Europe, microsporidia have never been recovered from gypsy moths collected from U.S. field populations (Podgwaite, 1981).

IMPORTATION OF PATHOGENS AS A BIOCONTROL STRATEGY

The importation of parasitoids and predators has resulted in the partial, substantial, or complete control of more than 157 insect species worldwide (Laing and Hamai, 1976). By contrast, few insect pathogens have been imported and then intentionally introduced into a pest population to provide a regulatory effect on succeeding generations (Harper, 1978). There are several examples where a pathogen that was accidentally introduced into a new location along with its pest host became a significant mortality factor in succeeding generations. The most noteworthy among forest insects were the introductions of the baculoviruses of the European spruce sawfly (Balch and Bird, 1944) and the gypsy moth (Glaser, 1915). The microsporidium *Nosema pyrausta* is an important biological control agent of the European corn borer in the United States but it too was introduced accidentally, presumably via the importation of contaminated parasitoids. To the best of our knowledge, microsporidia have never been intentionally imported into the United States for the control of insect pests.

Although it is not known why few exotic pathogens have been targeted for foreign exploration and eventual introduction into the United States for control of economic pests, we offer a possible explanation. Whereas protocols have existed for the importation of parasitoids and predators and quarantine facilities are maintained both here and abroad to receive candidate species, guidelines for the importation of entomopathogens have been developed only recently. These are discussed briefly in a forthcoming section. Exploration for parasitoids usually entails collecting large numbers of host insects which are then reared or

maintained until parasitoids emerge. Many of these activities can be performed by trained technical personnel. Searches for entomopathogen must be conducted by trained insect pathologists who can dissect and examine diseased tissues on site, identify the microbial pathogens, and then properly care for them, i.e., exclude contamination by secondary organisms and determine the best storage conditions for shipment. Whereas parasitoids usually are perceived as biological control agents that cycle in both low- and high-density pest populations and ideally maintain host populations below an economic threshold, pathogens, notably the baculoviruses, are perceived to cause epizootics only at high host densities and therefore to have little regulatory effect on their host populations before the economic threshold is exceeded. This is probably a misconception that reflects our poor understanding of many entomopathogens such as the microsporidia and their role in the dynamics of populations.

FOREIGN EXPLORATION

For several reasons we believed that there was scientific merit for importing European microsporidia as potential biocontrol agents of the gypsy moth: 1) microsporidia are known to be important biological control agents of many species of insects; 2) the foreign literature suggests that several species of microsporidia are important mortality-causing factors in the dynamics of gypsy moth populations in Eurasia; and 3) microsporidia have not been recovered from U.S. gypsy moth populations. With the support from a USDA Forest Service cooperative agreement and after consultations with many of our gypsy moth research colleagues in the United States, Maddox and Jeffords in the spring of 1986 searched for microsporidia in gypsy moth populations in Europe. Excellent cooperation was received from the following:

Portugal: Dr. Maria Teresa Cabral, Mr. Fernando Barbosa,
and Mr. Antonio Completo

Yugoslavia: Dr. Radovan Marovic and Mr. Aleksandar Mancic

Czechoslovakia: Dr. Jiri Vavra and Dr. Jaroslav Welsler

In Portugal, gypsy moth larvae were collected in cork oak forests within ca. a 150 km radius southwest of Lisbon. Larvae were returned to the Forestry Institute in Lisbon where tissues of the midgut, salivary glands, and the fat body of each larva were examined under a compound microscope. Nearly 1,700 larvae were dissected. Although the prevalence of microsporidian infections was low (< 5%) Maddox and Jeffords found two species of microsporidia infecting gypsy moths, a *Nosema* sp. and a *Vavraia* sp.

Gypsy moth populations were low in Yugoslavia in 1986--only 500 larvae from five different locations south of Belgrade were collected. No microsporidia were recovered from these collections.

Two different microsporidia from Czechoslovakia were obtained, both of which had already been isolated by Drs. Vavra and Weiser from gypsy moth populations in that country. These cooperators also provided a species of microsporidia that had been isolated from gypsy moths collected in Bulgaria.

CHARACTERISTICS OF MICROSPORIDIA OBTAINED FROM EUROPE

Five species of microsporidia were isolated from gypsy moth populations in Europe (Table 2) and returned to our laboratory for evaluation and potential introduction. We briefly discuss the characteristics and taxonomy of these species.

Species	Country	Tissues Infected
<i>Nosema</i> sp.	Portugal	SG, FB, MG
<i>Vavraia</i> sp.	Portugal	FB
<i>Vairimorpha</i> sp.	Czechoslovakia	MG, FB
<i>Vairimorpha</i> sp.	Czechoslovakia	MG, FB, SG
<i>Vairimorpha</i> sp.	Bulgaria	MG, FB, SG

FB = fat body; MG = midgut; SG = salivary gland.

We believe that the *Nosema* sp. from Portugal probably represents a new species, though it is similar to *Nosema serbica* (Weiser, 1964), a species described from gypsy moths collected in Yugoslavia and reported to occur in the Ukraine (Zelinskaya, 1980). The Portugal isolate should be compared to *N. serbica*; unfortunately, we do not have an isolate of *N. serbica* and there is no information on its ultrastructure and few details available on its life cycle.

The *Vavraia* sp. is similar if not identical to *V. schubergi*, a species that has been recovered from several species of Lepidoptera. It is not known if *V. schubergi* represents a single species with a extensive species variability, or several different species. Microsporidia similar to *V. schubergi* have been isolated from several species of Lepidoptera. These isolates usually have been considered subspecies of *V. schubergi*, but because no thorough studies have been conducted on these isolates, it is possible that they may be separate species (Sprague, 1977).

The three species of *Vairimorpha* obtained from Drs. Vavra and Weiser present taxonomic difficulties common to many microsporidia described from Lepidoptera before their dimorphic nature was recognized. The genus *Vairimorpha* was established as a repository for these dimorphic microsporidia. At present it is not clear whether these *Vairimorpha* spp. represent the dimorphic forms of *Nosema* and *Thelohania* spp. described previously (*Nosema lymantriae*, *Nosema serbica*, *Thelohania similis*, *Thelohania disparis*) or are new, undescribed species. To clarify these taxonomic relationships, we are conducting ultrastructural examinations and life cycle studies on the five species we now have. In cooperation with foreign cooperators, we plan to conduct parallel studies on additional isolates from Eurasian gypsy moths.

EXPERIMENTAL RELEASE OF EUROPEAN MICROSPORIDIA INTO U.S. GYPSY MOTH POPULATIONS

Regulatory Issues

Establishing guidelines for the introduction of nonindigenous pathogenic microorganisms has been viewed as a regulatory dilemma as there is a legitimate concern about introducing organisms that may pose an environmental hazard. Are such organisms to be regulated in a manner similar to that for pesticides, genetically engineered organisms, or parasitoids and predators? Because our experiments constitute the first deliberate effort to introduce nonindigenous microsporidia into the United States, and because the regulation of nonindigenous insect pathogens has been an enigmatic issue, we believe it is appropriate to describe in some detail the regulatory matters germane to our proposed introductions.

In December, 1984, the Environmental Protection Agency (EPA) proposed a mechanism for reviewing genetically engineered, nonindigenous, and pathogenic microbial pesticides under the Federal Insecticide, Fungicide and Rodenticide Act (FIFRA). Particular emphasis was placed on small-scale field trials (terrestrial field studies on plots of 10 acres or less) with genetically engineered and nonindigenous microbial organisms. All isolates of microsporidia that were recovered from gypsy moth populations in Eurasia are considered to be nonindigenous to the United States and therefore subject to review. The EPA established a notification policy as set forth in Federal Register Notice (Vol. 51, No. 123, p. 2313-2335, dated June 26, 1986) titled "Coordinated framework for regulation of biotechnology; Announcement of policy and notice for public comment." We have adhered to these regulations in our annual field releases and briefly discuss the protocols that have been established for past and future releases.

The nonindigenous microsporidia were imported into the United States under certification by the USDA Animal and Plant Health Inspection Service (APHIS). Laboratory studies were conducted for 2 years at the

Illinois Natural History Survey to determine the biological characteristics (host ranges, IC-50 and LD-50, tissues infected, etc.) and generic identity of the European microsporidia. After 2 years an Environmental Assessment (EA) was prepared for each organism as prescribed by the Agricultural Research Service (ARS) National Environmental Policy Act regulations (7 CFR 520), and was reviewed by APHIS. APHIS determined that, on the basis of the evidence submitted, there was no significant environmental impact, and issued a courtesy permit for a small scale-field test. The EPA recognized that there had been prior review and permits issued at the federal level by ARS/APHIS. The EPA then agreed to minimize its notification requirements under FIFRA for our field releases of microsporidia. Under this agreement, the following information was provided to the EPA for each microsporidian species to be introduced experimentally.:

1. Identity of the microorganism, including taxonomic characterization.
2. The geographic location and a description of the natural habitat from which the microsporidium was isolated.
3. The host range of the microsporidium.
4. A description of the experimental introduction including site location, crop to be treated, target pest, amount of material to be applied, and method of application.
5. Verification that the microorganism was subject to USDA/ APHIS regulation, and that the necessary APHIS permits were obtained for import, movement, and/or field testing of the microsporidia.

OBJECTIVES

The immediate objectives of our experimental introductions of microsporidia into gypsy moth populations were to:

1. Determine the best method for introducing these microsporidia into gypsy moth populations.
2. Estimate the horizontal transmission of the microsporidia in the field.
3. Evaluate the ability of each species of microsporidia to establish (overwinter) in U.S. gypsy moth populations.
4. Determine the spread of microsporidian infections outward from the central release point to other areas in the experimental gypsy moth population.

The long-range objectives are to establish the most appropriate microsporidia in U.S. gypsy moth populations and then evaluate their role as naturally occurring biocontrol agents in gypsy moth populations. These

objectives, however, will take many years to complete and logically follow the modest objectives listed.

METHODS

Introduction Methods

Although both inundative and inoculative releases have been used to introduce pathogens into insect populations, we chose an inoculative method involving the contamination of gypsy moth egg masses with small quantities of microsporidia (Jeffords et al., 1988). We contaminated egg masses by soaking 60 laboratory-reared egg masses (NJ F30 strain) per plot (woodlot) with the microsporidium to be introduced into that plot. Egg masses were soaked for 5 minutes in spore suspensions that contained a few drops of Tween 80 and concentrations of microsporidian spores varying from 1.3×10^5 to 3.3×10^6 , depending on the IC-50 and LD-50 for each particular species of microsporidium. The objective was to choose concentrations that would infect most hatching larvae but would cause little mortality in early larval instars. The treated egg masses were allowed to air dry for 2-4 hr and then were individually encased in a 2 x 2-cm saran mesh envelope before being transported to the field. The mesh gauge of the saran envelope was large enough to allow newly hatched gypsy moth larvae to easily exit the envelope.

At each woodlot the saran mesh packets containing the egg masses were distributed equally among 6-8 preferred host trees and stapled to the boles at approximately 1.5 m above the ground. We preconditioned the laboratory-reared egg masses so that they hatched within 2-3 days of the hatch of the feral population.

Several criteria were used to choose the experimental woodlots, all located in central Maryland. Woodlots were predominantly oak, were isolated from other woodlots and forested areas, and had a gypsy moth population estimated at 25-150 egg masses per ha.

We believe that there are several advantages to our egg-contamination method of introduction as opposed to inundative methods of release:

- (1) Very small quantities of the microsporidia are released into the environment.
- (2) Few if any nontarget organisms are exposed to the initial introduction of the microsporidia.
- (3) Laboratory-reared egg masses are free of the gypsy moth NPV which could interfere with the introduction process.
- (4) We can better evaluate the interaction between the microsporidia and the target gypsy moth population because we can better estimate both the number of infected larvae

- and the intensity of infections in larvae released into the woodlot relative to the density of the feral larval population.
- (5) The newly emerged larvae become infected as they exit the egg mass and exhibit their normal dispersal behavior; thus, the microsporidian infections are distributed naturally among the feral population.

By contrast, when a pathogen is sprayed inundatively onto a forested canopy it is virtually impossible to determine the proportion of the target population that is initially infected.

Larval Sampling Methods

Larval sampling methods have been described (Jeffords et al., 1988) but will be briefly reviewed here. Each woodlot was divided into four cardinal quadrants and into sampling zones as shown in Figure 1. Burlap bands were placed on all oak trees > 10 cm dbh within the sampling zone. Locations of burlap-banded trees within each site also were mapped so that the specific locations of all larval collections were known. Three sampling methods were used.

Method 1

First- and second-stage larvae were collected from foliage within 20 m of the center of each site to determine percentage of initial infection and spread of disease from the site center. Gypsy moth larvae collected in these samples were placed individually in cups containing artificial diet and reared at room temperatures until at least the 4th instar. This additional period of development allowed time for the infection to progress and enhanced its diagnosis. Larvae were then examined for incidence and degree of infection. For each larva collected, the site, quadrant, and sampling zone were recorded.

Method 2

Fourth- and fifth-stage larvae were collected from the burlap-banded trees to determine percent of infection, spread of disease from the site center, and persistence of disease within the populations. Approximately 10% of the larvae that were resting under the burlap were collected from each banded tree, placed individually in empty diet cups, and examined in the laboratory for infection.

Method 3

This method was used to determine percentage of infection on selected trees and was conducted at the same time as Method 2. All larvae remaining under the bands after the Method 2 sampling were collected from randomly selected banded trees at various distances from the site centers. All larvae were removed from individual trees, placed together in a container, and dissected within 12 hr after they were collected.

Diagnosis of Infections

Microsporidian infections were diagnosed in the laboratory by dissecting each larva, preparing wet tissue mounts and determining the presence and abundance of spores by observing the wet mounts under a phase-contrast light microscope. Depending on the species of microsporidia being diagnosed, midgut, fat body, and/or salivary glands were examined. The intensity of infections in individual larvae were subjectively rated as light, medium, or heavy depending on the number of spores present.

RESULTS

Because the specific results of our experimental introductions are lengthy (Jeffords et al., 1988) we will provide a synopsis of what we consider the major findings in our study.

The egg-contamination method was an acceptable procedure for introducing all five species of European gypsy moth microsporidia. For species such as *Vavraia* sp. and *Nosema* sp., the contamination method works best because the LD-50 and the IC-50 are far apart, making it easy to select a concentration of spores that will infect most of the larvae without causing much mortality. *Vairimorpha* spp. are much more pathogenic than *Vavraia* sp., making it more difficult to select a spore concentration that will infect most larvae and kill few. It is possible that for some other species of microsporidia the egg-contamination method is less appropriate.

Our larval sampling demonstrated that in all woodlots, infected larvae dispersed from the center release trees, where contaminated laboratory-reared egg masses were placed, into other areas of the woodlot. Thus, the spread of infection throughout the woodlot was facilitated by the natural dispersal habits of the larvae. Results from our dissections indicated that some degree of horizontal transmission was occurring in populations of gypsy moths infected with all five species of microsporidia.

One species, *Nosema* sp. from Portugal, overwintered and persisted in the gypsy moth population from 1986 to 1988; however, *Vavraia* sp., also from Portugal, did not persist. The three species of *Vairimorpha* were first introduced experimentally in 1987, so it is too early to evaluate overwintering success.

FUTURE STUDIES AND OBJECTIVES

Although we are optimistic about the results of our initial releases and the potential role of microsporidia in the dynamics of gypsy moth

populations in the United States, we recognize that additional studies are needed. Several of these can be conducted exclusively in North America, while others should be conducted in cooperation with our colleagues in other countries.

Acquisition of additional microsporidian isolates.

In selecting candidate pathogens for introduction, isolates should be sought that are particularly well adapted to the host's specific geographic or ecological environment. We have initially introduced microsporidia that were available to us into gypsy moth populations in the most expedient locations. It is likely that certain species or strains of microsporidia will become established more readily and be more successful biological control agents in some areas of the United States than in others. We believe that there are many additional isolates and species of microsporidia infecting gypsy moths in Europe and Asia that should be acquired and evaluated for subsequent introductions.

Taxonomy

As emphasized earlier, previously described species of microsporidia from gypsy moths as well as new isolates must be examined ultrastructurally to confirm their generic placement. There also is a need for studies to determine intraspecific variability and geographic distribution of species of microsporidia that infect gypsy moth populations worldwide.

It is extremely important that we be able to unequivocally identify any microsporidia recovered from gypsy moth populations as the microsporidian species that we released. To this end we are developing rRNA sequences for all microsporidia from the gypsy moth to assist us in identification and taxonomic placement.

Laboratory evaluations

Additional laboratory studies will be conducted to further characterize the five species of microsporidia we now have as well as additional isolates we may obtain in the future. We need to adapt the egg contamination method for more pathogenic species of microsporidia, to obtain quantitative information on the vertical and horizontal transmission of all available isolates, and to determine their sublethal effects on gypsy moth life stages. Ultimately, studies will be designed to evaluate the interactive effects of each isolate with other biological control agents affecting gypsy moth populations.

Field studies

Our field experiments have been aimed at answering two questions: what is the most appropriate method for introducing microsporidia into gypsy moth populations, and can introduced European gypsy moth microsporidia persist in U.S. gypsy moth populations?

If these nonindigenous microsporidia can persist in U.S. gypsy moth populations, and it appears that at least one species can, then many additional questions should be addressed, including the following:

- (1). What is the effect of these microsporidia on the population dynamics of the gypsy moth?
- (2). What factors are important in the horizontal and vertical transmission of the microsporidia within a population?
- (3). Should we consider a multiple release of several isolates of microsporidia rather than single-species releases?
- (4). Should we consider inundative releases or continue using inoculative releases?

In the months ahead, and after consultation with other scientists, we will address these questions and many others before we prioritize short- and long-term research needs.

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PREDATION: ITS INFLUENCE ON
POPULATION DYNAMICS AND
ADAPTIVE CHANGES IN
MORPHOLOGY AND BEHAVIOR
OF THE LYMANTRIIDAE

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INTRODUCTION

Predation is a major suppressive force on natural insect populations (Holling, 1965; Murdoch & Oaten, 1975). Although Connell (1975) suggests that predation is the single most important biotic factor affecting natural communities, most biologists believe it to be the third most important limiting factor, with food and intraspecific competition being first and second, respectively. One of the main characteristics of the living organism is that it possesses an overwhelmingly complicated system of mechanisms that protects it against adverse influences of the environment including predation (Tinbergen, 1951). Because the magnitude of predation depends on a large number of variables that interact with one another (Holling, 1959) it is exceedingly difficult to generalize about the role of predation on a particular lymantriid (prey) population. Predators, however, are often regarded as an essential factor in the regulation of endemic forest pest insect populations (Buckner, 1966; Campbell & Sloan, 1977; Mason & Torgersen, 1987; Wallner, 1987).

Two related but separate issues are involved in discussing the relationship between predation and Lymantriidae. First, what is the role of predation in the dynamics of insect populations? Second, what is its potential use in integrated pest management (IPM)? Our perceptions of the role of predators on the population dynamics of Lymantriidae and its use in pest management have been strongly influenced by (1) reports of early naturalists, whose observations were usually anecdotal in nature and (2) the realization through recent studies (Smith & Lautenschlager, 1981; Smith, 1985) of the complexity of predator-prey interrelationships that makes practical implementation of predation theory difficult. Successful management depends on our knowledge of the role of predation; however, insufficient basic knowledge is available to develop realistic management scenarios at the current time.

The objectives of this paper are threefold. First, to briefly discuss the evidence for an adaptive evolutionary influence by predators on the morphology and behavior of Lymantriidae. Second, to discuss the effect of predation on the population dynamics of Lymantriidae. Third, to discuss some mechanisms of predation that influence predation rate.

Because all of my research has been with gypsy moth (*Lymantria dispar*), the emphasis in this paper is on that species. However,

the discussion on adaptive relationships and on the mechanisms that interact to influence the level of predation is applicable to Lymantriidae.

PREDATORS AS AN AGENT IN NATURAL SELECTION

The relationship between predator and prey in the "game of survival" is as old as natural populations of organisms. Therefore, it seems appropriate in an overview of predation to begin with a coevolutionary perspective. Since the first interactions between predator and prey, a variety of adaptive strategies and/or characteristics in order to gain a survival advantage of one over the other have evolved. Dawkins & Krebs (1979) suggest that prey actually have an inherent evolutionary advantage over predators. Selection by the predator on the prey for defenses is stronger than selection by the prey on the predator for hunting (Vermeij, 1982). In spite of this, no prey has evolved a perfect defense. Actually, the selective advantage of a particular defense mechanism may be quite small but enough to account for its evolution in a variety of species. Ford (1957) considers an improvement of 1 or 2 percent in a prey's chances of evading a predator as being highly significant. Price (1987) reported "...responses of insects to hunting predators have provided evolutionary biologists with some of the best evidence available on the force of selection and the precision of the evolutionary process." He suggests that a defense mechanism confers a 30% advantage or more over individuals without the defense.

