

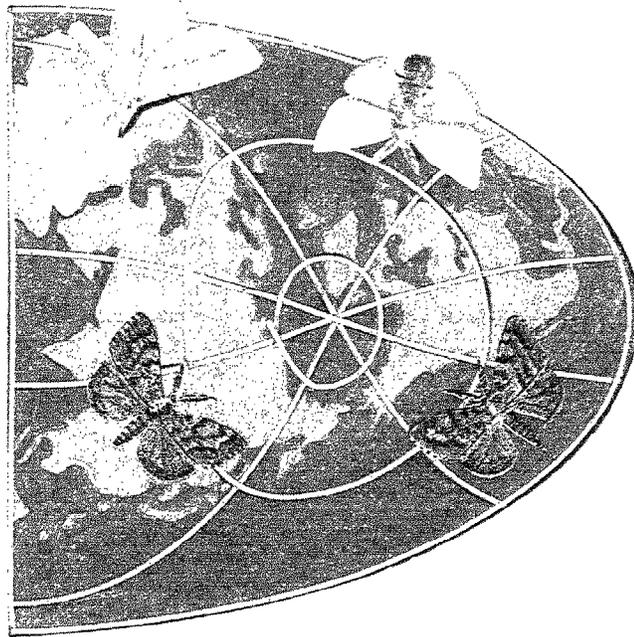


United States  
Department of  
Agriculture  
Forest Service  
Northeastern Forest  
Experiment Station  
General Technical  
Report NE-125



## 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 Lymantriid 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.

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## COVER

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

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

March 1989

**PROCEEDINGS**

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

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

Technical Coordinators:

William E. Walner and Katherine A. McManus  
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Northeastern Forest Insects & Diseases  
Hamden, CT 06514

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

### Welcoming Address

International cooperation on scientific issues  
of common interest

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

### Contents

#### FAMILY CHARACTERISTICS

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

#### POPULATION DYNAMICS

- T. S. Jensen* Latency characteristics of tussock moths  
(Lepidoptera: Lymantriidae)
- J. Schönherr* Outbreak characteristics of Lymantriids
- R. R. Mason* Monitoring population change in the Lymantriidae

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

#### GENETICS AND BEHAVIOR

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

#### HOST AND SITE RELATIONSHIPS

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

## BIOLOGICAL CONTROL AND POPULATION MANIPULATION

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

DIVERSITY IN FORM, FUNCTION, BEHAVIOR,  
AND ECOLOGY: AN OVERVIEW OF THE  
LYMANTRIIDAE (LEPIDOPTERA) OF THE WORLD

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INTRODUCTION.

The collective members of the family Lymantriidae represent a unique and peculiar group of moderate sized moths. Adults are not very colorful since many are cryptically colored, having evolved as well-camouflaged individuals against a background of tree bark, lichens or leaves on which they alight. Adults of many species are monochromatic -- white or shades of yellow. Adults have a non-functional haustellum (proboscis) and thus do not feed. Lymantriid caterpillars are often strikingly colored, many armed with abundant clusters of long setae formed into hair brushes, hair pencils, radiating clusters protruding from raised warts or veruccae, and some (e.g., many *Euproctis* spp.) possess urticating hairs which may cause severe allergic reactions when they come in contact with human skin. Caterpillars also possess two medial dorsal glands (rarely only one as in *Elkneria* spp.) on the 6th and 7th abdominal segments. These unique glands are somewhat eversible and are often brightly colored with shades of red, orange or yellow. Their function remains obscure, but is thought to involve defense. The lymantriid moths are often more easily identifiable as caterpillars than as adults. Life stages of four representative species showing some of the unique adaptations in the family are illustrated in Figure 1.

The uniqueness of lymantriid moths is further illustrated through several examples:

- two species of North American *Gynaephora* have life cycles that may require from 9 to 13 years to complete one generation;
- in tropical Africa more than one species of the genus *Anaphe* construct unique communal pupation webs from which several dozen adults may emerge;
- many species are diurnally active and possess correspondingly reduced compound eye size;
- *Gynaephora groenlandica* and a geometrid moth are the most northerly distributed of any lepidoptera, occurring on nunatacks in the northern Ellesmere ice sheet and at Kap Neumayer, Greenland, at 83° 18' North latitude;
- many species exhibit flightlessness in females through functional

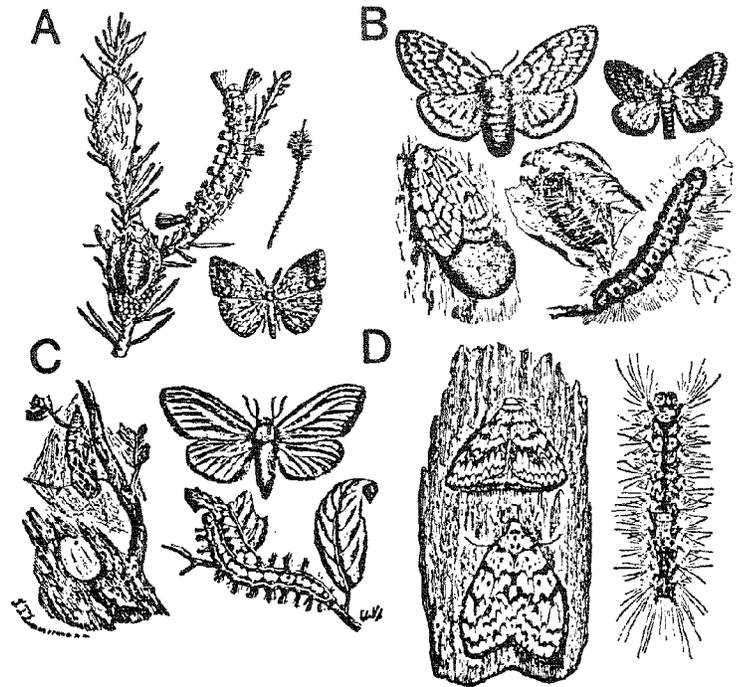


Figure 1: Representative Lymantriidae showing life stages.

- A. Rusty Tussock Moth or Vapourer, *Urgyia antiqua* (Linnaeus) (wingless female and eggs on cocoon).
- B. Gypsy Moth, *Lymantria dispar* (Linnaeus) (two whitish females on left, brown male on right)
- C. Satin Moth, *Leucoma salicis* (Linnaeus) (sexes similar)
- D. Nun Moth, *Lymantria monacha* (Linnaeus) (female below)

Note examples of extreme sexual dimorphism (A, B); female wing reduction (A); similar adult wing coloration (C, D); very hairy caterpillars (all); hair pencils and tufts (tussocks) (A); naked eggs (A); eggs covered by females hairs (B); eggs covered by hard froth (C). Although not illustrated, diurnal activity (A, B) and nocturnal (or crepuscular) activity (C, D) also represented and possibly diurnal activity correlated with dark male coloration (A, B).

(Illustrations taken from Musslin (1927) and reassembled.)

polymorphism to varying degrees or complete wing reduction;  
 --many species have evolved unique methods of egg protection, ranging from use of the setae from the female's abdomen, to a hardened foam, insertion of eggs under tree bark scales, and even collection of foreign material to adhere to the egg mass surface for camouflage;  
 --*Eloria noyesi* Schaus in South America is a pest on coca, the plant from which cocaine is refined. Apparently larvae can metabolize the precursors of this powerful drug; and  
 --*Orgyia thyellina* in Japan is bivoltine and has one generation with wingless females (producing summer-type, non-diapausing eggs) followed by a second generation of winged females capable of dispersal (producing winter type, diapausing eggs).

#### METHODS

Except for the author's personal exposure to lymantriid species in Japan and other parts of the Orient and the U.S., all information has been gleaned from the scattered literature on Lymantriidae. In the compilation of this information, an extensive bibliography of ca. 775 entries was generated. Only a fraction of this material is specifically cited in this review.

As no overview would be complete without some appreciation for the size of the family, I completed a preliminary assessment of the numbers of species and genera considered to currently belong in it. I began with the compilation by Bryk (1934), "Lepidopterorum Catalogus", part 62: Lymantriidae. This catalog listed 188 genera containing 2155 species (adjusting for duplicate entries for *Redoa*, *Dasychirinula* and *Mumenoides*) recognized as belonging in Lymantriidae in 1934. To update this list, I consulted all the Lymantriidae sections of the Zoological Record for the years 1933 to 1986 (vol. 70 - 123). All entries pertaining to the descriptions of new species, new name applications, and new synonyms were noted. All duplicate entries from these sources were reconciled. A new preliminary catalog was generated in this manner, however many conflicting nomenclatural interpretations have yet to be addressed. Nevertheless, this tentative catalog proved useful in providing insight into our present understanding of the family. At present, no such current comprehensive catalog of the Lymantriidae exists.

#### RESULTS AND DISCUSSION

##### Taxonomic Status

Over the years, many authors have contributed to the understanding of the Lymantriidae, including Aurivillius, Butler, Collenette, Distant, Holland, Kirby, Hampson, Hering, Herrich-Schaeffer, Hubner, Leech, Matsumura, Moore, Oberthur, Schaus, Snellen, Strand, Swinhoe, Walker, and Wallengren. Their contributions have been mostly descriptive taxonomy with few reports containing mention of larval stages, host plants, habitats or behavior.

In more contemporary times, names such as Barlow, Berio, Bryk, Chao, Dall'asta, de Freina, Ebert, Ferguson, Fletcher, Gomez-Bustillo, Griveaud, Gupta, Holloway, Inoue, Kozhanchikov, MacKay, MacNulty, Maes, Nam, Pinhey, Riotte, Robinson, Schaus, Sevastopulo, Viette, Wiltshire, and Witt all are contributors in varying degrees to knowledge of the Lymantriidae. Fortunately, use of genitalia as taxonomic characters and utilization of immature stages has more frequently infiltrated the contributions of these authors.

In 1982 the International Commission on Zoological Nomenclature ruled on the fixation of the name Lymantriidae as the correct name to apply to this moth family. This ruling became necessary since many names had been applied to the family over previous years. On the basis of general widespread usage, Lymantriidae Hamson 1893 was ruled to be valid over older the names Orgyiidae Wallengren 1861, and Dasychiridae Packard 1864, which both had precedence over Lymantriidae, but had only minor acceptance and usage in different parts of the world. Watson, Fletcher & Nye (1980) have done much to clarify this nomenclatural problem and Fletcher, Nye and Ferguson's (1980) application to the International Commission on Zoological Nomenclature and the resulting opinion has at last definitively clarified the family name.

At lower levels of classification, much work still needs to be done. Ferguson (in litt.), in a checklist being prepared of the Neotropical Lepidoptera, identified eight genera normally listed as Lymantriidae (as in Watson, Fletcher and Nye 1980) which he now believes are not Lymantriids.

The taxonomy of Lymantriidae will remain in a state of flux until such time as a worldwide revision is completed.

#### Species Distribution and Abundance

Representatives of the Lymantriidae are distributed on all continents except Antarctica, with species concentrated in the tropical areas of Africa, India, Southeast Asia and South America. Madagascar is unusually rich in species abundance with 258 species recorded (Griveaud 1977). Lymantriids are conspicuously absent on the islands of New Zealand, the Antilles (Ferguson 1978), Hawaii, and likely most islands of the South Pacific except Fiji, New Caledonia (Holloway 1979) and other more southwestern islands.

A global biogeographical analysis of Lymantriidae distribution was undertaken by Kozhanchikov (1950), who confounded the analysis because of the inclusion of the subfamily Acronictinae (now generally recognized as Noctuidae) in his concept of the Lymantriidae (as Orgyiidae). He attempted an overview of this assemblage of moths and focused on population dynamics and on an analysis of the biogeographical distribution of *Lymantria* (as *Ucneria*).

Regional faunistic studies or lists of species or pests (i.e. for North America (Ferguson 1978); Central and South America (Ferguson, in litt.); Madagascar (Griveaud 1977); USSR (Kozhanchikov 1950); Japan (Inoue 1956, 1957, Inoue et al. 1959); Korea (Nam & Kim 1981); India (Benson 1941); France (Herbulot 1958); Germany (Koch 1955); Hongkong (So 1967); East Africa (LePelley 1959); Southeast Asia (Barlow 1982);

Southern Africa (Pinhey 1979) and others) all help to illustrate faunal abundance or scarcity in some areas (Table 1). In temperate areas, the Palearctic region (Kozhanchikov 1950; Inoue 1976, 1977; Nam & Kim 1981) is richer in species diversity than the Nearctic (Ferguson 1978), although about 12% of North American species are Holarctic and common to both areas, due in a large part to accidental introductions into North America (e.g., gypsy moth, browntail moth and satin moth) (Table 2). In tropical areas, the faunas are not as well known. Examples of species adaptive radiation can be seen in the Neotropical fauna, genus Eloria, and the African fauna, again especially in Madagascar genera Lymantria (which contain many species previously considered Lymantria) and Mpanjaka (Griveaud 1977). However, some of these genera must be viewed in light of different nomenclatural interpretation of generic limits, especially in those species once classified as Dasychira (432 species) or Euproctis (796 species) (Table 3).

The tentative Lymantriidae catalog reveals about 355 valid generic names containing 2494 recognized species. This takes into account Ferguson's opinion on the misplacement of 8 genera containing 32 species of South American moths (Ferguson, in litt.) (Table 3). All genera with 20 or more species are considered "Major Genera". This listing of 21 genera contains 2159 species or over 70% of the total species known. Interestingly 55% of all lymantriid genera are monotypic and 66% of all genera contain only one or two species. Many genera are unique to certain geographical areas (i.e., Neotropical genera Eloria, Staetherinia, and Sarsina) with no evidence of phylogenetic relationships to other geographical areas.

Uneven distribution of species within genera suggests that species have been placed in genera such as Dasychira and Euproctis in a "catch-all" manner, because it is difficult to imagine that evolution has resulted in so many species in a few genera while evolving independently into so many generically different forms in so many other genera, e.g. 198 monotypic genera alone. In the final analysis, I believe the entire family needs careful revisionary study before we can fully accept the present worldwide classification of the Lymantriidae.

#### Food Plants and Pest Status

Food plants are recorded for only a minor portion of lymantriid species. In the north temperate regions, food plants are best known. In tropical areas where species richness is greatest, the feeding habits of species are poorly documented. Although patterns of food plant utilization have not been studied in detail, some generalities appear. Forest or shade trees serve as the principal food plants for the vast majority of lymantriids. Of lesser importance are shrubs, vines, herbs, and grasses. At least two species feed on lichens and one is known to feed on mistletoe.

#### Stenophagy

A few species are truly stenophagous and have evolved close associations with their host plants. Dasychira eurydice (Butler) in

Table 1. Tentative Numbers of Lymantriidae (Lepidoptera) Genera and Species in Various Geographical Areas.

Country/Region	No. Genera	No. Species	Reference
North America	6 <sup>a</sup>	46 <sup>a</sup>	Ferguson 1978 <sup>b</sup>
Brazil	4	9	d'Araugo e Silva, et al., 1968
Neotropics	8	132	D. Ferguson (pers comm.) <sup>c</sup>
Europe	10	28	Kirby 1903
England	9	12	Stainton 1857
France	9	12	Herbulot 1958
Germany	9	16	Koch 1955
Turkey	6	8	Iren & Ahmed 1973 <sup>d</sup>
East Africa	18	67	LePelley 1959 <sup>d</sup>
Madagascar	53	258	Griveaud 1977
Southern Africa	30	57	Pinhey 1979 <sup>d</sup>
Japan	14 <sup>a</sup>	45 <sup>a</sup>	Inoue 1956-57 <sup>b</sup>
Korea	14	37	Nam & Kim 1981
China	26	235	Chao 1978 <sup>b</sup>
	30	270	Sun (these Proceedings)
Thailand	11	30	Anonymous 1965 <sup>d</sup>
U.S.S.R.	16 <sup>e</sup>	65 <sup>e</sup>	Kozhanchikov 1950
India	11	47	Beeson 1941
Southeast Asia	17	29	Barlow 1982 <sup>c</sup>
Australia	18	60	Turner 1921

- a. Number adjusted based on subsequent information.  
b. Including subsequent report(s) by the same author.  
c. Based on a manuscript checklist (Area covered includes Mexico, Central & South America) by D. C. Ferguson which will be included in a forthcoming section of the Atlas of Neotropical Lepidoptera, J. B. Heppner, ed.  
d. This reference is not a revision of this family but does provide insight into the species diversity for that area.  
e. Exclusive of the Acronictinae, which is generally placed in Noctuidae by other authors.

Table 2. Accidental Introductions of Lymantriidae.

Name/Species	Year Found	Place Found	Origin	Reference
Gypsy moth, <u>Lymantria dispar</u> (L.)	1868	Medford, Mass. USA	France/ Belgium	Forbush, 1896
Satin moth, <u>Leucoma salicis</u> (L.)	1920	Malden, Mass. USA	Europe?	Burgess & Crossman, 1927
	1920	Vancouver, British Columbia	?	
	1922	Bellingham, Washington, USA	Canada?	same
Browntail moth, <u>Euproctis chrysorrhoea</u> (L.)	1897	Somerville, Mass, USA	France/ Holland	Marlatt, 1911
Rusty tussock moth, <u>Orgyia antiqua</u> (L.)	?	Santiago, Chile	Europe ?	Ferguson, 1978

Table 3. Major Genera and Number of Genera and Species in Lymantriidae.

Major Genera	No. Species	Major Genera	No. Species
<u>Aroa</u> Walker 1855	62	<u>Leucoma</u> Hubner 1822	90
<u>Calliteara</u> Butler 1881	55	(including <u>Stilpnotia</u> )	
<u>Collenettea</u> Griveaud 1977	22	<u>Lymantria</u> Collenette 1936	27
<u>Dasychira</u> Hubner 1809	432	<u>Lymantria</u> Hubner 1819	158
<u>Eloria</u> Walker 1855	54	<u>Mpanjaka</u> Griveaud 1976	37
<u>Euproctis</u> Hubner 1819	796	<u>Olapa</u> Walker 1855	21
(including <u>Porthesia</u> )		<u>Orgyia</u> Ochsenheimer 1810	52
<u>Eudasychira</u> Moschler 1887	30	<u>Pantana</u> Walker 1855	25
<u>Idalia</u> Hubner (1819) 1816	20	<u>Rahona</u> Griveaud 1976	22
(including <u>Caviria</u> , per Ferguson, pers. comm. 6/1988)		<u>Redoa</u> Walker 1855	38
<u>Lacipa</u> Walker 1885	25	<u>Rhyppopteryx</u> Aurivillius 1879	27
<u>Laelia</u> Stephens 1828	127	<u>Thagona</u> Moschler 1883	39
(Subtotal of 21 Major Genera:		2159 Species)	
Approximately 334 other Genera:		906 Species	
Tentative Total Genera:		355 Genera	
Tentative Total Species:		3065 Species	

Japan (Inoue 1956) and in Korea (as *Cifuna*) (Kim et al. 1982) feeds only on vines of *Vitis* spp. *Ivela auripes* (Butler) in the Orient is associated almost exclusively with *Cornus* sp. (Schaefer 1983). Many other species might appear to be limited in their food plants and listed in the literature as feeding only on one species or a very limited selection of hosts. It is often unclear if true stenophagy is present. Too often narrowness of diet is a function of the extent to which lepidopterists or plant protectionists have studied a species.

#### Polyphagy

On the opposite extreme, there are some species which have exhaustive host plant records and are truly polyphagous. The gypsy moth, *Lymantria dispar* (L.), exemplifies a species with a capacity of maximal utilization of available plants. Forbush and Fernald (1896) compiled a list of 458 plant species upon which the gypsy moth fed in Massachusetts and they provided a supplemental list of 78 species, mostly trees and shrubs, which were considered the principal food plants in the field. In Japan alone, I have compiled a list of ca. 152 plant species scattered among 53 plant families that may serve as food plants for the Japanese form of the gypsy moth (Schaefer et al. 1988).

Other notorious polyphagous species include the holarctic vapourer or rusty tussock moth, *Orgyia antiqua* (L.), in both Eurasia and North America. Tietz (1972) lists 38 species and genera food plants in North America. This species makes little differentiation between hardwoods and conifers as it will feed readily on trees in either category. The North American relative, the white-marked tussock moth, *Orgyia leucostigma* (J. E. Smith), is far more polyphagous having a recorded food plant list of 143 species (Tietz 1972), including both deciduous and coniferous trees.

#### Oligophagy

Between the above extremes in plant utilization are the vast majority of species. These species have evolved to utilize relatively limited plant resources, often evolving along coniferous or deciduous tree lines. Some species specific for the coniferous trees include *Lymantria fumida* Butler on *Abies* and *Larix* in Japan; *Dasychira pinicola* (Dyar) and *D. manto* (Strecker), both feeding on *Pinus*, and *D. dominickaria* (Ferguson) feeding on *Taxodium*, in North America (Ferguson 1978). In Japan *Parocneria furva* (Leech) may be a serious defoliator of *Chamaecyparis* and *Juniperus* spp. (Inoue 1957). *Dasychira argentata* Butler in Korea is known to feed only on *Cryptomeria japonica* Don. (Kim et al. 1982). In Southern Africa, a number of species are *Pinus* feeders (perhaps not exclusively), i.e. *Euproctis subalba* (Janse) (Swain & Prinsloo 1986), *Euproctis terminalis* (Walker) (Pinhey 1979), and *Bracharoa dregei* (Herrlich-Schaffer) (Swain & Prinsloo 1986). *Oligeria hemicalla* (Lower) is a *Pinus radiata* feeder in Australia (Moore 1968).

Similarly, many species of *Dasychira*, *Lymantria*, *Leucoma*, and *Orgyia* in the temperate latitudes are exclusively deciduous tree feeders. Likewise many tropical species feed only on hardwoods trees. Oligophagous species probably represents the largest

assemblage of lymantriid species with examples too numerous to cite.

#### Specialized Feeders

Some species have evolved as grass and sedge feeders. *Laelia coenosa* (Hubner) in Japan (Inoue 1956) and China (Li 1987) feeds on *Phragmites* (and so might be useful for the biological control of this weed) but also feeds on rice, *Oryza sativa*, (Inoue 1956) and probably other useful grains. In India, *Euproctis virguncula* Walker feeds on wheat (Sandhu & Deol 1975), *Porthesia xanthorrhoea* Koller (Munshi et al. 1970), and *Psalis pennatula* Fabricius feed on rice (Garg & Sethi 1980), and *Laelia exclamatoris* Kollar and *Laelia devestita* Walker both feed on grasses (Beeson 1941). Rice is also food to *Laelia suffusa* Walker in Malaya (Evans 1952), and *Euproctis cervina* (Moore) in Pakistan (Mohyuddin 1987). Thus a number of lymantriids are pests of grain crops.

Perhaps the most novel food plant associations are shared by three diverse lymantriids and are perhaps more stenophagous than their relatives that feed nearly exclusively on one or two tree species mentioned above. In Australia, *Euproctis edwardsi* Newman feeds on the mistletoes (Lorentaceae) which are parasitic on *Eucalyptus* trees (Watson & Whalley 1975) and because of this habit the moth is locally referred to as the Mistletoe browntail moth (Carne et al. 1980).

The other unusual food resource occurs in two African species that both feed on lichens. *Paraproctis calamolopha* Collenette in Uganda (Collenette 1936; MacNulty 1966) and *Dasychira octophora* Hampson in southern Africa (Pinhey 1979) have apparently completely lost their ability to survive on the higher plants and instead rely exclusively on the cryptogamic flora.

#### Pest Status

The vast majority of lymantriid moths can not be considered pests. Many are so poorly known that they are considered rare. However, when necessary food resources of species conflict with human agricultural interests those species are considered pests. A comprehensive overview of tropical pest species compiled by Hill (1983) listed 47 tropical pest/plant associations involving lymantriid moths as pests of 36 tropical crops. One additional tropical South American crop is coca, on which *Eloria noyesi* feeds and may cause defoliation (Wille 1935).

In temperate areas, lymantriid species appear more dependent on tree species for food and are therefore forest and shade tree pests. Many of these species show tendencies for massive population outbreaks, for example gypsy moth, douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) or nun moth (*Lymantria monacha* Linnaeus), all in the holarctic region. At such outbreak times, species may become pests simply by their unusual abundance, causing a nuisance to communities and homeowners. A particularly unusual form of nuisance was reported in Japan when larvae became so abundant during the height of an outbreak that they congregated on railroad tracks in such numbers that the crushed larvae on the rails inhibited train movement (Esaki 1934). Finally, several groups contain species which have

unusually severe urticating properties. Crushing of the larval setae against unprotected human skin cause severe urtication. In some instances, these setae possess a histamine which greatly enhances the reaction caused from the mechanical action alone. Urticaria occurs in the browntail moth, Euproctis chrysorrhoea (Linnaeus) in Eurasia and in North America, Euproctis flava (Bremer) in Japan, Euproctis edwardsi Newm. in Australia (McKeown 1945); Euproctis terminalis in South Africa, (Watson & Whalley 1975; Skaife 1953); Euproctis molundiana aurivillius in West Africa (Sevastopulo 1967) and Euproctis (as Porthesia) similis in England (Eltringham 1913) and in Shanghai, China, where a serious epidemic occurred (Su 1981). Although less severe than in Euproctis spp., other groups may produce dermal irritation principally from mechanical action. Gypsy moth larval spines will cause unpleasant irritation in sensitive people. Occasionally, under outbreak conditions, small larvae caused rashes to humans over wide areas, as happened in Pennsylvania in 1981 (Aber et al. 1982). Wirtz (1984) reviewed the urticaria phenomenon in arthropods, including lymantriid moths.

#### Biological and Ecological Specializations

Perhaps the most unique aspect of the Lymantriidae is found in the overall diversity expressed by representatives of this group. We generally think of moths as having a life history progressing from eggs, larvae and pupae into winged adults which fly, mate, and lay eggs without much variation in the the general theme. In the subsections which follow, focus is on these expressions of variation, diversity, behavior, and ecology in the broadest sense.

#### Female Wing Reduction and Flightlessness

Evolution of wing reduction has occurred in several lymantriid genera, for example Lymantria, Orgyia, Thea, Enome, and Gynaephora. Wing reduction reaches its extreme in Orgyia where females are totally wingless with the wings being reduced to little more than lobes. Some Orgyia have females with partially reduced wings as in Orgyia hopkinsi Collenette native to Africa (Collenette 1937). Still another African species, Orgyia basalis Walker, has wings but yet does not fly (Sevastopulo 1951). Whether females are physically capable of flight remains unclear.

Wing reduction reaches a unique compromise in Orgyia thyellina Butler, native to China, Korea and Japan. Being bivoltine, females of a summer generation are winged (producing non-diapausing eggs) while those of a fall generation are wingless (producing larger diapausing eggs which overwinter). Kimura & Masaki (1977) have shown control of this wing reduction to be photoperiodically induced. Interestingly, the larger, diapausing eggs are usually deposited on the female's cocoon, spun on objects other than suitable food plants. Dispersal in the spring is thus left to the newly-hatched larvae.

Loss of flight capacity in females with apparently fully developed wings occurs rather commonly. Arctic species of Gynaephora have nearly fully developed wings but apparently do not fly, probably in adaptation to the harsh climatic conditions in the tundra or alpine

habitats. Winds whipping over the dwarfed vegetation might carry flying moths out of suitable habitats where individuals would be lost from the population. Presence of wings may also provide a degree of insulation from strong winds and may contribute to enhanced solar absorption in a habitat where net solar warming greatly influences development and behavior of these moths that require extended periods for development -- estimates of up to 14 years to mature (see Kukul & Kevan 1987; Kevan et al. 1982; Schaefer & Castroville 1979).

The complete range of wing reduction occurs in the genus Lymantria. Brachypterism is most pronounced in the Indian L. ampla Walker where females have only lobes for wings. The female Indian gypsy moth, L. obfusca Walker, has wings reduced to about 1/2 normally expected size. At the other end of the range are many species that possess fully developed wings which the females readily use for flight. Examples include the nun moth, L. monacha Linnaeus, of Eurasia, L. mathura Moore and L. fumida Butler both of Japan. Intermediate between these extremes is an interesting case of functional polymorphism in the gypsy moth. In western Europe and in North America (where gypsy moth was accidentally introduced (Table 2)) females do not fly, that is they are incapable of sustained or ascending flight. In the rest of Eurasia (including nearly all of the U.S.S.R. and apparently some eastern European countries) and eastward into Japan, gypsy moth females are fully capable of ascending flight. In Japan, Korea or China (Schaefer, unpubl. data; Kenda 1959; Kosugi 1954), females are attracted to lights at night. The same is reported in the Moscow area of U.S.S.R. (Gornostaev 1962). Perhaps in gypsy moth, we are seeing the first stages in the evolution of brachypterism. At present we must accept this functional polymorphism as a factor having significant bearing on the ecology and evolutionary trends in the two population forms.