Today, it would seem difficult for a naturalist to dispute the impact that natural enemies (including predators and parasites) have had on the evolutionary biology of any insect species and that all have developed to some degree an anti-predator defense. That natural enemies have had a profound affect on Lymantriidae is even evident in the family common name "tussock moth," a name derived from the "tussocks" or conspicuous dorsal tufts of protective hair on certain larval segments of some species.

The Lymantriidae is a highly diverse family. Although some 2,500 species have been described worldwide, lymantriids show only modest diversity in temperate regions. Worldwide descriptions of Lymantriidae are remarkably similar. Tillyard (1926) wrote the following description of Lymantriids in Australia and New Zealand:

Larvae very hairy, often with tufts or brushes of hairs, sometimes with urticating hairs, frequently conspicuously colored and distasteful to birds; many species have gregarious larvae living within a large bag-like shelter, spun between twigs and leaves of trees. Pupae in a cocoon often with larval hairs spun into it.

Metcalf et al. (1962), in describing North American species, stated:

...the larvae make up for the plainness of their parents. They are frequently of striking or beautiful appearance,

bearing tufts or pencils of beautifully cropped, close-set hairs of gaudy colors or brilliantly colored tubercles partially concealed by the hairs of their bodies. Hairs play an important part in the economy of life of these insects. Some of the hairs of the larvae are netting and no doubt serve to protect their lives from certain enemies;

It is suggested from these descriptions and those of others (Forbes, 1948; Seitz, 1913; Craighead, 1950) that predators have had a major influence on the morphology of Lymantriidae and subsequently an array of defensive mechanisms have evolved (i.e., changes in color, size and pattern of hairs, urticating spines and tubercles). It is most probable that the principle selective force for particular color patterns is predation by vertebrates (especially birds) (Ford, 1945).

Harvey & Greenwood (1978) and Jarvi et al. (1981) write that certain insect species "have evolved distastefulness as a means of defense against predators...and...many such unpalatable species are brightly colored." Bright aposematic coloration is common among Lymantriidae. According to Harvey et al. (1983), three conditions of biological importance favor the evolution of aposematism and seem particularly applicable to my observations pertaining to gypsy moth larvae. First, aposematism is favored when prey families are found at low densities and, second, the predator must easily recognize the prey and remember. It has been shown that birds quickly learn to avoid aposematic prey after only a few trials and remember to associate particular color patterns in prey for several months (Brower, 1958; Brower et al., 1963). Third, the prey must not be too easily recognized. The aposematic coloration of the gypsy moth is conspicuous only when viewed closely by a predator; however, when viewed from a distance, even in aggregations, they appear cryptic. This relationship appears to be characteristic of lymantriids even though it would seem less obvious with the brilliantly colored larvae of *Dasychira pudibunda*, a tussock moth distributed in Europe and the forest zones and steppes of European USSR. The full-grown larva is yellow-green and is cryptic on or near the foliage in the crown until pupation. However, the larvae are very conspicuous when viewed closely. They have black transverse cuts and erect bundles of yellow hairs on the 4th and 7th segments and a long reddish tail in the 11th segment.

Bright coloration among unpalatable diurnal prey is usual (Turner, 1975; Gittleman & Harvey 1980). Palatability is difficult to determine and various defensive adaptations will affect it differently. It is not usually because of color alone but rather a combination of disagreeable attributes such as hairiness, bad flavor, and conspicuous coloration that affords the greatest protection against predators. Taken individually, hairiness seems to offer the greatest protection from the attack of birds (Judd, 1899). Except for cuckoos, I am unaware of any species of birds that has adapted itself to specialize in hairy caterpillars. It appears all others prefer hairless larvae.

Many Lymantriids have developed hairiness to a high degree and in certain regions of the body grow urticating hairs especially

modified for defense (example, browntail moth, Euproctis chrysorrhoea). An interesting account of the importance of these hairs to survival in the yellowtailed moth (E. similis) in Europe was presented by Ford (1955). The hairs on this lymantriid actually take the form of barbed spicules and protect throughout the life of the moth. Most insect-eating birds avoid eating the pupa because the irritating spicules are spun up among the silk. When the female moth emerges, she collects the spicules on the yellow tuft of hair on the end of the abdomen. Therefore, the yellow-tail moth (in the female) is as irritating as the larva. The spicules produced by the larvae are then used to protect the eggs as they are incorporated into the yellow-down egg mass during egg deposition.

In this discussion of adaptive influence of natural enemies of Lymantriidae, it is appropriate to focus on the morphological and behavioral changes in the immature stages of L. dispar. Larvae of gypsy moth undergo complex changes in morphology and behavior immediately following the third molt. It is generally accepted that older (IV-VI instar) larvae within innocuous densities descend from the canopy at dawn to aggregate in sheltered places and ascend at dusk to resume feeding. It is important to note that the timing of larval movements to and from feeding and resting sites occurs before and after birds are foraging especially actively, thereby reducing risk to predation by birds (Allen, 1925). Interestingly, Campbell & Sloan (1976) were the only researchers in North America to hypothesize that this behavior evolved in order for larvae to evade natural enemies in Europe in spite of all the evidence to suggest such a relationship. They made no reference, however, to the morphological changes.

Coincidental with this behavioral change are morphological changes. It is my contention that these changes coevolved with behavioral changes as adaptive protective mechanisms to reduce mortality from natural enemies, particularly predators. Changes in coloration would appear to serve little function against parasites as larvae moved away from the canopy. Certainly, movement should increase vulnerability to predators and additional protection of larvae in getting to and from resting locations, often 20 m from where they fed in the canopy, was essential.

In larval instars IV-VI, the head of the gypsy moth has yellow markings that interrupt the previously all black head. It is my contention that they create the illusion of two large "eye" spots. The body remains dusky or sooty-colored and hairy; however, there is now a prominent double row of five pairs of blue tubercles followed by a double row of six pairs of red tubercles on the dorsum. Each tubercle bears numerous urticating setae.

Although it has not been shown experimentally for gypsy moth to what degree the bright coloration (red and blue tubercles) or "eye" spots intimidate predators, it is reasonable (based upon studies with other Lepidoptera) to assume they serve a similar function. Caterpillars of several species have eye spots with some being very large, almost cartoon-like (Owens 1980). Small birds have an innate fear of large eyes and are easily startled. Blest (1957) tested the effectiveness of frightening patterns on bird foraging behavior. In his experiments, birds were somewhat troubled by even a pair of vertical or parallel bars and were progressively frightened as the

pattern became more "eye-like." Certainly, this would suggest that the large "eye" markings on the head of gypsy moth instars IV-VI would be sufficient to trigger a startle response in many birds and thereby reduce predation. Adding credence to my contention is the fact that electron microscopy failed to reveal any structural differences between the "eye" bands and the rest of the head capsule. Also, I am unaware of any reported physiological function of these bands.

Whalen et al. (in press) present further evidence that supports the idea that predation by birds could have had a major influence on these adaptive changes. Heritable propensity to attack gypsy moth larvae, measured in an aviary, was greatest among those species that forage in the mid and upper canopy. Therefore, the evolution of a behavioral pattern to move away from the stratum where the greatest amount of predation would likely occur would have obvious survival value to the species. In addition, their study concluded that earlier instars are preferred over later instars, giving further credence to the hypothesis that earlier instars are at greatest risk to predation. It is also important to note that the en masse arrival of migratory insectivorous species, particularly warblers, which also forage in the canopy, occurs during the availability of instars I-III. Recent data of stomach analysis of insectivorous birds show a significant decline in consumption of mature larvae (larvae after the third molt). Rejection due to increased size alone is not a likely explanation. Jones (1932) found that when birds were fed Lepidoptera and Coleoptera of various sizes (small, medium and large) the highest acceptability within each group was for the largest.

There is also evidence to support the relationship between distastefulness and conspicuous coloration in gypsy moth larvae. Aside from protective hairiness, which has a major influence on palatability, it has been shown that fifth instar larvae contain four times the histamine content of first instar larvae (Sharma et al., 1982). It is also possible that increased tannin levels in maturing larvae that fed on oaks (*Quercus* spp.) will further reduce palatability. The gut of gypsy moth larvae is rejected by white-footed mice in the wild (Smith & Lautenschlager, 1978).

Because these changes in morphology and behavior appear so abruptly in the development of the gypsy moth, adaptive theory would suggest that survival of later instar larvae is a critical link in the next generation. It is argued that instars IV-VI is a key age interval in deciding whether sparse populations of *L. dispar* will remain at innocuous levels (Campbell & Sloan, 1977).

Evidence shows that predators have had a profound affect on Lymantriidae. They have changed their appearance and their behavior. These adaptive changes persist in natural populations today suggesting that the forces that brought about these changes are still operative and are still potentially regulating factors in the dynamics of Lymantriidae.

Understanding the dynamics of Lymantriidae requires the detailed knowledge of a host of complex, interrelated factors interacting on the insect's life system. Predation is one process that can have a substantial impact on populations of lymantriids. Although accounts of predator interactions with a variety of lymantriid species are commonly found in the literature, the roles of predation on Douglas-fir tussock moth (*Orgyia pseudotsugata*) and the gypsy moth are the only well-documented cases. Typically, many tussock moth populations are relatively stable at low densities most of the time and only occasionally erupt to outbreaks (Mason & Luck, 1978). Most gypsy moth populations are usually maintained at innocuous densities once the original outbreak has subsided (Campbell, 1981). Within both of these sparse, stable population systems, predation seems to play a major role (Campbell & Sloan, 1977; Mason et al., 1983; Mason & Torgersen, 1987).

Early naturalists studying predators of the gypsy moth emphasized the importance of birds and Forbush and Fernald (1896) considered them to be the primary predators of gypsy moth. Subsequently, other studies have suggested that the regulatory impact of predators on endemic gypsy moth populations in North America results predominantly from the accumulative effect of birds and mammals (Campbell & Sloan, 1977; Smith & Lautenschlager, 1981). The greatest impact is attributed to predation of pupae by small mammals. The impact of invertebrate predators on gypsy moth populations has not been well documented. Smith (1985), studying risk to predation by pupae placed at various densities in selected microhabitat locations, determined that pupae located above the ground were more vulnerable to predation by invertebrates than vertebrates.

Calosoma sychophanta, a large carabid beetle imported from 1906 to 1926, may be abundant during outbreaks and can account for as much as 25% of pupal mortality (Campbell, 1967). However, because it depends on prey density, it is not effective on sparse populations. This is also true in Europe (Patočka & Capek, 1971).

Campbell & Sloan (1977) hypothesized that year-to-year numerical stability (among the sparse populations they studied) was determined largely by a combination of predaceous birds that tended to concentrate on instar IV-VI larvae, and small mammals, especially *Peromyscus leucopus*, which tended to concentrate on the pupae. Unfortunately, their study produced ambiguous results regarding the actual role of birds. The exclusion of birds alone produced no effect while the exclusion of mammals plus birds had the greatest effect on change in gypsy moth egg-mass density.

Although nearly 50 species of birds are known to occasionally eat gypsy moth, their effect on the dynamics is less clear than that of small mammals. Predation of gypsy moth by birds at sparse densities is variable and can be very low. Diets (based on stomach content analysis) of 251 individuals of eight insectivorous bird species revealed that only stomachs of the black-capped chickadee (*Parus atricapillus*), tufted titmouse (*Parus inornatus*), and yellow-billed cuckoo (*Coccyzus americanus*) contained gypsy moth

(Whitmore et al., 1987, unpublished progress report). Smith (1985) examined frequency of occurrence of gypsy moth in 557 stomachs of 17 species of insectivorous birds collected in areas of high gypsy moth (outbreak) densities in Massachusetts and New York. All but two species had eaten some gypsy moth; however, frequency of occurrence was < 25% in 13 species. Overall, 24% ate some gypsy moth (19% with cuckoos excluded from sample). Evidently, hairs on the larvae caused a significant reduction in predation by birds as evidenced by the high rate of predation of other hairless Lepidoptera. Predation by birds actually involves two separate periods (instars I-III and instars IV-VI). Birds inherently prefer early instars over later instars of gypsy moth. Therefore, the *en masse* migration of insectivorous birds, especially the warblers, which coincides with the availability of these young larvae, may account for high mortality of these larvae while they are still vulnerable in the canopy. Predation by birds of instars IV-VI, although still of potentially important magnitude, would decline dramatically due to a combination of larval defense mechanisms and the availability of alternative foods.

Bess et al. (1947) were the first to suggest that small mammals (mice and shrews) were important predators of the gypsy moth. Bess (1961) indicated that in mesic forests survival is low when gypsy moths rest in the litter and innocuous populations predominate. Campbell & Sloan (1976, 1977) presented further evidence that predation by vertebrates is essential in maintaining low populations and showed conclusively that small mammals are a major factor in the dynamics of these populations. Campbell & Torgersen (1983) further reported that birds and small mammals contributed about 27% of the killing power during the gypsy moth generation, and about 47% between instar V and adults. In this life system, small mammals compensated for birds but not the converse. However, to conclusively answer the question of "regulation" by predators, it still must be shown that changes in mortality rates due to predators and not other agents occurs prior to changes in the overall dynamics of the gypsy moth.

Survival of pupae at different densities and in selected microhabitats (litter, bole, bark flaps) was studied by Smith (1985). In this study, predation was significantly ($P < 0.001$) greater in the litter than on the bole or under bark flaps at all densities (Table 1). However, vertebrates and invertebrates evidently differed in foraging behavior. Essentially, all vertebrate predation was by small mammals. At the two higher densities, small mammal predation in the litter accounted for most mortality. Evidently, at the lowest density, litter aggregations (Table 1) were too scarce to be found whether by random encounter or by a learning-search-image response. Invertebrates, being omnipresent, attacked pupae uniformly in all locations and at all

¹Whitmore, R.C., Cooper, R.J., and Smith, H.R. 1987. Vertebrate predator and gypsy moth population interactions and their influence on defoliation. Unpublished Progress Report, Gypsy Moth Program. 7 pp.

Table 1. Percent survival of gypsy moth pupae within different microhabitats and at different densities. (Smith, 1985).

No./ha	Location	Percent- age eaten by verte- brates	Percent- age eaten by inver- tebrates	Percent- age dead of other causes	Percent- age sur- vival
2,491	Flap	13	19	15	52
	Bole	14	17	17	52
	Litter	45	22	8	25
712	Flap	7	15	11	68
	Bole	22	19	11	49
	Litter	42	25	7	26
237	Flap	2	13	6	78
	Bole	3	14	8	76
	Litter	9	37	3	52

densities. Most invertebrate activity was attributed to ants. The high proportion eaten by invertebrates (37%) at the low density may have resulted from reduced competition from the small mammals. Moth survival was greatest at all densities under bark flaps.

Figure 1 shows the pattern and amount of predation that occurred at each aggregation within the high-density area. In the illustration it is apparent that invertebrate pressure is much more uniform between locations than predation pressure from the vertebrates. Clearly, mortality by vertebrates (specifically small mammals) was concentrated in the litter. This illustration would also suggest an example of Darwinian selection (see Ford, 1945; Dobzhansky, 1970; Darlington, 1980) by gypsy moth larvae to rest and pupate on the bole if it can be shown that gypsy moth larvae have a genetically based difference in behavior for the selection of their resting locations. Predation by birds on early instars in the canopy may have resulted in selection for a behavior that involves seeking refuge in bark crevices, flaps, and litter. This behavior may then subsequently reduce mortality by birds and/or other natural enemies. However, larvae that attempt to pupate in the litter have been shown here to have the lowest survivorship. Therefore, predation by small mammals in the litter would favor the survivorship of individuals in the gypsy moth population to rest and pupate above the litter. Because predation by invertebrates seems to be more uniform there does not appear, on their part, to be any spatially related survivorship or any selective advantage to relocate. Conversely, predation pressure from small mammals could be the selective agent causing pupation sites above the litter. Observations made during a 1986 visit to the Ukraine, USSR, also support this contention. No larvae were observed resting in the litter and all egg masses (previous generation) were found only at

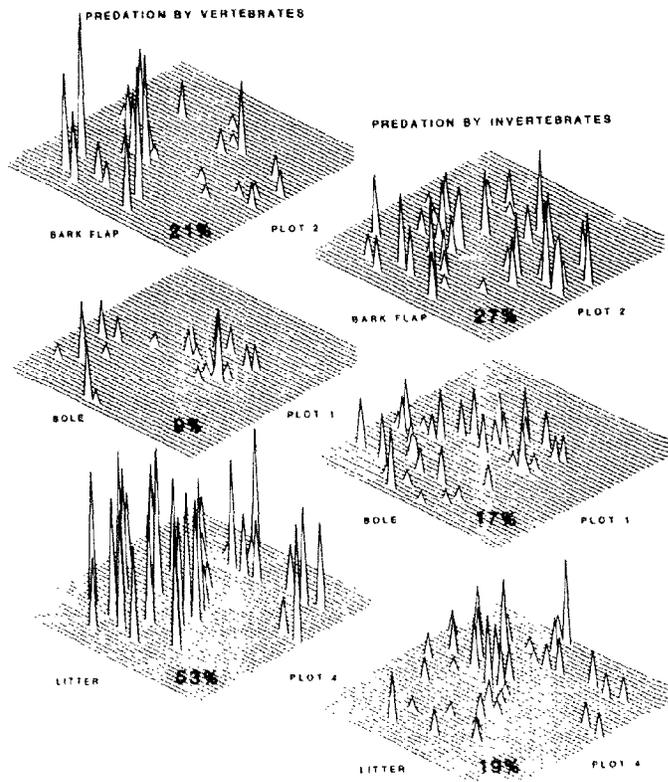


Fig. 1. Pattern and percentage of predation of gypsy moth pupae by vertebrates and invertebrates within selected microhabitats. (Peak indicates range of mortality from 1 to 12.)

the base of the tree. A census of small mammals estimated the combined density of *Apodemus* spp. and *Clethrionomys glareolus* to be nearly 100 per hectare, which would certainly represent a formidable predation potential. Rothschild (1958) observed remains of gypsy

moth larvae and pupae in the stomachs of Apodemus sylvaticus and A. flavicollis in the Soviet Union. In the U.S., Campbell et al. (1975) reported that bark flaps provided virtually the only pupation locations within the highest density stratum studied where female pupae had a reasonable survival probability. Interestingly, within the lowest density stratum studied only about 16% of the female insects pupated in places other than the litter or bark flaps, but survivorship of these from "other places" represented nearly half of the adult females and, presumably, egg masses within that stratum. References to vertebrate predation on gypsy moth in the Eurasian literature are fairly common and all except Rothschild (1958) emphasize the importance of birds. Bruns (1960) concluded that birds can remove substantial proportions of low-density insect populations and Turcek (1950) noted that birds probably play a role in maintaining gypsy moth populations at low levels. Furuta (1982) reported that birds intensely devoured the larvae of higher density subpopulations and caused density-dependent mortality on the population. He concluded that predation by insectivorous birds was the most important factor in determining the density within innocuous density levels. These observations are certainly in contrast to gypsy moth populations in North America. Another difference is the predation by birds of egg masses. In Europe, bird predation of egg masses has been reported to average 34% and up to 90% in sheltered areas (Schaefer, 1980). In the Soviet Union, seven species of birds reportedly exterminated up to 35% of the overwintering eggs (Kondakov, 1961). Reichart (1959) reported, following a gypsy moth outbreak, that tits (Parus sp.), nuthatches, and tree-creepers attacked 34-76% of the egg masses and destroyed from 25% to 78% of the eggs. In an attempt to gain insight into the amount of predation by birds on egg masses in North America, 104 egg masses located predominantly on oak (Quercus spp.) were monitored from January to April in Connecticut. Forty-nine percent were at least partially destroyed and 13% were completely destroyed presumably by birds. White-breasted nuthatch (Sitta carolinensis), black-capped chickadee (Parus atricapillus), and Downy woodpecker (Picoides pubescens) were observed eating eggs.