#### Sexual Dimorphism

Apart from female wing reduction, there are other expressions of sexual dimorphism among some lymantriids. Perhaps one of the most extreme forms is in coloration of the gypsy moth, where males have shades of light to dark brown coloration yet the females are basically white to buff with some black markings. Dark brown males and white females also occurs in a recently discovered New Caledonian species, Euproctis dimorphissima Holloway (Holloway 1979). Similar extreme sexual dimorphism is seen in Perina nuda F. in Southeast Asia. Adult females are a uniform yellow to cream coloration, whereas the males emerge as a dark brown moth but wing scales on the forewings and a patch on the hindwing promptly sluffs off resulting in hyaline wings. The clear-winged appearance of these males bears no resemblance to females of the same species. Vastly different appearances are found in the two sexes of the very striking Oriental Numenes spp. in which males only similarity to females is the reduced white line patterns on the black color of the forewing (Inoue 1975).

Gravid females of a species are larger than males whether females bear wings or not. Colorational sexual dimorphism is usually expressed as more melanistic males relative to their respective females. This phenomenon seems to be closely correlated with diurnal

flight behavior, as in many Orgyia spp. and Lymantria dispar sensu lato.

#### Diurnal Flight Behavior and Compound Eye Size

Evolution of diurnal activity appears to have evolved in at least three separate ways:

- (A) Invasion of Arctic habitats where continuous summer daylight occurs. Two species are known in this category, Gynaephora rossii Curtis and G. groenlandica Wocke. Diurnal behavior must have been modified some in the relict Alpine populations of G. rossii (Schaefer & Castrovillo 1979) since these moths are subjected to a distinct scotophase, unlike arctic populations.
- (B) Diurnal activity by conspicuous species (pure white or yellow) possibly having evolved as butterfly mimics. Support for this theory might be the discovery that these species are distasteful to bird predators. Examples include Ivela auripes Butler in Japan, Eloria noyesi Schaus and perhaps all other South American Eloria spp. (Collenette 1950), and Euproctis sinuinigra Holloway in Borneo (Holloway 1976).
- (C) Diurnal activity by inconspicuous, camouflaged species that often exhibit sexual dimorphism which may include female wing reduction. Examples include the holarctic Orgyia antiqua (L.), Lymantria dispar (L.), and Orgyia pseudotsugata (McDunnough), in which diurnal and crepuscular flight behavior was demonstrated (Wickman et al. 1975). A list of species recognized as being diurnally active is presented in Table 4.

In conjunction with diurnal flight, a corresponding reduction in compound eye size has evolved. Ferguson (1978) mentioned the phenomenon of reduced eye size in diurnal species. He noted it in O. antiqua and O. pseudotsugata, but also noted a deviation in a subspecies of the latter, which possessed larger eyes and thus may not be strictly diurnal. Schaefer (unpublished data) has quantified this relationship for some Oriental species in a search for species that show reduced eye size. By identifying these species, although they are rare or unusual, a notion of possible diurnal behavior was inferred. This study showed that eye reduction in Lymantria dispar was unique in the genus Lymantria for Japanese and Korean species and that when compared to L. monacha, eye size was reduced ca. 32%. Overall, observations indicated that diurnal activity could be found in a variety of genera (Table 3), but was poorly represented in the two largest, Dasychira and Euproctis. Field confirmation was the next logical step, but was possible only in Ivela auripes in an area studied in Japan (Schaefer 1983).

#### Incomplete Adult Emergence

In a South African lymantriid, female Bracharoa dregei Herrich-Schaeffer never emerge from their cocoons. Emergence is simply a shedding of pupal skin and the female remains within her cocoon. Mating and oviposition take place therein. On hatching, the

Table 4. Diurnally Active Species of Lymantriidae.

Species	Location	Reference
CONFIRMED SPECIES		
<u>Apina callisto</u> Doubleday	Australia	Froggatt 1907
<u>Aroa biformis</u> Holloway	Borneo	Holloway 1976
<u>Aroa cinerea</u> Holloway	Borneo	Holloway 1976
<u>Aroa translava</u> Holloway	Borneo	Holloway 1976
<u>Birnara bicolor</u> Walker	Borneo	Holloway 1976
<u>Bracharoa dregei</u> Herrick-Schaffer	South Africa	Watson et al. 1975
<u>Eloria noyesi</u> Schaus	Peru, Bolivia	Collenette 1950
<u>Euproctis sexinacula</u> Swinhoe	Borneo	Holloway 1976
<u>Euproctis sinuigrana</u> Holloway	Borneo	Holloway 1976
<u>Gynaephora groenlandica</u> (Wocke)	Arctic Canada	Kukul & Kevan 1987
<u>Gynaephora (=Byrdia) rossi</u> Curtis	Japan	Inoue et al. 1959
	Maine, USA	Schaefer & C. 1979
<u>Ivela auripes</u> Butler	Japan	Inoue et al. 1959,
<u>Leucoma wiltshirei</u> Collenette	Iraq	Wiltshire 1957
<u>Lymantria dispar</u> (L.)	North America	Ferguson 1978
<u>Lymantria dispar japonica</u> Motsch.	Japan	Inoue et al. 1959
<u>Ocnerogyia amanda</u> Stgr.	Iraq	Wiltshire 1957
<u>Orgyia antiqua</u> (L.)	North America	Ferguson 1978
	Eurasia	Gillanders 1908
<u>Orgyia pseudotsugata</u> (McDunnough)	North America	Ferguson 1978
<u>Orgyia recens approximans</u> Hubner	Japan	Inoue et al. 1959
<u>Orgyia thyellina</u> Butler	Japan	Inoue et al. 1959
ADDITIONAL UNCONFIRMED SPECIES BASED ON COMPOUND EYE SIZE		
<u>Aroa socrus</u> Geyer	Taiwan	Schaefer unpubl. data
<u>Aroa substrigosa</u> Walker	Taiwan	Schaefer unpubl. data
<u>Dasychira nachiensis</u> Narumo	Japan, Taiwan	Schaefer unpubl. data
<u>Dura alba</u> Moore	Taiwan	Schaefer unpubl. data
<u>Lymantria suarezia</u> Mabilie	Madagascar	Schaefer unpubl. data
<u>Lymantria ampla</u> Walker	India	Schaefer unpubl. data
<u>Lymantria apicebrunnea</u> Gaede	China	Schaefer unpubl. data
<u>Lymantria marginata</u> Walker	China	Schaefer unpubl. data
<u>Lymantria obfuscata</u> Walker	India	Schaefer unpubl. data
<u>Lymantria tacita</u> Hering	East Africa	Schaefer unpubl. data
<u>Medama diplaga</u> Hampson	Taiwan	Schaefer unpubl. data
<u>Medama basimaculata</u> Matsumura	Taiwan	Schaefer unpubl. data
<u>Numenes takamukui</u> Matsumura	Taiwan	Schaefer unpubl. data
<u>Orgyia triangularis</u> Butler	Japan	Schaefer unpubl. data
<u>Pantana albipes</u> Matsumura	Taiwan	Schaefer unpubl. data
<u>Pantana infuscata</u> Matsumura	Taiwan	Schaefer unpubl. data
<u>Pantana simplex</u> Leech	Taiwan	Schaefer unpubl. data
<u>Perina nuda</u> Fabricius	Hongkong	Schaefer unpubl. data
<u>Pida niphonis</u> Butler	Korea	Schaefer unpubl. data

larvae consume the female cadaver before emerging from the cocoon in search of food plants (Watson et al. 1975).

#### Communal Activities

Apparently in the interest of energy conservation and protection within groups, some species have developed novel communal activities. In Euproctis chrysorrhoea (L.), communal webs normally provide a means for all siblings from a single egg mass to overwinter. All activities, including feeding, are gregariously undertaken only during the Summer and Fall periods. By late Fall, this gregarious activity produces a tightly-spun communal web amongst the twigs and leaves of the host plant, often positioned on a terminal twig that literally "flags" that tree as infested. Within the web are numerous cells in which small groups of larvae eventually diapause. This behavior has presumably evolved to enhance survival during overwintering (Schaefer 1974, 1986).

Other communal activities include gregarious feeding by younger larvae only in E. chrysorrhoea. Similarly, Olapa travatensis Holland in West Africa is a gregarious feeder (MacNulty 1966). Gregarious feeding to a much later stage occurs in Euproctis pseudoconsersa Strand in Japan, Euproctis flava (Bremer) in China, and probably many other poorly studied species. Presumably "safety in numbers" also applies to Lymantriids.

A unique communal activity is the communal pupation web or "cocoon-bag" produced by some African species (Holland 1893). In both Anaphe moloneyi Druce and Decura goodii Holland in tropical West Africa, late stage larvae construct a rough silken bag ca. 15 - 20 cm in diameter. As larvae mature, they enter this web, pupate and eventually emerge as adult moths from these cocoon-bags. Several dozen moths may emerge from the same bag over extended periods according to Holland.

#### Egg Protection and Oviposition

Sevastopulo (1967) noted that a grass-feeding species, Mylantria xanthospila Plotz, lay loose or scattered eggs (not in masses), typical of grass-feeding Lepidoptera. Among tree-feeding species, some Lymantriid females lay naked egg masses, for example Orgyia antiqua, Orgyia thyellina, Gynaephora rossii, and many Dasychira spp. Many other species attempt to cover their eggs for protection. This is accomplished in one of several ways:

- (1) Covering the mass with setae from the abdomen of the female. This occurs in some Lymantria spp. (dispar, sakaguchi, obfuscata) and some Euproctis spp. (chrysorrhoea, pseudoconsersa).
- (2) Use of a solidified foam or froth to cover the mass. This process seems to have evolved into two methods of application. (2A) Masses are attached to a solid substrate such as the bark of a tree and the foam simply covers the surface to mask any appearance of eggs beneath it. This method occurs in the satin moth, Leucoma salicis (L.). A second subtype (2B) involves inserting the eggs beneath a bark scale or crack and applying the solidified foam to seal the

crack, as found in *Lymantria monacha*, *L. fumida* and *L. mathura* (at least in Hokkaido, Japan). Some females may also adhere setae to the exposed cement for added protection or disguise. (3) Application of material from the environment to the egg mass surface. This method is used by *Ivela auripes* Butler in Japan (Schaefer 1983). Females lay a geometric single-layer egg mass on the trunk of the host tree, *Cornus controversa* Hemsl. but during the oviposition process females "dust" the surface of the mass with an abrasive material harvested by the female during her preovipositional period. This abrasive material appears as a gray dust, which is crystalline, inert, and more dense than water. The source of this material is unclear, but it appears to be harvested from the surface of the trees on which the eggs are laid and may have an origin associated with lichens.

#### SUMMARY

Lymantriidae contain some species which possess some unusual traits, many found in few other moth families. Much is yet to be learned on the life histories and habits of many of the more unusual species. Relatively little is known on host-plant relationships, parasites and predator associations, except in certain well-studied lymantriid pests. The taxonomic limits of the family, of individual genera, and certainly of individual species are not well-delineated and will continue to evolve as our knowledge of this worldwide moth family increases. In those species well-known, recognition of such interesting phenomena as sexual dimorphism, diurnal flight behavior and compensatory compound eye reduction, brachypterism and female flightlessness, gregarious behaviors, and various methods of egg protection all illustrate some of the diversity which has evolved in the family.

During consideration of the various topics covered in these proceedings, let us continue to marvel at the diversity in form, function, behavior and ecology that has evolved in these moths. Let us also recognize those areas where our knowledge is weakest and also strive to build on our present understanding a greater knowledge and appreciation for the moths we recognize as members of the family Lymantriidae.

#### LITERATURE CITED

- Aber, R., T. DeMelfi, T. Gill, B. Healey, M. A. McCarthy, et al. 1982. Rash illness associated with gypsy moth caterpillars -- Pennsylvania. *Morb. Mortal. Wkly. Rep.* 31:169-170.
- Anonymous. 1965. A host list of the insects of Thailand. Dept. Agric., Royal Thai Govt. & U.S. Operations Miss. to Thailand. Thai-American Audiovisual Ser., 149 pp.
- Barlow, H. S. 1982. An introduction to the moths of south east Asia. The Malayan Nature Soc., Kuala Lumpur & E. W. Classey, Garingdon, Oxon, UK., 305 pp.
- Beeson, C. F. C. 1941 (reprinted 1961). The ecology and control of the forest insects of India and the neighboring countries. Govt. India, 767 pp. (part. 485-490).

- Bryk, F. 1934. Lymantriidae. In Strand, Lepidoptera Catalogus 62, 1-441, W. Junk, Berlin.
- Burgess, A. F. & S. S. Crossman. 1927. The satin moth, a recently introduced pest. U. S. Dept. Agric. bul. no. 1469, 22 pp.
- Carne, P. B., L. D. Crawford, M. J. Fletcher, I. D. Galloway & E. Highley. 1980. Scientific and common names of insects and allied forms occurring in Australia. Commonwealth Sci. & Indust. Res. Org., Australia, 95 pp.
- Chao, C.-L. 1978. Lepidoptera: Lymantriidae. In Memoirs of Chinese Economic Entomology. Vol. 12, Sci. Publ. Center, Beijing, 121 pp.
- Collenette, C. L. 1936. New African Lymantriidae (Lep.). Entomologist, London, 69:178-181.
- Collenette, C. L. 1937. New African Lymantriidae (Lepidoptera, Heterocera). Ann. Mag. nat. Hist., London, (10) 20:604-617.
- Collenette, C. L. 1950. A revision of the genus *Eloria* Walker (Heterocera: Lymantriidae). Ann. Mag. nat. Hist. London (12) 3:813-865. ZR 87:614
- d'Araujo e Silva, A. G., et al. 1968. Quarto catalogo dos insetos que vivem nas plantas do Brasil. Seus parasitos e predadores. Part II. Insetos, hospedeiros e inimigos naturais. Minist. Agric., Lab. Central Patologia vegetal, Rio de Janeiro, Brazil. 622 pp.
- Eltringham, H. 1913. On the urticating properties of *Porthesia similis* Fuess. Trans. ent. Soc. Lond. 1913:424-427.
- Esaki, T. 1934. Diplopods disturbing railway trains. Shokubutsu-oyobi dobutsu 2(5):821-833. (in Japanese)
- Evans, J. W. 1952. The injurious insects of the British Commonwealth (except the British Isles, India and Pakistan) with a section on the control of weeds by insects. Commonw. Inst. Entomol., London. 242 pp. (part. 169 - 170).
- Ferguson, D. C. 1978. Noctuoidea, Lymantriidae. The Moths of America North of Mexico, Fascicle 22.2. E. W. Classey Ltd. & Wedge Entomol. Res. Found., 110 pp, 9 pls.
- Ferguson, D. C. (in litt.). Check list of Neotropical Lymantriidae. In Check list of Neotropical Lepidoptera. J. B. Heppner, ed.
- Fletcher, D. S., I. W. B. Nye & D. C. Ferguson. 1980. Lymantriidae Hampson 1893 (Insecta: Lepidoptera) proposed precedence over Orgyiidae Wallengen 1861 and Dasychiridae Packard 1864. Bull. zool. Nom. 37(1): 40-46. Z.N.(S): 2216
- Forbush, E. H. 1896. The gypsy moth, *Porthetria dispar* (L.). Part I. In Forbush, E. H. & C. H. Fernald, The gypsy moth. Wright & Potter Print. Co., Boston, MA, (Reprinted Arno Press, N.Y., 1977).
- Froggatt, W. W. 1907. Australian insects. Wm. Wesley & Son, London, 449 pp.
- Garg, A. K. & G. R. Sethi. 1980. Tussock caterpillar, *Psalis pennatula* (Fabricius) feeding on rice at Delhi. Indian J. Entomol. 42(2):306-308.
- Gillanders, A. T. 1908. Forest Entomology. Edinburgh & London: W. Blackwood & Sons, 422 pp.
- Gornostaev, G. N. 1962. Mass flight of the gypsy moth, *Lymantria dispar*, to a mercury lamp in the Moscow area. Byull. Mosk. O-Va. Ispyt. Prir. Otd. Biol. 67:124. (in Russian).
- Griveaud, P. 1977. Insectes lepidopteres Lymantriidae (Ire partie). Fauna Madagascar 43(1):1-293. (2e partie) 43(2):295-588.

- Herbulot, C. 1958. Atlas des lepidopteres de France. II. Heterocerces. Editions M. Boubee, Paris, 145 pp.
- Hill, D. S. 1983. Agricultural insect pests of the tropics and their control. 2nd edit. Cambridge Univ. Press, Cambridge, 746 pp.
- Holland, W. J. 1893. Communal cocoons and the moths which weave them. *Psyche* 6(202):385-391.
- Holloway, J. D. 1976. Moths of Borneo with special reference to Mount Kinabalu. Malayan Nature Soc., Sun U Book Co, Kuala Lumpur, Malaysia, 132 or 264 pp + 32 pls.
- Holloway, J. D. 1979. A systematic account of the New Caledonian Macrolepidoptera. pp. 259-540, in J. D. Holloway, A survey of the Lepidoptera, Biogeography and Ecology of New Caledonia. Dr. W. Junk, B.V. Publ. The Hague.
- Inoue, H. 1956. A revision of the Japanese Lymantriidae (I). *Jap. J. M. Sc. & Biol.* 9: 133-163.
- Inoue, H. 1957. A revision of the Japanese Lymantriidae (II). *Jap. J. M. Sc. & Biol.* 10: 187-219.
- Inoue, H. 1975. On the species of the genus *Numenes* from Japan and neighbouring countries (Lymantriidae). *Japan Heteroc. Journ.* 83:377-383. (in Japanese)
- Inoue, H. et. al. 1959. *Iconographia Insectorum Japonicorum Colore naturali* edit. Volume I. Lepidoptera. Hokuryukan, Tokyo, 284 pp. (part. 166-169).
- Iren, Z. & M. K. Ahmed. 1973. The microlepidoptera and deciduous fruit pests of Turkey. *Plant Prot. Inst., Ankara, Plant Prot. bul. suppl. 1*, 96 pp.
- Kenda, I. 1959. On the biology of gypsy moth which are attracted to light traps. *Forest Protection News* 8:73-75. (in Japanese)
- Kevan, P. G., T. S. Jensen, & J. D. Shorthouse. 1982. Body temperatures and behavioral thermo-regulation of high arctic woolly-bear caterpillars and pupae (*Gynaephora rossii* (Lymantriidae: Lepidoptera) and the importance of sunshine. *Arctic & Alpine Res.* 14(2): 125-136.
- Kim, C.-H., S.-H. Nam & S.-M. Lee. 1982. Illustrated flora and fauna of Korea. Vol. 26. Insects (VIII), Samwha, Seoul, Korea, pp. 588-615. (in Korean)
- Kimura, T. & S. Masaki. 1977. Brachypterism and seasonal adaptation in *Orgyia thyellina* Butler (Lepidoptera: Lymantriidae). *Kontyu* 45(1):97-106.
- Kirby, W. F. 1903. The butterflies and moths of Europe. Cassell & Co., Ltd, London.
- Koch, M. 1955. *Wir Bestimmen Schmetterlinge*. II. Baren, Spinner, Schwärmer, und Bohrer, Deutschlands, Neumannverlag-Radebeul und Brelin, 148 pp.
- Kosuai, K. 1954. Investigations on the number of gypsy moths caught by light traps and on the distribution of egg masses and their hatch. *Forest Protection News* 27:6-7. (in Japanese)
- Kozhanchikov, I. V. 1950. *Orgyidae*. In *Fauna SSR, Insecta-Lepidoptera*, Moscow, vol. 12, 583 pp. (in Russian)
- Kukal, O. & P. G. Kevan. 1987. The influence of parasitism on the life history of a high arctic insect *Gynaephora groenlandica* Wocke (Lepidoptera: Lymantriidae). *Can. J. Zool.* 65(1):156-163.
- Le Pelley, R. H. 1959. Agricultural insects of East Africa. East Africa High Commission, Nairobi, Kenya, 307 pp.

- Li, Hongke. 1987. Control of *Laelia coenosa candida* Leech and *Chilo hyrax* Bls., two major pests of reed, with *Bacillus thuringiensis*. Chinese J. Biol. Control 3(3):127-128.
- MacNulty, B. J. 1966. Outline of life histories of some West African Lepidoptera. Part I. Lymantriidae. Proc. S. Lond. ent. nat. Hist. Soc. 1966:69-84.
- Marlatt, C. L. 1911. Danger of general spread of gipsy and browntail moths through imported nursery stock. U.S. Dept. Agric. Farmers' Bull. 453, 22 pp.
- McKeown, K. C. 1945. Australian insects, an introductory handbook. Royal Zool. Soc. New South Wales, Sydney, 303 pp.
- Mohyuddin, A. I. 1987. A catalogue of insects and mites in the reference collection of PARC-CIBC Station up to 1986. Vol. 1, Lepidoptera. Commonw. Inst. Biol. Control, Pakistan Stn., rept. 34 pp.
- Moore, K. M. 1968. Observations on some Australian forest insects. 14. A preliminary list of insects attacking *Pinus* spp. in New South Wales. Australian Zool. 13(1):69-77.
- Munshi, G. L., S. Singh & R. Singh. 1970. A new record of *Porthesia xanthorrhoea* Kollar (Lymantriidae: Lepidoptera) on paddy in Jammu, J & K State. Indian J. Entomol. 32:390.
- Nam, S.-H. & C.-W. Kim. 1981. A synonymic list of tussock moths (Orgyidae: Lep.) in Korea. Entomol. Res. bul. 8: 73-100.
- Nusslin, O. 1927. Forstinsektenkunde. Paul Parey Pub., Berlin, 625 pp.
- Pinhey, E. C. G. 1979. Moths of Southern Africa. A. A. Balkema, Rotterdam, 273 pp.
- Sandhu, G. S. & G. S. Deol. 1975. New records of pest on wheat. Indian J. Entomol. 37(1):85-86.
- Schaefer, P. W. 1974. Population ecology of the browntail moth (*Euproctis chrysorrhoea* L.) (Lepidoptera: Lymantriidae) in North America. Ph.D. Thesis, Univ. Maine, Orono, 246 typr pp.
- Schaefer, P. W. 1983. *Ivela auripes* Butler in Hokkaido: Behavior and morphology of females; host egg defense mechanism against parasitism by *Trichogramma* sp. nov. Kontyu 51(2): 298-307.
- Schaefer, P. W. 1986. Bibliography of the browntail moth, *Euproctis chrysorrhoea* (L.) (Lepidoptera: Lymantriidae) and its natural enemies. Agric. Expt. Stn., Univ. Delaware, Newark, DE, Bul. no. 464, 66 pp.
- Schaefer, P. W. & P. J. Castrovillo. 1979(81). *Gynaephora rossii* (Curtis) on Mt. Katahdin, Maine, and Mt. Daisetsu, Japan, and comparisons to records for populations from the Arctic (Lymantriidae). J. Res. Lepid. 18(4): 241-250.
- Schaefer, P. W., K. Ikebe, & Y. Higashiura. 1988. Gypsy moth, *Lymantria dispar* (L.) and its natural enemies in the Far East (Especially Japan). Annotated bibliography and guide to the literature through 1986 and host plant list for Japan. Delaware Agric. Exp. Stn. bull. 476, 160 pp.
- Sevastopulo, D. G. 1951. Sluggishness of Lymantriid females. Entomol. Record 63:298-299.
- Sevastopulo, D. G. 1967. Lymantriidae -- East versus West Africa. Proc. S. Lond. Ent. Nat. Hist. Soc. 1967:15-17.
- Skaife, S. H. 1953. African insect life. Longmans Green & Co., Lond. 387 pp.

- So, P.-Y. 1967. A preliminary list of the insects of agricultural importance in Hong Kong. Agric. & Fisheries Dept., H.K.
- Stainton, H. T. 1857. A manual of British butterflies and moths. vol. 1. John van Voorst, London, 338 pp.
- Su De-Long, S. 1981. Mulberry tussock moth dermatitis: a study of an epidemic of unknown origin. J. Epidemiol. Comm. Health 35:1-4.
- Sun, X.L. (in litt.). Lymantriid forest pests in China. (Elsewhere in these Proceedings)
- Swain, V. M. & G. L. Prinsloo. 1986. A list of phytophagous insects and mites on forest trees and shrubs in South Africa. Entomol. Mem., Dep. Agric. & Water Supply, Rep. So. Africa, no. 66, 91 pp.
- Tietz, H. M. 1972. An index to the described life histories, early stages, and hosts of the macrolepidoptera of the continental U.S. and Canada. Allyn Mus. Entomol., Sarasota, FL, 2 vol., 1041 pp.
- Turner, A. J. 1921. Revision of Australian Lepidoptera -- Liparidae. Proc. Linn. Soc. N.S.W. 1920, 45:474-499.
- Watson, A. & P. E. S. Whalley. 1975. The dictionary of butterflies and moths in color. McGraw-Hill Book, Co., N.Y., 296 pp.
- Watson, A., D. S. Fletcher & I. W. B. Nye. 1980. Generic names of the moths of the world. Vol. 2: Arctiidae, Ctenuchidae, Dioptidae, Lymantriidae, Notodontidae, Thaumetopoeidae, Thyretidae. Publ. British Museum (Nat. History), London, No. 811, 228 pp.
- Wickman, B., R. R. Mason, & H. G. Paul. 1975. Flight, attraction, and mating behavior of the Douglas-fir tussock moth in Oregon. Environ. Entomol. 4(3):405-408.
- Wille, J. 1932. Der Coca-Strauch Perus und sein Schädling. TROPENPFLANZ 35:9-25, 47-94.
- Wiltshire, E. P. 1957. The Lepidoptera of Iraq. Nicholas Kaye Ltd., Iraq, 162 pp.
- Wiltshire, E. P. 1958. New species and forms of Lepidoptera from Afghanistan and Iraq. J. Bombay nat. Hist. Soc. 55:228-237.
- Wirtz, R. A. 1984. Allergic and toxic reactions to non-stinging arthropods. Ann. Rev. Entomol. 29, 47-69.

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

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S U M M A R Y

There are 35 species of Lymantriidae in Europe (De Freina & Witt, 1987), but research is concentrated nearly exclusively on the 7 most destructive: Lymantria dispar (L.), Lymantria monacha (L.), Euproctis chrysorrhoea (L.), Euproctis similis (Fuessly), Calliteara (Dasychira) pubibunda (L.), Leucoma (Stilpnotia) salicis (L.) and Orgyia antiqua (L.). Although E. similis also attacks oak and other tree species in forests, it is primarily a pest of orchards and has been omitted from this selected overview of research carried out mainly since 1978, on the distribution, hosts, biology, natural enemies, outbreaks and control of these economically important insect species. This research gained impetus from the development of methods of artificial rearing, identification and synthesis of pheromones, response to concern about the effects of insecticides on the ecosystem, and production of microbial and environmentally safer insecticides. As even-aged coniferous plantations in Europe expanded considerably since 1930, calamities such as the one caused by L. monacha from 1978-1984 in Poland, may well recur.

G y p s y M o t h  
L y m a n t r i a d i s p a r ( L . )

Distribution and hosts

The gypsy moth (GM) occurs in Europe from the west coast of the mainland to the Urals, limited in the North by a line stretching from Central Sweden through Moscow and in the South by the Mediterranean Sea including islands such as Corsica and Sardinia. In altitude it is limited to the growth zone of Quercus. Its optimum development is reached in the broadleaved forests of S. and S.E. Europe. More than 300 hosts have been recorded; Quercus is regarded as the preferred food plant, followed by other Fagaceae such as Fagus, Carpinus and Castanea. A third group of food plants consists of Salix, Populus, Robinia, Betula, Acer and Tilia. Larix is a common

coniferous host, but Pinus is not (Wellenstein & Schwenke, 1978). The inefficient feeding of GM (and of L. monacha), is one of the causes of their destructiveness; this trait may be related to polyphagy (Baranchikov, 1983).

#### Biology

The egg clusters of GM, which are hair-covered and normally contain between 50-800 eggs, overwinter and hatch in spring. Larvae often start feeding on flushing buds and later on flowers and leaves. The coincidence of bud burst and hatching is considered important for population development. Female larvae pass through an additional 6th stage and are more prone to parasitization, predation and diseases. They are also more sensitive to changes in food quality. Warm and dry summers shorten their larval period resulting in a sex ratio favourable for outbreaks. Male adults are active diurnally; females hardly fly. Dispersal is effected by first instar larvae carried on silken threads by wind. GM is very closely related to L. monacha, which shares many features of its biology. GM larvae and adults vary greatly in morphology and colour, having many geographical forms and races.

#### Parasites, predators and pathogens

One hundred sixty-five parasite species have been recorded; 109 hymenopterans and 56 dipterans. Of these, the tachinids Blepharipa scutellata, B. pratensis, Parasetigena segregata and Compsilura concinnata are dominant species. The egg parasites Anastatus japonicus and Ooencyrtus kuvanae are also important. Dermestids (Kotenko, 1982) and cantharids, e.g. Megatoma pici, Dermestes, Justus floralis and Malachius bipustulatus are important egg predators. Panina (1984) describes a method to determine the effectiveness of these predators. The carabid Calosoma sycophanta is an effective predator. However, the most important factor influencing GM populations during an outbreak is a nuclear polyhedrosis virus (NPV). Its impact increases as the epidemic progresses until it ultimately causes the total collapse of the population. Rain, birds and predators are major factors in the dissemination of NPVs (Patkistlo, 1986). The occurrence of cytoplasmic polyhedrosis viruses (CPV) is less frequent, but a CPV causing 42% mortality in GM larvae was recorded in Austria; the disease presumably also killed the larval parasites (Jahn, 1979). Zelinskaya (1980), studying the role of 4 microsporidia (Nosema lymantriae, N. serbica, Thaloshania diggarii and Fleisstophora schubergi) during a GM outbreak, concluded that apart from killing the larvae, the infections also lowered the fecundity and mating capacity of adults. Streptococcus faecalis has been isolated from larvae in Bulgaria (Grigorova et al., 1982).

#### Outbreaks: conditions and damage

Site and climatic conditions are important in the development of

outbreaks; drought, high temperatures and light are the main outbreak-inducing factors. Most countries have traditional outbreak centres, where conditions are favourable for GM population development. Extensive studies have been carried out to define the factors that influence the population dynamics of GM (Znamenskii & Lyamtsev, 1985). The forecasting of outbreaks has been studied by Belov (1986), Ekk et al. (1980), Kireeva (1978) and others. In several countries, outbreaks appear to be cyclical; however, the intervals between outbreaks may vary; between 6 to 8 years (in Yugoslavia) to 14 years in France and 36 in Switzerland. In countries with optimal outbreak conditions, the periodicity seems to be ruled by intrinsic factors (Wellenstein & Schwenke, 1978). Fratian (1985) noted that in oak stands treated with microbials and insecticides, later population peaks recurred with the same frequency as in untreated stands. Host tree species appear to influence the duration of outbreaks. In areas with less favourable outbreak conditions, drought is considered a main factor for population build-up. Population fluctuations are probably influenced directly by the host condition [e.g. sugar content of the leaves before and during the course of an outbreak (Schwenke, 1968; Patocka, 1973)]. In addition, parasite, predator and pathogen populations influence the development of outbreaks. Economic losses can be considerable; despite the general capacity of oaks and other broadleaves to recover from defoliation, up to 25% mortality has been observed in *Q. robur* stands in Romania. But Nizi & Prosperi (1973) report that after a severe outbreak of GM in central Italy, yield loss was equivalent to 20% of the cost of aerial spraying. One year after the outbreak, additional growth had nearly obliterated earlier reduction. Magnoler & Cambini (1968) report a mean annual reduction of 33-39% in radial growth during a 3-year defoliation of *Q. suber*. Mortality in older age classes of oak may also be due to subsequent epidemics of oak mildew (Abramenko & Samilyak, 1983).

#### Monitoring and forecasting

After racemic disparlure and its (+)enantiomer became available, pheromone traps were used to estimate population density and to predict outbreaks. However, Bednyi & Kovalev (1978) found monitoring indicative only in pre-outbreak populations; Luciano & Prota (1985), obtained unsatisfactory results, as no relationship could be established between the numbers of egg clusters and the numbers of males caught. Population density was best estimated on the basis of counts of egg clusters.

#### Control

Results of mass trapping and mating disruption have also been inconclusive (Maksimovic, 1980). Bednyi et al. (1980) indicate that disruption of mating in spaces saturated with disparlure is a consequence of adaptation of the chemoreceptors of male adults rather than disorientation or other presumed causes. Much research was done by the the International Organization for Biological Control's

Working Group on Microbial Control of Lymantria dispar. The effect of microbials in outbreaks (Zelinskaya, 1980), and the selection of varieties of Bacillus thuringiensis (Bt) (Carrado & Brussino, 1985; Ovcharov, 1982) and races of Borrelina spp. (Skatulla, 1985; Magnoler, 1985) or synergistic combinations of both pathogens, including the effect of these microbials on natural enemies, have been studied. A general review on the application of Bt in plant protection is given by Krieg (1983). Spraying of an exceptionally virulent strain of NPV on GM egg masses has been reported to give excellent control in an outbreak affecting 1400 ha (Orlovskaya, 1970). Bt has been noted to be effective only when the daily temperature exceeds 13°C (Korchagin, 1980); Galani (1978) determined that the optimum temperature for Bt infection was 25°C. Under the same field conditions, Trigiani (1979) obtained good control with Bt but not with NPV. Recovery of larvae after infection with NPV was observed by Bakhvalov et al. (1982). According to Burgerjon et al. (1981) the increased resistance of older larvae is not attributable to weight nor to the amount of treated leaf area consumed. Although Bt and NPV reduced feeding activity, defoliation is often continued, the effects of treatments being more pronounced in the following year (Injac & Vasiljevic, 1978). The inactivation of NPV (Timans, 1982) and Bt spores by ultraviolet radiation is one of the causes of their limited effect under field conditions. A review of the attempts to protect NPVs from radiation is given by Entwistle and Evans (1985). Nosema lymantriae, was used in a field test against GM larvae, causing a mortality almost twice as high as in controls. The infection had a favourable effect on parasitization and predation; including the number of hatching eggs of the next generation, the population was reduced to 10% of the control (Weiser & Novotny, 1987). Simchuk (1982) defined optimal rearing conditions for Pleistophora schubergi, another microsporidian attacking GM. Sidor & Jodal (1983) found that host tree species influence the mortality caused by Nosema serbica and NPV.

Few studies have been done on the release of parasites in biocontrol; Chernov (1976) reports that the release of 3.8 million laboratory-reared adults of the egg parasite Ooencyrtus kuvanae during an outbreak of GM, resulted in 60% higher egg parasitization than in control areas. Maksimovic & Sivec (1984) added GM eggs to test plots to maintain a low density of the defoliator and consequently of its natural enemies. Eight years after the additions were started, reductions of about 70% were caused by Cotesia melanoscelus, Glyptapanteles porthetriae, tachinids and diseases.

Crosses between races of GM can result in a marked excess of male adults. However, the sex ratio is restored in the next generation and in backcrosses (Clarke & Ford, 1983). Crosses of inbred males with wild moths resulted in early larval hatching and high mortality; in this case, early hatching was maintained in following generations. Release of inbred males in low density populations of GM might further reduce the population level for some generations (Marovic, 1981).

Chemical control has moved from environmentally harmful, broad-spectrum insecticides like DDT to more selective chemicals such as the chitin inhibitors (Lyachenko & Andreeva, 1979; Szmidt & Sliwa, 1980) or synthetic pyrethroids such as permethrin (Svestka, 1978).

Combinations of sublethal doses of these insecticides with microbials have in many instances proved to be synergistic (Novotny, 1988; Videnova, 1980).

At least two components of air pollution (NaF and SO<sub>2</sub>) have been shown to result in high mortality rates of GM (Selikhovkin, 1981; Kataev, 1981).

#### Artificial rearing

GM is reared on artificial diets in many European countries such as France, Germany, Italy (Magnoler, 1970), Poland, Russia and Yugoslavia (Vasiljevic & Injac, 1971). A method for rearing Ooencyrtus kuvanae is described by Bjegovic (1972).

#### Nun moth Lymantria monacha (L.)

#### Distribution and hosts

The nun moth (NM) occurs in most European countries; it has been known as a pest of conifers since 1820 in the European USSR and has since spread widely, reaching the Ukraine in 1949-1952 and central European Russia and W. Siberia in 1954-1957 (Marushina, 1978). In N. and N.W. Europe, its distribution is limited to S. England, Norway, Sweden, and Finland; its northern limit extends approximately along the parallel of 60° N. Lat. through Leningrad to the Urals. In the South, its area is limited to the northern parts of Spain, Portugal, Corsica, Italy, Yugoslavia, Greece, and Bulgaria. NM manifests itself principally as a pest of the coniferous forests of central Europe and since 1920 also of the pine forests in the mountain areas of central Spain, where temperate climatic conditions prevail. NM is polyphagous; its northern limit coincides with the distribution of Q. robur. Preferred hosts belong to the genera Picea, Pinus, Larix, Abies, and Fagus. Of the deciduous trees, Carpinus, Betula, Quercus, Ulmus, Acer, and several other genera can be attacked.

#### Biology

Since NM is very closely related to GM only a few salient data are mentioned here. Females possess a long flexible ovipositor by which naked egg clusters (70-300 eggs) are deposited in crevices and behind the bark scales of conifers. As 50% or more of the eggs are oviposited on the lower 4 m of the trunk, the number of eggs found there can be used to forecast outbreaks. Feeding begins in May on young needles of flushing shoots, but male inflorescences, buds, or old needles may also serve as emergency food. In some years, the lack of synchrony of flushing of buds and hatching of eggs caused collapse of populations (Slyzinsky, 1970). The racemic mixture of disparlure attracts male NM; both species live in reproductive isolation because NM is nocturnally active whereas GM males are

active mainly at midday. In addition, their pheromones have a different composition of enantiomers. Hansen (1984), estimates that the pheromone of NM consists of 10% (+)- and 90% (-)-disparlure, while that of GM is almost 100% (+)-disparlure. Klimentz et al. (1976) found that in the field, the response of NM increased with the concentration of (+)-disparlure regardless of the concentration of (-)-disparlure, while the response of GM diminished as the concentration of (-)-disparlure increased. A reduction in response of GM to increased additions of (-)-disparlure was also reported by Kovalev et al. (1980). Preiss (1985), however, indicates that (-)-disparlure has no effect on the orientation of GM to (+)-disparlure.

#### Parasites, predators and pathogens

Some 88 primary parasites have been listed; 45 dipterans and 43 hymenopterans (Thompson, 1946; Herting, 1976). The tachinid Parasetigena silvestris and the braconid Cotesia melanoscelus are most important; Trichogramma evanescens and Telenomus phalaenarum have been recorded as egg parasites but their incidence is low (Mills & Schoenberg, 1985). Predators include Calosoma sycophanta and birds. Tits (eggs), cuckoos (larvae) and jays (pupae) are considered major predators during outbreaks but it is doubtful if they are of great influence (Wellenstein & Schwenke, 1978). For more than a century it has been known that natural NPV epizootics are the main factor for the collapse of NM outbreaks. The latent stage of the virus is present in all stages of the insect; it is activated under stress conditions such as lack of, or low quality food, and adverse weather. Bakhvalov et al. (1979) activated NPV in larvae by exposing them to temperatures of 4°C. Chemicals, sublethal doses of insecticides or Bt act as stressors and increase larval susceptibility to NPV.

#### Outbreaks; conditions and damage

Weather, site conditions and stand composition are the most important outbreak-inducing factors. A late but sudden spring promotes the coincidence of bud burst and egg hatching (Svestka, 1971). In addition, warm, dry summers result in a higher proportion of female adults; normally, females constitute only 15% of the population but during progradations their share may amount to 80%. Bejer (1985), found no correlation between outbreaks of NM in Denmark and the overall climate, forest composition or the size of mature stands. However, the eruptions seemed to be triggered by 3-4 years of high summer temperatures and low summer rainfall. Forests on poor, sandy soil appeared particularly susceptible. Cramer (1962) indicated that in Germany NM outbreaks occurred when the sum of the average monthly temperature of May and June in 3 consecutive years exceeded 32.6°C and the average precipitation in May of these years remained under 80 mm. In the Netherlands, where NM epidemics are rare, a large scale eruption recurred in the same locations that had been affected 78 years earlier. Lunderstadt (1983), studying the eco-physiological relationship between NM and spruce, concluded that

several protein-bound amino acids are relevant for the control of mass-flux within the plant-insect system. A relation between the occurrence of NM epidemics and sunspots suggested by Jahn, could not be confirmed statistically, although population increases appeared to occur two years after a sunspot maximum (Klimentek, 1976). Fluoride-polluted spruce needles had a detrimental effect on the development of NM larvae (Mitterbock & Fuhrer, 1988).

Growth losses and mortality can be high and prolonged due to the slow recovery of coniferous trees. Subsequent epidemics of bark beetles often take a heavier toll than primary NM outbreaks. Spruce is killed if it has been defoliated for 70-80%; pine is more resilient, while larch usually recovers. NM outbreaks often affect extensive areas of forest plantations. During the massive outbreak in Poland in 1978-1984, 6.3 million ha of Scots pine, Norway spruce and mixed stands were affected, of which 0.5% was killed. (Sliwa & Sierpinsky, 1986). In E. Germany in 1983 and 1984, extensive control activities were necessary to control a NM epidemic on more than 300,000 ha of coniferous forest (Majunke et al., 1985). The effect of defoliation on increment has been studied (e.g. by Blagovidov, 1986) while Abramenko & Myasoedov (1983) calculated the economic effect of aerial control in relation to the mortality percentage of trees.

#### Monitoring and forecasting

Methods have been developed for monitoring and forecasting epidemics based upon counts per tree of larvae, pupae, adults and eggs (Wellenstein & Schwenke, 1978). In Hungary, light traps are used for forecasting outbreaks of several injurious forest insects (Szontagh, 1974). Monitoring of NM by using the sex pheromone of live females started as early as 1932 in Czechoslovakia (Skuhravy, 1987); monitoring research increased considerably after racemic disparlure was synthesized in 1970 and proved to be attractive to NM (Schonherr, 1972). However, the relationship between the number of males caught and the number of females or egg clusters has often been unreliable (Jensen & Nielsen, 1984). No defoliation occurred in a Norway spruce forest in Austria, where maxima of 2000-3000 males per trap were caught (Schmutzenhofer, 1986). Stand density was found to influence trap catches.

#### Control

The use of racemic disparlure for control has focused on the development of mating disruption techniques. In Denmark, application of micro-encapsulated disparlure resulted in 2.5-3 times fewer eggs and larvae than in untreated areas (Jensen, 1983), while in Austria, a significantly reduced population resulted after spraying 20 g disparlure/ha (Schmutzenhofer, 1986). Mating disruption and mass trapping are adversely influenced by high density populations (Altenkirch, 1985; Schroter & Lange, 1975). Cross-infectivity of NPVs isolated from several lymantrids demonstrated that NPV from NM was not only pathogenic to GM but, more importantly, a strain of virus

isolated from *L. salicis* had high pathogenicity for *L. dispar*, *O. antiqua*, and *E. chrysorrhoea* (Skatulla, 1985). In addition, a virus strain from NM was found to be pathogenic to *Panolis flammea* (Lobinger & Skatulla, 1986). Since NPV production is costly, one of the obstacles to its wider application, a multiple-host NPV, would be extremely useful. A review of the production of pathogens is given by Huber & Miltenburger (1986). In field applications, foliage protection of NPV-treated areas is often inadequate, but mortality of trees may be prevented (Wellenstein, 1973). Although larval mortality usually exceeds 90% (Altenkirch et al., 1986; Glowacka-Pilot, 1983), long incubation periods and dense populations, account for the lack of protection. The feeding intensity of infected larvae only diminishes a few days before death (Glowacka-Pilot, 1983). Significant reduction in feeding was obtained under laboratory conditions by mixing sublethal doses of Bt with NPV (Schonherr & Ketterer, 1979). Although higher initial mortality of first instar larvae was confirmed by Altenkirch et al. (1986) in field trials with a Bt/NPV combination, complete defoliation could not be prevented. According to Marchenko & Emelyanchik (1981), Bt treatments should be applied against 1st and 2nd instar larvae at the onset of the eruptive phase of an epidemic. During progradations, all instars are less susceptible to Bt. Suppression of NM populations with Bt and mortality over 90% have been reported by Bakhvalov et al. (1984), and Zaripov (1981). However, other authors obtained mortality rates of only 53% in lab trials (Altenkirch et al., 1986) or 76% in the field (Bejer, 1986).

In 1935 and 1936, the first aerial applications of insecticides took place against NM in East Prussia in a forest of strategic importance. Ten planes were used to distribute 322 tons each of calcium-arsenate and dinitro-cresol over 20,000 ha of Norway spruce. In addition to the death of nearly all songbirds, beneficial insects, 3 deer, 30 roes and a hare, one of the pilots was killed in a crash, and 18 cows, 3 of which were later slaughtered, were affected by the arsenic dust. The treatment killed ca. 80% of the NM population (Wellenstein, 1979). Since then, the efficiency of chemical control has improved due to chitin inhibitors, pyrethroids and other chemicals less harmful to the environment and LV and ULV spraying. Although chemical control is still widely applied (Harris & Lavers, 1985; Majunke et al. 1985; Brinkmann, 1982) because it is cheap, effective and rapid, research is focused increasingly on biocontrol methods.

#### Artificial rearing

NM can be reared on artificial and semi-artificial diets for NPV production and other purposes (Grijpma, 1987).

### B r o w n t a i l M o t h E u p r o c t i s c h r y s o r r h o e a ( L . )

#### Distribution and hosts

The browntail moth (BTM) occurs in most European countries; in N. and N.W. Europe, its distribution is limited to S. Sweden and S.E. England from where its area extends to S.Russia. The Mediterranean Sea, including islands such as Sicily and Sardinia, forms its southern European border. BTM is a pest of broadleaved trees and shrubs; it is a major pest of orchards and cork oak plantations. Other hosts recorded, belong to Betula, Crataegus, Hippophae, Populus, Prunus, Pyrus, Quercus, Rosa, Salix, and Ulmus. In the northwestern part of its range epidemics occur on Hippophae rhamnoides in coastal areas or the dunes of North Sea islands. On the Adriatic coast, Arbutus unedo is a preferred host, while extensive areas of oak shrubs and coppice are attacked in Yugoslavia and other Balkan states. Food plant species and food quality influence pupal weight and the size of egg masses (van der Linden, 1967).

#### Biology

BTM is a pest of open forests, brushwood, hedges and lane trees. It is univoltine in N.W. and central Europe and bivoltine in the southern and southeastern countries. Winter is passed as 2nd and 3rd instar larvae in nests spun together from leaves at branch tips; larval feeding resumes in spring and culminates in summer. The larvae possess urticating, barbed hairs which cause skin irritation and injury to eyes and the respiratory tract. The inflammatory reactions are attributable to combined mechanical and toxic effects (de Jong & Bleumink, 1977). Pupation occurs in clustered cocoons within folded or loosely tied leaves. Adults deposit hair-covered egg masses, containing 100-500 eggs on the underside of peripheral leaves in midsummer (Skatulla & Schwenke, 1978). Larvae skeletonize the upperside of the leaves until autumn, when a communal winter nest is formed that contains an average of 750 larvae.

#### Parasites, predators and pathogens

Some 92 parasite species have been recorded: 68 hymenopterans and 24 tachinids (Auersch, 1955). Of the tachinids, Palesia nudiculata, Masicera sphingivora (Sisojevic et al., 1976), Carcelia lucorum and Lydella nigripes are considered most important. In Sardinia, Pales pavidus was the most numerous tachinid, and a Telenomus sp. parasitized 36.7% of the eggs (Delrio & Luciano, 1985). Of the other hymenopteran parasites, Meteorus versicolor and Eupteromalus nidulans have been recorded frequently. Polyphagy and hyperparasitism reduce the effectiveness of most parasites. C. sycophanta, tits and cuckoos are listed as major predators. Epizootics of fungi (Empusa aulicae), NPV (Borrelina euproctis) and microsporidia (Pleistophora schubergi, Nosema kovacevicici) generally cause the collapse of BTM outbreaks. Mortality caused by these pathogens, alone or in mixed infections, varied between 72 and 77% (Purrini, 1979; Sidor et al., 1975).

#### Outbreaks; conditions and damage

Temperature and light are important requirements for the development of BTM epidemics which can be stimulated by thinnings (Tseitgamel, 1974). In its optimal development area in S. and S.E. Europe, outbreaks are more frequent and last longer than in central or N.W. Europe. In Portugal, where *Q. suber* occupies some 650,000 ha, epidemics may last 7-8 years and reduce cork production. Loss in work time of cork strippers due to severe rashes and eye irritation is an additional economic effect. In Yugoslavia, BTM outbreaks occur practically every year, but most economic damage is caused to fruit orchards, where buds, flowers and fruits are attacked by larvae. In oak, increment losses prevail, although repeated attacks may cause mortality of trees. High daytime and low night temperatures in April and May results in delayed flushing of oak and increased damage to buds (Fankhanel, 1959). Consequently, varieties of late flushing oaks are subject to more damage by larvae than early flushing varieties (Pokozii, 1962).

#### Monitoring and forecasting

The sex pheromone of BTM has not been identified, light traps (Szontagh, 1974) and population parameters such as the number, size or weight of egg masses and the number or weight of winter nests are used to monitor and predict population development (Malayi, 1978; Longo, 1983). In order to get correct estimates in forecasting, overwintering larvae should be examined for infective diseases.

#### Control

Winter nests on small trees and shrubs in orchards, parks and roadside plantings are still manually removed and destroyed. By putting winter nests in holes dug in the ground and applying insecticide around the edges to prevent dispersal of the larvae, parasites such as the braconid *Eupteromalus nidulans*, can be saved for biocontrol (Uchinaka, 1973). The effectiveness of Bt preparations against BTM in laboratory and field conditions was studied by Korchagin (1983) who found that Bt var. *galleriae* and Bt var. *dendrolimus* are effective only when the temperature exceeds 18°C. Under semi-natural conditions, Dipel (Bt var. *kurstaki*) caused almost immediate cessation of feeding but mortality (< 50% in 14 days) was slower than with chemical insecticides (Ruelle et al., 1978). In Czechoslovakia, the same preparation was considered more effective than Bt var. *thuringiensis* and caused 99% mortality of BTM larvae in 14 days (Vankova & Novak, 1985). Mortality rates between 76-95 % after 3 weeks were obtained by Gatignol et al. (1972) and Gorbunov & Mishnev (1983). According to Malyi & Ovsynanikova (1978), the effect of Bt treatments depends on the phase of the outbreak; larvae are most susceptible towards the middle and end of an epidemic. Foodplants can influence the effectiveness of treatments (Cabral, 1977). The addition of sublethal doses of insecticides to Bt treatments generally produced synergistic effects. In chemical control, DDT, lindane, trichlorphon, carbaryl and, more recently, the pyrethroids and diflubenzuron have been used to suppress BTM

populations (Gorlitz et al., 1978; Strand & Sylvester, 1981). A large-scale outbreak of BTM in roadside plantings of oak trees that had lasted for 12 years in the South of the Netherlands was brought under control by aerial application of diflubenzuron in 1978. Few trials have been done on the use of microsporidia and NPV for control of BTM. In laboratory tests, Atanasov (1984) obtained 100% mortality of 2nd instar larvae that had been sprayed with 2.9 million polyhedra/cm<sup>3</sup>. Skatulla (1985) isolated a NPV from L. salicis with high pathogenicity for BTM, GM and O. antiqua.

#### Rearing

Natase (1974), reared BTM in January in the laboratory on leaves obtained by forcing Populus nigra var. italica.

#### Satin moth Leucoma salicis (L.)

#### Distribution and hosts

The oligophagous satin moth (SM) is distributed throughout Europe where the host genera Populus and Salix occur: from N. Scandinavia (Lapland) to the Mediterranean Sea, including Corsica and in the whole of European Russia. Damage on willows is usually less important than on poplars. In the genus Populus, the selection Aigeiros, with species such as P. nigra, the introduced P. deltoides and their hybrids, are most susceptible to attack but species of other selections such as P. alba, P. canescens, P. tremula, and P. tremuloides may also be defoliated. Increased larval mortality has been noted when larvae fed on the latter species. Under laboratory conditions, 100% mortality was obtained when SM larvae were reared on P. trichocarpa-leaves; late instar larvae and pupae showed symptoms of hormonal deviations (Grijpma, unpublished).

#### Biology

SM is univoltine in northern and central Europe but has two generations in its southern range (e.g. Italy and Spain). Adults appear in early summer; males are active nocturnal flyers but females are sluggish and rarely disperse over long distances (Nef, 1978). Egg batches, covered with a white spumilin layer containing 50-500 eggs, are deposited on tree trunks or undersides of leaves. Larvae skeletonize the leaf underside before overwintering as 2nd or 3rd instars in silken hibernacula in bark crevices. Feeding resumes in early April and lasts until early June. Moulting and pupation occurs in large groups on the trunks or near branch axils.

#### Parasites, predators and pathogens

Pisica et al. (1978) listed 42 hymenopterans and 15 tachinids parasites. The egg parasite Telenomus nitidulus is one of the most important hymenopterans and may attain average parasitization percentages from 7-22% (Zakharieva, 1983) up to 53% (Teodorescu, 1980). Temporal and spatial distribution of this parasite was studied by Nef (1976), and host specificity and oviposition behaviour by Grijpma & van Lenteren (1988). Data on T. nitidulus were used in a study on sib-mating and sex ratio strategies by Waage (1982). Trichogramma also attacks SM eggs but is of less importance as it only parasitizes eggs that are not covered by the spumilin layer. Of the other hymenopterans Cotesia melanoscelus, Apanteles spp., Meteorus versicolor and Rogas spp. are among the most frequently recorded. According to Obozov (1968), Apanteles rubripes and Rogas pelluscens destroyed ca 70% of SM larvae during an epidemic in the Caucasus. The beneficial effect of most parasites is often counteracted by hyperparasites (Vasic & Minic, 1979).

Of the tachinids, species of Linnaemya (Dondikov, 1974), Carcelia, Exorista and Zenilla play a major role. Khubenov (1983) recorded SM as a new host for Exorista pratensis. In W. Germany and Austria, the parasitic nematode Hexameris albicans was recovered from SM and GM larvae. Of the pathogens, NPV (Sidor et al., 1978) and CPV have been found in SM larvae, the former occurring more frequently (Ziennicka, 1981). Skatulla (1985) isolated a strain of NPV, highly pathogenic to GM, BTM and O. antiqua. Slizynski & Lipa (1975) obtained a CPV from Dendrolimus pini that was also pathogenic to SM, GM, BTM and O. antiqua. An epizootic of an unidentified Fusarium ended a large-scale epidemic of SM in Russia (Ogarkov & Ogarkova, 1979).

#### Outbreaks; conditions and damage

Extensive areas of even-aged poplars are the origin of SM epidemics; in addition, high temperatures and drought in years preceding epidemics favour the development of SM populations. Marikovskii (1977) suggests that drought may result in the loss of nectar-producing plants and subsequent lack of parasites. Luitjes (1973) calculated increment and financial losses due to an SM outbreak in the Netherlands. Complete defoliation may result in increment losses as high as 60% per year but rarely causes mortality. After 4-5 weeks, trees have recovered full foliage.

#### Monitoring and forecasting

In the Krasnoyarsk region of Siberia, SM epidemics have a cycle of 10-11 years; they precede outbreaks of Dendrolimus sibiricus and could serve as indicator for the latter (Galkin, 1976). Critical numbers of larvae (i.e. the number of larvae causing complete defoliation) as related to the age and foliage volume of poplar trees are reported by Nef (1978).

#### Control

The effectiveness of NPV stored at 4-5°C for 4 years is not reduced and causes 100% mortality in larvae after 17 days. Young larvae are more susceptible to NPV than older ones; first instars are infected during hatching if the surface of the egg cluster is contaminated with NPV (Sidor et al., 1978). The possibility of combining NPV and sex pheromones in open traps with a view to spreading the virus in SM populations has been suggested (Grijpma et al., 1986). The effectiveness of NPV strains may differ considerably; Lameris et al. (1985), found that an isolate from Poland was about 7 times as infective as a Yugoslavian isolate. Temperature and host species influence the mortality caused by NPV (Kusevska, 1972). An epidemic on poplar in an area of 100 ha in Switzerland was successfully controlled by applying Bt; mortality rates were between 92-94% a week after treatment (Maksymov, 1980). Kuzmanova et al. (1980) selected a highly effective strain of Bt that caused 100% SM mortality in a field test after 2-6 days. Bt var. kurstaki was found more effective than var. galleriae and var. dendrolimus (Szalay-Marszo et al., 1981). Nef (1972), compared the effectivity of DDT, Bt, and NPV and concluded that Bt reduced larval populations of SM as effectively as DDT but with comparatively little effect on parasites. The initial effect of NPV was slight but continued in later development stages of SM larvae. In Yugoslavia, diflubenzuron has been used in field applications against SM; feeding stopped in 5-7 days and resulted in complete control.