Douglas - fir tussock moth
Orgyia pseudotsugata

Considerable effort has been made in recent years to understand the dynamics of tussock moth populations particularly the processes that maintain sparse, stable populations. When tussock moth numbers are low and food is plentiful, vertebrate and invertebrate predators are a primary cause of mortality (Mason & Wickman, 1988). Predation is considered to be a major regulatory process in sparse populations (Mason et al., 1983; Mason & Torgersen, 1987). All life stages of the tussock moth are eaten by predators. However, unlike the gypsy moth (impact on pupae), the greatest impact by predators is on larvae. The most important factor affecting change was the disappearance of larvae, which accounted for 63% of the total generation mortality and exceeded by several times the other causes of mortality (Mason et al., 1983). Predation of pupae and eggs

accounted for 9% of the total generation mortality. Because predators often consume the entire insect, "predation" and "disappearance" are difficult to quantify. Mason and Torgersen (1987) found that vertebrate and invertebrate predators were responsible for removing a large portion of the larvae that disappeared. Spiders and predaceous ants commonly attacked small tussock moth larvae (Mason & Torgersen, 1983), and a variety of passerine birds preyed on larvae of all ages but were significantly responsible for the removal of late instar larvae. Torgersen et al. (1983) identified 21 species of birds as predators of the tussock moth.

Early-instar larvae appeared to be preyed on mostly by foliage-foraging arthropods, and late larvae by birds. Although individually none of the estimated mortality factors qualified alone as a key factor (based on analysis of k-values), Mason & Torgersen (1987) concluded that predation was independent of prey density and the major mortality factors interacted in a compensatory way so that their combined effects were delayed density-dependent and regulatory.

PREDATION BY OTHER LYMANTRIIDAE

With the exception of one reference by Jensen (1986), a search of the literature failed to reveal any studies of other lymantriid-predator relationships except for general accounts of an anecdotal nature. Jensen reported that during a decline phase following an outbreak of nun moth (*Lymantria monacha*) in Denmark, 81-86% of adult mortality could be attributed to birds. The following year a decrease in larval and pupal density from 1 to 2,000 larvae per tree to almost nil could only be explained as a result of bird predation. Pratt (1972), writing about the browntail moth in Maine, considered birds, next to disease, to play the most important role in helping to check the spread of this insect. Species commonly known to feed on other hairy caterpillars were mentioned as predators, however, he felt the northern oriole (*Icterus galbula*) and blue jay (*Cyanocitta cristata*) were the most important. Similarly, birds were reported to "undoubtedly consume many larvae of the satin moth," (*Leucoma salicis*) (Burgess, 1927). Unfortunately, from these and numerous other reports one can determine little regarding the role of predators in the dynamics of these insects.

Conversely, based on what is known regarding gypsy moth and Douglas-fir tussock moth, it is reasonable to hypothesize that predation is an integral process in sparse stable dynamics of other lymantriids.

UNDERSTANDING MECHANISMS OF PREDATION

Over the past decade our knowledge of the basic importance of predation on sparse stable gypsy moth populations has actually changed little while our understanding of the interrelationships between mechanisms that effect the magnitude of predation has changed dramatically.

It is evident from the earlier discussion in this paper that defense mechanisms influence predation rates. Yet, in spite of them, predators often appear to regulate certain sparse stable insect populations. It is also known that these insect populations are regulated indefinitely and the occurrence of outbreaks testifies to the inability of predators to maintain their control. Understanding the mechanisms that contribute to the variability in predation impact is essential from an IPM perspective. While population release is a complex phenomenon, tied to several biotic and abiotic factors, reduced predation could be a releasing mechanism.

Although the various components of predation are well known (Holling, 1959), their interactive effects on the magnitude of predation and the role of predation to the susceptibility of forests to defoliation by gypsy moth has not been well documented. The relationships between predator diversity and density, prey vulnerability and microhabitat, alternative foods and site characteristics (structural features offer refugia for prey and vegetative cover for predators) to survivorship of gypsy moth were examined in a series of comparative studies conducted with stocked cohorts of pupae in a resistant and a susceptible forest in Vermont.

New England forests vary in susceptibility to defoliation by gypsy moth. Susceptible forests characteristically are on dry, open ridgetop sites where trees (mainly oaks) are scrubby with numerous structural features (i.e. bark flaps, wounds and deep bark fissures) that provide refuge for the gypsy moth (Valentine & Houston, 1979). These sites are open and have little or no leaf litter. The predominance of lowbush blueberry (*Vaccinium* spp.) is a positive index of susceptibility (Bess et al., 1947). Blueberries, along with huckleberries (*Gaylussacia* spp.) provide small mammals an ample supply of a very palatable food at the same time gypsy moth pupae are available. By contrast, resistant stands are mesic. They are commonly areas of deep loamy soils and possess well-developed litter layers. Resistant stands are well stocked with vigorously growing trees that are relatively free of gypsy moth refugia. Understory plants often create a well-defined shrub layer. In addition, the closed nature of resistant stands is not favorable to the production of berries.

Species diversity and density was shown to be greater in resistant than susceptible stands for both birds and small mammals (Smith, 1985). Numbers of avian species and density of birds were, respectively, 3 and 4 times greater in the resistant stands. Shrew density (*Blarina* and *Sorex* spp.) was also 2-1/2 times greater in the resistant stands; however, *Peromyscus*, a habitat generalist, had densities that were remarkably similar between sites. The importance of reduced predator abundance to increased insect population growth has been demonstrated experimentally by Campbell & Sloan (1977) and also reported by Khanislamov et al. (1962) in the

Soviet Union. This would suggest that differences in vertebrate predator communities can directly influence stand susceptibility. Structural features (previously mentioned as refuges for insects) also contribute significantly to predation impact potential. As the number of refuges increases, the number of insects resting in the litter decreases. Therefore, survival of gypsy moth larvae and pupae will generally be much higher in susceptible stands because of reduced vulnerability to litter foraging predators (Fig. 1). Comparative survivorship curves of gypsy moth pupae (Figs. 2, 3) indicate that differences exist between susceptible and resistant stands. For example, in 1985 all pupae (all locations, litter-bole-bark flap) were destroyed by predators within 4 days in the resistant stand compared to 12 days in the susceptible stand. Detailed methodology and results of these studies will be presented in subsequent manuscripts. Average *P. leucopus* densities (based on minimum number known alive, 1.2 ha) in the resistant and susceptible stand for 1985, 1986, and 1987 were 65, 43, and 28, and 61, 42, and 34, respectively. Coinciding with the trend in declining mouse density was an obvious annual increase of berry abundance on the susceptible ridge site. In addition to the various factors already mentioned that influence site susceptibility, the abundance, availability, and palatability of alternative foods are of major importance. The opportunistic foraging behavior of *P. leucopus* is evident in Table 2. In the susceptible stand, as the abundance of ripe berries increased, their consumption increased with a corresponding decrease in the consumption of arthropods which undoubtedly reduced the effectiveness of these important predators. Conversely, in the resistant stand, the summer diet of mice remained predominantly arthropods due to the unavailability of berries. The

Table 2. Percentages of major food groups observed in stomachs of *P. leucopus*.

Food	June 7-10	June 21-24	July 6-7	July 19-21	August 9-10
-----Susceptible-----					
	(4)	(8)	(6)	(5)	(7)
Arthropods	52	98	79	59	13
Berries	0	0	19	32	86
Mast	48	0	0	8	0
-----Resistant-----					
	(9)	(11)	(13)	(15)	(16)
Arthropods	52	37	86	93	90
Berries	0	0	0	2	7
Mast	48	60	1	2	0

(n) Bryant Mountain, 1983.

unanticipated selective logging of the resistant stand (fall 1983), which opened the canopy, caused a rapid influx of raspberries and

blackberries along the logging roads. This resulted in a significant change in the foraging behavior and food selection of these mice. Consumption of berries (volumetric percentage) increased from 5%-22% by 1985. Berries have continued to increase since 1985 and its effect in combination with a declining mouse population is reflected in the 1987 survivorship curve (Fig. 2). The influence of an alternative food that reduces predator impact is especially appropriate when discussing lymantriids because of the

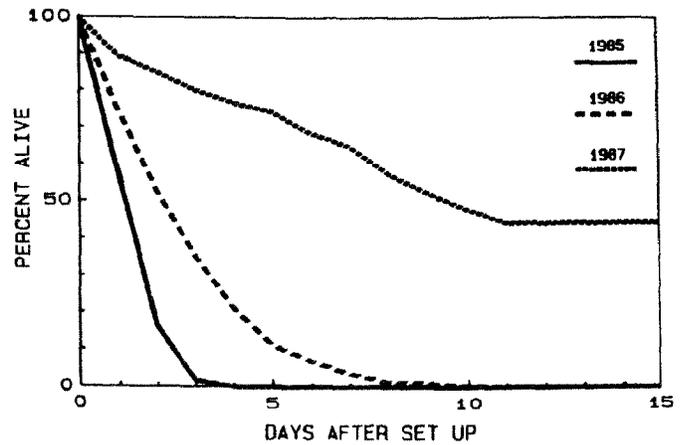


Figure 2. Survivorship curves of gypsy moth pupae in a resistant forest.

hairiness of these larvae and some pupae. Not only will the coincidental availability of berries reduce predation on lymantriids but the presence of hairless caterpillars will greatly mollify the magnitude of predation. One interesting example was reported nearly a century ago by Howard (1897). He wrote,

One of the early results of the introduction of the English sparrow was the practical extermination by this bird of cankerworms... The removal of the cankerworm afforded room for the multiplication of the white-marked tussock moth (*Orgyia leucostigma*) which, from the fact that its larvae are hairy, was not eaten by the sparrows, and consequently multiplied with rapidity.

One other important factor worthy of mention in relation to predation rate and site susceptibility is habitat structure, particularly vertical stratification of cover. *Peromyscus*, although a habitat generalist, prefer greater densities of cover in order to reduce their own risk of predation. Density of cover has a major effect on foraging behavior and food selection by mice. Gypsy moths resting on boles or under bark flaps in areas where associated shrub cover is moderate to dense (resistant forest) are much more likely to be eaten by mice than those resting above the litter in more "open" areas (susceptible forest). The only pupae that survived (1986) in the susceptible stand all rested above the litter. These studies show conclusively that predator effectiveness is of major importance to the concept of site susceptibility to defoliation. These studies also reemphasize the overall impact potential of predation on sparse insect dynamics but more importantly demonstrate (1) the causal relationships explaining variability of impact on survivorship and (2) can provide valuable forest management implications. The mechanisms and ecological principles involved in these studies may apply to lymantriids around the world. These were evident as I observed habitat selection, utilization, and foraging behavior by ecological equivalents of North American gypsy moth predators in the Soviet Union.

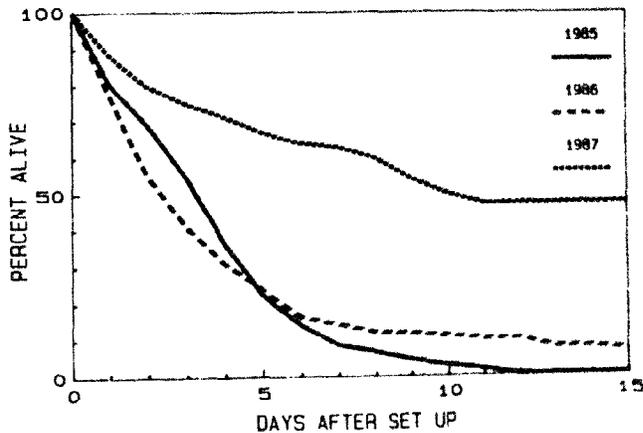


Figure 3. Survivorship curves of gypsy moth pupae in a susceptible forest.

SUMMARY

Predators were shown to be important agents of natural selection in the evolution of insect defenses among Lymantriidae. Adaptive changes in morphology and behavior demonstrate the impact predators had and still have on these insects. Studies on natural regulation of sparse Douglas-fir tussock moth and gypsy moth populations suggest that predation can regulate these populations indefinitely. However, predator effectiveness is influenced by several interactive mechanisms. Studies of these mechanisms have shown a causal relationship between site susceptibility or resistance to defoliation and predation. Reduced predation can have a "releasing" effect on an insect population. The interactions between predator density (a declining *Peromyscus* population), increasing availability of a preferred food (berries), and site differences in vertical stratification of cover accounted for the differences in rate of predation of gypsy moth, the total survivorship of pupae within years, and trend in survivorship between years.

These studies also helped to put in proper perspective the role of predation in the management of forest pest insects. Predators should not be regarded as ineffective simply because they cannot be "applied" as other control agents such as insecticides or viruses. The interactions between predator and prey are more complex, often subtle, but effective. Predation theory can be integrated into effective management schemes capable of extending the innocuous phase of insect populations. For example, a significant reduction or elimination of a palatable alternative food that could be achieved by the application of a chemical that would prevent fruit set (on blueberries) would reduce the survival of target insects. This could have a dramatic effect on survivorship of gypsy moth.

Sufficient knowledge of predation is also necessary for the successful utilization of other biological control agents in IPM (i.e., the release of parasites or sterile insects). Finally, understanding the relationship between the mechanisms that determine predation rate is critical to the development of "useful" population models and population forecasting. Particular emphasis in future studies should be on those mechanisms that affect both functional and numerical responses of predators. Although a great deal of evidence suggests the importance of predators, little actual documentation on the actual role exists.

In conclusion, predators have had a profound effect on the morphology and behavior of Lymantriidae; predation undoubtedly continues to have a significant impact on the dynamics of Lymantriidae and predation can play an important role in future attempts to manage these forest pest insects.

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PREDATION OF LYMANTRIIDS BY
ARTHROPODS

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INTRODUCTION

It is difficult to obtain definitive results in predation studies. Even when a conspicuous predator attacks an easily-observable prey, the relationships between the two are often not well known (Taylor 1984). When arthropods prey on arthropods, especially if prey or predators are small and arboreal, it may be particularly difficult to obtain reliable information. Predators often leave no identifiable remains, so prey just seem to disappear. It is usually impossible to determine whether dispersal, predation, disease, or sometimes even parasitism is responsible. The large "unknown mortality" category in many life tables attest to the difficulties of assessing the effects of predators, but also suggests the important roles they play.

Some studies have begun to show that arthropod predators can have substantial impacts on lymantriids. Evidence varies from observations of associations between predators and prey to controlled experiments involving prey-exposures. The studies have so far only touched on the impact of these predators. Rigorous research is needed to clarify their roles, not only so dynamics of prey populations can be better understood, but in order to find out if and how these predators can be made more effective in suppressing prey populations.

My intent is to review known cases where arthropods attack lymantriids, paying particular attention to effects of predators on prey and methods used to obtain results. By pointing out areas where I feel more research is needed, I hope to encourage more study on these important natural enemies.

GENERAL PREDATORS

These are arthropods that feed on a wide range of prey, among which lymantriids may be of greater or lesser importance. In most cases, general arthropod predators are effective biological control agents only when prey populations are low. In this, they are like vertebrate predators. Because they are not dependent on a particular organism for their survival, they are not closely linked to the populations of any one prey species. As a consequence, general predators usually have little ability to influence prey populations when the latter are at high densities. They may be able to keep prey populations low, but in no case is this known for sure because the population dynamics of the relevant natural enemies are not well enough

understood. The following survey will demonstrate the true of this last statement but will also detail some encouraging research directions.

Among hemipterous insects, the pentatomid, Dinorhynchus dybowski, is known to prey upon lymantriids in Japan (Schaefer et al. 1979). Feeding studies showed that D. dybowski is an obligate predator. Nymphs and adults readily feed on larvae, pupae, and adults of the gypsy moth, Lymantria dispar, and also attack other lymantriids such as Leucoma candida, L. salicis, and Ivela auripes. However, apart from field observations that the bug does feed on caterpillars, little is known about its impact on prey. The species has been imported and released in the United States, but is not known to be established. Other species of pentatomids are known at least occasionally to feed on gypsy moths, but reports are only anecdotal.

Polyphagous predaceous Coleoptera include the coccinellids, Anatis rathvoni and Neomysia subvittata, found in association with (but not necessarily feeding on) the Douglas-fir tussock moth, Orgyia pseudotsugata, (Mason 1976). Ground beetles have been implicated as being either predaceous or saprophytic on gypsy moths because of prey-specific antigens in their gut contents (Cameron, personal communication). Also, Mason and Ticehurst (1984) observed larvae of a dermestid, Cryptorhopalum ruficorne, on about 3% of gypsy moth egg masses in parts of Pennsylvania, U.S.A. Laboratory tests showed the beetle was a predator of gypsy moth eggs. However, its frequency of occurrence was low.

Matsui (1976) found that mantids not only directly kill young larvae of pine caterpillars, Dendrolimus spectabilis, but dislodge them so they fall to the ground. This apparently often resulted in their death by other, ground-foraging predators.

Furuta (1983) investigated predation on gypsy moths by the Japanese paper wasp, Polistes jadwigae, in southern Honshu by placing gypsy moth larvae on small (1.5-2 m high) forest trees, observing the predators, and determining disappearance rates of caterpillars. Wasps primarily fed on large caterpillars, and aggregated in the plots having the most gypsy moths. They were observed to capture prey in about 50% of attempts. Larvae that escaped usually did so by falling to the ground. Wasps failing on the first try often searched for other prey, especially at high larval densities. They spent more time searching (1.2 times more) and did not always capture prey when prey populations were low. The number of larvae that disappeared from a study plot was linearly and positively correlated to the number of wasps seen in that plot. Furuta concluded that the wasps were largely responsible for this disappearance. They also apparently learned to forage in areas where they had previously been successful, because the number of wasps visiting a site increased after it was artificially stocked with larvae.

Disappearance rates of gypsy moth caterpillars were rapid enough that most larvae were gone after 10 days. Furuta felt that both birds and wasps were responsible, but he could not be definite because in this experiment prey were not continuously observed.

I have described Furuta's study in detail because it illustrates how useful data can be gathered through careful research. It seems

clear from his study that *P. jadvigae* is a significant predator that aggregates to prey clumps and thus can be expected to act in a density-dependent manner. The favorable circumstances under which he worked undoubtedly contributed to his success, but his tactics (direct observations, coupled with exposures of different densities of prey) could be used in other situations as well.

Spiders are among the more prominent predators that attack lymantriids. Sometimes they have only been seen in association with potential prey, as reported by Dahlsten, et al. (1977) for the Douglas-fir tussock moth. However, Wickman (1977) observed unidentified spiders actively preying on newly-hatched tussock moths. Furuta (1977) made a rather detailed study of spiders in Japan. He released different numbers of gypsy moth third instars on trees in a pine plantation that had populations of two hunting spiders, *Oxyopes sertatus* and *O. badius*, and noted that over 9 days, only 5% of caterpillar mortality could be attributed to the spiders. Most mortality was due to the paper wasps previously noted. At very low prey densities, spiders responded in a direct density-dependent manner but only up to 15 larvae per tree. In another field experiment with the pine caterpillar, *Dendrolimus spectabilis*, Furuta (1977) found the numbers of spiders did not seem to be affected by numbers of caterpillars on trees, and thus the former apparently did not aggregate to clumps of prey. He also found that these spiders could not feed successfully on large caterpillars, and so concluded that spiders are not a very important predator of lymantriids in Japan. However, Matsu (1976) indicated that spiders are quite effective in destroying first-stage pine caterpillars.

Fairly good evidence about the nature of spider predation on Douglas-fir tussock moths is given by Mason and Torgersen (1983). The exposed cohorts of larvae on branches placed over drop-trays and recorded the numbers found dead or disappeared. While it was not possible to definitively determine that larvae had been killed by spiders, the shriveled nature of those found dead in drop-trays was very similar to those killed by *bona fide* spider predation in the laboratory, and spiders (dominated by species in the families Theridiidae, Thomisidae, and Salticidae), were often found in the drop trays. Most of the predation occurred on instars I and II (8.7%) and III and IV (6.6%), and, unless larvae were removed from the branches before being discarded by predators (which the authors felt was unlikely owing to sticky-barriers at branch bases), spider predation was probably not more than this because ants were also associated with the caterpillars.

Harvestmen (*Leiobunum longipes* and *L. politum*), were observed to feed on artificially-exposed gypsy moth pupae and "appear to have considerable predator potential" (Smith and Lautenschlager 1981). Spiders occasionally feed on gypsy moth larvae as well (personal observations).

The evidence concerning predation on lymantriids by spiders and other arachnids is somewhat sketchy, but where reasonably-well documented their effects appear to be rather small. What impact they have seems to be greatest on young larvae. However, they need to be better known, and study on them is encouraged.