#### Artificial rearing

A continuous rearing method based on leaf-producing poplar cuttings yielded a non-diapausing strain of SM with 5-6 generations/year (Grijpma et al. 1986).

R u s t y t u s s o c k m o t h  
O r g y i a a n t i q u a ( L . )

#### Distribution and hosts

The rusty tussock moth (RTM) or common vapourer, occurs throughout Europe from N. Scotland, Sweden and Finland to the Urals including in the South, the Mediterranean countries and the Balkan States. Outbreaks have occurred on spruce at elevations up to 1600 m. It is a highly polyphagous species that attacks trees, shrubs and herbs. Important broadleaved host genera are: Fagus, Quercus, Betula, Carpinus, Populus and Ulmus; the conifers attacked include Picea, Abies, Larix and Pinus (Wellenstein, 1978). RTM is an important pest of orchards.

#### Biology

Single-layered egg clusters, deposited by the wingless female on the remains of the cocoon, contain 50-300 naked eggs that overwinter (Wellenstein, 1978). In its northern distribution area, RTM has one

generation a year while in warmer countries (e.g. Spain) 2 generations occur. In the latter case, adults are present in summer and again in late summer or early autumn. In the Crimea, as many as 3 generations may occur (Galetenko & Pastukh, 1980). The larvae bear tufts of yellow and brown poisonous hairs. Under unfavourable field conditions, larval development lasted 98 days (Skatulla, 1974). According to Wellenstein (1978) female larvae pass through an additional 5th instar, but Littlewood (1984) indicates that both sexes experience 5 moults. Pupation occurs between the foliage or in the undergrowth during epidemics. In Russia, research has been done to synthesize and test the RTM sex pheromone (Smetnik et al., 1980). RTM is attracted to the sex pheromone of *O. pseudotsugata* (Brewer et al., 1985).

#### Parasites, predators and pathogens

At least 28 hymenopterans and 8 tachinids have been recorded as parasites (Wellenstein, 1978). Of the Hymenoptera, the egg parasite *Telenomus dalmanni* is of major importance; parasitization of over 50% and 61% of the eggs was reported respectively by Wellenstein & Fabritius (1973) and Kanecka et al. (1987). The former authors also list additional egg parasites found in Russia, e.g. *Ooencyrtus pinicola* and *Trichogramma evanescens*. *T. dalmanni* and *Trichogramma cacoeciae* are also important parasites in orchards (Niemczyk et al., 1978). Of the other Hymenoptera, the effectivity of *Phobocampe crassiuscula* which parasitized 16% of 3rd instar larvae (Skatulla, 1974), was greatly reduced by hyperparasites (*Gelis* spp.). *Pimpla turionellae* and *P. instigator* parasitized pupae but were of minor importance. Of the tachinids, *Carcelia amphion*, *C. lucorum* and *Comptosia concinnata* have been recorded frequently (Mills and Schoenberg, 1985). Birds, in particular tits and the pentatomid *Picromerus bidens* are major egg predators. Under laboratory conditions, the red wood ant, *Formica polyctena*, did not predate on 3rd instars but plucked out the hairs of older larvae. On average, 62% of these larvae died before pupation (Schmidt, 1985). Of the pathogens, the fungus *Paecilomyces farinosus* and NPV have been recorded as main factors that controlled an RTM epidemic in 1972 in southern Germany (Skatulla, 1974). An NPV was also isolated from RTM larvae in Bulgaria (Atanasov et al., 1983).

#### Outbreaks: conditions and damage

RTM is not a major forest pest; outbreaks usually occur in relatively small areas and collapse in 2-3 years. Epidemics over areas larger than 1000 ha have occurred in Sweden, Finland and recently in Czechoslovakia, where over 3300 ha of Norway spruce were attacked in the Bohemian Moravian Mountains in 1985/86 (Kanecka et al., 1987). Direct damage is limited to increment losses; but in coniferous forests, subsequent bark beetle attacks may cause additional damage. In central Europe, epidemics occur at intervals of 50-60 years; outbreaks often start in the middle of the forest but otherwise few preferences regarding site conditions have been

recognized. Trees of all ages are attacked (Wellenstein & Fabritius, 1973). Pinder & Hayes (1986), indicate that above average winter rainfall and below average summer rainfall occurred prior to an outbreak of RTM on 50 ha of Picea sitchensis in central Scotland. In addition, increased severity of defoliation was associated with lower relative height growth and lower phosphorus and potassium content of the needles.

#### Monitoring and forecasting

The sex pheromone of O. pseudotsugata attracts RTM (Brewer et al., 1985) but possibly due to the long intervals between epidemics, no data were found on methods for monitoring RTM populations in forests. Several authors (Bogenschutz, 1975; Lipa, 1983) stress the need to determine the rate of parasitism, predation and infection by pathogens as an element of forecasting in order to evaluate the necessity of applying any control. During the 1985/1986 outbreak in Czechoslovakia, control was limited to only 300 of 3326 ha because T. dalmanni parasitized 61% of the eggs and other natural enemies eliminated another 25% of the larvae (Kanecka et al., 1987).

#### Control

Nearly all references on the control of RTM refer to the use of Bt, pyrethroids, diflubenzuron and other chemical insecticides in orchards. As treatments and effects are probably quite different under forest conditions, only a few are included here. Deltamethrin and bioresmethrin were not toxic to T. dalmanni and T. cacoeciae during their development in eggs of RTM (Niemczyk et al., 1979). Lipa et al. (1977) applied 3 varieties of Bt at 4 concentrations and found that all treatments were effective in reducing the number of larvae below the economic threshold. A combination of Bt with a sublethal dosage of chlordimeform was even more effective. The effect of Bt on the histology of 2nd and 4th instar larvae was described by Galani (1973). According to Dronka et al. (1978), Bt var. kurstaki gave excellent control and was as effective as the insecticides fenitrothion, malathion, trichlorphon and dichlorvos. Skatulla (1973) tested the effect of Bt sprayed on different food plants, and found that the same concentration killed 100% of RTM larvae on pear in 3 days, while on spruce only 48% were killed in 9 days. Antibiotics and other factors in food plants are responsible for differences in effectiveness. Application of Bt during an RTM outbreak in a mature spruce forest caused 53% mortality; within 10 days the disease spread to untreated parts of the forest (Skatulla, 1974). Svestka & Vankova (1978) obtained good results with a combination of Bt with a sublethal dosage of permethrin.

#### Rearing

RTM can be reared on a general artificial diet (e.g. Berger, 1963).

P a l e t u s s o c k m o t h  
C a l l i t e a r a (D a s y c h i r a)  
p u d i b u n d a (L.)

#### Distribution and hosts

The taxonomy of the pale tussock moth (PTM), has been elucidated by Halloway (1982). PTM occurs throughout Europe between 42° and 60° N latitude. Its European distribution area is limited to the East by the Urals and to the West by Wales and Portugal. The species is highly polyphagous on deciduous trees, bushes and herbs; excepting Larix, it usually avoids coniferous trees. The main host is Fagus; other genera attacked are Carpinus, Quercus, Ulmus, Populus, Juglans, Tilia, Acer, Betula, Calluna, Vaccinium, Vitis, and many others including several orchard trees. The natural range of beech primarily determines the range of PTM.

#### Biology

PTM has one generation a year; it overwinters as pupae and adult activity occurs from late May to mid-June. Single-layered, naked egg masses containing 50-300 eggs are deposited throughout the forest vegetation on trunks, branches and leaves. Larvae hatch 3 weeks after oviposition and remain colonial for a few days before feeding. They feed for approximately 6 weeks during which they moult 4-8 times. (Vite, 1952; Vite & Kliefoth, 1955). Due to their inefficient feeding, the ground is usually covered with partly consumed leaves. Pupation takes place in a cocoon in the soil or in sheltered places.

#### Parasites, predators and pathogens

At least 21 hymenopterans and 9 tachinids have been recorded as parasites, of which the Hymenoptera Pimpla instigator, Gregoniimpla inquisitor, Automalus alboguttatus and Microgaster globatus and the tachinids Carcelia gnava and C. amphion have been found most frequently (Wellenstein, 1978; Herting, 1960; Vite & Kliefoth, 1955). PTM was recorded as a host for a new dipteran, Rhacodinella apicata (Larvaevoridae) in Poland (Karczewski & Draber-Monko, 1978). Birds, mice and carabids are major predators but it is doubted if they are responsible for the collapse of epidemics; that role is usually attributed to CPV (Urban, 1967) and NPV diseases (Jahn & Weber, 1966). A CPV isolated from PTM was tested on a cell line of GM by Skatulla (1987) but less than 1% of the cells replicated the virus.

#### Outbreaks; conditions and damage

In Germany, two consecutive warm and dry summers in areas with extensive forests of mature beech, often resulted in PTM outbreaks

(Wellenstein, 1978). Klimitzek (1972), determined a positive linear relationship between the extent of beech forests and the frequency of outbreaks. Although PTM epidemics were numerous in the first half of the 19th century in Germany, they have become less frequent, possibly because of milder winters, wetter summers and a decrease in area of beech forests. Since PTM is a late summer feeder, increment losses are usually limited and do not exceed 7% (Schneider, 1954). Measurement of the nutrient fluxes in a beech forest during an outbreak in 1971-1973 in S. Sweden indicate that increment losses cannot be clearly attributed to defoliation. In 1973, nitrogen, phosphorus and potassium in throughfall precipitation was three times that of 1971 (Nilsson, 1978).

#### Monitoring and forecasting

The sex pheromone of PTM has not yet been synthesized; therefore, outbreak density of the population is predicted on the basis of pupal counts (Zwölfer, cited in Wellenstein, 1978).

#### Control

Although increment losses are usually low and control is not recommended, chemicals have been applied successfully in a beech forest to save a major seed crop for the purpose of forest regeneration (Konig, 1954). In order to maintain high populations of predatory birds, nest-boxes are installed. No reports on the application of microbial control methods against PTM were found.

#### Rearing

PTM can probably be reared artificially on a general purpose diet (e.g Berger, 1983).

### EPILOGUE

The importance of the species dealt with in this overview is indicated by the estimation of area affected in some European countries (Table 1). The areas affected by GM and BTM include orchards, plantations of cork oak, brushwood and coppice. All other areas refer to epidemics in forests.

The NM calamities in Poland (1978-1984) and East Germany (1983-1984) started in large-scale Scots pine plantations on poor sandy soils. As the lymantrids are notorious forest pests not only in Europe but also in Africa, Asia and North America where the areas of forest plantations are continuously increasing, damage caused by this insect family may be expected to increase. A joint international effort to develop control strategies for stemming the losses caused by this insect family appears feasible and of high priority.

Table 1. Total area (1000 ha) infested by Lymantriid species during 1972-1987.

Countries	GM	LM	BTM	SM	RTM	PTM
Austria	0.3	-	-a	-a	-	-
Czechoslovakia	18.1	0.4	-	0.4	8.1	0.1
Denmark	-	2.3	-a	-	-	0.1
France	220.0	-	-a	-b	-	-
Germany (FRG)	-	5.0c	-a	-a	-	0.4c
Germany (GDR)	-b	300.0d	-b	-b	-b	-b
Hungary	53.0	-b	18.7	2.4	-b	-b
Italy	234.0c	-a	631.6c	-b	-	-
The Netherlands	0.2	3.3	-a	0.8	-	-
Poland	-b	6,300.4a	-b	-b	-b	-b
Switzerland	0.1	-	0.5	0.1	-	-
United Kingdom	-	-	-a	-	0.1	-
Yugoslavia	2,593.3	1.7	112.1	0.5	0.1	-
Total	3,118.8	6,612.7	762.9	4.3	8.3	0.6

a) Defoliation of lane trees, hedges, shelterbelts; area unknown. b) No data provided. c) Data refer to part of the country or period. d) Area actually controlled.

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## REFERENCES

- ABRAMENKO, I.D.; SAMILYAK, S.I. 1983. [Oak dieback in the ancient oak forest near the 'Forest on the Vorskla' and in surrounding forest steppe woodlands]. *Lesoved. Agrolesosmelior.* 67: 36-40 [Ru].  
 ABRAMENKO, I.D.; MYASHKOV, V.P. 1983. [Detrimental effects of needle-feeding insects and economic evaluation of their control by aerial spraying]. *Lesoved. Agrolesosmelior.* 66: 49-53 [Ru].  
 ALTENKIRCH, W. 1935. [Investigations on the biological control of

- the nun moth (*Lymantria monacha* L.) with the aid of the confusion technique.] Forst u-Holzw. 4:102-104 [De].
- ALTENKIRCH, W.; HUBER, J.; KRIEG, A. 1986. [Field trials on the biological control of the nun moth (*Lymantria monacha* L.) Z. Pflanzenschutz. Pflanzenschutz 93 (5):497-493 [De].
- ATANASOV, A. 1984. [Nuclear polyhedrosis virus in larvae of the browntail moth]. Rast. Zashch. 32(4): 30-31 [Bg].
- ATANASOV, A.; LECHEVA, I.; TRENCHEV, G. 1983. [Nuclear polyhedrosis of larvae of the cherry geometrid and the common vapourer]. Rast. Zashch. 31(8): 23-24 [Bg].
- BAKHVALOV, S.A.; LARIONOV, G.V.; ZHIMERIKIN, V.N.; CHERNYAVSKAYA, O.A. 1979. [Development of induced nuclear polyhedrosis in the nun moth (Lepidoptera, Orgyidae, *Lymantria monacha* L.) in experimental conditions]. Izv. Sibir. Otd. Akad. Nauk SSSR, Biol.10 vyp.2: 65-70 [Ru].
- BAKHVALOV, S.A.; LARIONOV, G.V.; BAKHVALOVA, V.N. 1982. [Recovery of the gypsy moth, *Lymantria dispar* L. (Lepidoptera, Lymantriidae) after experimental virus infection]. Entomol. Obozr. 61 (4):755-758 [Ru].
- BAKVALOV, S.A.; ZURABOVA, E.R.; PESHKOV, G.P.; BARANOVSKII, V.I.; LARIONOV, G.V.; USOVA, G.P. 1984. [Limiting the numbers of *Lymantria monacha* with the aid of Lepidocide]. Les. Khoz. 4: 49-50 [Ru].
- BARANCHIKOV, YU.N. 1983. [The effectiveness of consumption of excised needles by insect communities of European larch]. Izv. Sibir. Otd. Akad. Nauk SSSR, Biologicheskikh Nauk 3: 112-115 [Ru].
- BEDNYI, V.D.; KOVALEV, B.G. 1978. [Basis for the use of disparlure for determination and prediction of numbers of the gypsy moth]. Khemoretseptsiya Nasekomykh 3: 147-151 [Ru].
- BEDNYI, V.D.; CHERNICHUK, L.L.; CHEKANOV, M.; CHEKRIZOVA, V.L. 1980. [The influence of preliminary maintenance of males of the gypsy moth in an atmosphere saturated with disparlure on their mating ability]. Khemoretseptsiya Nasekomykh 5:123-125 [Ru].
- BEJER, B. 1985. Nun moth (*Lymantria monacha* L.) outbreaks in Denmark and their association with site factors and climate. Res. Dev.Pap., For. Comm. London 135: 21-26 [En].
- BEJER, B. 1986. Outbreaks of nun moth (*Lymantria monacha* L.) in Denmark with remarks on their control. Anz. Schaedlingsk., Pflanzenschutz 59 (5): 86-89 [En].
- BELOV, A.N. 1986. [The effect of insect defoliators on the growth of oak stands]. Les. Khoz. 4:67-69 [Ru].
- BERGER, R.S.1963. Laboratory techniques for rearing *Heliothis* species on artificial medium. USDA Presentation Pap. ARS: 33-84. 4p[En].
- BJEGOVIC, P. 1972. [Reproduction of *Ooencyrtus kuvanae* Howard (Hymen., Encyrtidae) in irradiated eggs of the gypsy moth (*Lymantria dispar* L.) Zast. Bilja 23 (117/118): 3-6 [Sh].
- BLAGOVIDOV, A.K. 1986. [The effect of defoliation of pure pine stands in different forest-growth zones]. Lesoved. 4:39-44 [Ru].
- BOGENSCHUTZ, H. 1975. [Parasite studies as aids to decision-making in the integrated control of forest pests]. Z. Angew. Entomol. 78(1): 1-4 [De].
- BREWER, J.W.; KRAMPL, F.; SKUHRAVY, V. 1985. Forest Lepidoptera attracted to six synthetic pheromones in Czechoslovakia. Z. Angew. Entomol. 100(4): 372-381 [En].

- BRINKMANN, G. 1982. [Control of the epidemic of *Lymantria monacha* L. in Poland]. Allg. Forstzeitschr. 3: 82-83 [De].
- BURGERJON, A.; BIACHE, G.; CHAUFoux, J.; PETRE, Z. 1981. [Comparative susceptibility, as a function of age, of larvae of *Lymantria dispar*, *Mamestra brassicae* and *Spodoptera littoralis* to nuclear polyhedrosis virus] Entomophaga 26 (1): 47-58 [Fr].
- CABRAL, M.T.E.C. 1977. [The influence of the food of *Lymantria dispar* L. and *Euproctis chrysorrhoea* L. on the effect of *Bacillus thuringiensis*]. An. Inst. Super. Agron. (Lisboa) 37: 179-221 [Pt].
- CHERNOV, T. 1976. [Biological control of forest pests]. Rast. Zashch. 24 (4): 5-8 [Bg].
- CLARKE, C.; FORD, E.B. 1983. *Lymantria dispar* (L.). A third reassessment. Proc. Roy. Soc. Lond. 218 (1212): 365-370 [En].
- CRAMER, H.H. 1962. [The possibility of forecasting outbreaks of forest pests with the aid of meteorological data]. Schreibe Forstl. Abt. Univ. Freiburg 1: 238-245 [De].
- CUNNINGHAM, J.C. 1982. Field trials with Baculoviruses: control of forest insect pests. In: Kurstak, E. (ed.) Microbial and viral pesticides, Marcel Dekker Inc. New York, p. 335-386 [En].
- CURRADO, I.; BRUSSINO, G. 1985. [Control experiments with *Bacillus thuringiensis* Berl. in the forests of Piedmont]. Difese delle Piante 8 (2): 339-343 [It].
- DE FREINA, J.J.; WITT, J. 1987. [The Bombyces and Sphingides of the West Palearctic], Forschung und Wissenschaft Verlag, Munchen. 708 pp.
- DELRIO, G.; LUCIANO, P. 1985. [The parasites and predators of *Euproctis chrysorrhoea* L. in Sardinia (preliminary note)]. In: Atti XIV Congr. Naz. Ital. Entomol. : 825-832 [It].
- DONDIKOV, N.M. 1974. [*Stilpnotia salicis* in the Altai region]. Zashch. Rast. 9: 47 [Ru].
- DRONKA, K.; NIEMCZYK, E.; OLSZAL, R. 1978. [The effectiveness of the bacterial preparation Dipel and some insecticides for the control of the rusty tussock moth (*Orgyia antiqua* L.) (Lepidoptera: Lymantriidae) in apple orchards]. Roczn. Nauk Roln., E 7(1): 75-80 [Pl].
- EKK, I.; KISS, M.; NOWINSKY, L.; SZABO, S.; TOTTH, G. 1980. The coefficient of population and its application in plant-protecting prognosis. Folia Entomol. Hung. 33(2): 23-32 [En].
- ENTWISTLE, P.F. 1986. Epizootiology and strategies of microbial control. In: Franz, J.M. (ed.) Biological plant and health protection. Progress in Zoology, G. Fisher Verlag, N. York, V. 32: 257-278 [En].
- ENTWISTLE, P.F.; EVANS, H.F. 1985. Viral control. In: Gilbert, L.I.; Kerkut, G.A. (eds.) Comprehensive insect physiology, biochemistry and pharmacology, Pergamon Press, V. 12: 347-412 [En].
- FANKHANEL, H. 1959. [On the influence of temperature and humidity levels on the speed of development, food consumption and larval mortality of the browntail moth, *Euproctis chrysorrhoea* L. (Lepidoptera)]. Beitr. Entomol. 9(3/4): 303-322 [De].
- FRATIAN, A. 1978. [Influence of defoliations caused by *Lymantria dispar* on the growth and viability of oak stands]. Zast. Bilja 29 (1/2): 163-168 [Fr].
- FRATIAN, A. 1985. Some aspects of population dynamics of the gypsy moth (*Lymantria dispar*) and oak leaf roller moth (*Tortrix viridana*) in chemically and biologically treated oak stands. Res.

- Dev. Pap., For. Comm.(London) 135: 100-103 [En].
- GALANI, G. 1973. [On the histology of larvae of Orgyia antiqua L., (Lepid., Lymantriidae) after treatment with a preparation of Bacillus thuringiensis]. Anz. Schaedlingsk., Pflanzenschutz 46(10): 150-152 [De].
- GALETENKO, S.M.; PASTUKH, T.I. 1980. [The common brushtail]. Zashch. Rast. 9: 49-50 [Ru].
- GALKIN, G.I. 1976. [Outbreaks of Dendrolimus sibiricus and solar activity]. Lesn. Khoz. 8: 83-85 [Ru].
- GATIGNOL, J.; MATOURET, D.; BIC, G. 1972. [The effectivity of Bacillus thuringiensis against the browntail moth]. Phytoma 24(237): 35-38 [Fr].
- GLOWACKA-PILOT, B. 1983. [Control of Lymantria monacha in Scots pine stands with nuclear polyhedrosis virus]. Pr. Inst. Badaw. Lesn. 616/620: 55-65 [Pl].
- GLOWACKA-PILOT, B. 1986. [Pathogenic micro-organisms of the nun moth (Lymantria monacha L.) and their use for forest protection]. Z. Pflkrankh. Pflanzenschutz 93 (5): 494-502 [De].
- GORBUNOV, A.F.; MISHNEV, A.K. 1983. [Needle-eating pests of forest stands in southern Ukraine]. Lesovod. Agrolesomeliior. 66: 53-58 [Ru].
- GORLITZ, H.; TRENKMANN, L.; HEROLD, H. 1978. [Incidence and control of Euproctis chrysorrhoea in 1977 with special reference to the Leipzig district] Nachrbl. Dtsch. Pflschdienst (Berlin) 32(3): 47-50 [De].
- GIGOROVA, R.; NAUMOVA, M.; STOYANOVA, M. 1982. [Study on newly isolated insect pathogenic Streptococcus]. Acta Microbiol. Bulg. 11:127-133 [Bg].
- GRIJPMMA, P. 1987. Artificial diets and rearing of the nun moth, Lymantria monacha. Entomol. exp. appl. 45: 219-225 [En].
- GRIJPMMA, P.; VAN LENTEREN, J.C. 1988. Telenomus nitidulus (Hymenoptera: Scelionidae), egg parasite of the satin moth, Leucoma salicis (Lepidoptera: Lymantriidae). In: Trichogramma and other egg parasites. Inst. Nat. Rech. Agron., Paris. Les Colloques de l'INRA no.43: 181-189. [En].
- GRIJPMMA, P.; PERSOONS, C.J.; PETERS, D.; VLAK, J.M. 1986. Biological control of the satin moth with pheromones and baculoviruses. Project Report 1985. European Economic Community; R & D Programme: Wood as a renewable raw material. Wageningen, Dorschkamp Rapport 443. 19pp.
- GRINENKO, YU.I. 1986. [Monitoring the populations of Lymantria dispar in Kazakhstan]. Lesoved. 4:45-49 [Ru].
- HANSEN, K. 1984. Discrimination and production of disparlure enantiomers by the gypsy moth and the nun moth. Physiol. Entomol. 9 (1): 9-18 [En].
- HARRIS, B.A.; LAVERS, A. 1985. Poland: management of forest pests. Span 28 (1): 8-10 [En].
- HERTING, B. 1960. [Biology of the westpalaeartic parasite-flies (Dipt., Tachinidae)]. Monogr. Angew. Entomol. 16, 188 pp. [De].
- HERTING, B. 1976. A catalogue of parasites and predators of terrestrial arthropods. Section A Vol. 7, Lepidoptera, Part 2 Macrolepidoptera, Farnham Royal; Commonw. Agr. Bureaux. 221 pp. [En].
- HOLLOWAY, J.D. 1982. The generic placing of Phalaena (Bombyx)

- pudivunda* L. and *Phalaena* (*Bombyx*) *fascelina* L. (Lepidoptera: Lymantriidae). Proc. and Transact. British Ent. Nat. Hist. Soc. 15(1/2): 44 [En].
- HUBER, J.; MILTENBURGER, H.G. 1986. Production of pathogens. In: Franz, J.M. (ed.) Biological plant and health protection. Progress in zoology, G. Fisher Verlag, N. York, V. 32: 167-181 [En].
- HUGER, A.; KRIEG, A. 1958. [About a cytoplasmatic polyhedrosis virus of the nun moth larva (*L. monacha*)]. Naturwissenschaften 45: 170-171 [De].
- INJAC, M.; VASILJEVIC, L. 1978. [Aerial control of the gypsy moth (*Lymantria dispar* L.) by nuclear polyhedrosis viruses (*Baculovirus*)]. Zast. Bilja 29 (1/2):43-56 [Fr].
- JAHN, E. 1979. [On the occurrence of a cytoplasmic polyhedrosis during the collapse of the outbreak of *Lymantria dispar* (Lepidoptera: Lymantriidae) in the Leitha mountains of Austria in 1973]. Zeit. Angew. Entomol. 66(1): 9-14 [De].
- JAHN, E.; WEBER, T. 1966. [On the polyhedrosis of *Dasychira pudibunda* and its transmittance]. Anz. Schaedlingsk. Pflanzenschutz 39(3): 39-42 [De].
- JENSEN, T.S. 1983. Registration and control of the nun moth, *Lymantria monacha* L. Mitt. Dtsch. Ges. Allg. Angew. Entomol. 4 (1/3): 146-149 [En].
- JENSEN, T.S.; NIELSEN, B.O. 1984. Evaluation of pheromone catches of the nun moth, *Lymantria monacha* L. Effect of habitat heterogeneity and weather conditions in the flight period. Z. Angew. Entomol. 98 (4): 399-413 [En].
- KANECKA, P.; SVESTKA, M.; PECHA, J. 1987. [The significance of the parasites and predators of the red tussock moth]. Lesn. Prace 4: 167-172 [Cs].
- KARCZEWSKI, J.; DRABER-MONKO, A. 1978. [A contribution to the knowledge of the biology and morphology of *Rhacodineella apicata* (Pandelle, 1896) (Diptera, Larvaevoridae)]. Polski Pismo Entomol. 48(1): 97-103 [De].
- KATAEV, O.A. 1981. [Some aspects of the effects of human activity on forest pests]. In: Aukstikal'ne, A.M. (ed.) Noveishie dostizheniya lesnoi entomologii. Institut Zoologii i Parazitologii Akademii Nauk Litovskoi SSR p.69-73 [Ru].
- KHUBENOV, Z.K. 1983. [Contribution to the study of the family of the Tachinidae (Diptera)]. Acta Zool. Bulg. 23: 57-61 [Bg].
- KIREVA, I.M. 1978. [Predicting a mass outbreak of *Lymantria dispar*]. Lesn. Khoz. 4:86-87 [Ru].
- KLIMITZEK, D. 1972. [*Dasychira pudibunda* in the Palatinate] Allg. Forst- u Jagdztg. 143(9): 192-195 [De].
- KLIMITZEK, D. 1976. [Fluctuations of insect populations in relation to sunspot activity]. Forstw. Centbl. 95 (4): 226-238 [De].
- KLIMITZEK, D.; LOSKANT, G.; VITE, J.P.; MORI, K. 1976. Differences in pheromone perception between gypsy moth and nun moth. Naturwissen. 63 (12): 581-582 [En].
- KONIG, E. 1954. [Control of the pale tussock moth in the Pfalz Forest by helicopter]. Forstarchiv 25: 87-94 [De].
- KORCHAGIN, V.N. 1980. [The gypsy moth]. Zashch. Rast. 11:64-65 [Ru].
- KORCHAGIN, V.N. 1983. [The thorn butterfly and the browntail moth]. Zashch. Rast. 12: 48-49 [Ru].
- KOTENKO, A.G. 1982. [Hide beetles (Coleoptera, Dermestidae), natural