Using ants as biological control agents is an ancient practice. Weaver ants (Oecophylla smaragdina F.) have been used by the Chinese to control citrus pests for millennia (DeBach 1964). Red wood ants (Formica spp.) are encouraged in European Forests (Finnegan 1971), and forest ants are credited with suppressing populations of some forest insects (Donley 1983, Fowler and MacGarvin 1985). There are a number of reports of ants feeding on lymantriids. Torgersen and Mason (1987) observed a Camponotus sp. pull several eggs from a Douglas-fir tussock moth egg mass and finally carry one away. Ants sometimes remove all eggs from a mass of gypsy moth eggs (Campbell 1975). Mason and Torgersen (1983), in the before-mentioned exposure of Douglas-fir tussock moth larvae over drop-trays, noted ants as well as spiders in the trays. The most common species were Lasius pallitarsis and Tapinoma sessile, both small and omnivorous species that were particularly abundant when caterpillars were young. What impacts they had on the prey populations were apparently restricted mainly to the first two instars, and cannot really be separated from the predation due to spiders already mentioned.

Kim and Murakami (1983) investigated the effects of the ant, Formica yessensis, on the pine caterpillar, Dendrolimus spectabilis, in Korea. They carried out a number of experiments on small trees on which specific numbers of caterpillars of different ages were placed. If instars I to III were placed on trees from which ants were excluded by flypaper around the trunk and other predators excluded by cages, they suffered 37% mortality after 14 days. If the flypaper and cages were not present, mortality went up to 46%. With an ant nest at the base and no flypaper, all larvae were destroyed, whether or not trees were caged. The authors felt that much of this mortality occurred when larvae became dislodged and fell to the ground where ants were foraging. If post-diapause pine caterpillars (instar IV and larger) were used, mortality was never higher than 17%, even with an ant nest at the tree base. Thus, F. yessensis appeared to have a strong impact only on young pine caterpillars.

In some situations ants have the greatest impact on older, not younger, lymantriid larvae. Schmidt (1985) found that laboratory colonies of the red wood ant, Formica polyctena, did not recognize stage one to three of the rusty tussock moth, Orgyia antiqua, as prey. However, ants killed almost 60% of instars four to six that were offered to them.

Predation by ants of large gypsy moth larvae also occurs (Weseloh in press). Gypsy moth fifth instars were tethered by tying pieces of thread around their bodies and anchoring these in leaf litter by means of wire stakes. Caterpillars were placed in litter because large gypsy moth larvae often rest here during daylight hours. These were observed hourly for 24 hr periods. Ants, particularly the carpenter ant, Camponotus ferrugineus, and a brown forest ant (Formica fusca group) were observed attacking and removing up to 30% of these larvae in a 24 hr period. Ants were active both day and night, but mainly when the forest floor was dry.

While it is not entirely clear what effect tethering had on these predation rates, interpretations of preliminary data suggest that at least the carpenter ants probably attack free-living prey with the same

success that they do tethered larvae. Large gypsy moth larvae may be particularly vulnerable to such ground-foraging predators because of their habit of resting in leaf-litter during the day.

Ants may also successfully attack pupae of lymantriids. Torgersen et al. (1983), exposed laboratory-reared Douglas-fir tussock moth pupae in field plots. Two kinds of predation were observed--pupae and cocoons were either entirely removed or cocoons were torn open and pupae were missing or in fragments. The authors attributed the former to birds and at least some of the latter, in which pupal fragments remained, to carpenter ants, probably Camponotus modoc Wheeler. Because of uncertainties about how much of the predation could be attributed to ants, their real impact remained unknown.

Carpenter ants (C. pennsylvanicus and C. ferrugineus) were often observed to attack gypsy moth pupae placed in leaf-litter (Smith and Lautenschlager 1981). Vertebrate and invertebrate predation could be distinguished based on characteristics of pupal remains, and invertebrates, with ants prominent among them, were concluded to be important predators of gypsy moth pupae. Again, however, the impact of ants vs. other invertebrates could not be determined readily because of ambiguities in identifying effects due to one or another predator.

As the above survey shows, information on the impact of general invertebrate predators on lymantriids is not definitive. (I wish to stress that I am not trying to denigrate the efforts of researchers saying this, but only to point out that evaluating predation is hard to do.) It is sometimes possible to determine that invertebrate predators are involved, but not always which ones. Predation by invertebrates certainly exists, and in some cases may be quite important. The predators for which most data have been gathered are ants, and these emerge at present as the most important ones. However, comparable studies need to be done with true bugs, spiders, harvestmen, and other invertebrates known to prey upon lymantriids before anything definite can be said about the importance of any of them. Their further study should be encouraged, not only to fill in the "unknown" or "disappeared" mortality categories of life-tables but to see if any can be used as effective natural enemies. Their contributions to the mortality of lymantriids at low densities may lead to ways to keep populations low, and so enable the elusive goal of pest management to become a reality.

CALOSOMA SYCOPHANTIA, A SPECIFIC PREDATOR

Specificity in predators is probably an uncommon occurrence. None of the predators so far considered feed only on one species of prey. However, the carabid beetle, Calosoma sycophanta, feeds primarily on gypsy moth larvae and pupae. C. sycophanta is not actually monophagous, because in the laboratory and sometimes in the field it readily consumes other caterpillars (Burgess 1911). Its specificity is based on behavior and life history characteristics to ensure this beetle is virtually never found except in association with high gypsy moth densities (Smith and Lautenschlager 1981, personal

observations). Through progeny production, it appears in some cases to be able to cause prey populations to decrease from outbreak levels (Bess 1961, Smith and Lautenschlager 1981, Weseloh 1985b), something that none of the other predators are able to do. In fact, largely because of its unique characteristics, *C. sycophanta* is the only predator attacking gypsy moths which is known to have been successfully introduced into North America from Europe. I am treating it separately here because of these unique characteristics and because the information known about it is different and perhaps more extensive than for most of the other invertebrate predators.

The life-cycle of the beetle is well-adapted for preying on the gypsy moth. Adult beetles pass the winter in soil and emerge in June to climb trees in search of the large gypsy moth caterpillars present then. In late June, females lay up to 500 eggs in the ground, which hatch in 4 to 7 days. Immature beetles are active tree climbers and feed on the available gypsy moth pupae, chewing characteristic jagged holes in them. Larval development takes about 26 days under usual field conditions, but feeding is often completed in the first 15 days or so. Third instars pupate in the soil and transform to adults in about 2 weeks. Beetles then stay in soil until the next spring (Burgess 1911). Thus the predator's phenology is well synchronized with that of the gypsy moth, and its dormancy through summer and winter ensure that it need not depend on any other prey. There is even some evidence that *C. sycophanta* can determine when gypsy moth numbers are high. Vasic (1972) in Yugoslavia placed adult beetles in cells in soil and over several years periodically re-examined them. He found that in years when gypsy moth numbers were low, most beetles remained in the ground, apparently dormant. Only when prey numbers were high did the predators initiate significant activities above ground. Adult beetles are known to live for 3-4 years, and perhaps they live longer if dormant. Long-life would be necessary if significant numbers survive from one prey outbreak to the next, which in North America is 8-10 years or more (Campbell 1981). Perhaps beetles emerge each year and, if prey are not available, briefly feed on nectar and/or honeydew and re-enter the soil. The adult beetle is known to survive well on sugar sources such as fruits (Vasic 1972). However, the beetles are also known to be strong fliers (Doane and Schaefer 1971), and the importance of long-range dispersal is unknown.

In my own studies, I used a mark-recapture technique to determine population levels and dispersal potential of beetles (Weseloh 1985a). In a year when gypsy moths were abundant, adult beetles were active, very visible, and produced many progeny that probably helped cause the decrease in the prey population that occurred that year (Weseloh 1985a, 1987). The next year at this same site gypsy moths were scarce. *Calosoma* adults were present in as high numbers as in the previous year, but were very inactive and did not reproduce. Virtually no emigration of beetles from the site occurred (Weseloh 1987), supporting the results of Vasic (1972) that beetles in non-outbreak years are inactive.

The number of adult beetles required to substantially affect gypsy moth population densities is quite small, no more than about 200 beetles of each sex per ha (Weseloh 1985a, 1985b). They have a large

impact probably because each female can produce from 200-500 eggs per season (personal observations). These eggs are large (2.4 X 5.2 mm), and the first instar averages 9.3 mm long. To produce such a mass of progeny, each reproducing female consumes hundreds of large caterpillars (Burgess 1911). While there are no data on field hatchability of eggs or the survivorship of beetle larvae, it is known that the soil-deposited eggs hatch only a few days after they are laid, that first instars can travel about 2 km in search of food (Burgess 1911), and that larvae grow rapidly. Thus, there would be little time for eggs or larvae to be killed by predators, and survivorship is probably high. Many progeny would therefore live to destroy large numbers of gypsy moth pupae.

The special relationship that *C. sycophanta* has with the gypsy moth may be exploitable. The beetle is very seldom effective during the first year of an outbreak, and even in older infestations its incidence may be spotty (Smith and Lautenschlager 1981). This is probably because relatively few beetles survive from one outbreak to the next, even though they are dormant in the soil. Thus, if beetle populations could be augmented by releasing a relatively few number of adults into increasing prey populations, the pest might be controlled before it has a chance to cause much damage. If this could be demonstrated, the most important practical problem will be to obtain enough of the beetles for releases. It can be reared, but larvae are cannibalistic and must be handled individually, greatly adding to cost. Trapping the beetle in areas where it is abundant may be the most effective procedure, as a rather efficient trap already exists (Collins and Holbrook 1929).

DISCUSSION

If *C. sycophanta* can be used effectively against the gypsy moth, it may also be effective against other lymantriids and other lepidopterous pests that have life-cycles similar to the gypsy moth. I can think of no reason why it should not thrive on any prey that meets its requirements of seasonal availability.

The effectiveness of other invertebrate predators might be enhanced as well. Ants are especially attractive possibilities. As already mentioned, they have been purposefully manipulated in Europe for biological control of forest caterpillars. Ants, however, often tend aphids or other honey-dew producing Homoptera (Fowler and MacGarvin 1985). Such trade-offs must be considered. To be effectively used, more definitive information on predator ecology and behavior is needed. Some of the research methods discussed, particularly prey-exposure techniques, can be used to obtain such information. Researchers should also be more willing to simply watch individual prey and predators, as Furuta (1983) has done with paper wasps preying on gypsy moths. I suspect that many entomologists who are accustomed to encountering large numbers of insects in field experiments feel that watching individuals does not produce enough data. However, when organisms are closely observed, deep insights

about their behavior and effects on population biology can often be made. One need only look at the extensive behavioral literature on invertebrates to appreciate the effectiveness of this approach. The difficulties of observing small arboreal organisms are, of course, not trivial, but the information gathered can be very valuable. I urge researchers to follow such paths whenever possible.

SUMMARY

The importance of arthropods which prey on lymantriids is discussed in relation to the impact of the predators on prey populations and the methods used to assess this impact. General predators of lymantriids are quite common, and include insects in the orders Hemiptera (Pentatomidae), Coleoptera (Carabidae, Coccinellidae, Dermestidae), and Hymenoptera (Vespidae, Formicidae), as well as spiders (various families). They only have significant impacts when prey populations are low. Evidence on predator effectiveness is best for the Hymenoptera and spiders. Through host-exposure techniques, the paper wasp, Polistes jadwigae, was found to be a significant mortality agent to large larvae of the gypsy moth, Lymantria dispar, in Japan. Spiders feed on the small caterpillars of gypsy moths, pine caterpillars (Dendrolimus spectabilis), and Douglas-fir tussock moths (Orgyia pseudotsugata), but generally appear to have only a small impact. Ants have been perhaps the best researched general invertebrate predators. They attack primarily small larvae of the pine caterpillar and Douglas-fir tussock moth, but will feed on pupae of the latter and on large larvae and pupae of the gypsy moth. Sometimes their impact is quite large, especially near a nest. The carabid beetle, Calosoma sycophanta, owing to its life-cycle and behavioral characteristics, is quite specific to the gypsy moth and is most important at high prey population densities. Through progeny production, the beetle is sometimes able to cause crashes in its prey's population. The feasibility of using releases of C. sycophanta to control gypsy moth populations is discussed, and a plea for more detailed study of all invertebrate predators is made.

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A COMPARISON OF THE PARASITE
COMPLEXES ATTACKING TWO
CLOSELY RELATED LYMANTRIIDS

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INTRODUCTION

The gypsy moth (GM), *Lymantria dispar*, was accidentally introduced into North America 120 years ago, and is probably the most serious pest of forest and shade trees in the northeastern U.S. Moreover, it imperils other regions, notably southern forests, as it continues to expand its range. Being an introduced insect, it was considered a prime candidate for biological control, and efforts to import and release natural enemies of this pest have been conducted intermittently from 1905 to the present time.

The early work (done prior to 1960), summarized by Dowden (1962) and by Clausen (1978), resulted in the establishment of 10 species of parasites and one predator. Although these introduced natural enemies were believed to have ameliorated the impact of GM to a certain extent, primarily by retarding outbreaks and reducing their severity, population explosions still occurred with troubling frequency.

Consequently, foreign explorations were resumed during the late 1960's and early 1970's in three regions: Europe, the Far East, and India (Coulson et al. 1986, Doane and McManus 1981). Although most of the early exploration work had been done in Europe, it was felt that additional work there was warranted for the following reasons: (1) The race of *L. dispar* in North America came from Europe (Campbell 1974). (2) Present-day rapid transit and modern rearing techniques could permit the establishment of species received and released in inadequate numbers during earlier efforts. (3) Augmentation of the gene pool of species already established in North America could increase their effectiveness. (4) The early work in Europe stressed mass collections in GM outbreaks (Burgess and Crossman 1929), so low host density parasites possibly were overlooked (Pschorn-Walcher 1977). (5) The southward dispersal of GM into the Middle Atlantic States raised the possibility that suitable alternate hosts might be available for some of those parasites requiring them that had not become established earlier. (6) The possibility existed that a "new" or previously untried natural enemy might be found. Exploration work in the Far East was resumed because previous explorations there had been limited, being confined to Japan (Burgess and Crossman 1929). Moreover, the genus *Lymantria* is believed to have originated in Asia (Goldschmidt 1934);

therefore, a mature, well-balanced complex of natural enemies could be expected to exist there. In support of this view, Townes (1971) noted that 25 ichneumonids had been recorded from lymantriids in Japan and Korea alone. Because there have been examples of successful biological control of pests by natural enemies originally associated with closely related host species (Hokkanen and Pimentel 1984), explorations and importations of natural enemies of the closely related Indian gypsy moth (IGM), *Lymantria obfusca*, were started during the 1960's. In pursuing the various lines of research associated with this biological control project, it became apparent to us that the complexes of parasites attacking GM in Europe, North America, and the Far East, and IGM in India had many interesting similarities and differences, which we review in this paper. The scope of this review is limited to primary parasites and a few species which are facultative hyperparasites. Because of this restriction, species which are exclusively secondary or hyperparasites remain undiscussed.

METHODS

In certain respects, this is a review paper since we are integrating the results of our earlier research in Europe, North America, and India with those reported elsewhere in the literature for these regions and the Far East. In many cases, methods used for rearing parasites from field collected hosts are not given in the literature. However, methods used by one of us in Europe (Drea and Fuester 1979) are probably typical of those used by most investigators.

Since many records, particularly those in the older literature, could be faulty owing to misidentifications of parasites or contamination of host rearing cages, we have relied primarily on our own rearings or those which are cited recently. Although many names cited in the older literature have been reduced to synonymy, the taxonomy of the most important groups has been reviewed recently: braconids by Marsh (1979), ichneumonids by Gupta (1983), and tachinids by Sabrosky and Reardon (1976), and it has been possible to establish the correct current name in many cases. Highly questionable recoveries (for example, those of parasites not previously recorded from Lepidoptera) have been omitted from our discussion.

RESULTS

Brief Description of Host Life Cycles

Both GM and IGM have similar life histories. There is one generation per year, with the eggs hatching in the spring and the larvae completing feeding 7-12 weeks later depending upon climatic or meteorological conditions, population density, or host plant. Young larvae of GM are blackish in color. Older GM larvae from Europe and North America are mottled grey and black and may be recognized by the

five pairs of blue spots and six pairs of red spots on the dorsum. Older larvae from the Far East are similar, but, in addition, have bright yellow markings on the dorsum. Older larvae of IGM tend to be more brownish in color than those of GM. After feeding, the larvae pupate, and adult moths emerge in about two weeks. Shortly after the female emerges, she mates and deposits egg masses on trees, rocks, or other objects. Females of IGM and of GM from Europe and North America have well-developed wings but cannot fly. In the Far East, however, adult females of *L. dispar* are capable of sustained flight which can serve as a major means of population dispersal (Schaefer 1978). Females of both GM and IGM deposit a single egg mass which bears a protective covering of buff-colored female vestiture. The egg masses of GM females from Europe and North America contain 100 to 1,000 eggs with means generally falling into the 300-700 range. Larvae and adults of GM from the Far East are somewhat larger, and egg masses tend to be somewhat larger containing 120-1,100 eggs. On the other hand, IGM larvae and adults tend to be smaller than those of GM, and egg masses contain 70-500 eggs (Rao 1966).

The gypsy moth is very polyphagous, and in Europe and North America is a defoliator primarily of hardwoods, especially oaks (*Quercus*), but after the larvae are half-grown, they will attack conifers. In the Far East, many outbreaks occur on larch (*Larix leptolepis*), and other preferred hosts include oaks, persimmon (*Diospyros*), chestnut (*Castanea*), and various fruit trees, particularly *Prunus*. The IGM prefers poplar (*Populus*), willow (*Salix*), oaks, alder (*Alnus*), and also defoliates apple, apricot, pear, plum, and other fruit trees.

Although the natural distribution of GM includes most of the Palaearctic region, its distribution in North America is limited primarily to the northeastern United States and adjacent areas in Canada. The IGM is restricted to the western Himalayas of India and Nepal. Ramaseshiah and Bali (1987) have noted that previous reports of this species from southern India are in error.

Because of the biological differences (e.g., flight of females, host plant preferences) exhibited by *L. dispar* in different geographic areas, its taxonomy is unsettled, and Pintureau (1980) concluded from biometrical studies that the Honshu form was a distinct species (*L. japonica*), and the Hokkaido form, a subspecies (*L. d. hokkaidensis*).

Inventory of Parasite Species

Inventories published for parasites of *L. obfuscalis* in India (Dharmadhikari et al. 1985) and of *L. dispar* in North America (Simons et al. 1979) and Europe (Fuester et al. 1981) are somewhat incomplete and do not reflect current taxonomy in all groups. No recent inventories have been published for the Far East, except in the case of certain groups in limited areas, e.g. the publication on tachinid parasites of Lymantriidae in Japan by Schaefer and Shima (1981). Coulson et al. (1986) updated many of the recent changes in scientific nomenclature on recent importations in the U.S.

In comparing quantitative aspects of the inventories compiled for the complexes of parasites attacking *L. dispar* and *L. obfuscalis* (Table 1), numbers of both genera and species are highest (and more or less

comparable) on *L. dispar* in the Far East and Europe, lowest on *L. dispar* in North America, and intermediate on *L. obfuscata*. Obviously, the disparity between North America, where the gypsy moth is introduced, and the other regions would be even greater were it not for the biological control projects which resulted in the importation and establishment of two species from the Far East and 10 species from Europe, essentially half of the complex. In addition, one parasite from the Far East, *Ooencyrtus kuvanae* was intentionally introduced into Europe following its introduction into North America (Anderson 1976). Although older listings show complexes numbering 100 or more species, our lower numbers reflect the elimination of recent synonyms and dubious records, many of which have been perpetuated in the literature for many years.

Table 1. Numbers of parasite taxa attacking gypsy moth and Indian gypsy moth in different regions.