- enemies of the gypsy moth in the southern Ukraine]. Vestn. Zool. 1: 41-45 [Ru].
- KOVALEV, B.G.; BEDNYI, V.D.; KARDE, R. 1980 [Attractiveness of enantiomers of disparlure to the gypsy moth and the nun moth]. Khemoretseptiya Nasekomykh 5: 109-112 [Ru].
- KRIEG, A. 1983. [Insect pest control in plant protection by *Bacillus thuringiensis* preparations and their influence on the environment. 2nd report]. Anz. Schaedlingsk. Pflanzenschutz 56(3): 41-52 [De].
- KRUSHEV, L.T.; MARCHENKO, Ya.I. 1981. [Against the nun moth]. Zashch. Rast. 11: 35 [Ru].
- KUSEVSKA, M. 1972. [The influence of ecological conditions on the occurrence and development of polyhedrosis in larvae of *Stilpnotia salicis*]. Fragm. Balc. 9(2): 9-19 [Ma].
- KUZMANOVA, I.; SAPUNDZHIEVA, K.; CHARNEV, T. 1980. [Perspective strains of *Bac. thuringiensis* for controlling forest pests]. Nauchni Trudove, Entomologiya, Mikrobiologiya, Fitopatologiya 25(3): 141-148 [Bg].
- LAMERIS, A.M.C.; ZIEMNICKA, J.; PETERS, D.; GRIJFMA, P.; VLAK, J.M. 1985. Potential of baculoviruses for control of the satin moth, *Leucoma salicis* L. (Lepidoptera: Lymantriidae). Meded. Fac. Landbouwwet. Rijksuniv.(Gent) 50(2a): 431-439 [En].
- LIPA, E.Ya. 1983. [Insect natural enemies and entomopathogenic organisms as an element of forecasting pest abundance]. Zashch. Rast. 2:40 [Ru].
- LIPA, J.J.; BAKOWSKI, G.; RYCHLEWSKA, M. 1977. [The effectiveness of the microbial insecticides Bactospeine, Dipel, Selctzin and Thuricide against the rusty tussock moth, *Orgyia antiqua* L. (Lepidoptera, Lymantriidae) on apple trees]. Prace Nauk. Inst. Ochr. Rosl. 19(1): 183-190 [Pl].
- LITTLEWOOD, S.C. 1984. Ecdysis and larval size of *Orgyia antiqua* (L.) (Lepidoptera: Lymantriidae). Entomol.Gaz. 35(3): 144 [En].
- LOBINGER, G.; SKATULLA, U. 1986. [Crossinfection tests with two virus strains (NPV) against the nun moth, *Lymantria monacha* L. (Lep., Lymantriidae) and the pine beauty, *Panolis flammea* Schiff. (Lep., Noctuidae)] Anz. Schaedlingsk., Pflanzenschutz 59 (8): 147-148 [De].
- LONGO, S. 1983. [First observations on the population dynamics of *Euproctis chrysorrhoea* L. in Sicily]. Atti XIII Congr. Ital. Entomol.: 375-382 [It].
- LUCIANO, P.; PROTA, R. 1985. [Two methods of evaluating population density in *Lymantria dispar* L.]. In: Atti XIV, Congr. Naz. Ital. Entomol. Palermo. Accademia Nazionale Italiana di Entomologia p.599-606 [It].
- LUITJES, J. 1973. [The effect of defoliation by *Leucoma salicis* on the growth of poplar]. Ned. Bosb. Tijdschr. 45(2): 45-53 [Nl].
- LUNDERSTADT, J. 1983. [Principles controlling the ecological-physiological relationship between forest trees and phytophagous insects]. Z. Angew. Entomol. 96 (2): 157-165 [De].
- LYACHENKO, P.I.; ANDREEVA, G.I. 1979. [Dimilin against forest pests]. Zashch. Rast. 6: 21-23 [Ru].
- MAGNOLER, A. 1970. A wheat germ medium for rearing of the gypsy moth, *Lymantria dispar* L. Entomophaga 15: 401-406 [En].
- MAGNOLER, A. 1985. [The use of two baculoviruses in the control of *Malacosoma neustria* L. and *Lymantria dispar* L. in the oak woods of

- Sardinia. Difesa delle Piante 8 (4): 451-462 [It].
- MACNOLER, A.; CABBINI, A. 1968. [Radial increment of *Quercus suber* and effects of defoliations caused by the larvae of *Lymantria dispar* and *Malacosoma neustria*. I. Experiments on trees not subject to bark stripping]. Memoria, Stazione Sperimentale de Sughero No.27; 16 pp.[It].
- MAJUNKE, C.; HAUSSLER, D.; WALTER, C. 1985. [Control of *Lymantria monacha* and other foliage pests of pine in the East German lowlands in 1984]. Beitr. Forstwirts. 19 (2): 89-91 [De].
- MAKSIMOVIC, M. 1980. [The use of pheromone for controlling the gypsy moth by disrupting mating]. Zast. Bilja 31 (4): 303-307 [Sh].
- MAKSIMOVIC, M.; SIVCEV, I. 1984. Further studies on the numerical increase of natural enemies of the gypsy moth (*Lymantria dispar* L.) in forests. Z. Angew. Entomol. 98 (4): 332-343 [En].
- MAKSYMOW, J.K. 1980. [Biological control of the satin moth *Stilpnotia salicis* L. with *Bacillus thuringiensis* Berliner]. Anz. Schaedlingsk., Pflanzenschutz 53(4): 52-56 [De].
- MALAYI, L.P. 1978. [Determining the degree of threat from needle-and leaf-eating insects]. Lesn. Khoz. 31(3): 79-80 [Ru].
- MALYI, L.P.; OVSYANIKOVA, T.Yu. 1978. [The susceptibility of larvae of *Euproctis chrysorrhoea* to Dendrobacillin]. Lesoved. 2: 73-75 [Ru].
- MARCHENKO, Ya.I.; EMEL'YANCHIK, G.M. 1981. [Susceptibility of caterpillars of the nun moth to bacterial infection] Lesoved. 5: 85-89 [Ru].
- MARIKOVSKII, P.N. 1977. [A mass outbreak of the satin moth] Zashch. Rast. 9: 29 [Ru].
- MAROVIC, R. 1981. Results of the crossing inbred strain of gypsy moth, *Lymantria dispar* L., with wild moths. Z. Angew. Entomol. 91 (1): 107-111 [En].
- MARUSHINA, N.G. 1978. [The nun moth]. Zashch. Rast. 3:38-39 [Ru].
- MILLS, N.J. & SCHOENBERG, F. 1985. Possibilities for the biological control of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lymantriidae), in Canada, using natural enemies from Europe. Biocontrol News and Information, Vol. 6 (1): 1-18 [En].
- MITTERBOCK, F.; FUHRER, E. 1988. [Effects of fluoride-polluted spruce needles on nun moth larvae *Lymantria monacha* L. (Lep., Lymantriidae)]. Z. Angew. Entomol. 105: 19-27 [De].
- NEF, L. 1972. [Influence of chemical and microbial treatments on a population of *Stilpnotia (=Leucoma) salicis* L. and on its parasites]. Z. Angew. Entomol. 69(4): 357-367 [Fr].
- NEF, L. 1976. [Ecological studies on *Telenomus nitidulus*, parasite of the eggs of *Stilpnotia (=Leucoma) salicis*]. Z. Pflanzenkr. Pflanzenschutz 83(1/2/3): 109-119 [Fr].
- NEF, L. 1978. [*Leucoma salicis* L.] In: Schwenke, W. [The forest pests of Europe] Parey, V.III: 375-380 [De].
- NIEMCZYK, E.; MISCZAK, M.; OLSZAK, R. 1979. [The toxicity of pyrethroids to predacious and parasitic insects]. Roczn. Nauk Roln. E, 9(2): 105-115 [Pl].
- NIEMCZYK, E.; OLSZAK, R.; POPINSKA, H. 1978. [The role of parasites in limiting numbers of overwintered eggs of the vapourer moth, *Orgyia antiqua* L. in apple orchards]. Polski Pismo Entomol. 48(4): 665-675 [Pl].
- NILSSON, I. 1978. The influence of *Dasychira pudibunda* (Lepidoptera)

- on plant nutrient transports and tree growth in a beech (Fagus sylvatica) forest in southern Sweden. *Oikos* 30(1): 133-148 [En].
- NIZI, G.; PROSPERI, G. 1973. [Notes on the wood increment of forest trees of the genus Quercus defoliated by Lymantria dispar L.]. Note e Appunti Sperimentali di Entomologia Agraria 14: 67-78 [It].
- NOVOTNY, J. 1988. [The sensitivity of Lymantria dispar L. (Lep., Lymantriidae) to Bacillus thuringiensis and two moulting inhibitors, pure and in combinations. *Anz. Schaedlingsk., Pflanzenschutz* 61: 11-14 [De].
- OBOZOV, A.N. 1968. [The white satin moth]. *Zashch. Rast.* 13(9): 46 [Ru].
- OGARKOV, B.N.; OGARKOVA, G.R. 1979. [Fungal epizootics of insect pests in the Irkutsk region]. *Mikol. Fitopatol.* 13(1): 10-12 [Ru].
- ORLOVSKAYA, E.V. 1970. [A microbiological method for the control of the gypsy moth]. *Zashch. Rast.* 15(9): 39-40 [Ru].
- OVCHAROV, D. 1982. [Evaluation of the activity of bacterial preparations in forestry]. *Rast. Zashch.* 30(8): 16-18 [Bg].
- PANINA, N.B. 1984. [Methods of determining the effectiveness of predators of Lymantria dispar]. *Lesn. Khoz.* 12: 49-50 [Ru].
- PATOCKA, J. 1972. [Influence of temperature on hunger resistance and mortality of the larvae of several oak moths (Lepidoptera)]. *Acta Entomol. Boh.* 69(4): 243-250 [De].
- PATOCKA, J. 1973. [Influence of food and location on the mortality of some injurious insects living on oak] *Vestn. Cesk. Spol. Zool.* 37(4): 282-292 [De].
- PINDER, P.S.; HAYES, A.J. 1986. An outbreak of vapourer moth (Orgyia antiqua L.: Lepidoptera Lymantriidae) on Sitka spruce (Picea sitchensis (Bong.) Carr.) in central Scotland. *Forestry* 59(1): 97-105 [En].
- PISICA, C.; LACATUSU, M.; TUDOR, C.; TEODORESCU, I.; NASTASE, I. 1978. [The natural enemies of the defoliator Stilpnotia salicis L. (Lepidoptera, Lymantriidae) in Europe and Romania]. *Travaux du Museum d'Histoire Naturelle 'Grigore Antipa'* 19: 297-301 [Fr].
- POKOZII, I.T. 1962. [Euproctis chrysorrhoea and its destructiveness in forest belts]. *Tr. Kharkovsk. Sel'skokhoz. Inst.* 36(73): 116-148 [Ru].
- PREISS, R. 1985. Lack of effect of (-)disparlure on orientation towards (+)disparlure source in walking and flying gypsy moth males. *J. Chem. Ecol.* 11 (7) 885-894 [En].
- PURRINI, K. 1979. [On natural diseases of Euproctis chrysorrhoea L. (Lep., Lymantriidae) 1977 in Bayern]. *Anz. Schaedlingskde., Pflanzenschutz* 52: 56-58 [De].
- RUELLE, P.; NEF, L.; LEBRUN, P. 1978. [Effectiveness and persistence of Bacillus thuringiensis: test in semi-natural conditions on Euproctis chrysorrhoea]. *Parasitica* 34: 199-206 [Fr].
- SCHMIDT, M. 1985. [Studies on feeding the red wood ant (Formica polyctena F.; Hym., Formicidae) with the hairy caterpillars of Orgyia antiqua L. (Lep., Lymantriidae)]. *Anz. Schaedlingsk., Pflanzenschutz* 58(4): 70-72 [De].
- SCHMUTZENHOFER, H. 1986. [Monitoring and mating disruption of the nun moth, Lymantria monacha L., with the pheromone disparlure]. *Anz. Schaedlingsk. Pflanzenschutz* 59 (7): 125-130 [De].

- SCHNEIDER, G. 1954. [Is it worthwhile to control the pale tussock moth?]. Forst- u. Holzwirt 9: 378-379 [De].
- SCHONHERR, J. 1972. [The effect of Disparlure on the nun moth, *Lymantria monacha* L.]. Z. Angew. Entomol. 71: 260-263 [De].
- SCHONHERR, J.; KETTERER, R. 1979. [On combined applications of polyhedrosis virus and *Bacillus thuringiensis* for control of the nun moth, *Lymantria monacha* L. (Lepidoptera)]. Z. Pflanzenkr. Pflanzenschutz 86: 483-488 [De].
- SCHROTER, H.J.; LANGE, R. 1975. [Field investigations on the influence of the female sex pheromone on the flight activity of the male of *Lymantria monacha* L.]. Z. Angew. Entomol. 77(4): 337-341 [De].
- SCHWENKE, W. 1968. [New indications for a dependency of the reproduction of leaf- and needle feeding forest insects on the sugar content of their food]. Z. Angew. Entomol. 61: 365-369 [De].
- SELIKHOVKIN, A.V. 1981. [The effect of sulfur dioxide on the development of the gypsy moth (*Porthetria dispar* L.)]. In: Aukstikal' nene, A.M. (ed.) Noveishie dostizheniya lesnoi entomologii. Institut Zoo- logii i Parazitologii Akademii Nauk Litovskoi SSR p. 148-151 [Ru].
- SIDOR, C.; JODAL, I. 1983. [Results of a study on the physiological condition of the gypsy moth (*Porthetria dispar* L.) on the acacia forest "Bagremara" near Backa Palanka]. Zast. Bilja 34(4): 445-455 [Sh].
- SIDOR, C.; DUSANIC, L.; VUJIN, M. 1975. [The most important diseases of the European browntail moth, *Euproctis chrysorrhoea* L. caused by micro-organisms in 1972-1974 in the Macedonian Republic]. Acta Entomol. Jugosl. 11(1/2): 125-134 [Sh].
- SIDOR, C.; ZAMOLA, B.; KAJFEZ, I.F. 1978. [Polyhedral viral disease of *Leucoma salicis* L. in Voivodina, Yugoslavia]. Arhiv za Higijenu Rada i Toksikologiju 29: 219-233 [Sh].
- SIMCHUK, P.A. 1982. [The importance of environmental conditions in the rearing of Microsporidia]. Zash. Rast. 1:32 [Ru].
- SISOJEVIC, P.; SERAVIMOVSKI, A.; KUSEVSKA, M.; CEPELAK, J. 1976. [Tachinid parasites of the browntail moth (*Euproctis chrysorrhoea* L.) in Macedonia, 1972-1974]. Zast. Bilja 27(2): 167-179 [Sh].
- SKATULLA, U. 1973. [Differential effects of *Bacillus thuringiensis* on *Orgyia antiqua* in relation to the food plant]. Anz. Schaedlingsk., Pflanzenschutz 46(3): 46-47 [De].
- SKATULLA, U. 1974. [On the outbreak of the vapourer moth, *Orgyia antiqua* (L.) in 1971/72 in Bavaria]. Anz. Schaedlingsk., Pflanzenschutz 47(6): 89-93 [De].
- SKATULLA, U. 1985. [The effect of a polyhedrosis virus, isolated from *Leucoma salicis* (Lep., Lymantriidae), on some Lymantriidae species]. Anz. Schaedlingsk., Pflanzenschutz 58 (3): 41-47 [De].
- SKATULLA, U. 1986. [On the effect of two virus strains on the larvae and pupae of the gypsy moth, *Lymantria dispar* L. (Lep., Lymantriidae)]. Anz. Schaedlingsk. Pflanzenschutz 59(2) 25-29 [De].
- SKATULLA, U. 1987. [Studies on the susceptibility of a cell line of *Lymantria dispar* L. (Lep., Lymantriidae) to some virus strains]. Z. Ang. Entomol. 103(2): 203-208 [De].
- SKATULLA, U.; SCHWENKE, W. 1978. [*Euproctis chrysorrhoea* L.]. In: Schwenke, W. (ed.). [The forest pests of Europe]. Parey, V.III: 368- 374 [De].

- SKUHRAVY, V. 1987. A review of research on the nun moth (Lymantria monacha L.) conducted with pheromone traps in Czechoslovakia, 1973-1984. Anz. Schaedlingsk. Pflanzenschutz 60: 96-98 [En].
- SKUHRAVY, V.; ZUMR, V. 1981. Nocturnal and seasonal flight of the nun moth Lymantria monacha L. (Lepidoptera, Lymantriidae) as determined by pheromone and light traps. Z. Angew. Entomol. 92 (3): 315-319 [En].
- SLIWA, E.; SIERPINSKI, Z. 1986. [Outbreak of Lymantria monacha in Poland from 1978 to 1984]. Anz. Schaedlingsk. Pflanzenschutz 59 (5): 81-86 [De].
- SLIZYNSKI, K. 1970. [The feeding of the nun moth Ocneria monacha L. (Orgyidae, Lepidoptera) on the male inflorescences of pine, Pinus sylvestris L.]. Polski Pismo Entomol. 40 (4): 871-876 [Pl].
- SLIZYNSKI, K.; LIPA, J.J. 1975. A cytoplasmic polyhedrosis virus of pine moth Dendrolimus pini L. (Lepidoptera: Lasiocampidae). Prace Nauk. Inst. Ochr. Rosl. 17(2): 29-60 [En].
- SMETNIK, A.I.; SHUMAKOV, E.M.; LANDA, V. 1980. [The use of pheromones of insects as a means of protection of plants]. Informatsionnyi Bulletin 1: 73-77 [Ru].
- STRAND, R.J.; SYLVESTER, N.K. 1981. Control of browntail moth, ULV compared with conventional low volume spraying. Intern. Pest Contr. 23(2): 43,44,58 [En].
- SVESTKA, M. 1971. [The influence of climatic factors and natural enemies in the spring of 1967 on the population dynamics of Lymantria monacha in Norway spruce stands in S.W. Moravia]. Prace VULHM 40: 17-34 [Cs].
- SVESTKA, M. 1978. [The effectiveness and persistence of the synthetic pyrethroid permethrin]. Lesnictvi 24 (3): 267-284 [Cs].
- SVESTKA, M.; VANKOVA, J. 1978. [On the effect of Bacillus thuringiensis combined with a synthetic pyrethroid]. Anz. Schaedlingsk. Pflanzenschutz 51(1): 5-9 [De].
- SZALAY-MARZSO, L.; HALMAGYI, L.; FODOR, S. 1981. Microbial control experiment against Stilpnotia salicis L., pest of poplar stands in northwest Hungary. Acta Phytopathol. Acad. Sci. Hung. 16(1/2): 189-197 [En].
- SZMIDT, A.; SLIWA, W. 1980. [Use of Dimilin in forest protection]. Sylwan 124 (11): 39-46 [Pl].
- SZONTAGH, P. 1974. [The significance of light trap research in forecasting injurious forest insect epidemics]. Pol. Ent. Hung. XXVII.-Suppl.: 153-157 [De].
- TEODORESCU, I. 1980. [Contribution of the oophagous scelionids (Proctotrupoidea-Scelionidae) to the limitation of attack by some defoliating Lepidoptera]. Stud. Cercet. Biol., Biologie Animale 32(2) 177-180 [Ro].
- THOMPSON, W.R. 1946. A catalogue of the parasites and predators of insect pests. Section 1. Parasite host catalogue, parts 5-9. Parasites of the Lepidoptera. Belleville; Imperial Service, 627 pp. [En].
- TIMANS, U. 1982. [The effect of UV radiation on the nuclear polyhedrosis virus of the gypsy moth, Lymantria dispar L. (Lep., Lymantriidae)]. Z. Angew. Entomol. 94(4): 382-401 [De].
- TRIGIANI, A. 1979. [Preliminary control tests with Bacillus thuringiensis Berl. and Borrelinavirus reprimens against the larvae of Porthetria (Lymantria) dispar L. (Lep: Lymantriidae) on Macedonian

- oak (*Quercus trojana* Webb.)). Entomologica 15: 103-113 [It].
- TSEITGAMEL, Yu.S. 1974. [The population dynamics of *Euproctis chryso-rrhoea* in the Central Chernozem State Reservation]. Zool. Zhur. 53(2): 292-296 [Ru].
- UCHINAKA, V.A. 1973. [*Eupteromalus nidulans* against the browntail moth *Euproctis chryso-rrhoea*]. Lesn. Khoz. 12: 65-66 [Ru].
- URBAN, S. 1968. [The occurrence of a cytoplasm polyhedrosis virus in *Dasychira pudibunda*]. Arch. Forstw. 16(6/9): 837-840 [De].
- VANKOVA, J.; NOVAK, K. 1985. [Effects of the biopreparations Bathurin and Dipel on larvae of the browntail moth (*Euproctis chryso-rrhoea* L.) in field conditions]. Sbornik UVTIZ Ochrana Rostlin 21(4): 307-309 [Cs].
- VASIC, K.; MINIC, D. 1979. [Fauna of hyperparasites in cocoons of solitary *Apanteles* species and *Meteorus versicolor* Nees., primary parasites of the gypsy moth (*Porthetria dispar* L.) and the satin moth (*Leucoma salicis* L.) in Yugoslavia]. Arh. Biol. Nauka. 28(3/4): 175-188 [Sh].
- VASILJEVIC, L.; INJAC, M. 1971. [Artificial diet for the gypsy moth (*Lymantria dispar* L.)]. Zast. Bilja 22 (115/116): 389-396 [Sh].
- VIDENOVA, E. 1980. [Dipel, - a highly effective biopreparation. Ways and means of increasing effectiveness] Rast. Zash. 28(2): 10-12 [Bg].
- VITE, J.P. 1952. [Mass outbreak of the pale tussock moth]. Holz-Zentralbl. 78: 1711-1712 [De].
- VITE, J.P.; KLIEFOTH, R. 1955. [Experience with the pale tussock moth]. Holz-Zentralbl. 81: 511-512 [De].
- VSHIVKOVA, T.A. 1978. [Rate of development of *Lymantria dispar* on different species of food plants]. In: Vladyshevskii, D. V. (ed.) Ekologiya pitanya lesnykh zhivotnykh p. 88-96 [Ru].
- WAAGE, J.K. 1982. Sib-mating and sex ratio strategies in scelionid wasps. Ecol. Entomol. 7(1): 103-112 [En].
- WEISER, J.; NOVOTNY, J. 1987. Field application of *Nosema lymantriae* against the gypsy moth, *Lymantria dispar* L. Z. Angew. Entomol. 104: 58-62 [En].
- WEISMANN, L.; SVATARAKOVA, L. 1974. Toxicity of sodium fluoride on some species of harmful insects]. Biologia, Czechoslovakia, B 29(11): 847-852 [En].
- WELLENSTEIN, G. (ed.). 1942. [The nun moth in East Prussia (1933-1937)]. Monogr. angew. Ent. 15. [De].
- WELLENSTEIN, G. 1973. The use of insect viruses for the protection of forests. OEPP/EPP0 Bull. 9: 43-52 [En].
- WELLENSTEIN, G. 1978. [*Dasychira pudibunda* L.]. In: Schwenke, W. (ed.) [The forest pests of Europe]. Parey, V.III: 318-325 [De].
- WELLENSTEIN, G. 1978. [*Orgyia recens* Hbn.]. In: Schwenke, W. (ed.) [The forest pests of Europe]. Parey, V.III: 327-331 [De].
- WELLENSTEIN, G. 1979. [Retrospect on 4 years study and control of *Lymantria monacha* in East Prussia]. Allg. Forst-u. J.Ztg. 150 (2): 25-30 [De].
- WELLENSTEIN, G.; FABRITIUS, K. 1973. [Observations on the vapourer moth (*Orgyia antiqua* L.) and its parasites]. Anz. Schaedlingsk.. Pflanzenschutz 46(2): 24-30 [De].
- WELLENSTEIN, G.; SCHWENKE, W. 1978. [*Lymantria* Hbn.]. In: Schwenke, W. [The forest pests of Europe]. Parey, V.III: 334-368 [De].

- ZAKHARIEVA, A. 1983. [Species composition and role of parasites of Stilpnotia salicis l. in Bulgaria]. Nauchni Tr. Vissh. Lesotekh. Inst. Sofiya, Ozelenyavane 27/28: 107-113 [Bg].
- ZARIPOV, I.N. 1981. [Dendrobacillin against the nun moth]. Zashch. Rast. 9: 19 [Ru].
- ZELINSKAYA, L.M. 1980. [The role of microsporidia in the population dynamics of the gypsy moth (Porthetria dispar L.) in forest plantations in the lower Dnieper region]. Vestn. Zool. 1: 57-62 [Ru].
- ZIEMNICKA, J. 1981. Studies on nuclear and cytoplasmic polyhedrosis viruses of the satin moth (Stilpnotia salicis L.) (Lepidoptera, Lymantriidae). Prace Nauk. Inst. Ochr. Rosl. 23(1): 75-142 [En].
- ZNAMENSKII, V.S.; LYAMTSEV, N.I. 1985. [Indicators of an outbreak of Lymantria dispar]. Lesn. Khoz. 2: 60-62 [Ru].

LYMANTRIID FOREST PESTS  
IN CHINA

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INTRODUCTION

The Lymantriidae are among the most important pests of Lepidoptera, distributed throughout the world(1). There are about 2500 known species in the world, 270 of which are recorded in China, 93 of which are forest pests and about 12 are important defoliators (1,2, 20). Lymantriids may infrequently cause damages to many tree species though only a little research work has been done on them. Many coniferous and deciduous trees and trees of economic importance could be infested over a large area. After outbreaks, tree growth usually is slowed, sometimes a great number of trees are killed. Since 1950, a number of papers on the fauna, biology, infestation and control measures of lymantriids have been published. Extensive efforts have been made to control lymantriid pests more effectively, but so far, they still cause considerable economic losses in national economy.

Brief introductions on the fauna of Lymantriidae in China and the host plant, distribution, biology, infestation and control measures of 12 forest lymantriids are given below.

## FAUNA OF LYMANTRIIDAE IN CHINA

Number of species in various genus of Lymantriidae  
recorded by Chao Zongling

generic name	number of species
Lymantria	27
Dasychira	41
Gynaephora	1
Orgyia	10
Aroa	4
Cifuna	5
Laelia	6
Arctornis	9
Stilpnotia	10
Ivela	3
Leucoma	4
Redoa	8
Kanchia	1
Pantana	8
Pida	12
Numenes	11
Daplasa	2
Parocneria	1
Perina	1
Topomesoides	1
Porthesia	10
Euproctis	78
Mardara	3
Imanus	1
Sura	1
Medana	2
Heracula	1
Parakanchia	1
Cispia	6
Imaida	2
<hr/>	
Total	270

Pine lymantriid, Dasychira axutha Collenette

Host: *Pinus massoniana*, *P. tabulaeformis*, *P. ellioti*,  
*P. taeda*.

Distribution: Guangxi, Guangdong, Hunan, Jiangxi,  
Zhejiang, Liaoning, Heilongjiang.

## Biology and infestation:

They may often occur in admixture with D.punctatus in masson pine plantation. They can consume up all the pine needles in a stand and reduce tree growth or kill the trees. But sometimes they serve as intermediate hosts for the natural enemies of D.punctatus. There are 3-4 generations a year in Guangxi and Henan. It overwinters in the stage of mature larva or pupa, depending upon locality and season. Adults fly in mid- or late May. Larvae of various generations feed from April to November. Irregular egg masses are laid on pine needles, consisting of 50-100 eggs, averaging 40 eggs. Larvae usually hatch in the early morning. After hatching, young larvae cluster round the chorin and consume part of it, then eat the edges of needles. Third-instar larvae begin to consume whole needles, leaving an inch of needle's basal part on the twig. They start to eat from the middle of needles and leave a lot of broken needles tips on the ground. This is somewhat different from the damage caused by D.punctatus. The mature larvae pupate in the debris around the basal part of trunk or in the weeds or roots of shrubs, besides they also pupate in the bark crevices, limbs of branches, mud holes or under the stones.

In Guangxi province, they often occur in the stands facing south and back to the wind with a bigger canopy density. It was reported that severe outbreaks had occurred both in Guangdong and Guangxi provinces.

It has a variety of natural enemies such as Telenomus dasychiri, Trichogramma dendrolimi and Anastatus spp. are

egg parasites; Casinarina nigripes and Apanteles ordinarius are larval parasites; Xanthopimpla pedator, Brachymeria spp. Blepharipa zebina, Carcelia rasella and Myxexoristops bicolor are pupal parasites; Beauveria bassiana, Thuringensis sp. and a NPV are microbial parasites.

Nun moth Lymantria monacha (L.)

Host: Fortune Keteleeria, Pinus yunnanensis, Armand pine, Chinese Douglas fir.

Distribution: Heilongjing, Jilin, Liaoning, Zhejiang, Sichuan, Yunnan, Guizhou, Taiwan.

Biology and infestation:

In an outbreak, they may infest the deciduous trees and also agricultural crops like corn and rice near the forest. When in severe outbreak, conspicuous defoliation can be seen and trees may be killed if they are infested 2-3 years consecutively. Since 1953, fortune keteleeria plantation covered an area of about 100,000 hectare in Yunnan and Guizhou border were infested, among which mortality of the trees in individual plot reached 70%. Economic losses were caused both in forestry and agriculture.

There is one generation a year in Yunnan province. Fully developed young larvae overwinter in the eggs. Young larvae hatch in mid- and late March. Newly hatched larvae cluster on the trunk and consume part of the chorin. After 3-4 days, they scatter to the needle clusters on crowns. First and second instar larvae only eat a little and can spit silk to disperse. Third instar larvae eat much more than the young larvae. At first, they infest the needles on the lower crown and then crawl upwards to the upper crown. When in severe outbreak, they feed on the needles day and night, and eat up all of them. The larvae prefer

to migrate to shady places and stop eating when the sunlight is strong. But on rainy days, a few of them may continue to eat. Mature larvae pupate in tree holes or bark crevices. Cocoons are thin and sparse, locating under sparse mud along fields, debris on the forest floor or in shrubs. The pupal stage lasts 15-20 days. Adults fly in early June. The peak time for flight is from early June to early July, and eggs are laid in 3-5 days after emergence. Egg masses consist of 15-20 eggs usually locating in the coarse bark crevices. Each female may lay 97-304 eggs, averaging 200.

Gypsy moth, Lymantria dispar (L.)

Host: oak (*Quercus* spp.), larch (*Larix* spp.), persimmon, poplar, plum, salix, elm, betula, spruce, maple, linden, apple, apricot, etc., about 500 species.

Distribution: It was recorded in all provinces that lie completely north of the 30°N latitude, as well as Hunan and Guizhou provinces situated south of that line.

Biology and infestation:

Gypsy moth is a widespread pest in China, where in general it occurs more commonly in the northern half of China. There is one generation a year. It overwinters in the egg stage. There are variations in larval color morphology: most of them are generally mottled dark gray, others are unusually yellow, and a few of them are black-backed mutants (14). Larvae hatch in late April or early May. After hatching, young larvae remain on the egg cases for some time. They feed first on young buds and then the new leaves, when the weather gets warmer. The larval stage usually lasts one and a half months. Starting from mid-June, mature larvae begin to pupate in tree holes or trunk crevices, on twigs or branches, or under stones.

Both males and females can and begin to fly in late June (14). The peak time for flight is from mid- to late July. Egg masses are laid on tree trunks or branches, on stumps or stones or under roofs. A female may lay 400-1200 eggs. The males can also be attracted by the American disparlure enantiomers and there are many natural enemies for gypsy moth in China(14,15).

It is reported that the epidemic cycle is about 8 years: 1 year for latent phase, 2-3 years for propagation phase and 2 years for epidemic phase. There are epicenters in endemic phase. If under condition of adverse weather, for example in drought, the propagation phase may be shortened and the epidemic phase prolonged. In 1974-1976, there was an severe outbreak in the southern part of Liaoning province. A lot of oaks, poplars, elms and apples were damaged.

*Dasychira melli* Collenette

Host: Chinese fir

Distribution: Jiangsu, Zhejiang, Hubei, Hunan, Jiangxi, Sichuan, Guangdong, Guangxi, Fujian

Biology and infestation:

There are 3 generations a year in Hunan. They overwinter as pupae under litter or stones on the forest floor. Adults appear in April of the following year. The larval stages of the 3 generations are: May-June; July-August; October-November. It was reported that in 1981, there were outbreaks in You County and Liling County, Hunan province, over an area of about 300 ha, about 100 ha of which were severely defoliated. The damage brought serious losses to the timber production.

Lymantria dissoluta Swinhoe

Host: Pinus massoniana, P. tabulaeformis, P. thunbergii,  
Quercus sp. cypress

Distribution: Anhui, Jiangsu, Zhejiang, Hubei, Hunan,  
Jiangxi, Fujian, Taiwan, Guangdong, Guangxi

Biology and infestation:

There are 3 generations a year in Anhui.

Overwintering is in the egg stage. Eggs start to hatch in May. Newly hatched larvae feed gregariously on the needles at night. It pupates in mid-June. Pupae are formed in the bark crevices on trunk about 2M or below from the ground. Adults fly in late June, which are attracted by light and lay eggs in the evening. Egg masses are mostly located in bark crevices or on tree limbs. A female may lay 180-250 eggs. Larvae of the second generation appear in early July, and those of the third generation in early August. Adults of the third generation appear in late September. It was reported that there was an outbreak in massion pine stands in the region between the Yantze River and Yellow River over an area of 10,000 ha.

Lymantria xyliana Swinhoe

Host: horsetail beewood, Eucalyptus, willow, oilteatree,  
oriental plane tree, and other fruit trees.

Distribution: Fujian, Guangdong, Taiwan.

Biology and infestation:

There is one generation a year in Fujian.

Overwintering is in the egg stage. Eggs hatch in May. There are seven instars in the larval stage, which is from mid-March to mid-June. The adult stage is from late May to late June. Newly hatched larvae have a habit of aggregation and can spit silk and disperse by the wind.

Third instar larvae begin to eat more. Mature larvae pupate in tree limbs or leaves. The pupal stage lasts 5-14 days. A female lay only one egg mass of about 1000 eggs with a maximum of 2435 eggs. It was reported that there was a severe outbreak in the horsetail beewood shelterbelt in Putian Region in Fujian over an area of 6000 ha. sometimes it causes very severe infestations.

Stilpnolia salicis (L.)

Host: poplar, willow, filbert, maple.

Distribution: Heilongjiang, Jilin, Liaoning, Hebei, Shanxi, Inner Mongolia, Xinjiang, Qinghai, Ningxia, Gansu, Tibet.

Biology and infestation:

There is one generation a year in Inner Mongolia. The second instar larvae overwinter in the trunk crevices. They begin to feed on the leaves in May. Usually severe defoliation are caused in June. Larvae are active in daytime. Cocoons are formed in bark crevices on trunk. Adults appear in July. Eggs are laid on tree trunk, tender twig or back of leaf. A female may lay one egg mass of about 250 eggs. Outbreaks are often occurred in Inner Mongolia and Xinjian.

Stilpnolia candida Staudinger

Host: poplar, willow, tea tree.

Distribution: Heilongjiang, Jilin, Liaoning, Inner Mongolia, Hebei, Shanxi, Henan, Hunan, Sichuan, Fujian, Jiangxi, Beijing, etc.

Biology and infestation:

There are two generations a year in Beijing.

Overwintering is in the larval stage. Larvae begin to feed on the leaves in April. Larvae usually crawl down the tree and hide themselves in the shade, feeding on the leaves at night. Mature larvae pupate in bark crevices or tree limbs. Adults appear in early June, laying eggs on tender twigs, tree trunk or back of leaf. Larvae of first generation appear in mid- and late June and adults appear in late July. Larvae of second generation appear in August. Young larvae overwinter in late October. It is an important pest of shade trees and shelterbelts.

Parocneria orientalis Chao

Host: Chinese arbor vitae

Distribution: Zhejiang, Sichuan, Hubei.

Biology and infestation:

There are two generations a year in Sichuan.

Overwintering is in the egg stage. First generation lasts from February to mid-June. Second generation lasts from mid-June to October. Larvae of first generation infest seriously from early May to late May, while those of second generation from late August to mid-September. But the infestation of first generation is heavier than the second one. Outbreak occurs infrequently.

Parocneria furva (Leech)

Host: juniper, cypress, Chinese arbor vitae.

Distribution: Hebei, Shangdong, Henan, Liaoning, Shanxi,

Anhui, Jiangsu, Zhejiang, Hubei, Hunan,

Jiangxi, Sichuan.

Biology and infestation:

There are two generations a year in Beijing area.

Overwintering is in the larval stage. Larvae start to infest leaves in April. Cocoons are formed in June. Adults appear in mid- and late June. Eggs are laid on petioles or leaves in irregular piles consisting of 20-65 eggs. The egg stage lasts for about 14 days. Larvae of first generation appear in early July and feed on leaves at night. In daytime they move downward and hide themselves under barks or tree limbs. There are seven instars in the larval stage, lasting about 65 days. Cocoons are formed in the leaf clusters or bark crevices. The pupal stage lasts 5-18 days. Adults are attracted by the light traps. In early spring, larvae are fond of eating tender buds, causing serious damage to trees. Sometimes the trees are defoliated seriously.

Euproctis yunnanpina Chao

Host: *Pinus yunnanensis* Franch, *P. knasya* Royle et Cond.

Distribution: Yunnan, Guangxi.

Biology and infestation:

There are two generations a year in Yunnan.

Overwintering is in the larval and pupal stages. Larvae of first generation feed on needles from June-August. They begin to pupate in mid-August. Adults of second generation appear in early September. Larval infestation to the needles is serious, making trees turn to yellow over a large area. The larval hairs are somewhat poisonous to humans, causing a skin rash or other form of allergy. Pupae are formed in mud crevices and tree roots or under litter on forest floor. In 1980-1981, there were infestations over an area of 100,000 ha in Yunnan, among which 6000 ha of the forest were heavily damaged.

Pantana phyllotachysae Chao

Host: bamboo

Distribution: Zhejiang, Jiangxi, Hubei, Hunan, Guangxi,  
Sichuan

Biology and infestation:

There are 3 generations a year in Jiangxi. Overwintering is in the egg stage. Eggs are laid mostly on bamboo leaves, a few on bamboo rods. Eggs hatch in late February. Adults appear in mid- and late June. Eggs of second generation hatch in late June, those of third generation in mid August. Adults fly in October. The adult stage lasts 10-13 days. Larvae feed on bamboo leaves. When in severe infestation, they cause the bamboo groves turn into yellow, even kill bamboos over a large area. In 1973, accumulated infested area in Liuzhou, Guangxi province, reached more than 100 ha.

CONTROL

There are usually 4 kinds of method for control the lymantriids in China:

1. Chemical control is the principal method, in which spray of diptrex, cygon and malathion diluted with water or chemical smokes are used.
2. On occasion, Bt or Beauveria bassiana are used to control Pantana yunnanpina and Dasychira axutha in southern China.
3. Light traps sometimes are used for collecting adults.
4. Physical control, such as ploughing in the trees or piling soil around tree trunks on the ground is used to kill larvae or pupae.

## SUMMARY

In general, Chinese forest lymantriids occur with periodic outbreaks. Species in the South are much more numerous than those in the North, so is the seriousness. The fauna of Lymantriidae in China is quite clear. The research on Chinese forest lymantriids stressed mainly on biology and control, and need of deepened research in various other respects. More efforts are needed for better understanding and control.

## LITERATURE CITED

1. Chao Zhongling. 1982. Iconographia Heterocerorum Sinicorum 2. Science Press, Beijing. (in Chinese)
2. Chao Zhongling. 1983. Distinction of some serious forest lymantriids in China in recent years. Forest Pest and Disease. 1:39-43
3. Chinese Academy of Forest Science. 1983. Chinese forest insects. Chinese Forestry Press. Beijing.
4. Cheng, C. J. 1978. A preliminary study of the nuclear polyhedrosis virus of gypsy moth(Lymantria dispar L.) Sci. Silvae Sin. 3:44-46
5. Chen Zepo et al. 1960. Discovery of Dasychira axutha Collenette in Guangxi. Entomol. Knowledge 5:159
6. Chen Yangchuan et al. 1982. A preliminary study on Pantana phyllostachysae. Sci. Silvae Sin. 3:343-346
7. Huang Dingfang. Preliminary study on habits and control of Orgyia parallela Gaede. Forest Pest and Disease 3:10-11(1984)
8. Kuoh J.L. 1952. A preliminary study of Euproctis Lubblaya Bum. Acta Entomol. Sin. 2:87-102
9. Li Yougong et al. 1981. Study on the lymantriid moth Lymantria xyliana Swinhoe. Acta Entomol. Sin. 2:174-183
10. Liang Hsingshan. 1966. Behaviour and population fluctuation of Stilpnotia ochropoda Eversmann in relation to meteorological factors. Acta Entomol. Sin. 4:327-332
11. Liu Yunfu. 1958. A preliminary observation on Orgyia antiqua L. and Erannis ankeraria STGR. Sci. Silvae Sin. 3:308-318
12. Niu Hongxin. 1972. Study on the biology and control of Stilpnotia salicis L. Sci. Silvae Sin. 3:14
13. Schaefer P.W. et al. 1984. Natural enemies of gypsy moth Lymantria dispar L. (Lepidoptera: Lymantridae) in China. Sci. Silvae Sin. 4:434-440
14. Schaefer P.W. et al. 1984. Gypsy moth Lymantria dispar

- L. (Lepidoptera: Lymantridae) in the People's Republic of China. *Environ. Entomol.* 13:1535-1541
15. Wallner W.E. et al. 1984. Gypsy moth Lymantria dispar L. attractancy to disparlure enantiomers in the PRC. *J. Chem. Ecol.* 10:753-757
  16. Wang Wenxue. 1981. Biology of Telenomus euproctidis Wilcox (Hymenoptera: Scelionidae), an egg parasite of tea lymantriid, Euproctis pseudoconspersa Strand (Lepidoptera: Lymantridae) *Acta Entomol. Sin.* 4:384-389
  17. Wu Peiyu. 1982. Control of Euproctis flava and survey of its natural enemies. *Entomol. Knowledge.* 2:29
  18. Xie Chenmei. 1983. Observation and isolation of nuclear polyhedrosis virus of Pantana phyllotachysae. *Forest Sci. Technol.* 2:26
  19. Xu Caoji. 1980. Some notes on occurrence and control of Orgyia ericae Germar. *Sci. Silvae Sin.* 1:70
  20. Yan Shouyuan et al. 1981. A catalogue of Chinese forest insects. Chinese Forestry Press. 330p
  21. Yu Huiqi. 1984. A preliminary study on Euproctis yunnanpina Chao. *Forest pest and disease.* 1:4-5

OVERVIEW OF PEST LYMANTRIIDAE  
OF NORTH AMERICA

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INTRODUCTION

Although over 2,500 species of Lymantriidae have been described worldwide, only 33 species are native to the United States and Canada; most are from the Old World tropics. Species from the genera *Lymantria*, *Leucoma*, and *Euproctis* have been introduced into the United States and Canada from the Old World and, together with native lymantriids, they constitute the most economically important family of forest Lepidoptera in North America. More than 30% are considered pests; these species have, for that reason, received the greatest research attention. An overview of the history, distribution, and immediate and past research efforts is described for three native and three introduced lymantriid pests. Subspecific distributions are also given for the three lymantriids native to North America. Ferguson (1978) relegated these to subspecies rank based upon morphological traits. However, subspecies integrity needs further clarification using isozyme analyses or host plant acceptance.

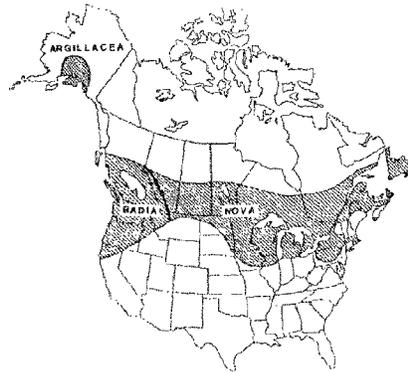
Research emphasis has been related directly to those lymantriids that present the most serious threat; support funding traditionally has been correlated with hectares of defoliation. The gypsy moth, *Lymantria dispar* (L.), and Douglas-fir tussock moth, *Orgyia pseudotsugata* (J.E. Smith), received accelerated USDA research funding during periods of excessive damage. Although research support for these species has diminished markedly, substantial financial and administrative support still exists to conduct continuing high-priority studies on latent and expanding populations. The concepts of monitoring, early intervention in population cycles, and the attempt to integrate various suppression strategies are among present goals. The current status of research on these as well as other lymantriids follows.

NATIVE LYMANTRIIDS

R u s t y   T u s s o c k   M o t h  
*Orgyia antiqua* (L.)

The rusty tussock moth (RTM) is a holarctic species and the most northern member of the genus *Orgyia* in North America. It ranges across southern Canada and northern United States, south to the Middle Atlantic States and northern California. The range of food plants is extremely diverse including more than 50 species of

deciduous trees and shrubs as well as nearly all conifers with the exception of Juniperus spp. Preferred hosts include fir, spruce, larch, pine, hemlock, Douglas-fir, birch, alder, willow, poplar, maple, cherry, apple and elm (Tietz, 1972). This broad host range may reflect the action of three distinct subspecies, O. antiqua nova Fitch, O. antiqua badea Henry Edwards, and O. antiqua argillaceae; nova closely approximates European nominate subspecies (Ferguson, 1978).



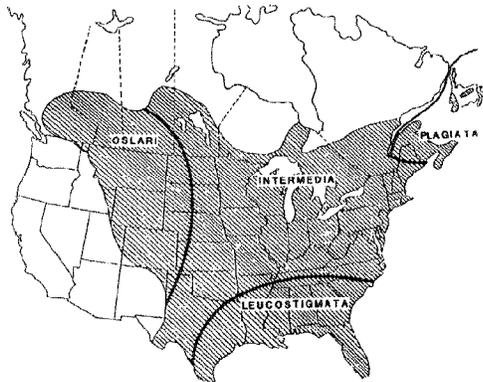
Distribution of the rusty tussock moth, Orgyia antiqua, and its subspecies in North America

Despite its broad distribution and host plants, emergence of RTM adults is remarkably consistent--early August to mid-September. In the Eastern and Western United States, at the southern fringes of its range, a few early summer adult records suggest the existence of two broods per year.

Winter is passed as eggs deposited in single-layered, naked masses on cocoons; larvae develop as solitary feeders after dispersing as first instars. Populations are occasionally found in insect surveys with moderate to broad amplitudes in abundance (Canada Dept. For., 1962). Periodically, the RTM causes conspicuous defoliation. Outbreaks are most common in Canada, although locally heavy defoliation has been reported from Montana and Idaho in the United States. Traps baited with the Douglas-fir tussock moth (DFTM) (O. pseudotsugata) pheromone attract RTM males as well as three other western tussock moth species (Daterman et al., 1976). Interspecific pheromone responses by seven tussock moth species to the Z-isomer of the DFTM pheromone suggest it is a sex pheromone component for a number of species. While RTM and whitemarked tussock moth (WMTM) can hybridize in the laboratory, they are isolated temporally in nature by differences in adult periodicity (Grant, 1977). Research specific to the RTM is scarce because it has a non-economic pest status.

Whitemarked Tussock Moth  
Orgyia leucostigma (J.E. Smith)

Distributed widely throughout the United States and Canada, the whitemarked tussock moth (WMTM) is extremely common in urban areas and seldom a forest pest. Accounts during the late 1900's report it as mainly a pest of orchards and other roseaceous hosts. Coincidental to the introduction and rapid increase in numbers of the English sparrow in the United States, WMTM rapidly increased in cities. Studies by LeConte (1874) demonstrated that its numbers increased dramatically due to the action of the English sparrow which displaced native birds that foraged on WMTM. Since then, WMTM has been observed as common with a fairly broad amplitude of variation in numbers in the Eastern United States and Canada.



Distribution of the whitemarked tussock moth, *Orgyia leucostigma*, and its subspecies in North America

*O. leucostigma* has been subdivided into four taxonomic subpopulations with quite different hosts. *O. leucostigma* is a generalist feeder and these host listings undoubtedly reflect subspecies geographical range. *O. leucostigma intermedia* is the most widespread and economically important subspecies, with over 140 food plants and two generations per year. *O. leucostigma leucostigma* is a species of the Deep South (U.S.) with two or more broods per year. It has a diverse host list but most commonly is recorded from willow, salt cedar, live oak, redbud, apple, pyracantha, Franklin-tree, and mimosa. *O. leucostigma plagiata* is single-brooded and found in northeastern North America on willow, alder, white pine, birch, and larch; it is especially damaging to balsam fir Christmas tree plantings in Nova Scotia. *O. leucostigma oslari* is a rare, single-brooded, high elevation (2000-3000 m) species about which little is known (Ferguson, 1978; Tietz, 1972).

Dense populations of WMTM tend to be sporadic and limited to streetside trees; extensive defoliation seldom occurs. The most recent report of defoliation to forest plantings was in 1985-86 in western Newfoundland where some 100 ha of white birch, speckled alder, and other hardwoods were damaged. Aerial sprays of *Bacillus*

thuringiensis were used to suppress populations; an Entomophthora species also was observed causing mortality (Clarke & Carew, 1985).

Few definitive studies on the population dynamics and natural control factors of WMTM have been conducted. The most comprehensive study was by Howard (1897) who identified 15 hymenopteran and six dipteran primary parasites. Pimpla inquisitor and Chalcis orata were the dominant parasites. Predators included dermestids feeding on eggs and three Heteroptera that fed on larvae; the spined soldier bug, Podisus maculiventris Say, was most common. While avian predators prefer not to feed upon larvae because of their protective coloration and abundant setae, the real impact is unclear. Certainly, WMTM is subject to attack by parasites common to other Lymantriidae. Wallner & Grinberg (1984) demonstrated that Rogas lymantriae, a primary endoparasite of gypsy moth, will attack WMTM as well as brown-tail moth and Douglas-fir tussock moth.

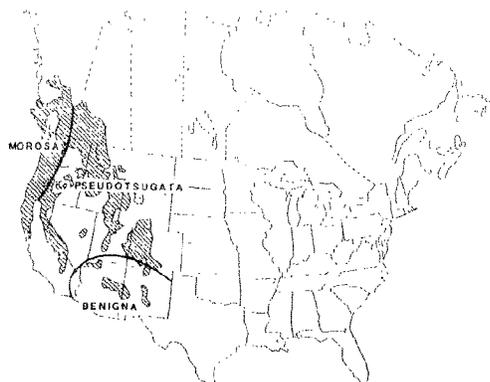
In efforts to establish parasites from Sicily for gypsy moth control in the United States, Schaffner (1934) found that Cotesia (Apanteles) melanoscelus survived solely on WMTM. Verly likely, other shared natural enemies exist. Damage by WMTM is so limited and sporadic that it has received little research attention except for the occasional report that relates it to other more economic Lymantriidae (Grant, 1977).

#### D o u g l a s - F i r T u s s o c k M o t h Orgyia pseudotsugata (McDunnough)

Widespread in the mountain regions of western North America, the Douglas-fir tussock moth (DFTM) is one of four western Orgyia species, and by far the most serious pest, in the genus. While it may feed on a variety of hosts during outbreaks, DFTM is nearly host specific preferring Douglas-fir, grand fir, and white fir under forested conditions. In urban areas, ornamental spruces and firs are attacked but rarely completely defoliated.

O. pseudotsugata has been classified into three subspecies; O. pseudotsugata pseudotsugata (the nominate species), O. pseudotsugata morosa, and O. pseudotsugata benigna. In making these determinations, Ferguson (1978) noted in his examination of subspecies that O. pseudotsugata morosa specimens were rare and not associated with outbreaks. Interestingly, this corresponds with the outbreak areas presented by Mason & Wickman (1988) who do not ascribe subspecies or their locations.

Outbreaks of DFTM were first observed in 1916 in southern British Columbia and from 1927 to 1930 in northwestern United States. Outbreaks of various severities have occurred since then at roughly 7- to 9-year intervals; most recently during the early 1970's in the Pacific Northwestern United States and southern British Columbia, and again in southern British Columbia during the early 1980's. Outbreaks tend to erupt abruptly over thousands of hectares of forest type, defoliation ensues for 3 to 4 years and then collapses dramatically; four phases are evident during this cycle (Mason & Wickman, 1988). Under urban conditions, outbreak cycles are



Distribution of the Douglas-fir tussock moth, Orgyia pseudotsugata, and its subspecies in North America

more prolonged and do not coincide in occurrence with those on forested areas, and trees are seldom totally defoliated (Loomis et al., 1985).

The severity of DFTM damage in the West, coupled with the chronic gypsy moth problem in the Northeast, and southern pine beetle, prompted the development of the Combined Forest Pest Program in 1973. These 5-year research, development, and application programs were intended to accelerate research and implement findings. Objectives and accomplishments for DFTM included: (1) Methods for detecting larvae, pupae and eggs. Under the program, this was accomplished for outbreak levels and research is continuing for sampling low, innocuous population levels. (2) The use of the sex attractant for monitoring and detecting potential outbreaks. Pheromone trapping has defined the natural range of DFTM and its outbreak area. Work is continuing to use trap results as an early warning system. (3) Find methods to predict changes in DFTM populations and subsequent damage. Stand characteristics are useful predictors of susceptibility to defoliation. Incidence and intensity increases in multistoried stands of mature grand fir and Douglas-fir, particularly those on upper slopes or ridgetops with southerly exposures. Trees growing on deep volcanic ash soils are less susceptible to defoliation. (4) Evaluation of natural mortality showed that some 30 species of Diptera and Hymenoptera parasitize all developmental stages; but the egg parasite Telenomus californicus is most important, causing up to 60% egg mortality; others such as the tachinid, Carcelia yalensis and the Ichneumonid Phobocampe pollipes also cause significant mortality. The dark-eyed junco and mountain chickadee are among 11 species of birds that caused up to 50% predation of all life stages; arboreal spiders and ants also are important. At low DFTM levels, parasites and vertebrate and invertebrate predators are the most important causes of mortality. (5) Field and safety studies on the DFTM nucleopolyhedrosis virus demonstrated its efficacy and is registered as TM Biocontrol-1<sup>®</sup>, for use for DFTM control. Bacillus thuringiensis was evaluated as

several different formulations as were the chemical insecticides Trichlorfon® and Carbaryl®, and the insect growth regulator, Diflubenzuron®. All provide acceptable control. (6) Aerial spray technology was increased for these products. Included were determination of optimum droplet size, extent and control of spray drift, development of a monitoring system with electronic spray delivery and better understanding of meteorological factors affecting spray deposits. (7) Finally, an integrated pest management system using three computer models (stand prognosis, stand outbreak, and socio-economic) was developed for making forest management decisions (Brookes et al. 1978; Mason & Wickman, 1988; Shepherd et al. 1984).

Following these expanded research program efforts, studies on DFTM have been continued by federal, state, and university personnel. Some, but certainly not all, include cryptic shelters for sampling and monitoring population change and pupal parasitism and refinement and registration of DFTM pheromone for mating disruption for control (U. Cal. Berkeley), identification of additional components of DFTM pheromone (Simon Fraser Univ.), biosynthesis and pathways of action of DFTM pheromone (SUNY, Stonybrook), use of Bt for suppressing outbreaks (USFS-Corvallis and LaGrande, OR), use of TM Biocontrol-1 for outbreak suppression, expand and refine DFTM pheromone for monitoring populations (Can. For. Serv., Victoria, BC; USFS, Corvallis, OR). The dramatic, synchronous outbreak pattern and rapid collapse has often caught forest managers off guard; present knowledge hopefully will permit continuous monitoring of populations, predict outbreaks and intervene pre-emptively to minimize the impact of future outbreaks.

#### INTRODUCED LYMANTRIIDS

Three lymantriid species have been introduced into North America; each has developed quite different patterns of geographic distribution. While all are considered pests, the gypsy moth is by far the most notorious. There are a number of striking similarities among these species; apparent ineffectiveness of native parasites to control these introduced pests, degree of susceptibility of host attack based upon physiography, and the importance of introduced parasites from Europe and Asia that attack all three genera.

#### S a t i n M o t h Leucoma salicis (L.)

Sometime before 1920, the satin moth (SM) was inadvertently introduced and became established at two widely separated locations in North America: near Malden, Massachusetts, and New Westminster and Vancouver, British Columbia. The origins of these infestations are not known. The SM gradually expanded its range at both locations in the Maritimes; it was estimated to have spread northward at 8-13

miles per year (Reeks & Smith, 1956). Host availability has undoubtedly influenced its distribution since SM can complete development only on poplar and willow. Before 1967, outbreaks were confined to single, or small groups of exotic shade and ornamental trees in residential areas. Since then, SM has attacked native poplars causing widespread defoliation and tree mortality (Clarke & Pardy, 1971). Wagner & Leonard (1979b) reported little change in host preference for SM after 60 generations in North America. They found eastern cottonwood and Lombardy poplar as the most suitable hosts whereas balsam, Simon and white poplars were least suitable. Parental and progeny diet, developmental time, body weight and survival were parameters investigated.

The SM has a split-year, univoltine cycle; first and second instar larvae skeletonize leaves, third instars overwinter in hibernacula on tree boles and resume feeding the following spring when larvae consume entire leaves except leaf veins. Commonly, there are seven larval instars, although eight have been reported (Reeks & Smith, 1956). Adults of both sexes are capable of flight; the female flies after depositing the first of up to five masses containing a total of 650 eggs (Wagner & Leonard, 1979a).