Host Species	Region	Numbers of Taxa Recorded	
		Genera	Species
<i>L. dispar</i>	Far East	32	44
	Europe	29	45
	North America	19	22
<i>L. obfuscata</i>	India	25	36

Surprisingly, only 11 parasite species were shared by both host species: an egg parasite, *Anastatus japonicus* (= *disparis*); 5 larval parasites, *Dolichogenidea lacteicolor*, *Cotesia melanoscelus*, *Glyptapanteles liparidis*, *Compsilura concinnata*, and *Pallexorista inconspicua*; and 5 pupal parasites, *Brachymeria intermedia*, *B. lasus*, *Coccygominus disparis*, and *Monodontomerus aereus*. With the exception of *D. lacteicolor*, *C. melanoscelus*, and *G. liparidis*, these species are broadly polyphagous. In a few cases, species attacking IGM were recovered from GM in Europe but not the Far East (e.g., *P. inconspicua* or vice versa (*C. disparis*)). As expected, the similarity was greatest between the parasite complexes of *L. dispar* in Europe and the Far East and 20 species were recovered in both regions. Most differences involved minor, polyphagous members of the complex. Several species known to occur throughout the Palaearctic Region have been reared from *L. dispar* in Europe but not the Far East. Examples include *D. lacteicolor* a parasite of *Euproctis chrysorrhoea*, and the polyphagous *intermedia*. However, many more studies have been made in Europe than in the Far East, and we suspect that additional field studies would reveal an overlap of parasite species on the order of 60%.

Ecological Homologues

In some cases, species of parasites missing from one host or region appear to be replaced by ecological homologues, closely related species that have life cycles very similar to those of the species replaced. Some of these are shown in Table 2.

Table 2. Ecological homologues in parasite complexes of gypsy moth and Indian gypsy moth.

Host Stage Attacked	Genus	L. dispar		L. obfuscata India
		Europe	Far East	
Egg	<u>Anastatus</u>	<u>japonicus</u>	<u>japonicus</u>	<u>kashmirensis</u>
Larval	<u>Cotesia</u>	<u>ocneriae</u>	<u>schaeferi</u>	?
	<u>Glyptapanteles</u>	<u>portheidae</u>	?	<u>indiensis</u>
	<u>Hyposoter</u>	<u>tricoloripes</u>	<u>vierecki</u>	<u>lymantriae</u>
	<u>Exorista</u>	<u>larvarum</u>	<u>japonica</u>	<u>rossica</u>
Pupal	<u>Brachymeria</u>	<u>intermedia</u>	<u>lasus</u>	both spp.

With most forest insects, major parasites are rarely absent from different regions within the natural home of the pest (Pschorn-Walcher 1977). In our analysis, we have found a few instances where major parasites are absent and not represented by ecological homologues (Table 3).

Table 3. Significant lacunae in parasite complexes of gypsy moth and Indian Gypsy Moth.(1)

Host Stage Attacked	Genus	L. dispar		L. obfuscata India
		Europe	Far East	
Egg	<u>Ooencyrtus</u>	<u>kuvanae</u> (2)	<u>kuvanae</u>	--
Larval	<u>Rogas</u>	--	<u>lymantriae</u>	<u>indiscretus</u>
	<u>Meteorus</u>	<u>pulchricornis</u>	<u>japonicus</u>	--
	<u>Parasetigena</u>	<u>silvestris</u>	<u>silvestris</u>	--
	<u>Blepharipa</u>	<u>pratensis</u>	<u>schineri</u>	--

- (1) Lacunae indicated by dashes (--).
 (2) O. kuvanae not indigenous in Europe.

No obvious gaps were present in the Far East complex, but there were two in Europe (*Q. kuvanae* counted because it was imported into Spain in 1923), and four in India. The absence of *Meteorus* in India is noteworthy because members of this genus are often important natural enemies of Lymantriidae. An example is *Meteorus versicolor*, an important parasite of the brown-tail moth, *Euproctis chrysorrhoea*, and the satin moth, *Leucoma salicis* (Clausen 1978). The absence of the univoltine tachinids *Parasetigena* and *Blepharipa* in India is also surprising in view of the fact that the host is univoltine.

Structure of Parasite Complexes

Pschorn-Walcher (1977) divided the parasite complexes of forest pests into four guilds corresponding to parasitological niches: egg parasites, larval parasites, pupal parasites, and hyperparasites. We are inclined to follow this arrangement (omitting the hyperparasites).

Eggs of Lymantriids are attacked by a variety of chalcidoids and scellionids (Anderson 1976). The dominant egg parasites of *L. dispar* are *Anastatus* spp. (Eupelmidae) and *Q. kuvanae* (Encyrtidae). Other egg parasites frequently recorded from gypsy moth include the scellionids *Gryon* spp. and *Ielenomus* spp. from Europe (Fuester et al. 1981) and *Trichogramma dendrolimi* from the Far East (Schaefer et al. 1988b). These species are rare with the possible exception of *G. howardi* which reportedly parasitized 75-85% of the gypsy moth eggs in the Crimea (Mokrzecki and Ogloblin 1931).

Most larval parasites of Lymantriidae are endoparasites from three families: Braconidae, Ichneumonidae, and Tachinidae. Small larvae of *Lymantria* are attacked by braconids (*Cotesia*, *Glyptapanteles*, and others formerly considered *Apanteles*), *Meteorus*, and *Rogas*, as well as by porizontine ichneumonids (*Casitaria*, *Hyposoter*, and *Phobocampe*). Large larvae of *Lymantria* are attacked by several genera of tachinids, the most prevalent being *Blepharipa*, *Carcelia*, *Exorista*, *Palexorista*, and *Parasetigena*. In addition, large larvae are often attacked by multivoltine, gregarious braconids such as *Glyptapanteles liparidis* (Fuester et al. 1983). In addition, a few species of gregarious, ectoparasitic eulophids have been reported, but never in large numbers, for example, *Elachertus* sp. from *L. dispar* in the Far East (Schaefer et al. 1984). Larval parasites exhibit widely differing degrees of host specificity from apparent monophagy in the case of *Phobocampe uncinata* to broad polyphagy in the case of the tachinid *Compsilura concinnata*.

Most of the pupal parasites are polyphagous chalcidoids (*Brachymeria*, *Monodontomerus*) and ephialtine ichneumonids (*Coccygomimus*, *Iheronia*). Some of these (e.g., *Monodontomerus* and *Iheronia*) are facultative hyperparasites.

Of special interest are the dominant members of the parasite complex. They are often dominant by virtue of a high degree of adaptation to the host, superior host-finding ability, high reproductive capacity, or some other advantage.

The dominant parasites of the gypsy moth in the Far East are shown in Table 4 together with information on rates of parasitization and alternate host requirements. The ranges of egg parasitization shown in Table 4 are somewhat misleading since Schaefer et al. (1988b) found

overall egg parasitization in Japan and Korea to be rather low, on the order of 1.3% and 10.0%, respectively. They cited large host egg mass size, hyperparasitization by *Ityndarichus navae*, poor parasite dispersal ability, and predation of host egg masses by birds as contributing factors. They further noted a total absence of egg parasitization in some larch plantations, which tend to be highly artificial habitats lacking in diversity.

Table 4. Dominant parasites of the gypsy moth in the Far East.

Host Stage Attacked	Name of Parasite	Percent Parasitization	Alternate Host Needed
Egg	<i>Anastatus japonicus</i>	0-17%	No
	<i>Ooencyrtus kuvanae</i>	0-71	No
Larval	<i>Cotesia melanoscelus</i>	0-11	No
	<i>Glyptapanteles liparidis</i>	0-70	Yes
	<i>Rogas lymantriae</i>	0-33	Yes
	<i>Phobocampe lymantriae</i>	0-11	Yes
	<i>Exorista japonica</i>	0-73	Yes
	<i>Parasetigena silvestris</i>	0-40	No
	<i>Blepharipa schineri</i>	0-100	No
	<i>Brachymeria lasus</i>	0-42	Yes
Pupal			

Far and away the dominant larval parasite in the Far East is *G. liparidis*, which has two generations per year on gypsy moth and two generations per year on its primary alternate host, the pine caterpillar, *Dendrolimus spectabilis* (Kamiya 1938). Parasitization of gypsy moth is frequently high, greater than 20%, in both generations. Other species often attacking significant percentages of gypsy moth were *E. japonica*, *P. silvestris*, *B. schineri*, and *B. lasus*. About half of the species require alternate hosts. Little is known about the biology of many species in the Far East (Schaefer et al. 1984).

Dominant species of parasites of the GM in Europe are shown in Table 5. As in the Far East, about half require alternate hosts. Over most of Europe, *A. japonicus* is the dominant egg parasite of GM (Fuester et al. 1981). The introduced egg parasite, *O. kuvanae*, is common in southern Europe, but is not yet abundant further north. For example, Fuester et al. (1983) recovered only a single specimen in Austria. None were recovered from egg masses collected in Poland (Fuester et al. 1981). Parasitization by *O. kuvanae* is generally 15-20%, and where both it and *A. japonicus* occur, total parasitization is ca. 20-30%. Interspecific competition does not appear to be an important consideration as mean rates of parasitization by *A. japonicus* in areas where it occurred with and without *O. kuvanae* were more or less comparable, 9.6% and 11.3%, respectively.

Table 5. Dominant parasites of the gypsy moth in Europe.

Host Stage Attacked	Name of Parasite	Percent Parasitization	Alternate Host Needed
Egg	<u>Anastatus japonicus</u>	0-28%	No
	<u>Ooencyrtus kuvanae</u>	0-30	No
Larval	<u>Glyptapanteles porthetriae</u>	0-48	Yes
	<u>Cotesia melanoscelus</u>	0-42	No
	<u>Glyptapanteles liparidis</u>	0-17	Yes
	<u>Hyposoter tricoloripes</u>	0-32	Yes
	<u>Phobocampe uncinata</u>	0-19	No
	<u>Exorista larvarum</u>	0-15	Yes
	<u>Cerantia samarensis</u>	0-80	?
	<u>Parasetigena silvestris</u>	0-44	No
	<u>Blepharipa pratensis</u>	0-77	No
	Pupal	<u>Brachymeria intermedia</u>	0-33

The European complex of larval parasites (Table 5) differs from that in the Far East in several respects. G. liparidis is not nearly so important as in the Far East, rates of mean parasitism for the 1st and 2nd broods being less than 5% and 10%, respectively. The dominant parasite of early instars is C. melanoscelus, which appears to be more important in Europe than in Asia. Several other species are important in certain areas: G. porthetriae in the Mediterranean area and H. tricoloripes in central France. Although Phobocampe lymantriaae, a polyvoltine species, is also present in Europe, the univoltine P. uncinata is far more abundant. Likewise, B. schineri is present in Europe (Sabroskey and Reardon 1976), but is rarely recovered from L. dispar, and the most consistent tachinids are B. pratensis and P. silvestris. Recent host exposure studies conducted in low host density populations in eastern France by Mills (1984) show that C. samarensis, a parasite recovered only rarely at a very few locations during the 1970's (Fuester et al. 1981), often parasitized very high percentages of GM. This tachinid has a partial second generation (Mills and Dewar 1988), which probably utilizes an alternate host.

All of the dominant parasites of the gypsy moth in North America are exotic species that became established following their importation as part of the biological control program to control the gypsy moth (Table 6). Although the gypsy moth has been present in North America for ca. 120 years, none of the native species, even those with broad host ranges (e.g., Exorista mella) have become sufficiently adapted to the gypsy moth to attack it consistently. With the exception of the tachinid C. concinnata and the chalcidid B. intermedia, both broadly polyphagous species, none require alternate hosts. It is noteworthy, perhaps, that egg parasitization is generally much higher than in Europe and the Far East, ca. 25-50%. It is generally felt that the introduction of natural enemies from the Old World has resulted in partial control of GM (Leonard 1974, Clausen 1978).

Table 6. Dominant parasites of the gypsy moth in North America.

Host Stage Attacked	Name of Parasite	Percent Parasitization	Alternate Host Needed
Egg	<u>Ooencyrtus kuvanae</u>	10-82%	No
	<u>Anastatus japonicus</u>	0-40	No
Larval	<u>Cotesia melanoscelus</u>	0-50	No
	<u>Phobocampe uncinata</u>	0-30	No
	<u>Compsilura concinnata</u>	0-60	Yes
	<u>Parasetigena silvestris</u>	0-80	No
	<u>Blepharipa pratensis</u>	0-56	No
Pupal	<u>Brachymeria intermedia</u>	0-67	Yes

The dominant species in the parasite complex attacking the Indian gypsy moth appear in Table 7. The most striking differences between the complex of parasites on Indian gypsy moth and those on the gypsy moth are (1) significantly overall lower parasitization on Indian gypsy moth, and (2) the much higher proportion of species that require alternate hosts.

Table 7. Dominant parasites of the Indian Gypsy Moth

Host Stage Attacked	Name of Parasite	Percent Parasitization	Alternate Host Needed	
Egg	<u>Anastatus kashmirensis</u>	0-30%	No	
Larval	<u>Glyptapanteles indiensis</u>	0-30	Yes	
	<u>Cotesia melanoscelus</u>	0-25	Yes	
	<u>Glyptapanteles flavicoxis</u>	0-15	Yes	
	<u>Glyptapanteles liparidis</u>	0-15	Yes	
	<u>Hyposoter lymantriae</u>	0-8	Yes	
	<u>Rogas indiscretus</u>	0-25	Yes	
	<u>Exorista rossica</u>	0-25	Yes	
	<u>Palexorista spp.</u>	0-30	Yes	
	Pupal	<u>Brachymeria intermedia</u>	0-30	Yes
		<u>Brachymeria lasus</u>	0-20	Yes

Only one egg parasite of any significance, A. kashmirensis, is present, and rates of parasitization are more or less comparable to those observed in Europe. Although recorded from IGM, A. japonicus is

very rare (Dharmadhikari et al. 1985). The gregarious braconids, *G. flavicoxis* and *G. liparidis* seem to occupy similar parasitological niches the former dominating in the Kulu Valley, and the latter in Kashmir. Weseloh (1982) noted that the Indian strain of *C. melanoscelus* differs from the U.S. strain in not having a photoperiodically induced diapause in the cocoon stage. This appears to be due to the fact that the Indian strain can readily attack satin moth which occurs on the same host plants (*Salix* and *Populus*) when gypsy moth larvae are no longer available. The ichneumonid *H. lymantriae* achieves high parasitism in localities where cool humid weather prevails. In this respect, it resembles *H. tricoloripes* in Europe. The polyphagous tachinids, *E. rossica* and *Palexorista inconspicua*, appear to be the most consistent parasites.

Role of Parasites in Host Population Dynamics

In North America, only a few long term studies have been made on the impact of parasites on populations of *L. dispar*. Bess (1961) working in New England and New York from 1937 to 1945, concluded that parasites were not as important as predators, but that *C. melanoscelus*, *B. pratensis*, and *C. concinnata* appeared to be the most important species. He further noted that *B. pratensis* did poorly in xerophytic areas where populations of the moth are likely to be high. Egg parasitization generally was 20-40%, but there was no density dependent relationship with host abundance. Ticehurst et al. (1981) working in a first cycle outbreak in Pennsylvania concluded that the parasite complex had been ineffective in preventing host populations from reaching outbreak levels but that high parasitism by *B. intermedia* together with nucleopolyhedrosis virus and stress had contributed to the collapse of the host population and that high parasitism (60-70%) by tachinids, primarily *P. silvestris*, during the post-culmination period had been responsible for reducing populations to very low levels. However, the results of Elkinton et al. (1988), presented elsewhere in these proceedings, suggest that parasites may play an important role in regulating low populations of GM in North America.

In Europe, there are instances where parasites appeared to be the major factor causing gypsy moth outbreaks to collapse: *G. liparidis* in the USSR (Burgess and Crossman 1929), *G. porthetriae* in Poland (Burgess and Crossman 1929) and Yugoslavia (Vasic 1958), and *B. pratensis* in France (Fuester, unpublished data). Studies in Yugoslavia (Sisojevic 1975) and Austria (Fuester et al. 1983) indicate that the oligophagous, univoltine tachinids *B. pratensis* and *P. silvestris* are major factors in reducing populations during the first and second post-culmination years of the gypsy moth gradation, respectively. Sisojevic (1975) also noted that polyphagous, polyvoltine species such as *E. larvarum* and *C. concinnata* are dominant during the latent and progression phases of the host gradation. Outbreaks of gypsy moth seem to occur most frequently in southern Europe (Spain, Sardinia, Corsica, and Yugoslavia), and in some cases, appear to result from collapse of the natural enemy complex. Working in Yugoslavia, Maksimovic and Sivcev (1984) found that they could maintain populations of natural enemies (primarily *G. porthetriae* and *Cotesia melanoscelus*) during the latent period by

adding eggs of *L. dispar* to test plots. The increase in abundance of natural enemies that resulted from a steady supply of gypsy moths kept populations of the pest at low levels.

There have been relatively few studies on population dynamics of the gypsy moth in the Far East, but there are reports of outbreaks being triggered by unusual weather conditions (Nomura 1947), sunspot activity (Kono 1938), and fluctuations in numbers of parasites and predators (Ishii 1941). Parasites do not appear to be as important as birds in maintaining sparse populations, but Furuta (1981) noted that *R. lymantriae* and *E. japonica* produced significant density-dependent mortality at certain localities. Disease organisms, primarily NPV and the fungus *Entomophthora*, generally cause outbreaks to terminate. High rates of parasitization have been reported frequently for *G. liparidis*, *E. japonica*, and *B. schineri* (Table 4), but the stage of the gradation is seldom indicated, so it is difficult to evaluate the effectiveness of these species or the extent to which they regulate low populations.

Very few studies have been conducted on the impact of parasites on the Indian gypsy moth. The only in-depth studies were life tables developed by P. R. Dharmadhikari and the late V. P. Rao (Dharmadhikari 1972), which are discussed elsewhere in these proceedings (Mills 1988). In brief, the most important parasite over most of the study appeared to be *E. rossica* followed by "*Apanteles*" spp., *Palexorista* spp., and *B. intermedia*. Although generational mortalities ranged from 89-99%, the residual populations often were sufficient to produce high populations the following year.

DISCUSSION

The parasite complexes attacking gypsy moth in Europe and the Far East appeared to be the most complete and well-balanced (Tables 4 and 5), but even the one in Europe had a few lacunae (Table 3). Since the most complete complex of natural enemies should be present in a pest's native land, this lends credibility to the theory that *L. dispar* had its origins in Asia. The complex of parasites of Indian gypsy moth appeared to be relatively immature being composed largely of mildly and broadly polyphagous species with only one species, *A. kashmirensis*, entering diapause and having no need of alternate hosts. It appears possible that *L. obfusca* represents the remnant of an accidental introduction of *L. dispar* to the Indian subcontinent during antiquity. Were it not for the introduction of parasites from Europe and the Far East, the complex of parasites attacking gypsy moth in North America undoubtedly would be very depauperate, since about half of the species presently known would be missing.

Though many of the most important members of the the parasite complexes attacking gypsy moth in Europe and the Far East are monophagous or oligophagous species that do not require alternate hosts, some important species, notably *G. porthetriae* in Europe and *G. liparidis* in Asia, do have such requirements. Studies by Vasic (1958) and Fuester et al. (1983) suggest that, in certain localities, these species may be important in maintaining sparse populations of gypsy moth. Alternate hosts of *G. liparidis* are well known, but those of *G.*

orthetriae are not (Marsh 1979). Stocking patterns using trees preferred by alternate hosts of these or other important species would probably result in higher attack rates on L. dispar and could become an effective method of conserving or augmenting natural enemies.

Since most of the dominant parasites of the gypsy moth in Europe and the Far East have already been introduced (successfully or not) in North America, there are only limited possibilities for future importations. Many of the most promising species that failed to become established did so because of stringent alternate host requirements. It might be worthwhile to attempt development of strains of these parasites that would attack North American species closely related to their habitual alternate hosts by artificial selection.

Since there appears to be a dearth of well-adapted oligophagous species attacking the Indian gypsy moth, it appears logical to attempt the introduction of univoltine species such as P. uncinata, B. pratensis, or P. silvestris. Since parasitism by Q. kuvanae is negatively correlated with egg mass size (Brown & Cameron 1979), and egg masses of L. obfusata are smaller than those of dispar, it seems possible that Q. kuvanae could prove to be an effective parasite of L. obfusata.

Although efforts to obtain biological control of the gypsy moth have been beneficial, they have not been 100% successful. It is possible that new approaches in augmentation, classical importation, or conservation may provide improved control. However, the question arises as to whether it is worthwhile to attempt biological control of Lymantriidae. According to Clausen (1978), classical importation projects directed at the satin moth in the U.S. and Canada were successful. Concerning the project directed against the brown-tail moth in New England, he noted that a decline in moth populations followed the importation of natural enemies from Europe, but that the proper evaluation work was not done, and that an in-depth assessment of the mortality factors affecting the pest should be made.

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SUMMARY

Lymantria dispar, the gypsy moth, and Lymantria obfusata, the Indian gypsy moth, are defoliators of deciduous trees, the former in the Far East, Europe, and North America (where it is introduced), and the latter in northwestern India. The parasite complexes attacking gypsy moth in the Far East and Europe had the most species whereas that on the gypsy moth in North America had the least. The number of

species attacking Indian gypsy moth was intermediate. Species attacking the gypsy moth in the Far East and Europe seemed to be better adapted to their host than those attacking the Indian gypsy moth. A sizeable proportion of the former were oligophagous having no alternate host requirements, but most of the latter were polyphagous and required alternate hosts. Oligophagous parasites seem to be good at stabilizing host populations following outbreaks, whereas polyphagous species may play at least a minor role in maintaining sparse host populations or slowing down their increase.

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A REVIEW OF TECHNIQUES FOR
MEASURING THE IMPACT OF
PARASITOIDS OF LYMANTRIID S

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INTRODUCTION

Accurately measuring the impact of parasitoids on pest insects is an important component of entomological research. Values of percentage parasitism, calculated in various ways, are used for purposes such as estimating the effectiveness of inundative parasitoid releases, determining the effect of management treatments on parasitism levels, and constructing life-tables. In many studies, however, insufficient thought is given to the methods used to derive values of percentage parasitism and the biases that affect them (Van Driesche 1983). For this reason, the results of many prior attempts to estimate parasitoid impact on Lymantriid populations are difficult to interpret and have been generally unsatisfactory. In addition, researchers have often not been sufficiently specific when describing methods used to obtain values of percentage parasitism.

The impact of a parasitoid on its host population can be measured in two ways. One can measure the proportion of individuals that enter the host stage(s) susceptible to parasitism that are ultimately attacked by parasitoids (stage-specific parasitism) or the proportion of individuals present at the beginning of a time interval that are attacked during the interval (time-specific parasitism). Most of the values of percentage parasitism reported in the literature purport to estimate the stage-specific impact of parasitoids but these values are often severely biased. These biases can be the result of either host and parasitoid population phenologies and mortalities or biases inherent in the method of calculating percentage parasitism. In this paper we will review the advantages and disadvantages of each of four methods for estimating stage-specific percentage parasitism that have been used in the past (peak sample percentage parasitism, "pooled"

percentage parasitism, the graphical method of Southwood & Jepson (1962), and direct measurement of host and parasitoid recruitment) and one method for estimating time-specific parasitism which has recently been developed (time-specific k-value analysis).

Method 1: Peak Sample Percentage Parasitism

This method involves collecting a series of samples of hosts and dissecting them or rearing them until they die or molt to a non-susceptible stage. Most often, values of percentage parasitism for such samples are calculated as the number of parasitized hosts divided by the total number of hosts in the sample. The largest value of percentage parasitism (the "peak" when graphed) is often used as an estimator of the impact of the parasitoid (e.g. Ticehurst et al. 1978 for *Lymantria dispar* L. and Dharmadhikari et al. 1985 for *Lymantria obfuscata* Walker). Values of peak percentage parasitism are not necessarily good predictors of stage-specific parasitism, however. Values of parasitism seen in samples are easily biased by the pattern over time of the recruitment of hosts and parasitoids into the sampled stages, their relative rates of mortality in the sampled stages, and the timing of host and parasitoid molt to their next life stages (Van Driesche 1983).

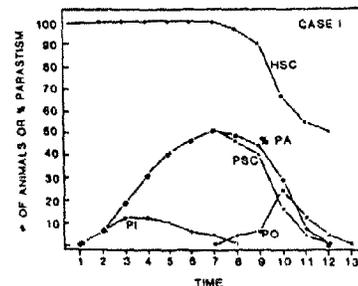


Fig. 1. Trends in sample percent parasitism values, under Case 1. HSC = Host Standing Crop, PSC = Parasitoid Standing Crop, %PA = Percent parasitism, PI = Parasitoid oviposition, and PO = Parasitoid emergence. Reprinted with permission from Environmental Entomology. Copyright 1983, Entomological Society of America.

Only under certain conditions does peak percentage parasitism accurately estimate stage-specific parasitism. This can be seen by considering a series of examples drawn from Van Driesche (1983) in which stage-specific parasitism was set at 50%. First consider Case I where 1) host recruitment to the susceptible stage is complete prior to the beginning of parasitoid oviposition, 2) no hosts molt to a nonsusceptible stage during the sampling period, 3) mortality of parasitized and healthy hosts is the same, and 4) parasitoid recruitment and parasitoid emergence do not overlap (Fig. 1). Under these conditions, there exists a period of time after parasitoid oviposition is complete and prior to the start of parasitoid emergence when sample percentage parasitism (the peak value) accurately reflects the level of parasitism for the susceptible stage. Samples must be taken frequently, however, so that the peak value is not missed.

Frequently the conditions just described are not met and values of peak percentage parasitism do not accurately reflect stage-specific levels of parasitism. For example, if unparasitized hosts develop to the next life stage during the sampling period more rapidly than parasitoids develop in and emerge from the hosts and if only the susceptible stages are being sampled, parasitized hosts will be over-represented in samples. This is due to an artificial concentration of parasitized hosts that results from longer residence times of parasitized hosts (as compared to healthy hosts) in the set of animals from which samples are drawn. This causes values of percentage parasitism to overestimate actual parasitoid impact (Fig. 2, Case II). The greater the proportion of unparasitized hosts that leave the susceptible stage, the greater the error will be in overestimating parasitism. Unparasitized hosts may leave the susceptible stage faster because their development to the next host stage requires fewer heat units than is required for parasitized hosts to reach the point of parasitoid emergence. The same result may occur if mortality of unparasitized hosts (by other mortality agents) is greater than that suffered by parasitized hosts. Alternatively, if parasitized hosts develop to their next stage faster or suffer higher levels of mortality than healthy hosts, sample percentage parasitism values will be depressed rather than inflated.

Another process that can affect values of peak percentage parasitism is the degree to which parasitoid oviposition and parasitoid emergence overlap (Fig. 3, Case III). For example, if the immature stage of a particular species of parasitoid is relatively brief but adults are long lived, considerable overlap of oviposition and emergence may occur. If such overlap occurs, there is never a point in time when all

parasitized hosts occur together in the population and are available for sampling. In such cases, peak values of sample percentage parasitism always underestimate the stage-specific level of parasitism.

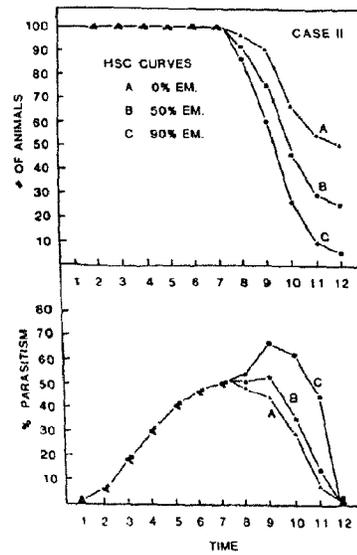


Fig. 2. Effect of early emergence (EM) of non-parasitized hosts.

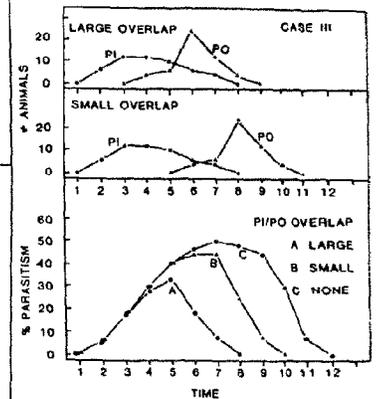


Fig. 3. Effect of overlapping parasitoid oviposition and emergence.

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In cases where hosts enter the susceptible stage gradually and concurrently with parasitoid oviposition, leave the susceptible stage concurrently with parasitoid emergence, or both, percentage parasitism will be higher than in Case I during both the recruitment period and the period when hosts are advancing to the next stage (Fig. 4, Case IV). If neither parasitoid oviposition and emergence nor host recruitment and advancement to the next stage overlap, a period may exist when the peak percentage parasitism accurately represents the stage-specific parasitism level. There is no reason, however, for such precise timing to occur and in most systems it is likely

that hosts and parasitoids will gradually enter and leave the system resulting in complex overlapping patterns (Fig. 5, Case V). When this occurs, values of peak percentage parasitism do not estimate stage-specific levels of parasitism because sample percentage parasitism at any given moment results from the net balance of four competing processes (cumulative parasitoid oviposition, parasitoid emergence or death, host recruitment, and host loss due to advancement or death) and bears no relationship to values of stage-specific parasitism.

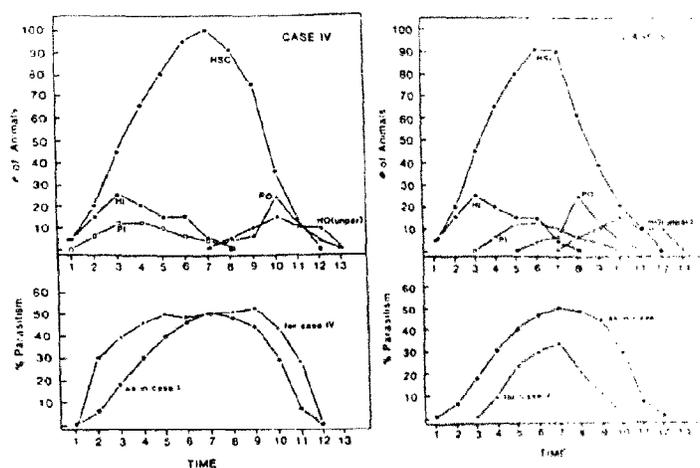


Fig. 4. Effect of gradual entry and exit of hosts.

Fig. 5. Effect of competing entry and leaving rates between parasitoids and hosts.

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Two advantages of using values of peak percentage parasitism are that they are easy to measure and it is not necessary to estimate the number of individuals entering a stage. Peak percent parasitism can be a good estimator of stage-specific parasitoid impact but only under specific conditions. Knowledge of the phenologies of host and parasitoid recruitment and loss are essential before values of peak percentage parasitism are used to estimate losses from parasitoids.

Two alternative uses of values of sample percentage parasitism sometimes employed are to take the mean percentage parasitism of a series of samples (i.e. Weseloh & Anderson 1975 and Weseloh et al. 1983 for L. dispar) or to take only one sample of a given life stage to estimate parasitism (i.e. Mason & Torgersen 1987 for Orgyia pseudotsugata McDunnough). From the previous discussion it follows that such values have a greater probability of being biased than peak values and should be avoided.

Method 2: "Pooled" Percentage Parasitism

The most common method of estimating stage-specific parasitoid impact is to use values of "pooled" percentage parasitism (e.g. Barbosa et al. 1975, Reardon 1976, Ticehurst et al. 1978, Blumenthal et al. 1979 for L. dispar; Massodi et al. 1986 for L. obfuscata; and Kukul & Kevan 1987 for Gynaephora groenlandica Wocke). "Pooled" percentage parasitism is calculated as the total number of parasitoids emerging from hosts in a series of samples divided by the sum of all the hosts collected. It is not clear what this value means in terms of stage-specific parasitism. Some of the samples are taken when values of sample percentage parasitism are increasing because of parasitoid oviposition and some when these values are decreasing due to parasitoid emergence. By pooling these samples with samples taken at the time of peak percentage parasitism one is essentially taking an average of sample percentage parasitism during the period of parasitoid occurrence. If "pooled" percentage parasitism is calculated for Case 1 (Fig. 1) where there are no complications due to host or parasitoid phenologies, parasitoid impact is underestimated as 32% (stage-specific parasitism was set at 50%). Another potential problem is that some samples may include hosts that were not susceptible to parasitoid attack because they were too young or too old when collected to be acceptable to parasitoids for oviposition or because they were collected prior to the seasonal onset of parasitoid oviposition. The combination of these two biases will nearly always lead to underestimates of the stage-specific impact of parasitoids.

In general, "pooled" percentage parasitism will accurately estimate generational parasitism only for nondynamic systems where each sample can be considered a replicate estimating a fixed condition (e.g. estimating egg parasitism in L. dispar from a series of samples taken during the late fall after parasitoid attack has ceased). This method should not be employed as a means

of estimating stage-specific parasitism levels for dynamic systems.

Method 3: Southwood & Jepson's "Graphical" Technique

The "graphical" method of Southwood & Jepson (1968) can be used to estimate numbers of hosts, parasitoids both that enter specified stages of a given generation (Bellows et al. 1988, 1989). To make such estimates, number of insects per sample unit is plotted versus accumulated degree-days as measured in the field. The area under the resulting curve has units of individual degree-days and when divided by the number of degree-days required for complete development of an individual, estimates of the number of individuals that entered the stage are obtained. Stage-specific parasitism estimates can be constructed from this approach by dividing a graphical estimate of numbers of parasitized hosts by graphical estimate of total hosts (in which counts of parasitized and healthy hosts are pooled). This approach assumes that being parasitized does not change the residence time of the host in the stage used to calculate total hosts, an assumption that may be true for some species and stages, but explicitly is not true for all cases. This method has been employed to date only in a few cases (Gargiullo & Berisford 1983, Schneider et al. 1988, Van Driesche et al. 1989) and only once in studies of Lymantrilidae (Kolodny-Hirsch et al. 1988, in a study of inundative releases of Cotesia melanoscela).

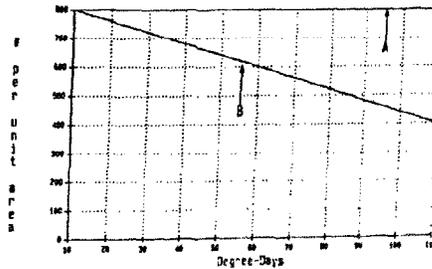


Fig. 8. The effect of mortality on estimates of the area under the curve and thus numbers entering a stage.
A: No mortality B: With mortality

The use of the Southwood & Jepson graphical method is complex and is subject to significant biases. In general, the Southwood and Jepson technique assumes that there is either no mortality during the stage or it occurs only at the end of the stage (Southwood 1978). Mortality occurring during the sampling period leads to a depression of the curve and to an underestimate of the number of individuals entering the stage. In a simulated population (Fig. 6), 800 individuals enter a stage which is subject to sampling. If there is no mortality (line A) the area under the curve divided by the developmental time accurately estimates that 800 individuals entered the system. In the case where mortality occurs throughout the stage (line B), the curve is depressed and an estimate of only 600 individuals results. As mortality increases so does the degree of bias in the resultant estimates of numbers entering the stage. When the technique is used to estimate both the number of hosts and the number of parasitoids (i.e. parasitized hosts) bias derives from: 1) mortality of healthy hosts, 2) mortality of parasitized hosts, and 3) the degree of parasitism. The interrelationships of these biases have been examined in detail by Bellows et al. (1988) and the method should only be applied to systems where biases are minimal.

Another potential problem with the use of the Southwood & Jepson graphical method is that developmental rates of individuals are usually calculated in the laboratory under conditions of constant temperature. Measurements of degree-days against which numbers per sample unit are plotted are taken in the field under conditions of fluctuating temperatures. In addition, temperature measurements are usually of a general ambient temperature; not necessarily of the microclimate temperature experienced by the insect. Lance (1987) found that the temperature of larvae in an outbreak population was 2-6°C warmer than those in a low-density population and that this temperature difference was due to density-related shifts in microhabitat. Laboratory studies indicated that this temperature difference could lead to a developmental difference of 1-2 weeks.

The Southwood & Jepson graphical method, while potentially useful, has significant risk of misuse if applied without careful consideration of the biases involved as determined by the biologies of the specific species under study. Also, to obtain an accurate estimate of the area under the curve, samples must be taken frequently. This may not be possible for some species of lymantrilids where sampling is extremely labor intensive.

Method 4: Direct Assessment of Host and Parasitoid Recruitment

Direct assessment of host and parasitoid recruitment provides a record of both total hosts and of parasitoid oviposition. This latter feature contrasts with the previously discussed methods which infer levels of parasitoid oviposition from observations of parasitoid emergence. Estimating parasitism from emergence data can be misleading if other mortality agents are selective in their attack on either parasitized or healthy hosts. Direct assessment of host and parasitoid recruitment is the only method that is not subject to this difficulty.

Methods to assess recruitment of herbivores (i.e. hosts) have been developed for a variety of species (e.g. Birley 1977, Van Driesche & Bellows 1988, Lopez & Van Driesche 1989). For *L. dispar* total host recruitment to the first instar may be determined by multiplying estimates of the numbers of egg masses per ha by the number of larvae hatching per egg mass (Buonaccorsi & Liebhold 1988 and Gould et al. in preparation). Recruitment to the pupal stage for *L. dispar* has been estimated by recording the number of new pupae appearing in small areas over short intervals of time. The numbers of new pupae per sample unit that are recorded during each interval are summed to obtain the total number of individuals entering the pupal stage for the generation (Gould et al. in preparation, Weseloh, personal communication).

Methods to directly assess recruitment of parasitoids to their immature stages have been developed more recently (e.g. Van Driesche 1988a,b, Lopez & Van Driesche 1989). Two general approaches to measuring parasitoid recruitment exist. One is to dissect field collected hosts to detect some brief, early stage in the life cycle of the parasitoid such as the egg or first instar larva, the duration of which may be determined under laboratory conditions (Van Driesche 1988a, Lopez & Van Driesche 1989). There is a risk, however, that small parasitoids may be overlooked when hosts are dissected.

An alternative approach is to deploy laboratory reared hosts in the field as trap hosts. After exposure to parasitoid oviposition in the field for limited intervals of time, trap hosts are recaptured and dissected or reared to detect the proportion that were attacked by parasitoids during the period of exposure. Parasitoid recruitment for each interval is then estimated as the attack rate on trap hosts times the density per sample unit of unparasitized, susceptible hosts in the field population. Total recruitment of parasitoids into the susceptible stage for the generation is then estimated by adding together the estimates of recruitment over all successive intervals during which

parasitoid oviposition occurred. Percentage parasitism for the stage is then estimated by dividing the number of parasitoids recruited by the number of hosts that entered the susceptible stage across all sample periods.

A basic assumption of this approach is that trap hosts are direct equivalents of field hosts. Factors such as trap host instar, density, pattern of occurrence in the environment, etc. may make trap hosts more or less susceptible to parasitoid attack. The suitability of trap hosts versus field hosts should therefore be experimentally verified (Van Driesche 1988a). The trap host approach is most often employed for sessile life stages (e.g. Torgersen et al. 1985 for eggs of Orgyia pseudotsugata McDunnough and Weseloh 1972 for eggs of L. dispar). The use of this technique is more difficult when mobile host stages are involved because parasitism rates can be affected by host behavior (e.g. Gould et al. in preparation) and because recovery of trap hosts may be difficult to achieve if hosts move from the release location. We have found that recruitment estimates of parasitism by Cotesia melanoscela Ratzeburg and Parasetigena silvestris Robineau-Desvoidy greatly underestimated the level of parasitism of L. dispar larvae (Gould et al. in preparation).

For species where accurate sampling procedures can be developed to measure host and parasitoid recruitment, this approach provides the most robust means of assessing stage-specific losses from parasitism of any of the methods discussed in this paper. It is not subject to complex or ambiguous biases and is easily computed and interpreted. We recommend its use whenever possible. The biology of many host/parasitoid systems may, however, make its use impractical.

Method 5: Time Specific K-Value Analysis

Because of the problems associated with the use of methods 1-3 and because direct assessment of recruitment is not always possible, an alternative approach has been developed by Elkinton (in preparation). This approach has advantages over Methods 1-3 in that it is not affected by host and parasitoid phenologies, estimations of host and parasitoid numbers are not necessary, and it estimates the proportion of hosts attacked by a given parasitoid, not the proportion that are ultimately killed. This method consists of quantifying mortality over time intervals rather than over specific stages or instars. Samples of hosts are taken at given intervals (e.g. weekly) without regard for the stage or instar of the individuals collected. Individuals in each sample are reared under field conditions until the next sample

is taken and the number of hosts that die due to each species of parasitoid during the interval is recorded. From these data estimates of the proportion of hosts in the natural population that die from each parasitoid during each interval can be obtained.

Except for the method of direct assessment of host and parasitoid recruitment, most methods of estimating parasitoid impact ignore the issue of simultaneous attack by more than one mortality agent. When hosts parasitized by more than one parasitoid are collected and reared (or dissected after considerable parasitoid development), one species is usually detected and considered to be the cause of mortality and there is no evidence of attack by the other species. The method of Elkinton (in preparation) expands upon the method developed by Royama (1981) and allows calculation of the simultaneous K-values or percent mortalities of each agent (see Royama 1981 for a full description of the method). "Marginal probability values" are calculated which are greater than the mortalities actually observed in rearings because they are estimates of the proportion of hosts that would have been killed by each parasitoid in the absence of mortality from the other simultaneous agents. In the method of Elkinton these values of the marginal probability of mortality are calculated for each interval, for each parasitoid species. They are then used to calculate K-values (Varley & Gradwell 1960, 1968) for each time interval. K-values are then summed over all intervals to obtain the estimate of the total impact of each parasitoid on the host population for the generation.