Distribution of the satin moth, *Leucoma salicis*, in North America

Outbreaks of SM are from 4 to 6 years in duration and the period between outbreaks is 2 to 6 years. Factors that control populations are severe winter temperatures, introduced parasites, pathogens and vertebrate predators. Mortality of larvae during overwintering is considered critical in reducing the duration of outbreaks and lengthening the period of latency. Not only are low winter temperatures (-28 C or lower) implicated, but also the activity of pathogenic fungi (*Paecilomyces* sp. and *Hirsutella gigantea*) appears to work in concert with overwintering weather conditions. A high proportion of overwintering larvae die from unknown causes. Native parasites exert less than 1% control over SM. However, the

several different formulations as were the chemical insecticides Trichlorfon® and Carbaryl®, and the insect growth regulator, Diflubenzuron®. All provide acceptable control. (6) Aerial spray technology was increased for these products. Included were determination of optimum droplet size, extent and control of spray drift, development of a monitoring system with electronic spray delivery and better understanding of meteorological factors affecting spray deposits. (7) Finally, an integrated pest management system using three computer models (stand prognosis, stand outbreak, and socio-economic) was developed for making forest management decisions (Brookes et al. 1978; Mason & Wickman, 1988; Shepherd et al. 1984).

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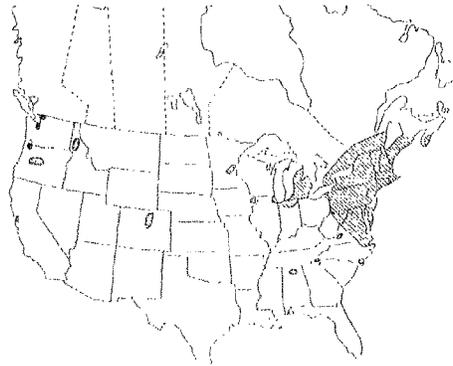
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Outbreaks of SM are from  $\frac{1}{4}$  to 6 years in duration and the period between outbreaks is 2 to 6 years. Factors that control populations are severe winter temperatures, introduced parasites, pathogens and vertebrate predators. Mortality of larvae during overwintering is considered critical in reducing the duration of outbreaks and lengthening the period of latency. Not only are low winter temperatures ( $-28$  C or lower) implicated, but also the activity of pathogenic fungi (*Paecilomyces* sp. and *Hirsutella gigantea*) appears to work in concert with overwintering weather conditions. A high proportion of overwintering larvae die from unknown causes. Native parasites exert less than 1% control over SM. However, the

hosts preferred by gypsy moth in Europe (black locust) and Asia (larch) are seldom attacked except under outbreak circumstances. Hosts of intermediate preference such as birch and maple show considerable variability which may be reflective of site conditions such as stand age and soil moisture. Furthermore, the capacity of a forest to sustain GM can be altered by defoliation by long-term changes in species composition and stand structure, and short-term changes in foliage quality (Montgomery & Wallner, 1988). Population behavior is significantly influenced by site and habitat conditions. Forests highly susceptible to GM defoliation occur on xeric sites such as ridgetops and deep sands and contain a high proportion of favored hosts such as chestnut oak, white oak, and black oak.



Distribution of the gypsy moth, *Lymantria dispar*, in North America

Resistant stands support vigorous tree growth; red oak is the dominant oak species but such sites also contain maple, black birch, tulip poplar, and ash. The susceptibility or resistance of a forest to GM defoliation can be classified based on tree species and structure features (Houston & Valentine, 1977).

Historically, GM has been subjected to a variety of research efforts since its initial establishment. Earliest studies (1869-1900) were descriptive and emphasized the biology, behavior, and influence of native predators and parasites. From 1901 to 1919 infestations rapidly increased. This prompted studies on dispersal, nucleopolyhedrosis virus, management of infested woodlots, and search for foreign parasites for importation. In 1912, a Federal domestic quarantine was enacted to limit the spread of GM. Despite these efforts, GM became established throughout New England, New York, New

Jersey, and Pennsylvania, and a barrier zone from Canada to Long Island, New York, was created in 1923 under which intensive eradication efforts were used. More intensive research was devoted to natural enemies, particularly those parasites already established and a search for additional foreign species for importation, studies on population dynamics, and effects of defoliation on trees were begun. The period from 1941-60 was characterized by terminating the unsuccessful barrier zone and broadscale use of a number of pesticides for control, including DDT, which was phased out and replaced by Carbaryl. Research during this period was minimal. Following the realization that eradication of GM was biologically impractical, more emphasis, during the 1960's, was placed upon researching biological pesticides (Bt and NPV), the synthetic GM pheromone was developed, and work was initiated on developing the use of the sterile male technique.

During the 1970's accelerated and expanded research was conducted on GM. Among the program accomplishments were (1) methods for predicting population trends, sampling procedures (mainly for egg masses), and measuring larval dispersal; (2) evaluating new chemical insecticides and ascertaining their environmental impacts. Several were tested and registered for use including the insect growth regulator, diflubenzuron; (3) procedures for measuring and predicting impacts of defoliation including socioeconomic and environmental impacts; (4) registration of NPV (Gypchek) and Bt as well as optimizing spray formulations was completed; (5) disparlure was developed and utilized for containment but its use for suppression (confusion of males and mass trapping) was tested but not proved efficacious. Additionally, a + enantiomer of disparlure was synthesized, tested, and found to be more highly active than the racemic fraction; (6) the study of existing and newly introduced parasites in controlling moderate to dense GM populations reveals that the importance of native species was negligible. Of the 10 introduced species (80 species have been imported and released), Cotesia (Apanteles) melanoscelus, Compsilura concinnata, Ooencyrtus kuvanae, Blepharipa pratensis, and Parasetigena silvestris all exert control but taken alone are not capable of preventing GM outbreaks; (7) mass-rearing technology was developed using an artificial diet for producing large quantities of high-quality GM year round. This accelerated efforts on NPV production, sterile male and parasite production and release. The accelerated program initialized research, the expanded program provided additional research but largely emphasized implementation and application of technology (Doane & McManus, 1981, U.S. Dep. Agric., 1987).

During the period 1979-83, GM caused more defoliation than had occurred during the previous 55 years (Loomis et al., 1985). This prompted additional research initiatives in 1983 that were directed principally toward extending the period of latency and reducing the amplitude of outbreaks. Goals included (1) determining the effects of gypsy moth on forests by developing tree growth and mortality functions, evaluating silvicultural practices and ascertaining mechanisms following defoliation; (2) improving the understanding of biology and population dynamics of GM at low densities by developing sampling procedures for all life stages, characterizing population processes in susceptible and nearly resistant forests, determining

the effect of gross climate and microclimate on GM behavior and survival, and understanding GM-host relationships; (3) developing the methodology to use parasites as regulators in low-level GM populations by measuring and enhancing GM mortality by parasites and ascertaining the relationship between parasites and pathogens; (4) determining the role of vertebrate and invertebrate predators in low GM populations by determining mortality caused by predators and manipulating predators to enhance GM control; (5) determining the role of pathogens for GM control specifically NPV, Bt, microsporidia and means to improve pathogen efficiency; and (6) investigating the role of integrated pest management (IPM) for GM control by evaluating technology and tactics, produce an IPM strategy for testing and developing a series of interactive models (U.S. Dep. Agric., 1987). An evaluation of GM management programs in the United States is given in Ravlin et al. (1987).

The voluminous publications on GM and space limitations preclude a complete literature presentation. Numerous studies are underway; some are completed and not yet published. Following are some studies, but certainly not all, that indicate the breadth of current GM research: GM population monitoring (USFS-Hamden, CT; University of Massachusetts-Amherst; Virginia Polytechnic Institute-Blacksburg), NPV epizootics and GM population dynamics (University of Massachusetts; USFS, Hamden, CT), forest vulnerability rating system (University of West Virginia and USFS, Morgantown, WV), GM population dynamics in susceptible and resistant forests (USFS, Hamden, CT; University of Massachusetts; University of Vermont-Burlington; Institute of Ecosystem Studies, Millbrook, New York), establishment of microsporidia (Illinois Natural History Survey, Champaign, IL; USFS, Hamden, CT), regenerating stands following GM damage (Pennsylvania State University, State College; USFS, Morgantown, WV), documenting role of GM focal sites and pre-outbreak intervention (USFS-Hamden, CT, University of Massachusetts, University of Vermont), NPV formulation and application (USFS, Hamden, CT), manipulation of GM densities and natural enemy response (University of Massachusetts; USFS, Hamden, CT), characterization of forest ecosystem susceptibility to GM (University of Michigan, Ann Arbor, MI; USFS, Hamden, CT), burlap band sampling of larvae in relation to field densities (USFS, Hamden, CT), spatial distribution of GM egg masses by forest physiography (Institute of Ecosystem Studies, Millbrook, NY; USFS, Hamden, CT; University of Massachusetts; University of Vermont), climate influence on GM defoliation (University of Connecticut, Storrs, CT; USFS, Hamden, CT), leaf quality variation and GM performance (Pennsylvania State University; USFS, Hamden, CT), the role of vertebrate and invertebrate predators in GM population dynamics (USFS, Hamden, CT), bioassays of 1100 Bt strains from USDA cultures against GM (USFS, Hamden, CT), technology of spray delivery through forest canopies (Pennsylvania State University; USFS, Hamden, CT), GM life system model development (USFS, Morgantown, WV and Portland, OR), evaluation of inherited sterility for GM control (APHIS, Otis AFB, MA; USFS, Hamden, CT), development of expert systems for aerial application (Pennsylvania State University; USFS, Hamden, CT), development of interactive computer models for GM IPM (Alabama Agriculture & Mechanical University; State of North Carolina; USFS, Morgantown, WV), aerial

spray model validation (Pennsylvania State University; University of Connecticut; USFS, Hamden, CT), neuro-mechanisms of feeding (USFS, Hamden, CT; University of Connecticut), protein and energy reserves (University of Massachusetts; USFS, Hamden, CT), enhancement of avian predation with nest boxes (Southern Connecticut State University, New Haven, CT; USFS, Hamden, CT), relationship between defoliation, tree condition and *Armillaria* attack (USFS, Hamden, CT), development of silvical guidelines for minimizing tree mortality and growth loss by GM defoliation (USFS, Morgantown, WV), development and phenology of GM eggs (Canadian Forestry Service, Sault Ste. Marie, Ontario), mitochondrial DNA of GM populations (Cornell University, Ithaca, NY; USFS, Hamden, CT), avian abundance and GM population levels (West Virginia University, Morgantown, University of Michigan; USFS, Hamden, CT). Details on the bioecology of GM have been purposely omitted but the reader is referred to Leonard (1981) and Montgomery & Wallner (1988) for the most current and comprehensive sources.

#### SUMMARY

Comparison of features of native and introduced lymantriid species substantiates differences and similarities. The inability to differentiate morphological subspecies in three introduced lymantriids in contrast to the ability to do so for native species in North America may reflect the limited gene pool introduced and warrants further study. Differences in the spread and pest status of the introduced species are striking. The aggressive spread and continual pest status of gypsy moth may reflect its broad host range and adaptive capacity. Certainly, the satin and browntail moths have not been nearly as dominant. However, the recent spread of browntail moth may indicate a resurgence due to adaptation or failure of natural controls. If it achieves the pest prominence similar to that of Eurasia, its future will not be as benign as its past. Unfortunately, only modest studies have been conducted on browntail and satin moths due to their non-economic status. One has to wonder, had extensive research been conducted to ascertain the mechanisms responsible for their control, whether such information could be used to mitigate against gypsy moth. While Douglas-fir tussock moth has been, and continues to be researched, this is an exception for native North American lymantriids. The recent establishment of gypsy moth in forests infested with Douglas-fir tussock moth in western North America offers a unique opportunity to ascertain biological interactions. The existence of shared natural enemies, host-site influences, and other biological similarities reinforces the concept that research on members of this family has reciprocal application. Regardless, comparisons should stimulate collaborative, worldwide research and should be useful in the event that additional introductions occur between North America and other continents.

#### REFERENCES

- BROOKES, M.H., STARK, R.W. & CAMPBELL, R.W. 1978. The Douglas-fir tussock moth: A synthesis. U.S. Dep. Agric. Tech. Bull. 1585.
- CANADA DEPARTMENT OF FORESTRY. 1962. Forest Lepidoptera of Canada Vol. 2, Bull. 128.
- CLARKE, L.J. & CAREW, G.C. 1986. Forest insect and disease conditions in Newfoundland and Labrador in 1985. Can. For. Serv. Inf. Rep. N-X-241.
- CLARKE, L.J. & PARDY, K.E. 1971. Biological control of the satin moth in Newfoundland. Bi-month. Res. Note, Can. Fish. For. 26: 36-37.
- DATERMAN, G.E., PETERSON, L.J., ROBBINS, R.G., SOWER, L.L., DAVES, JR., G.D. & SMITH, R.G. 1976. Laboratory and field bioassay of the Douglas-fir tussock moth pheromone, (Z)-6-heneicosen-11-one. Environ. Ent. 5: 1187-1190.
- DOANE, C.C. & MCMANUS, M.L. (eds.) 1981. The gypsy moth: research toward integrated pest management. U.S. Dep. Agric. Tech. Bull. 1584.
- FERGUSON, D.C. 1978. The moths of America north of Mexico. Noctuoidea, Lymantriidae. Fascicle 22.2. E.W. Classey Ltd., & Wedge Entomol. Res. Found. 110 p.
- GRANT, G.G. 1977. Interspecific pheromone responses of tussock moths and some isolating mechanisms of eastern species. Environ. Ent. 6: 739-742.
- HOUSTON, D.R. & VALENTINE, H.T. 1977. Comparing and predicting forest stand susceptibility to gypsy moth. Can. J. For. Res. 7: 447-461.
- HOWARD, L.O. 1897. A study in insect parasitism: A consideration the parasites of the whitemarked tussock moth, with an account of their habits and interrelations, and with descriptions of new species. U.S. Dep. Agric. Div. Entomol. Tech. Series No. 5.
- JONES, T.H., WEBBER, R.T. & DOWDEN, P.B. 1938. Effectiveness of imported insect enemies of the satin moth. U.S. Dep. Agric. Circ. No. 459.
- LECONTE, J.C. 1874. An instance of replacement of injurious insect by human agency. Proc. Am. Assoc. Adv. Sci. 23: 44.
- LEONARD, D.E. 1981. Bioecology of the gypsy moth. p. 9-29 In: C.C. Doane & M.L. McManus (eds.). The gypsy moth: Research toward integrated pest management. U.S. Dep. Agric. Tech. Bull. 1584.
- LEONARD, D.E. The browntail moth, *Euproctis chrysorrhoea* (Lepidoptera: Lymantriidae), on Cape Cod Massachusetts. In: Ecology and Management of Exotic Species. U.S. Dep. Interior, George Wright Soc. In press.
- LOOMIS, R.C., TUCKER, S. & HOFACKER, T.H. 1985. Insect and disease conditions in the United States 1979-1983. U.S. Dep. Agric., For. Serv., Gen. Tech. Rep. WO-46.
- MASON, R.R. & WICKMAN, B.E. 1988. The Douglas-fir tussock moth in the interior Pacific Northwest, p. 179-209, In A.A. Berryman (ed. Dynamics of Forest Insect Populations: Patterns, Causes, Implications. Plenum Publ. Corp.
- MONTGOMERY, M.E. & WALLNER, W.E. 1988. The gypsy moth: A westward migrant, p. 353-375 In A.A. Berryman (ed.). Dynamics of Forest Insect Populations: Patterns, Causes, Implications. Plenum Publ. Corp.
- RAVLIN, F.W., BELLINGER, R.G. & ROBERTS, E.A. 1987. Gypsy moth

- management programs in the United States: Status, evaluation and recommendations. Bull. Entomol. Soc. Amer., Summer 1987:90-98.
- REEKS, W.A. & SMITH, C.C. 1956. The satin moth, Stilpnotia salicis (L.), in the Maritime Provinces and observations on its control by parasites and spraying. Can. Ent. 88: 565-579.
- SCHAEFER, P.W. 1974. Population ecology of the browntail moth (Euproctis chrysorrhoea L., Lepidoptera: Lymantriidae) in North America. Ph.D. Dissertation, University of Maine, Orono, 249 pp.
- SCHAFNER, J.V. 1934. Introduced parasites of the browntail and gypsy moths reared from native hosts. Ann. Ent. Soc. Am. 27: 585-592.
- SHEPHERD, R.F., OTVOS, I.S., CHORNEY, R.J. & CUNNINGHAM, J.C. 1984. Pest management of Douglas-fir tussock moth (Lepidoptera: Lymantriidae): Prevention of an outbreak through early treatment with a nuclear polyhedrosis virus by ground and aerial applications. Can. Ent. 116: 1533-1542.
- SIMMONDS, F.J. & GREATHEAD, O.J. 1977. Introductions and pest and weed problems, p. 109-124 In J.M. Cherrett & G.R. Sagar (eds.). Origins of Pest, Parasite, Disease and Weed Problems Oxford: Blackwell Press.
- SNOWDEN, P. 1986. Biological evaluation of the browntail moth in 1985 on the Cape Cod National Seashore. U.S. Dep. Agric., Northeast. Region Memo. 9 p.
- TIETZ, H.M. 1972. An index to the described life histories, early stages and hosts of macrolepidoptera of the Continental United States and Canada. Allen Museum.
- U.S. DEPARTMENT OF AGRICULTURE. 1987. Annual Progress Report. U.S. Dep. Agric., For. Serv., Northeast. Sta. Gypsy Moth Res. Dev. Prog. 53 p.
- WAGNER, T.L. & LEONARD, D.E. 1979a. Aspects of mating, oviposition, and flight in the satin moth, Leucoma salicis (Lepidoptera: Lymantriidae). Can. Ent. 111: 833-840.
- WAGNER, T.L. & LEONARD, D.E. 1979b. The effects of parental and progeny diet on development, weight gain, and survival of pre-diapause larvae of the satin moth, Leucoma salicis (Lepidoptera: Lymantriidae). Can. Ent. 111: 721-729.
- WAGNER, T.L. & LEONARD, D.E. 1980. Mortality factors of satin moth, Leucoma salicis [Lep.: Lymantriidae], in aspen forests in Maine. Entomophaga 25: 7-16.
- WALLNER, W.E. & GRINBERG, P.S. 1984. Suitability of the white-marked tussock moth (Lepidoptera: Lymantriidae) as an alternate host for the imported gypsy moth (Lepidoptera: Lymantriidae) parasite, Rogas lymantriae Watanabe (Hymenoptera: Braconidae). Environ. Ent. 13: 986-989.

POPULATION STUDIES ON LYMANTRIID  
PESTS IN PAKISTAN

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INTRODUCTION

Three lymantriids, Elkneria (Dasychira) aff. mulleri Ebert, Euproctis lunata Walk., and E. subnotata Walk., have been recorded as forest pests in Pakistan. Elkneria aff. mulleri Ebert appeared for the first time in epidemic form in 1977 in chir pine (Pinus roxburghii) forests in Swat. A vast area covering dense to open crop consisting of pole to middle aged trees was defoliated seriously at an elevation of 1,000 to 1,700 m above sea level. In an overall outbreak, heavy defoliation occurred in patches.

E. lunata Walk. and E. subnotata Walk. exist in riverine forests and irrigated plantations of Acacia nilotica in Sind province. The pests normally remain under check due to their natural enemies but sometimes the population crosses the economic injury level.

Besides causing serious defoliation, larvae of these species have urticating hairs which cause irritation and inflammation on the human skin and are a source of nuisance for the field workers and visitors.

Ebert (1966) recorded and described 4 species of Dasychira from Afghanistan which includes D. mulleri Ebert. Sreenivasam et al. (1972) reported Dasychira plagiata (Wlk.) as an important defoliator of jack pine (Pinus banksiana) and red pine (P. resinosa) from northwestern Wisconsin and east-central Minnesota (U.S.A.). Bionomics of the pest is also given. Klimetzek (1972) described the occurrence of D. pudibunda (L.) in the Palatinate (West Germany) since 1810 analyzing historical data in forestry districts. The most important infestations have been reported in 1892-95, 1901-03, and 1941-44. From about 1940, this pest showed a marked increase which infested pine in the mountainous districts of central and northern Pfälzer Wald.

Sampo (1968) has published notes on three lepidopterous species that normally feed on the leaves of deciduous trees in Italy but have recently been observed on conifers. One of them is Dasychira selenitica (Esp.), which was found defoliating young larch trees during 1958 in reforestation areas of the Maritime Alps, having migrated to them from surrounding patches of Sarothamnus scoparius. Bullock and Smith (1968) found Epijoppa fumosa Morl. parasitizing pupae of Dasychira georgiana and effectively keeping the population under check. Bionomics and outbreak of the pest and its control with insecticides is also given.

Urban (1967) attributed the collapse of an outbreak of D. pudibunda (L.) to a cytoplasmic polyhedrosis virus (Smithiavirus pudibundae) in beech forests of the Neubrunn and Henneberg districts in Germany. Results are given of light and electron microscope

observations on infested larvae. Geispits and Zarankina (1963) worked out the photoperiodic reaction and the effect of temperature on the development of *D. pudibunda* (L.) in the Soviet Union, where this Lymantriid occurs from north of Leningrad to the extreme south sporadically, as a pest of various trees. The results showed that growth processes were affected by photoperiod and that the duration of development was prolonged as temperature increased.

*E. lunata* Walk. and *E. subnotata* Walk. have been reported from India infesting mulberry, castor, cacao, guava, and sorghum by Butani (1978), Sukhija et al. (1977), and Mogal et al. (1980).

#### METHODS

A map of the area defoliated by *Elkneria (Dasychira)* aff. *mulleri* Ebert spread over compartments 36 to 40, and 42 and 43 of Swat Range, and 15 and 16 of Buner Range was prepared from the forest range maps. Points were selected on different aspects in defoliated forests for assessment of pest population. Five trees were randomly selected at each point. The first tree was marked by walking straight in one direction to reach the 20th tree from the starting point. Taking this tree as a base, 4 other trees were selected at right angles from each other by walking straight and taking the 15th tree, one each on western, eastern, southern and northern directions. For assessment of population, every tree was divided into three parts: stem, main branches, and shoots of main branches as pupal cocoons were present on these parts only. All cocoons on stem and main branches were counted starting from the base and climbing up the tree while on shoots, counting was made from the ground. The population on all the parts was added to obtain total population of insect cocoons per tree. Five hundred cocoons were collected at each point from the randomized trees for the assessment of parasitism. Each cocoon was cut open in the laboratory at Peshawar and observation on living, dead, and parasitized pupae was recorded.

Assessment of larval and pupal populations of *Euproctis* spp. was made in the affected forests whenever defoliation was reported in Sind. Larval population was recorded by shaking branches of randomized babul (*Acacia nilotica*) plants on a cloth sheet. Pupal population was taken by digging the soil around tree bases in 1-m circles at different points.

#### RESULTS AND DISCUSSION

The pest population of *Elkneria (Dasychira)* aff. *mulleri* Ebert was found over an area of about 900 ha in chir pine forests falling mainly in Swat Range and partly in Buner Range. The trees carried varied population of the insect pest and accordingly the extent of defoliation

differed in various localities and aspects of the forests. The pest population census recorded on various site aspects is shown below.

Table 1. Relationship between aspect and population per tree.

Aspect	Population per tree	
	Average	Range
Southern	1,484	660-2856
Eastern	1,168	630-1460
Western	1,031	610-1900
Northern	506	383 -600
Shady places and water courses	208	130 -287

The pest preferred southern, eastern and western aspects with maximum population per tree (1,484) on southern aspect followed by eastern (1,168) and western (1,031) aspects. Population per tree was low (506) on northern aspect and the lowest (208) in most shady places and deep nullahs. The number of heavily defoliated trees was greater on southern aspect followed by eastern and western, where most of the trees were completely denuded of foliage. The number of trees defoliated up to 50% was highest on northern aspects and lowest on southern aspects. All trees were defoliated lightly in most shady places, on banks of water courses and negligibly attacked away from the centre of heavy defoliation and at the base of nullah.

Table 2. Larval population per tree on variously defoliated trees.<sup>1</sup>

Defoliation	Larval population	
	Average	Range
Complete	1788	1020-2856
Heavy	794	702- 903
Medium	571	383- 670
Light	208	130- 287

<sup>1</sup> Based on puparia present on the trees.

More than 1,000 larvae per tree (average, 1,788) defoliated trees of all ages completely when population reached the limit either of one generation or the other during April to November. Similarly, populations between 700 and 900 (average, 794) and about 400 and 700 (average, 571) per tree caused heavy and medium defoliation.

respectively, when populations reached the limits any time during this period. Defoliation remained light or insignificant when populations remained below 300 larvae per tree.

A hymenopterous parasite of the pest, Monodontomerus dentipes Boheman (Family, Torymidae) existed naturally in the area. At the time of pest population census, observations were also recorded on the extent of parasitism carried up to the end of the season in the month of December.

Table 3. Extent of parasitism on Elkneria (Dasychira) aff. mulleri Ebert.

<u>Larvae/pupae examined</u>	<u>Parasitized larvae/pupae</u>	<u>% parasitism in</u>		
		<u>larvae</u>	<u>pupae</u>	<u>total</u>
1681	1677	24.87	74.89	99.76

The parasite seems to have very high reproductive potential as it outnumbered and overpowered the pest population within 6-8 months. The insect pest population multiplied rapidly and caused serious defoliation of Pinus roxburghii over an area of about 190 ha. The parasite, finding plenty of food, also bred tremendously resulting in 99.76% parasitism of the pest population in December leaving only 0.24% population to carry forward to the next spring with enormous parasite population to starve to death. The pupae of the pest found parasitized were collected and kept in the laboratory which gave rise to 10-27 adult parasites per pupa.

The pests Euproctis lunata Walk. and E. subnotata Walk. caused defoliation of babul forests in Sukkur Forest Division in 1975. However, the pest population had subsided before population census was made. Larval and pupal population recorded after suppression was as under:

Table 4. Larval and pupal population of Euproctis spp. in Sukkur Forest Division during 1975.

<u>Locality</u>	<u>Larval population per 100 trees</u>	<u>Pupal population per 100 tree basis</u>
Ding Forest	50	20
Kitishah Forest	47	6
Kitiabad Forest	40	11

With the above minor population, the pest remained under complete control of bioagents until 1981. In 1982, resurgence of the pests occurred in Sukkur Forest Division while their population build-up was also reported from Hyderabad Forest Division. The pests were again checked by natural enemies in the same year. Larval and pupal population recorded after suppression was as follows:

Table 5. Larval and pupal population of Euproctis spp. in 1982.

<u>Forest division</u>	<u>Locality</u>	<u>Larval population per 100 trees</u>	<u>Pupal population 100 tree basis</u>
Hyderabad	Miani Forest	0	105
	Mutyari Forest	0	0
	Kabrani Forest	0	55
Sukkur	Ding Forest	20	15
	Kitishah	35	5
	Kitiabad	340	0

Pupae collected from Hyderabad produced 3 hymenopterous and 2 dipterous parasites but no moth emerged. Pupae collected from Sukkur produced one immature moth and no parasite emerged.

High population of babul defoliator was reported to occur from September to November in Sukkur and Hyderabad Forest Circles. Therefore, it was planned in 1983 to study pest population, record parasite complex, and carry out control experiments during October-November. On receiving the report of defoliation from Mulchand Forest, Hyderabad in December 1984, population survey was carried out in January 1985, which is reported below:

Table 6. Larval population of Euproctis spp. in 1985 in Mulchand Forest

<u>Compartment</u>	<u>Plants observed</u>	<u>Larvae collected</u>
4, 6, 7	3500	120
10	3000	86
42	1000	22
45	1000	42

Soon after development of the pest population, the natural enemies found plenty of food, multiplied rapidly, and overpowered the pests. The pests are still under the control of their natural enemies and no report of resurgence of pest population has been received since.

## SUMMARY

Population of Elkneria (Dasychira) aff. mulleri Ebert, a pest of chir pine, and Euproctis lunata Walk. and E. subnotata Walk., two pests of babul have been studied. An average population of E. aff. mulleri Ebert numbering 1,788, 794, 571, and 208 larvae per tree, respectively, caused complete, heavy, medium and light defoliation of Pinus roxburghii in 1977. The pest preferred southern, eastern and western aspects. An average population per tree on these aspects was 1,484, 1,168, and 1,031 larvae, respectively.

E. lunata Walk. and E. subnotata Walk. caused occasional defoliation of babul forests since 1974. An assessment of the available population is given.