DISCUSSION

Many Lymantrilids are major forest pests and considerable effort is expended to gain improved understanding of their population dynamics. Conclusions from such research influence management decisions, yet estimates of the significance of parasitoids as sources of mortality in such systems are often based in part on values of percentage parasitism derived using Methods 1-3. These estimates, unfortunately, may be severely biased and the impact of parasitoids may not be accurately assessed. It is important for researchers to have a good understanding of the temporal patterns of host and parasitoid recruitment and loss and other possible biases such as mortality, behavior of trap hosts, etc. before choosing the most appropriate method of estimating parasitoid impact.

SUMMARY

Accurately estimating the impact of a parasitoid species on the population dynamics of its host is a crucial component of much of the research on species of Lymantrilids. We review four techniques for estimating stage-specific parasitism that have been used in past studies and one technique for estimating time-specific parasitism that has recently been developed. We conclude that the use of values of peak sample percentage parasitism and the Southwood and Jepson graphical method is appropriate for some systems but these methods can be subject to significant biases. Knowledge of the temporal patterns of host and parasitoid recruitment to and exit from the stages susceptible to parasitism as well as mortalities suffered by host and parasitoid populations is essential before these methods can be utilized effectively. The method of "pooling" estimates of parasitism across a series of samples is a common approach but such values have little meaning and this method is not recommended for dynamic systems. We recommend direct assessment of host and parasitoid recruitment to the host stages susceptible to parasitism whenever possible but in many instances this may be difficult. When direct assessment is not possible the use of a recently developed method (time-specific k-value analysis) is recommended as an effective technique for estimating losses due to parasitism.

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MODELS FOR THE POPULATION DYNAMICS
OF LYMANTRIA DISPAR

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INTRODUCTION

The many advances in computer technology during the past 25 years, in combination with the increased quantitative understanding of population dynamics, have sparked the development of computer models that simulate the population dynamics of several forest insects. Among the Lymantriidae, such models have been developed primarily for the gypsy moth, Lymantria dispar (L.), and the Douglas-fir tussock moth, Orgyia pseudotsugata (McD.). Because of space limitations, this review has been restricted to models of gypsy moth population dynamics.

Computer models of biological systems are often classified as either empirical or process models, although many other sets of names have had greater popularity in the past (Bruce, in press). The former usually are regression-based models developed from direct measurements of each variable of interest in the system. Process models generally incorporate current knowledge of the biological, chemical, and physical processes that affect the system being simulated; often the primary goal of process models is a better understanding of the system or the ability to extrapolate from observed conditions to situations that are currently unmeasurable (Bruce and Wensel, 1988). Applying the term "empirical" to the former category of models mistakenly implies that empirical elements are never included in process models, so I prefer the term "regression-based". Most population dynamics models are really mixed models because they incorporate both empirical observations and theory about the processes involved, so that a continuum exists between the two extremes (Bruce and Wensel, 1988; Bruce, in press).

Models from the full continuum -- simple regression models to complex process models are covered in this review. Mathematical models that may not be available as computer programs are also included because advances in programming languages and increasing programming skills among researchers often allow rapid, easy translation of a mathematical model to computer code. Models that simulate within-generation processes that affect the population dynamics of gypsy moth are also covered; these models sometimes serve as the foundation for multi-generation population dynamics models.

WITHIN-GENERATION MODELS

Phenology

Several models are available to predict the timing of gypsy moth development and host foliage growth within a season based on weather and other factors. Most are process models that use stand-wide averages of daily minimum and maximum temperatures as weather input.

Johnson et al. (1983) predicted the dates of first and median egg hatch using a degree-day based model. In field tests conducted in New Hampshire, predicted dates of egg hatch initiation closely matched observed dates for 2 of 3 years; egg hatch started about 1 week earlier than predicted in the third year (Johnson et al., 1983).

To simulate the pattern of egg hatch, Waggoner (1984) incorporated a delaying function, by which the development of certain portions of the gypsy moth egg population is delayed each day, into a Poisson function. This model predicted a skewed pattern of hatch that is characteristic for gypsy moth. The standard deviation for differences between observed and predicted dates of mean egg hatch was 2/3 day in laboratory studies, and was smaller for this model than for a degree-day model.

Larval and pupal development was simulated by Casagrande et al. (1987) based on temperature-dependent development rates; they also used Weibull functions to describe the distribution of development times of individuals. Parameters for this model were based on data from gypsy moths reared on white oak foliage, and the authors provided indices based on the literature for development on other hosts relative to development on white oak. Tests of this model against independent data from both laboratory- and field-reared gypsy moths revealed close agreement (roughly 5% error) between observed and predicted development (Casagrande et al., 1987).

Models for predicting the timing of budbreak and leaf growth for six eastern hardwood species were presented by Valentine (1983a). Either degree-days (budbreak, leaf growth) or calendar-days (leaf growth only) were used as independent variables. No tests against independent data were conducted, but for leaf growth the mean square errors were much smaller for the degree-day model (.005-.066) than for the calendar-day model (.012-.082) (Valentine 1983a).

Published data on gypsy moth phenology and the Valentine (1983a) host phenology model have been incorporated into a comprehensive phenology model developed by Sheehan (in review). This degree-day model uses daily minimum and maximum temperatures to simulate sets of cohorts of female and male gypsy moths from egg hatch to adult emergence, by host species. During an initial test of this model, differences between observed and predicted dates ranged from 0.2 to 2.6 days for egg hatch initiation, 1 to 3 days for early larval development, and 0.3 to 4.0 days for budbreak initiation (Sheehan, in review).

Growth

Gypsy moth growth and consumption within a season have been simulated by Valentine and coworkers in a series of differential

equation models. Five state variables were used in Valentine et al. (1976): number of gypsy moths per hectare, average larval weight (g), cumulative foliage consumption by gypsy moths (kg/ha), actual foliage present (kg/ha), and potential foliage (kg/ha that would be present if no defoliation occurred). A daily time-step was used, gypsy moth growth and consumption parameters were based on larval rearings on artificial diets, and potential foliage growth parameters were estimated to meet expected final foliage amounts (kg/ha).

Subsequent models refined and extended portions of the initial model. A degree-day based model that simulated larval growth and consumption was developed from field observations on two red oaks (Valentine and Talerico, 1980). Additional mortality sources representing virus, starvation, other density dependent factors, and insecticides were added to the initial model, which was then linked to a forest growth model in Valentine (1981). Budbreak and leaf expansion models were developed for six hardwood species by Valentine (1983a) as described earlier. The sensitivity of this model to a series of assumptions regarding gypsy moth response to changes in foliage quality is described by Valentine (1983b). Although the refined models performed well against the data from which they were developed (Valentine and Talerico, 1980; Valentine, 1983a), they have not been tested against independent data.

Density, Location

Multiple-regression models have been developed to predict maximum density of third and fourth instars and the proportions of larvae and pupae found in different resting locations. Maximum larval density (per .01 ac) was predicted as a function of distance to the nearest oak mass, number of egg masses at that distance, bark flap density, and oak density (Campbell et al., 1975; $R^2 = .57$). The density and proportions of fourth through sixth instars were predicted for four resting locations (bark flaps on oak, other locations on oak, litter, and other locations) using two variables that reflect average life stage (Campbell et al., 1975; range in $R^2 = .66-.99$). All of these models were developed from sparse, stable populations in Eastford, CT.

Dispersal

Dispersal of newly-emerged first instars has an important role in the population dynamics of gypsy moth (Mason and McManus, 1981), and several models simulating first instar dispersal have been published. None of these larval dispersal models have been tested against independent data.

Mason and McManus (1981) developed an atmospheric dispersion model which predicted that most larvae disperse short distances (within 400m) and that the few larvae that traveled long distances landed within 1 km for non-mountainous terrain and within 3 km for mountainous terrain. Settling velocity was modeled by McManus and Mason (1983) as a function of larval weight and silk length based on laboratory observations.

Taylor and Relling (1986) developed a simple model that calculated horizontal displacement of larvae based on wind speed, updraft duration, and velocities for updrafts, downdrafts, and larval settling; during wind speeds of 25 km/hr (which is probably the upper limit above which gypsy moth dispersal declines [McManus and Mason, 1983]) and using velocities reported in the literature, their model predicted long range dispersal of 5-19 km. Based on aerial samples taken over one location in one year, Taylor and Relling (1986) also reported a model that describes the log-linear relationship of aerial density of larvae and height above sea level; using this model and previous egg-mass counts, they estimated that about 0.3% of newly-hatched larvae became airborne and thus possibly subject to long-range dispersal.

A three-dimensional, stochastic wind model was linked to a trajectory and Gaussian puff model for larval dispersal by Fosberg and Peterson (1986). In 300 simulations of dispersal given springtime wind patterns characteristic of a currently infested coastal California area, transport greater than a few hundred meters occurred in 2% of the simulations. Fosberg and Peterson (1986) then used their model and the range of settling velocities reported by McManus and Mason (1983) to predict the dispersal patterns associated with long-range transport. They estimated that the centroid of the distribution of dispersed larvae would range from 7.2 km (for a settling velocity of 120 cm/s) to 21.0 km (for a settling velocity of 40 cm/s); given an initial source of 1 million dispersing larvae, their model predicted that maximum larval densities in long-range transport episodes would range from 49 to 14 larvae per hectare.

Mortality Sources

Models of mortality that occurs during the course of a season have been developed for certain specific mortality causes (primarily egg parasites and pathogens) and for certain life stages.

The population dynamics of *Ooencyrtus kuvanae* (Howard) (Hymenoptera: Encyrtidae), a parasite of gypsy moth eggs, was simulated in a model developed by Brown et al. (1982). Using a Leslie matrix approach for this multivoltine parasite, this model accounted for the effects of egg-mass size and density, mutual interference, and age-specific parasite fecundity. Predictions of *O. kuvanae* densities closely matched observed parasite densities in gypsy moth outbreaks, but became poorer as gypsy moth densities declined. The authors concluded that *O. kuvanae* was not food limited, and that though it may be an important mortality source during outbreaks, *O. kuvanae*'s reduced host-finding capacity and the decreased proportion of eggs available for parasitism in large egg masses have limited its effectiveness at low gypsy moth densities.

The within-season effects of nucleopolyhedrosis virus (NPV) and *Bacillus thuringiensis* (Bt) on gypsy moth populations have been simulated by Valentine and coworkers. Valentine and Podgwaite (1982) modified the differential equation model of Valentine (1981) to include changes in the densities of healthy and virus-infected larvae and changes in polyinclusion-body density on foliage, bark, or litter during the course of the larval stage. Effects of Bt application were incorporated into the model of Valentine (1983b) by Valentine et al. (1986), who then analyzed the influence of gypsy moth density and timing

of Bt application on the net rate of gypsy moth increase. Valentine et al. (1986) reported that the optimal application date was very sensitive to the density-dependent mortality rate.

Campbell has reported a series of regression models that predict age-specific mortality rates based on studies conducted in two locations. Eastford, CT populations (a well-established infestation) were sparse and stable, while the densities of Glenville, NY (a newly-infested area) fluctuated tremendously during Campbell's studies. Except as noted, none of these models has been tested against independent data. Age-specific mortality models developed by Campbell include:

- * proportion of small larvae (first through third instars) that survive to fourth instar, a function of initial egg density (Campbell, 1976; $R^2 = .47$ for Glenville, NY and $.98$ for Eastford, CT)
- * percent of large larvae (fourth through sixth instars) that die from disease, a function of the density of newly-hatched first instars and site moisture index (Campbell, 1963a; Glenville, NY)
- * percent of large larvae that die from NPV and that survive but carry sublethal doses of NPV, a function of the percent of large larvae that die from disease (Campbell, 1963a; Glenville, NY)
- * proportion of large larvae that survive to the prepupal stage, a function of egg density (Campbell, 1976; $R^2 = .25$ for Glenville, NY and $.49$ for Eastford, CT) or the density of newly-hatched first instars (Campbell et al., 1977; Eastford, CT, $R^2 = .58$)
- * proportion of larvae that survive specific portions of the large larval stage, a function of the proportion of larvae in different resting locations, the current lifestage, and average life stage (Campbell et al., 1977; Eastford, CT, $R^2 = .58$)
- * proportion of prepupae that die from desiccation, a function of the number of eggs per mass at the end of the current generation (used as an estimate of relative density during the current generation) (Campbell, 1963a; Glenville, NY)
- * proportion of pupae (male and female combined) that survive to adults, a function of initial egg density (Campbell, 1976; Eastford, CT, $R^2 = .85$)
- * percent mortality for female and male pupae, a function of the number of eggs per mass at the end of the current generation (Campbell, 1963b; Glenville, NY)
- * percent mortality for female pupae caused by Ichneumonid parasites, a function of egg density at the start of the generation (Campbell, 1967; Glenville, NY, $R^2 = .82$)

Fecundity

A strong relation between pupal fresh weight and adult fecundity has been reported by Hough and Pimental (1978, $R^2 = .99$). Their model has been validated by Sheehan et al. (in preparation) using published observations of pupal weights and fecundity.

Other regression models that use gypsy moth density during a generation to predict fecundity at the end of a generation have been developed by Campbell. Based on data from Glenville, NY -- a relatively new infestation -- the number of eggs deposited per female was reported as a function of egg density at the start of a generation (Campbell, 1967, 1976; $R^2 = .72$ and $.80$, respectively) or the density of newly-

hatched larvae (Campbell, 1963a). A model based on the stable, Eastford, CT populations showed low correlation between initial egg density and fecundity (Campbell, 1976, $R^2 = .21$).

Campbell later developed a regression model that predicted the number of eggs per mass at the end of a generation based on the number of fourth instar larvae per hectare present during the generation (Campbell, 1978; $R^2 = .71$). This Glenville, NY model was compared to data sets from other sparse populations (Campbell, 1981). No significant differences were found between data sets from Glenville and from well established populations within the generally-infested area, while the differences between Glenville populations and those from newly infested areas or Cape Cod, MA (where repeated outbreaks have occurred) were statistically significant (Campbell, 1981).

Sex Ratio

Several regression models for pupal sex ratios have been reported. Based on a data set from Glenville, NY, Campbell described the percentage of females among pupae as a function of the percentage of disease and desiccation among larvae and pre-pupae (Campbell, 1963b) and as a function of egg density, precipitation in June, and the percentage of white oak foliage among the total overstory foliage (Campbell, 1967; $R^2 = .73$). Mauffette and Jobin (1985) predicted the proportion of males among pupae based on larval density as measured by either grass boards during late June ($R^2 = .76$) or tarpaper during mid-July ($R^2 = .74$).

Campbell (1976) reported two models that predict adult sex ratio based on initial egg density. One model was based on data from sparse populations in Eastford, CT ($R^2 = .97$), while the other was based on Glenville, NY data ($R^2 = .60$). None of the models for pupal or adult sex ratios have been compared to independent data.

MULTIPLE-GENERATION REGRESSION MODELS

Several models have been developed that use regression analysis to predict changes in gypsy moth numbers from year to year. Specific variables that are predicted across generations include egg density, egg-mass density, or changes in generation trend. Table 1 summarizes the factors included in several regression-based models, which are briefly discussed below.

Generation Trend

Campbell and Sloan (1978b) presented models that used egg density at the start of generation n to predict the trend in density from generation n to $n+1$. Because significant differences were found between data sets from an area with sparse, stable populations (Eastford, CT) and a recently invaded area (Glenville, NY), separate models were developed for each area ($R^2 = .71$ and $.68$, respectively). When each

Table 1. Summary of attributes included in regression-based models for multiple generations of gypsy moths.¹

Attribute	Trend				Egg Density C1	Egg-Mass Density			
	CS1	CS2	CS1	CS2		C1	B	C2	ZL
Egg Density	•	•			•				
Egg-Mass Density			•	•		•	•	•	•
Other GM Attributes		•		•				•	•
Weather					•	•	•	•	•
Stand Attributes					•			•	•
Tested	•								•

¹ CS1 = Campbell and Sloan (1978b), CS2 = Campbell and Sloan (1978a), C1 = Campbell (1967), B = Biging et al. (1980), C2 = Campbell (1973), and ZL = Znamenski and Liamcev (1983).

data set was compared to a subset from the IPS system of plots (an independent data set), significant differences in density-trend relationships were found ($P < .01-.05$), although visual inspection of the models did reveal general similarities.

A second model form that predicted egg density trend was reported by Campbell and Sloan (1978a), who used both egg density at the start of generation n and the coefficient of variation in egg density as independent variables. Data from the Glenville and IPS data sets of Campbell and Sloan (1978b) were used to develop this model. No test against independent data was conducted for this model, nor were any estimates of goodness of fit provided.

For situations in which fecundity estimates are not available, these authors also presented models that predicted egg-mass density trend using initial egg-mass density either alone (Campbell and Sloan, 1978b) or with the coefficient of variation in egg-mass density and the amount of precipitation in June (Campbell and Sloan, 1978a). Both models were developed from the Melrose Highlands data set, which is described by Campbell (1973b) and Biging et al. (1980). The R^2 values for the first model form (using egg-mass density as the only independent variable) ranged from .23 to .51, and no comparisons were made with independent data sets for either model.

The Melrose Highlands data was also used by Campbell (1973b) to develop a series of tables that listed the proportion of observations in each egg-mass trend category (increasing five-fold, decreasing five-fold, or intermediate) as a function of zone egg-mass density, stand egg-mass density, and the previous year's trend category.

Egg Density

Campbell (1967) presented a model that predicted egg density for generation $n+1$ as a function of egg density for generation n , precipitation in June during generation n , and the percentage of overstory foliage represented by swamp white oak. The Glenville data set was used to develop this model, which had an R^2 value of .48; no comparisons to independent data sets were reported.

Egg-mass Density

The Melrose Highlands data has been used to develop several models that predict egg-mass density. Campbell (1967) developed separate models for the periods from 1910-1921 and 1922-1930; both models calculated egg-mass density as functions of egg-mass density in generation n and precipitation in June. No tests against independent data were conducted for these models, whose R^2 values were .35 (1910-1921) and .37 (1922-1930).

Campbell (1973a) later reported another set of regression models based on the Melrose Highlands data, in which egg-mass density was predicted separately for poor food stands (with more than 50% of the overstory foliage composed of species that are not preferred by gypsy moths) and oak stands (with at least 50% of the overstory foliage composed of oaks). A second model for oak stands used only variables that can be observed by March 1 of a given year. Independent variables used in these models were gypsy moth density (egg-mass density at the start of generation n , percent of the surrounding zone with >500 and >5,000 egg masses per acre, and previous egg-mass trend), stand conditions (total foliage per acre; percentage of overstory foliage in three host categories -- most preferred, intermediate, and least preferred; percentage of overstory foliage in the red oak or white oak groups, and percentage of dominant trees in the stand in the most preferred host category), weather conditions (precipitation in May for generation n and in June for generation $n-1$, and mean minimum temperature for the coldest month experienced by generation n), and defoliation (stand-wide percent defoliation caused by generation n , and percent defoliation of food class A caused by generation $n-1$). The R^2 values for these models ranged from 0.66 to 0.74, and no comparisons to independent data sets were made.

Biging et al. (1980) used the Melrose Highlands data to develop a multiple-regression model that was tailored to tree species found in Wisconsin. These authors predicted egg-mass density at the start of a generation based on egg-mass density and weather data for the preceding two generations plus a stochastic error term based on observed mean square errors for egg-mass density. Weather variables included precipitation and temperatures for May and June, and mean winter temperatures. Separate models were developed for six host groups that were common to Wisconsin. Biging et al. (1980) ran a set of 10 or more simulations for each host group using weather data from 11 weather stations in Wisconsin, reporting the results as state-wide hazard maps. Models for all species groups consistently predicted higher populations in northern Wisconsin; the authors speculated that winter temperatures,

which played a relatively minor role in the Melrose Highlands models, may play a much different role in Wisconsin. This model has not been compared to an independent data set.

In the USSR, several models that use gypsy moth, weather, and stand variables to predict egg density (egg quantity per 100 shoots) have been developed by Znamienski and Liancev (1983). Separate models for all stands, oak stands only, and mixed stands were developed, with the following independent variables: number of eggs per mass, egg-mass density, and egg weight for the previous generation; mean temperatures for July-August and May-August, minimum temperatures for May, and the ratio of the minimum temperature for May to the 10-year average minimum temperature for May; and the proportion of oaks in the stand ($R^2 = .87-.88$). Because egg weight is often not available to pest managers, a fourth model that did not include this variable was developed for all stands ($R^2 = .85$). When this latter model was tested against independent data from three other areas, predicted densities closely matched observed densities.

Valentine and Campbell (1975) linked the egg-mass density model of Campbell (1973a) with other submodels that simulated defoliation and tree condition. Five state variables (egg-mass density, population trend, defoliation last year, and the percentages of the surrounding area that contain high and low egg-mass densities) plus a stochastic element were used to estimate defoliation. Transition probability matrices from Campbell and Valentine (1972) were used to estimate the effects of defoliation on tree condition and mortality. This model was intended to be a decision-making tool for forest managers who were considering gypsy moth suppression.

MULTIPLE-GENERATION PROCESS MODELS

Table 2 summarizes the general features of several process-oriented models that simulate gypsy moth populations for multiple generations. The objectives of most of these models were either to synthesize current knowledge and guide research and/or to project long-term impacts of gypsy moths in currently uninfested areas where forest conditions may differ greatly from those found in the northeastern United States. Accurate predictions were generally not objectives of these models, and none of them have been tested against independent data. These models are reviewed in approximate order of publication.

One of the earliest process models for gypsy moth was developed by Picardi (1973), who simulated female gypsy moth and Ichneumonid densities based on available literature and the guidance of a consulting entomologist. Six mortality sources were included: egg parasites, disease, small mammals, birds, *Calosoma*, and Ichneumonids. Sex ratio was simulated as a function of disease mortality, and both gypsy moth density and available foliage were used to calculate fecundity. The regular, 8-year cycles predicted by this model were due primarily to the actions of Ichneumonids, which were modelled as a delayed, density-dependent mortality source, and the density-dependent functions for disease and predation. Several pest control options were simulated, including insecticide application, mating disruption via pheromone

Table 2. Summary of attributes included in process models for multiple generations of gypsy moths.¹

Attributes	P	M/S	V	E	Br	By	S
Weather			•	•			•
Foliage	•	•	•	•		•	•
Growth/Consumption	•	•	•	•	•	•	•
Dispersal						•	•
Sex Ratio	•	•			•		•
Fecundity	•	•			•	•	•
Stand Model	•	•	•			•	•
General Density- Dependent Mortality		•	•	•	•	•	
Predators/Parasites	•				•		•
Starvation			•			•	•
NPV-natural	•	•	•	•	•	•	•
Insecticides	•	•	•				•
Other Controls	•		•				•

¹ P = Picardi (1973), M/S = Morse and Simmons (1979), V = Valentine (1981), E = Etter (1981), Br = Brown et al. (1983), By = Byrne et al. (1987), S = Sheehan et al. (in preparation).

release, and a combination of both insecticide and pheromone application. Picardi's (1973) model predicted that insecticide use would lead to 2-3 year cycles with tremendous population fluctuations, while pheromone release would lead to gypsy moth extinction after 25 years (if used alone) or 15 years (if used in combination with insecticides).

Another early process model concerning gypsy moth was developed by Morse and Simmons (1979) to explore the results of alternative gypsy moth management strategies. Their forest submodel used site quality, species composition, stocking, and average tree size to predict amounts of foliage present. Foliage consumption was predicted by a gypsy moth submodel using stage-specific mortality rates and consumption rates. A stochastic feature of the gypsy moth mortality section initiated outbreaks when population densities were low. Tree mortality was simulated as a function of site quality, current defoliation, and defoliation history for the previous two years. Morse and Simmons

(1979) concluded that annual aprays for eradication would fail because gypsy moth populations would persist at low densities during spray years and would rise once spraying stopped.

Brown et al. (1983) developed a simple process model to examine the effect of *O. kuvanae* on gypsy moth population dynamics. Mortality factors other than the egg parasite included NPV, vertebrate predation of pupae, and a general density dependent mortality factor. Foliage was assumed to be unlimited, and environmental factors were assumed to be constant and optimal for gypsy moths. Brown et al. (1983) compared simulations with and without egg parasitism using their model, Picardi's original model (Picardi, 1973), and Picardi's model modified to include three other parasites and to update the egg parasite and pupal parasite sections. Both the Brown et al. (1983) model and the original Picardi model predicted regular outbreak cycles, with *O. kuvanae* lengthening the time between outbreak, prolonging the duration of outbreaks, and lowering the average gypsy moth density over time by several orders of magnitude. In simulations with the modified Picardi model showed the egg parasite did not affect average gypsy moth density but did alter the regular 2-year cycle (in the absence of the egg parasite) to an irregular, acyclic pattern. Variation in parasitism rates predicted by all three models was found to be similar to that found in two independent data sets.

Two population models were briefly described by Etter (1981): a simplified NPV compartment model, and a more complex process model. The latter model simulated gypsy moth and host phenology, gypsy moth growth and foliage consumption, and mortality caused by NPV and by other factors. Etter (1981) reported that the process model was very sensitive to the degree of synchrony between budbreak and egg hatch, but details of this model have not been published.

To assess the influence of gypsy moths on existing oak forests, Valentine (1981) linked a forest growth model with a gypsy moth population model. Tree volume growth was modelled as a function of photosynthate production, which was assumed to decline when defoliation occurs, and respiration. Increased tree mortality was also simulated following defoliation. Valentine et al.'s (1976) model of gypsy moth growth and foliage consumption was the basis for the population model, to which mortality sources representing starvation, NPV, and other density-dependent factors were added. Application of either NPV or insecticides could be simulated. In 16-year projections with no defoliation, predicted basal area closely matched observations. The gypsy moth portion of this model was most sensitive to parameters affecting larval growth and consumption and foliage phenology.

Another forest-gypsy moth model was developed by Byrne et al. (1987) to explore potential long-term impacts of gypsy moth populations on succession in North Carolina forests. They used Johnson's (1977) forest succession model to simulate 12 forest types, each with 3 tree-size classes. Based on species composition, forest types were assigned to one of three preference groups, and gypsy moth populations were simulated using development times and mortality rates that varied with lifestage and preference group. Additional gypsy moth mortality due to first instar dispersal, starvation, and NPV was also included. For all but the least preferred hosts, this model predicted that gypsy moth populations would increase steadily until they reached densities that trigger a NPV epidemic and subsequent population crash. Forest mortality was simulated as a direct function of defoliation in the

current and previous years. Byrne et al.'s (1987) model predicted short-lived outbreaks at approximately 8 year intervals, with outbreak frequency and severity largely controlled by forest composition.

The most comprehensive forest-gypsy moth model developed to date is the Gypsy Moth Life System Model (GMLSM), which was initially developed through a series of workshops (McNamee and others, 1983) and later extensively revised and expanded (Sheehan, in press; Sheehan et al., in preparation). This degree-day model uses daily weather to drive the development of gypsy moth cohorts, foliage, and certain parasites. Within GMLSM, a stand submodel that was modified from previously existing stand models (JABOWA, from Botkin et al. [1972] and FORET, from Shugart and West [1922]) translates defoliation into effects on tree growth, mortality, and recruitment; a wide range of silvicultural treatments may be simulated. To predict defoliation, the gypsy moth submodel predicts gypsy moth growth and foliage consumption (based largely on Valentine and Talerico [1980]), foliage growth (taken from Valentine [1983a]), larval movement, and fecundity. Mortality sources that may be simulated by the GMLSM include: NPV (either naturally-occurring or applied), Bt, four predator groups, six parasite species, starvation, released pheromones, insecticides, or released sterile eggs or males. Aside from the gypsy moth and host phenology sections (Sheehan, in review), this recently-developed model has not been tested; testing will become a major emphasis in the ongoing work on this model.

SUMMARY

A wide range of mathematical models has been developed to simulate the population dynamics of gypsy moth. The primary goal of some of these models has been to forecast gypsy moth densities, while other models were developed to summarize existing knowledge, guide research, or predict what might occur in areas quite different from the current North American infestations. Two alternative approaches have generally been used: regression-based models, which use regression analyses to identify statistical relationships among observed variables, and process models, which quantify and incorporate the biological, chemical, and physical processes that affect population dynamics.

Potential users of these models often face a dilemma. Regression-based models that are available in the literature generally have been developed for only a limited number of locations and years, often include variables that can not be used in other areas (such as specific tree species with limited distributions), and cannot readily be modified to address new questions. On the other hand, process models that have been developed often include variables that are not easily measured, generally are either very complex (and difficult to interpret or evaluate) or very simple (with results obviously dictated by model structure and parameter values), and in many cases only cover a portion of the system under study. Only a small proportion of the models using either approach have been tested, especially for multiple-generation models.

Both approaches to modeling -- regression-based versus process -- have inherent strengths and weaknesses, and the best choice for a given situation depends on the objectives of the user, available data, and

current biological understanding of the system. The large number of untested models described in this review is a tribute to the need for model builders to place greater emphasis on model testing.

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NEW AND OLD WORLD LYMANTRIIDAE:
DISCUSSION AND RESEARCH
ISSUES

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Following each presentation, a 15-minute discussion period encouraged the expression of views and observations by participants. These discussions identified unresolved issues and indicated where additional research is necessary for their clarification. Statements made were not necessarily endorsed by all attendees and comments were recorded and later synthesized into general topics as follows.

OUTBREAK PERIODICITY

Is there outbreak periodicity for different species of Lymantriidae? In Europe, outbreaks of the nun moth are related to drought, particularly in forests that are not optimal for the insect. High summer temperatures preceded by low spring temperatures appear to be good predictors of outbreaks. There is a possible sunspot relationship for nun moth in Europe; defoliation often occurs 2 years following sunspots. In New England there appears to be local periodicity of 7-9 years between gypsy moth outbreaks. There is intensive defoliation by gypsy moth followed by years of decline. This pattern seems to occur from west to east in the state of Connecticut but has not been documented elsewhere.

The actual periodicity of gypsy moth outbreaks has not been proven. It has been suggested that periodicity shown on a spatial scale disappears when examined on a time scale. In Europe, where annual surveys of life stages of the gypsy moth are measured over the same area, periodicity of population peaks has been observed, but these peaks do not necessarily produce defoliating outbreaks. In the United States, where defoliation is used as the criterion for assessing outbreaks, population peaks are often missed and it has been difficult to demonstrate population periodicity. There is a need to look at the Eurasian and U.S. data on a similar scale (population peaks or defoliation, or both) to determine whether periodicity exists.

SYMPATRY OF LYMANTRIID SPECIES

Where there is sympatry of the brown-tail moth and the gypsy moth in Europe, the brown-tail moth tends to be displaced. The latter will relocate if gypsy moth already has stripped trees of foliage needed for egg deposition by the female brown-tail moth. This may have contributed to the decline of brown-tail moth populations in the United States. Mechanical destruction of nests has continued in the United States since the 1920's, but it is unlikely that this alone is responsible for the population decline. There is no effective method for surveying areas where the brown-tail

moth once occurred and there still may be residual localized populations that have gone undetected. Pathogens introduced against the brown-tail moth may have been the primary reason for its reduction. However, habitat/host relationships appear to limit the distribution of brown-tail moth to coastal regions of Europe and the United States. Are these regions less favorable to other *Lymantriids* so that sympatry is less intensive or is weather limiting survival to these discrete habitats? Is there evidence of other sympatric interactions, such as with Douglas-fir tussock moth and other Western United States *lymantriids*?

POPULATION DENSITY ESTIMATES

While protocols have been developed and others are being evaluated for low-density sampling of several *lymantriid* species, universal techniques are lacking. Factors that complicate this problem include differences in behavior and development of low- and high-density populations; effect of the spatial scale and forest physiography; and a poor understanding of the role of dispersal. All of these have a bearing on the size of research study areas. Dispersal also is important when assessing spray techniques. In the ridge and valley system of Pennsylvania the gypsy moth appears to have a greater range of dispersal than was previously reported. It has been difficult to evaluate spray efficacy in subsequent years because even in blocks of 1,000 hectares, reinvasion makes it difficult to distinguish the boundary of sample or treatment areas. This raises the question of the magnitude of the spatial scale of the sample area. What is the ideal sampling unit? The individual tree? A hectare plot? When sampling *Lymantriidae*, there always is the possibility of migration into or immigration from trees. Cooperation with other researchers to establish tests and evaluate standardized techniques internationally would be beneficial.

HOST AND STAND RELATIONSHIPS

It is generally agreed that host type, condition and stand structure influence various *Lymantriidae*. Yet we lack a complete understanding of these complex relationships. Host choices of the nun moth differ in various countries. In Japan, the nun moth develops fastest on larch; in Europe there are only small larch stands and nun moth outbreaks rarely begin there. Nun moth does not generally pose a problem in Western Europe, but in the French Alps, an outbreak of nun moth began on larch. Three outbreaks of nun moth are known in this century--usually triggered by a period of dry weather. However, where there are larch stands in an area of outbreak, the trees are defoliated but the larch produces new needles. When defoliation of spruce exceeds 80 percent, trees die; spruce stands are killed in the first year of the outbreak, pine trees survive one defoliation, and larch stands survive. Development of the caterpillars is faster on larch. A suggested reason for the decline in outbreaks of the nun moth on pine in the second year of defoliation is that the insect consumes the new flowering buds, which

depletes food in the following year. One generation consumes the food for the next generation causing the outbreak to die out.

The issue of the relationship of pollution and insect pests was addressed. In Oregon, there seemed to be no relationship between reduction in pollution and pest outbreaks. In fact, in recent years the worst tussock moth outbreaks have occurred despite improved air quality. The relationship between the Mount. St. Helen's eruption and a reduction in populations of Douglas-fir tussock moth and western spruce budworm is believed associated with ash deposits on the foliage.

There appears to be a similarity in host composition and stand structure in forests that are traditional epicenters for gypsy moth outbreaks. In fact, the physiography of susceptible stands in New York and Vermont are similar to outbreak sites in China and Crimea, U.S.S.R. Are there consistent habitat requirements for the *Lymantriids* per se? If so, how can factors associated with forest physiography be used by researchers and pest managers worldwide?

FECUNDITY

How important is the assessment of fecundity in *Lymantriidae*? In latent populations there is little difference in fecundity from one year to the next on a single host plant, but fecundity would vary significantly from host plant to host plant. Temperature also influences fecundity. It is not clear at what spatial scale fecundity should be calculated. Use of eggs per unit area will vary by forest type and condition. For example, species stands such as are found in Europe would probably require a different spatial scale than multispecies stands.

Do all *Lymantriidae* produce large numbers of eggs capable of outbreak proportions? Some species deposit their eggs intermittently (this is true of species that feed on grasses and sedges) while others deposit all of their eggs at one time. Some species are destined to outbreak; others seem to avoid it. Comparison of outbreak and nonoutbreak species on the basis of egg deposition characteristics and larval aggregations would be useful in understanding population dynamics and predicting outbreaks.

FEMALE FLIGHT

For gypsy moth, the difference between a descending flight, which more resembles a flutter of wings as the insect descends to a resting location (as found in the United States and Western Europe) and an ascending flight, where the insect can choose a variety of egg deposition sites, (as found in Eastern U.S.S.R. and Asia) is not clearly understood. There appears to be diminution in flight ability from Eastern to Western U.S.S.R. and only flightless females are found in the Federal Republic of Germany. One would expect that in those cases where the female has lost the ability to fly, dispersal is not lost but shifts to a different life stage, such as first-instar larvae. In Japan, deposition of egg masses by flying females is not affected by density. Nothing is known about the

genetics of flight in the overlap zone in the Soviet Union, where some females fly and others do not. Information is needed on the ecological correlates of wing reduction and dispersal and mate finding. Patterns of defoliation associated with difference in flying and nonflying female gypsy moth populations need to be assessed with respect to adult flight and vagility.

BIOLOGICAL CONTROL

Is biocontrol successful? Some parasites introduced into the United States are successful against several Lymantriids. However, there has been no documentation that parasites have been instrumental in reducing outbreaks or maintaining Lymantriid species at low levels. It is not clear whether the recent change in distribution and behavior of the brown-tail moth on Cape Cod, Massachusetts is due to the collapse of unknown control factors or whether a period of adjustment is required before an introduced pest increases dramatically.

What is considered "unknown" mortality by Tachinids might be overlooked. This would occur when a parasite attacks a larva that dies without producing a parasite. The difference between mortality in sites which favor Tachinids and those that do not might be correlated with this unassessed mortality.

There is considerable concern about the methods of determining percent parasitism. In the past, parasitism has been expressed as either the highest sample percent parasitism value or an average of all sample values. Since there are often large biases associated with these methods, a new method has been developed which uses "K values" which are calculated for short periods of time and added together to give the total impact of the parasitoid. It is apparent that there is a need for uniformity in reporting parasite assessments both in the field and the laboratory.

What is the proper spatial area to measure and what resolution is most appropriate for parasites? Should they be studied at a different resolution than that for predators? In fact, habitat has significant effects on the predator community in that extreme differences can be expected within short distances. Thus, the role of predators must be evaluated carefully with respect to habitat variation.

How should predation be assessed? For example, some small mammals are effective insect predators that in turn are preyed on by other animals. These relationships must be understood as insect management schemes are developed. This is true for the deployment and assessment of bird nest boxes as nest boxes may be used by animals other than those intended.

With the use of *Bacillus thuringiensis* (Bt) there is the problem of extended egg mass hatch period combined with a short effective period of Bt in the field. In the Western United States, 3-4 applications are used in field trials. The terrain in treated areas often encompasses a range of elevations. This makes it difficult to monitor individual sites where the geographic area is large and the hatch is sparse. An important question is why spray programs are not initiated before pest populations become too large. The answer seems

to be that it is difficult to obtain a financial commitment for such programs when populations are low. In the Northeastern United States much of the land is privately owned, making it difficult to obtain the necessary cooperation.

Should virus control be attempted for the brown-tail moth? In one report, the treatment area was 10-20 square meters. It is too early to determine whether virus control is economical. Reporting of results should be uniform as differences in formulation and application must be taken into account. Also, dosage (weight or international units) should be reported consistently.

The methodology of treating gypsy moth eggs with NPV varies. In the Federal Republic of Germany, there is no attempt to treat all of the egg masses--just enough to transport the virus into the population. This was recommended for isolated infestations. It is not recommended for large gypsy moth outbreak areas.

Infection of adults by gypsy moth NPV has not been determined completely. A sublethal dose of NPV fed to larvae with no evidence of NPV in the next generation does not necessarily mean the virus was not transmitted. Efforts should be made to determine the presence of the virus in the adult (female) stage of generation one.

Microsporidia evaluation is ongoing and needs input from studies of other populations in Europe. There is a need to clarify the taxonomy of the isolates on hand. The role of introduced microsporidia into North American gypsy moth populations requires careful assessment. Possible adverse effects from introduced microsporidia include: sublethal effects such as lower percent hatch, reduced fecundity, higher mortality of progeny in infected females, and poor mating of males. Spatial and temporal effects of microsporidia may have an impact on other factors such as parasitism and overwintering. Research on the spread of microsporidia from inoculated areas is being considered in the United States. Currently, only isolated infestations can be treated. In the laboratory, these microsporidia infect other Lepidoptera. But even though they could infect another host, microsporidia may not necessarily cause an epizootic. How microsporidia move between species would be an important line of international research.

GENETICS

Is the gypsy moth polymorphic since there are several known races? Controversy exists over the application of this term to certain insect species since polymorphism, when defined loosely as "distinct forms" conflicts with the classic genetic definition of "single gene difference." There is a need for a more accurate definition of terms.

There is a possibility (unconfirmed) that some gypsy moth escapees from Asia to the Western United States were not eradicated. However, they may not be identified easily if they occur in low numbers. The goal is to delineate the populations in Asia to see what differences can be identified. Genetic markers can answer some of the questions of origin if one is willing to devote the time and money involved. Through collaboration it is possible to look at populations from a genetic point of view for Oregon or other

subpopulations of gypsy moth in the United States. It has been suggested that no difference would be found without the use of high-resolution genetic analysis. The techniques for this analysis have been refined and now there is a need for samples from diverse areas. There are problems involved in crossing different populations of gypsy moth for control purposes. Genetic manipulation has inherent problems and it has been suggested that this is not a viable strategy. This is an area of research which would require a multinational cooperative effort.