## LITERATURE CITED

- BULLOCK, J.A. & SMITH, R.G. 1968. The bionomics and control of Argyrotagma niobe (Weym.) and Dasychira georgiana Fawc. Lep.: Lymantriidae on block wattle in Kenya. Bull. Entomol. Res. 58, pt. 2: 255-277.
- BUTANI, D.K. 1978. Insect pests of fruit crops and their control: 25 - Mulberry. Pesticides 12(8): 53-59.
- EBERT, G. 1966. Afghanische Bombyces and spinges. 1. Lymantriidae. Ergebnisse der 2. Deutschen Afghanistan Expedition (1966) der Landessammlungen für Naturkunde in Karlsruhe. Reichenbachia 10: 181-197.
- GEISPITS, K.F. & ZARANKINA, A.I. 1963. Some peculiarities of the photoperiodic reaction of Dasychira pudibunda L. Lepidoptera: Orgyidae. Rev. Entomol. URSS. 42 pt. 1: 29-38, Leningrad.
- GHAZI-BAYAT, A. 1967. On the morphology, biology and ecology of Dasychira selenitica (Esp.) (Lepidoptera: Lymantriidae). Z. angew. Entomol. 60 pt. 4: 467-492.
- KLIMETZEK, D. 1972. The occurrence of pale tussock moth (Dasychira pudibunda L.) in the Palatinate. Allg. Forest jagdztg. 143(9): 192-195.
- MOGAL, B., MALI, A.R., RAJPUT, S.G. & PAWAR, K.L. 1980. Relative toxicity of pesticides to sorghum earhead hairy caterpillar, Euproctis subnotata (Walk.). Pesticides 14(6): 30-31.
- RADHA, K. & RAWTHER, T.S.S. 1976. Pests and diseases of garden and land crops. Indian Farming 25(11): 31-35.
- SAMPO, A. 1968. On the allotropic liking for resin of some Lepidoptera of interest to forestry. Annali della Facolta di Scienze Agraria della Universita degli studi di Terino 4: 317-344.
- SREENIVASAM, D.D., BENJAMIN, D.M. & WALGENBACH, D.D. 1972. The bionomics of the pine tussock moth. Research Bulletin, College of Agriculture and Life Sciences, University of Wisconsin-Madison, No. 282. 36 pp.
- SUKHIJA, H.S., BRAR, K.S. & BAKHETIA, D.R.C. 1977. Toxicity of some new insecticides to Euproctis lunata Walk. J. Res., Punjab Agric.

- Univ. 14(3): 389-390.
- THONTAKARVA, T.S. & NALAVADI, U.G. 1969. Euproctis s  
Lymantriidae, Lepidoptera, as a pest of guava flower  
guava. Mysore J. Agric. Sci. 3(3): 334-335.
- URBAN, S. 1967. The occurrence of a cytoplasm polyhe  
Dasychira pudibunda. Arch. Forstw. 16(6/9): 837-840

GYPSY MOTH OUTBREAK AND CONTROL  
IN SOUTHWEST GERMANY, 1984 - 1986

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INTRODUCTION

In Central Europe outbreaks of the gypsy moth, *Lymantria dispar* L. (Lymantriidae), are not uncommon, yet it is not considered to be a forest pest. In his 1841 book, "Forest Pests and Their Enemies," Ratzeburg, the father of forest entomology, states: "Occasionally the large, voracious larvae can become dangerous." However, Schwerdtfeger (1981) mentions the gypsy moth without going into detail. He wrote: "Without importance in forests, only lasting outbreaks in oak-stands (especially in Southeast Europe) are to be noticed." If you want to know more about the population dynamics of the gypsy moth in the German literature, you have to consult the third of the five volumes of the handbook, "The Forest Pests of Europe," edited by Schwenke in 1978, where you can find details about the locations of past outbreaks which indicate the unimportant role of the gypsy moth in Central Europe (Table 1). Moreover, the table shows how the population dynamics depend on climate: Outbreaks are triggered by drought and heat.

Table 1. Area of European forests damaged by outbreaks of *Lymantria dispar*

Region	Country	Year	Area in ha
Southeast Europe (arid-continental)	Yugoslavia	1957	1,500,000
	Rumania	1958	600,000
	Soviet Russia	1933	206,000
Western Mediterranean Countries (dry, hot summers)	Spain	1958	100,000
	Portugal	1958	22,000
Central Europe (humid-maritime)	Switzerland	1924	75
	Germany	1973	50

(Schwenke, 1978)

In Europe, outbreaks are usually noticed only in oak-stands, but two German species, Quercus petraea and Quercus robur, suffer not only from gypsy moth but from many other phytophagous insects. The most important members of this "oak damaging community" are the green oak roller, Tortrix viridana, and the winter moths, Operophtera brumata and Erannis defoliaria. Although there are periodical outbreaks of these pests, control measures are seldom undertaken because of the high regeneration capacity of the oaks. Even after complete defoliation, the stands are green again within a few weeks. Therefore, heavy defoliation during several successive years causes loss of increment but does not kill trees. This is true only in healthy stands. The increasing "Waldsterben" forces a more careful assessment of the phytophagous insects. In addition to causing thinning of crowns these insects reduce stand vigor by reducing foliar biomass, especially in cases of oak-stands suffering from a new "Eichen-Sterben" (oak decay) (Altenkirch, 1987; Patocka & Novotny, 1987). In this context, the gypsy moth becomes more and more important also in Central Europe. Two leaflets dealing with gypsy moth biology, from Skatulla (1985) and from Niemeyer (1988) recently published in Germany, express this change.

An outbreak of the gypsy moth in Southwest Germany gave us the opportunity to study the population dynamics under current conditions. The outbreak area was situated 70 km north of Freiburg in the forest districts of Offenburg and Kehl. Defoliation was first noticed in a stand of 30-year-old red oak (Q. rubra) in July 1984. At the end of the feeding period, 70 ha of Q. robur and Q. rubra stands were heavily defoliated (Table 2).

Table 2. Area defoliated by Lymantria dispar in the forest districts of Offenburg and Kehl

Year	1983	1984	1985	1986	1987
Area in ha	0	70	1300	470	0

The defoliated area amounted to 1300 ha in 1985, an area larger than any other Central European outbreak area previously recorded (Wellenstein and Schwenke, 1978). Egg masses were counted to ascertain the population densities and their changes. In the winter of 1984-85, we restricted ourselves to the red oak stand where the attack was first observed. We counted egg masses on the stems of 100 trees from the ground to the bottom of the crown and found 388 egg masses. As 1500 red oaks grow on 1 ha at the experimental site, the egg mass density was estimated to be approximately 6000 per ha.

Six egg masses were sampled randomly to determine number/mass and viability; masses contained from 177 to 687 eggs. The mean was  $351 \pm 184$ . According to Wellenstein and Schwenke (1978) this number of eggs indicates the culmination of population density. Viability was high and since 99% of the larvae hatched, a population collapse was not expected. To predict the defoliation for 1985, we considered the following values: In 1984, we estimated an average of 4 egg

masses per tree each containing 350 viable eggs; that means a calculation of 1400 eggs per tree. The egg mass density was 6000 per ha. Wellenstein and Schwenke (1978) consider 600 eggs per tree to be critical to 30-year-old oaks in Europe. In the United States, a rule-of-thumb value of 1236 egg masses per ha is considered to be critical (Talerico, 1981). Both numbers of our experimental site exceeded by far these values, indicating total defoliation in the next season. In the winter of 1985-86 egg mass counts were undertaken more systematically. In the forest district of Offenburg we selected the most heavily infested plots of the stands - 1 per 10 ha - to determine egg mass density on 10 trees. The averages ranged from 0.8 to 10.7 (Table 3).

In the forest district of Kehl, egg mass densities were estimated on 10 trees/plot, but these plots were arranged in a regular 333 m grid. Egg densities were lower than in Offenburg; at 63 plots in three subdistricts the maximal egg mass per tree corresponded with the mean of Offenburg (Table 3). Analysis of randomly selected egg masses brought the following results: In the winter of 1985-86 the number of eggs per mass had decreased to one-half of the number in 1984-85; the collapse of the population was foreseeable. Nevertheless, heavy defoliation has to be expected at least in some heavily infested stands (last column, Table 3). This was an essential assumption for the two special investigations we planned for the 1986 season.

First, we wanted to study the parasite complex of the gypsy moth in the communal forest of Offenburg in detail since, in 1985, the larvae were highly infested by parasitic flies (Maier & Bogenschutz, in press).

Secondly, in 1985 we found no incidence of nuclear polyhedrosis virus (NPV) in field material. Collected dead larvae did not contain any polyhedral inclusion bodies (PIB's).<sup>1</sup> Therefore, we wanted to introduce NPV by spraying a virus suspension onto the egg masses to induce an epizootic (Campbell, 1983; Trzebitzky et al., in press).

#### The Evaluation of the Natural Gypsy Moth Antagonists

When we visited the outbreak area for the first time in the middle of June 1984, the population of *Lymantria dispar* had already pupated, but numerous relict egg masses indicated that the outbreak started in 1983. In the webs of the larvae we noticed many cadavers of larvae and pupae but we could not explain the reason for this mortality. We now assume that this was due to tachinid maggots which abandoned the dead bodies. On April 25, 1985, the eggs had hatched completely, but 15% of the larvae rested together inactively in a fine web below the egg mass. On June 28, the larvae matured, at which point parasitism by tachinids had reached about 80%. The flight period of gypsy moth was at its maximum in mid-July.

<sup>1</sup>We acknowledge the diagnosis of Dr. Alois Huger, Darmstadt.

Table 3. Population density of *Lymantria dispar* in the winter of 1985-86.

Forest district	Number of egg masses per tree		Number of eggs per egg mass		Number of eggs per tree	
	N <sub>1</sub>	max. mean	N <sub>2</sub>	mean	mean	max.
<u>Kehl</u>						
Communal forest of Neuried VI	16	5.1	1.8	22	164	294
Rheinau XXIII/XXV	14	3.9	2.3*	24	200	460
Rheinau XVII	33	3.5	2.0**	4	179	357
<u>Offenburg</u>						
Communal forest of Offenburg	25	10.7	4.7			
Subdistrict Spitalhof				32	180	938
Subdistrict West				60	118	616
						1480

N<sub>1</sub> = Number of plots with 10 trees in each; N<sub>2</sub> = number of egg masses. Not included, \* 8 plots resp.; \*\* 20 plots with a mean of less than 1 egg mass per tree.

More intensive studies of population dynamics were conducted in 1986 in three stands. The first was the epicenter of the outbreak area near Offenburg, in which an average of 9 egg masses per tree had been estimated the preceding winter. The other two were situated at the edges of the outbreak area. There were no apparent differences in the results from these three sites concerning the biotic mortality factors. In the following report we shall restrict ourselves to the results from the central outbreak area. On a weekly basis, we (Table 3) collected samples of 100 to 200 larvae from the stems and lower parts of the crown to ascertain parasitism.

The larvae concentrated under textile belts [burlap bands] fixed on the stem where they hid during the daytime, after having reached the third stage. In the laboratory we reared the larvae by means of oak leaves or dissected them to determine the parasitism percent and the degree of super-, multi- and hyperparasitism. In 1986, larval eclosion occurred later than in 1985 with first hatch on April 28; 80% of the larvae were in the second stage on May 12; pupation began by July 8 and adults occurred from July 20 to August 20.

In spite of the fact that egg density exceeded the critical value, defoliation remained about 5% in the experimental stand; a portion of which was caused by other phytophagous species such as *Tortrix viridana* and *Operophtera brumata*. In the other stands, the maximal defoliation was about 20%. Because of our 1985 results we concentrated on the activity of parasitic flies as the major mortality factors. On May 2, gypsy moth eggs began to hatch and we observed flies of *Parasetigena silvestris* (Robineau-Desvoidy) and *Blepharipa schineri* (Mesnill) visiting textile belts on leaves sprayed with sugar water. Eighteen days later, *Blepharipa pratensis* (Meigen) appeared (Table 4).

The first larvae with eggs of *P. silvestris* were found May 12; at that time, larvae were in the second instar. The percent of larvae with eggs attached quickly increased to more than 50% by June 24, but then decreased since only a few adult flies were still alive. Parasitism by *Blepharipa* can be ascertained only by dissecting larvae. The maggots penetrate into a ganglion of the central nervous system where they induce a tumor-like growth. In a similar way, *B. pratensis* infests intersegmental muscles. Other tachinids had only limited significance.

Table 4. Abundance of tachinid species observed as adults in the communal forest of Offenburg in 1986

Species	Number	Date of appearance
<i>Parasetigena silvestris</i>	202	2.5. - 1.7.
<i>Blepharipa schineri</i>	52	2.5. - 17.6.
<i>Blepharipa pratensis</i>	7	20.5. - 17.6.

Cocoons occasionally found on leaves or under textile belts indicated the activity of a hymenopterous parasite which only infested young larvae. Their effectiveness was low; parasitism by hymenopterans reached 20% in only one plot.

We found the first larvae infested by NPV on June 10, but an epizootic never occurred. While NPV was not important as a mortality factor in the epicenter, at the edges of the outbreak area 20% of the larvae died by this disease.

On June 17, about 50% of the gypsy moth population had reached the last larval stage. At that time, parasitism was nearly 100% as estimated by dissection. More than 90% of the larvae contained at least one *Parasetigena* larva, more than 80% were superparasitized. Superparasitism was as high as a mean of 3.4 maggots per host (Fig. 1). The distribution of maggots in the host correspond to that of egg deposition; the majority were found in the thoracic segments.

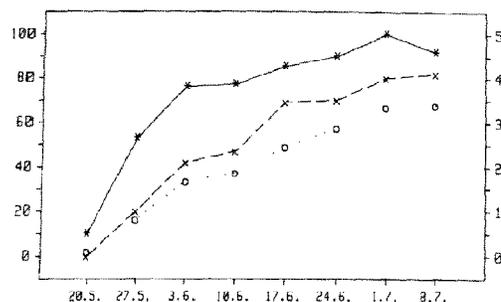


Fig. 1. *Parasetigena silvestris*: Percent parasitism and superparasitism of *Lymantria dispar* and number of maggots per host in the communal forest of Offenburg in 1986 (determined by larval dissection).

Maggots of *B. schineri* were found later than those of *Parasetigena* because larvae not yet entering a ganglion remained undetected. This species reached peak parasitism of more than 90% and superparasitism was very high with the average number of larvae per host being 3.9 (Fig. 2). Larvae occurred predominantly in the ganglia of abdominal segments 1 to 4.

The high parasitism of these two tachinids caused a high rate of multiparasitism. During the feeding period of *L. dispar*, multiparasitism reached 95% (Fig. 3). *P. silvestris* as well as *B. schineri* are univoltine parasites. After infesting the host, maggot development is arrested until the host begins to pupate when they develop rapidly and kill their host. Normally, only one maggot survives per host. Supernumerary individuals are excluded by intra-

or interspecific competition. Interspecific competition is decided in favour of the species with the most rapid development. The laboratory rearings gave more insight into parasite competition. We took a sample of 312 fourth to sixth instar larvae from the experimental stand. Six percent moulted to pupae, 85% were left by tachinid maggots, 7% died of NPV, and 2% of unknown reasons. In the cages, we found 425 tachinid puparia; 368 *P. silvestris*, 45 *Blepharipa* sp., 11 *Ceranthia samarensis* and 1 *Compsilura concinnata*. Assuming that the individuals of the three latter species each emerged from a single host, 237 gypsy moth larvae would remain for 368 *Parasetigena* puparia, an average of 1.6 maggots developing per host. We did not rear single gypsy moth larvae. However, we observed a few cases where two tachinids emerged from the same host; in one case, one gypsy moth larva yielded three maggots.

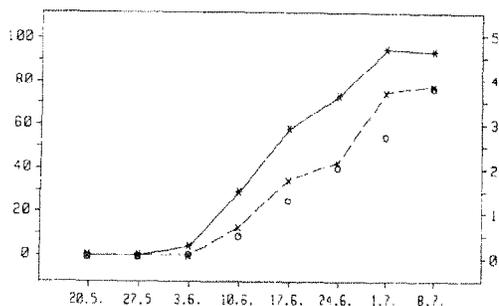


Fig. 2. *Blepharipa schineri*: Percent parasitism and superparasitism of *Lymantria dispar* and number of maggots per host in the communal forest of Offenburg in 1986 (determined by larval dissection).

The ratio of 8:1 in favour of *Parasetigena* puparia indicated that this species outcompeted *B. schineri*.

The results of the dissections and rearings demonstrate that the outbreak of *L. dispar* in Southwest Germany collapsed predominantly through the influence of the two tachinids, *P. silvestris* and *B. schineri*. As already mentioned, only 5% of the leaves were browsed in the experimental site. To document that a population collapse had occurred, we surveyed the flight of the moth by the use of sex pheromone traps. In 12 delta traps baited with 100 ug of disparlure, an average of only 46 males per trap was caught during the whole flight period from July 20 to September 1; maximum flight activity occurred during early August. New egg masses were also extremely rare.

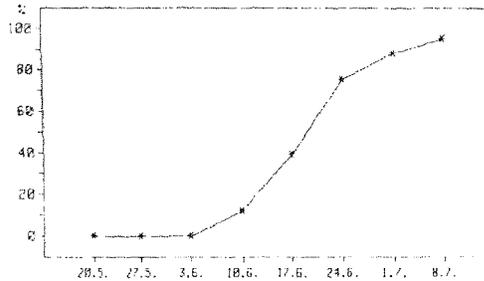


Fig. 3. Percent multiparasitism in Lymantria dispar larvae by Parasetigena silvestris and Blepharipa schineri (determined by dissection of host larvae).

The tachinids, especially P. silvestris, reached very high population densities. This univoltine species hibernates in a puparium in the ground as does B. schineri. Therefore, we expected intensive flight activities of these two species in the spring of 1987. However, the contrary occurred. On May 14 and June 12, the time of maximal activity in 1986, not one fly visited textile belts or leaves sprayed with sugar water which is difficult to explain. In spring, we predicted complete defoliation because of the high density of first instar gypsy moth larvae. The key mortality factor, parasitism by tachinids, affects only the last stage larvae that had completed feeding. Our methods obviously overlooked essential mortality factors such as predation. In addition, physiological dysfunction of the larvae may have limited food consumption.

We do not know whether the population collapsed because of unknown mortality factors or dispersed after hatching in search for alternative hosts.

#### The Effect of Spraying Egg Masses with Gypchek<sup>2</sup>

In the forest district of Kehl, we tested this method in an isolated stand that had a high egg mass density and no incidence of NPV the season before. The aim of our studies was to infect young larvae during hatching thereby transporting the virus into the crowns to induce an epizootic in the whole L. dispar population.

<sup>2</sup> Dr. J. Huber, Darmstadt, and Dr. K. Lohmann, Freiburg, participated in these investigations. Dr. J. Podgwaite sent us a sample of Gypchek. Many thanks to all these colleagues.

Our trials were divided into three successive phases:

- the estimation of the effective virus concentration in the laboratory;
- the treatment of the egg masses in the field and the monitoring of the NPV epizootic; and
- the identification of the effective NPV strain through restriction endonuclease analysis of the viral DNA.

To determine the effective virus concentration we sprayed each field collected egg mass few days before hatch with about 3.5 ml of Gypchek suspension. The concentrations were  $10^5$ ,  $10^6$ ,  $10^7$  and  $10^8$  PIB's per ml. We added 0.025% of the adjuvant Citowett (Celamerck, Ingelheim) to the suspension and in some trials 1% milk powder (sticker) and/or 20% sugar (phagostimulants). The larvae were held solitary or in groups of three in small containers on leaves or on an artificial medium (Bell et al., 1981). Dead larvae were counted every third day.

In all trials, mortality increased with the virus concentration. Routinely, 90% mortality was obtained 12 days after the concentrations  $10^7$  or  $10^8$  PIB's per ml were applied. Results of 15 different tests with larvae caged solitarily or in groups, fed with leaves or a medium, sprayed with or without sugar or milk powder, showed no significant differences. The average of the  $LC_{90}$  was  $2.7 \times 10^7$  PIB's per ml.

For the field trial, we chose a hardwood forest of 11 ha surrounded by agricultural areas. The oak stands had different ages, from less than 5 up to 140 years. In 1985, defoliation by gypsy moth was noted for the first time, egg mass density was high (> 2400 masses per ha) and culmination of the outbreak was expected in 1986.

On April 30, at the beginning of hatch, the egg masses on the lower part of the stems were treated with Gypchek with a portable high-pressure sprayer to the point of run off. The spray medium contained  $10^7$  or  $10^8$  PIB's per ml, 20% sugar and 0.025% Citowett. Weekly, we collected larvae, reared them in the laboratory and ascertained the rates of the infection and parasitism within treated and untreated plots. Mortality by NPV did not exceed 12% for the first 6 weeks of laboratory rearing. Beginning with the 7th week, the respective mortality ranged from 40 to 66% independent of the plots from which the larvae were collected (Fig. 4). Dispersal of young larvae by wind and transmission of NPV within the gypsy moth population by parasites had obliterated differences between experimental plots. Parasitism by tachinid flies increased total mortality up to 91% in weekly samples. The relative population density of *L. dispar* larvae calculated from the number of larvae in the first sample (=100%) minus the mortality rate in the successive samples decreased below 0.1%. By calculating the mortality induced only by NPV in each sample, we could show that it would have reduced the gypsy moth density below 5% even without considering mortality by parasites. The question whether the high mortality in the experimental area was induced by Gypchek sprayings or, perhaps, by an endogenous virus strain was still unknown. Restriction endonuclease analysis was undertaken to provide an answer. We isolated the virus DNA from the dry Gypchek prepate and from deep frozen NPV-infected larvae collected in the experimental stands respectively in the Offenburg area about 20 km to the south. The preparation followed

the methods described by Stiles and coworkers (1983). Each of the DNA preparations were treated with the four endonucleases Bam H I, Bgl II, Hind III and Eco RI. The electrophoresis was run in 0.7% (wt/vol) agarose gel for about 16 hours with 80 v. The gels were stained with ethidium bromide. Comparing the restriction profiles, we could positively identify the American NPV strain, Ldp-67 (Connecticut Standard) as the cause for the virus disease in the experimental stands. The band patterns from Gypchek DNA and from virus DNA from the treated area were identical in each enzyme treated but differed from that from the Offenburg material. No mixed infection was shown.

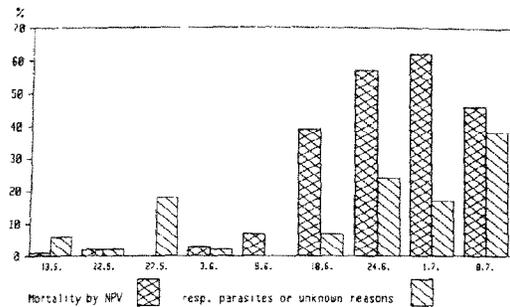


Fig. 4. Mortality rate of *Lymantria dispar* larvae in the plot treated with Gypchek ( $10^7$  PIB's per ml).

In comparison with former results, our treatments of egg masses with Gypchek in the laboratory and in the field proved to be very effective. Campbell (1983) induced a maximal mortality of 74% after 21 days with a concentration of  $10^6$  PIB's per ml in the laboratory. Yet, in the field, he obtained only 57% reduction of egg mass densities. In our studies, we observed high mortality to newly hatched larvae on egg masses which we treated with  $10^6$  PIB's per ml concentration. That means we did not succeed in using the larvae as a vector of the NPV with such a high concentration. After all,  $10^7$  PIB's per ml turned out to be the best concentration to treat egg masses. During 1986, also in the Kehl forest district, the gypsy moth outbreak was brought to an end by tachinid parasites, and, at least in the experimental stands, by NPV. In June, however, the density of the larvae was still so high that complete defoliation occurred in some stands. Nevertheless, we caught only an average of 56 males in 11 pheromone traps during the whole flight period. In addition, we found only four new egg masses in the whole subdistrict.

What consequences did the gypsy moth outbreak from 1984 to 1986 have on the forest economy? In addition to the defoliation by phytophagous insects, the second sprouting of *Q. robur* was heavily infected by the oak mildew, *Armillaria mellea*. All these damages led to the loss of 13 ha of plantation and 7 ha of pole-sized timber. In mature stands, single trees were harvested to avoid further loss through timber decay. The incidental felling amounted to about 2200 cubic meters.

## LITERATURE CITED

- ALTENKIRCH, W. & HARTMANN, G. 1987. Eichenprobleme. *Der Forst- und Holzwirt* 42: 445-448.
- BELL, R.A., OWENS, C.D., SHAPIRO, M. & TARDIFF, J.R. 1981. Development of mass-rearing technology. pp. 599-633. In: C.C. Doane and M.L. McManus, eds. *The Gypsy Moth: Research toward integrated pest management*. U.S. Dep. Agric. Tech. Bull. 1584.
- CAMPBELL, R.W. 1983. Gypsy moth control trials combining NPV, disparture and mechanical methods. *J. Econ. Entomol.* 76: 610-614.
- MAIER, K. & BOGENSCHUTZ, H. Die Bedeutung der Raupenfliegen (Dipt.: Tachinidae) beim Zusammenbruch einer Massenvermehrung von *Lymantria dispar*. *Mitt. Dtsch. Ges. Allg. Angew. Ent.* 6. In press.
- NIEMEYER, H. Erkennen, Überwachen und Bekämpfen wichtiger Forstschadlinge. Auswertungs- und Informationsdienst für Ernährung, Landwirtschaft und Forsten e.V., Bonn. In press.
- PATOČKA, J. & NOVOTNÝ, J. 1987. Share of insects in the mass decay of oak in Slovakia. *Vedecké Práce. VULH vo Zvolene*, 59-90.
- RATZEBURG, J.T.C. 1841. *Die Waldverderber und ihre Feinde*. Nicolaische Buchhandlung, Berlin.
- SCHWENKE, W. 1972-1986. *Die Forstschadlinge Europas*. Ein Handbuch in 5 Bänden. Verlag Paul Parey, Hamburg und Berlin.
- SCHWERDTFEGGER, F. 1981. *Die Waldkrankheiten*. 4 Aufl. Verlag Paul Parey, Hamburg und Berlin.
- SKATULLA, U. 1985. Eichenschadlinge - Schwammspinner (*Lymantria dispar* L.). *Waldschutz-Merkblatt* 8. Verlag Paul Parey, Hamburg und Berlin.
- STILES, B., BURAND, J., MEDA, M. & WOOD, H.A. 1983. Characterization of gypsy moth (*Lymantria dispar*) nuclear polyhedrosis virus. *Appl. Environ. Microbiol.* 46: 297-303.
- TALERICO, R.L. 1981. Evaluating populations. pp. 32-34. In: C.C. Doane and M.L. McManus, eds. *The Gypsy Moth: Research toward integrated pest management*. U.S. Dep. Agric. Tech. Bull. 1584.
- TRZEBITZKY, C., BOGENSCHUTZ, H., HUBER, J. & LOHMANN, K. Versuch zur Bekämpfung von *Lymantria dispar* L. (Lepidoptera: Lymantriidae) durch Behandlung der Eigelege mit Kernpolyederviren und Erfolgskontrolle durch Restriktionsanalyse der viralen DNA. *Mitt. Dtsch. Ges. Allg. Angew. Ent.* In press.
- WELLENSTEIN, G. & SCHWENKE, W. 1978. *Lymantria* Hbn. pp. 334-349. In: W. Schwenke, ed. *Die Forstschadlinge Europas*. 3 Band: Schmetterlinge.

N A T U R A L   D I S E A S E   O F   G Y P S Y   M O T H  
I N   V A R I O U S   G R A D A T I O N   P H A S E S

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

The family Lymantriidae is represented by several dendrophilous species in Slovakia. Gypsy moth (*Lymantria dispar* L.) is the most important species from the viewpoint of forestry. Its outbreak occurs in the period of 8-10 years. Each of its gradation phases (progression, culmination, repression) lasts in primary foci usually for one season (Novotný 1986). Under the conditions of Europe great bioregulative complex is connected with *Lymantria dispar*. Entomopathogenic microorganisms are the most important component of this complex. Their effect is concentrated mainly on larval stage of pest. Viruses (Guliy - Golosova 1975, Mihalache - Pirvescu 1980) are of the most significant effect, then follow bacteria (Weiser 1966, Mihalache - Pirvescu 1980) and protozoa (Weiser 1966, 1976, Zelinskaya 1980). The infestation by fungal pathogens (Weiser 1966, Glowacka 1983) is less frequent. In the dependance on population density of pest the overinfestation of population by pathogens is increasing or decreasing. It can be supposed that a relation exists between specific structure and activation of pathogenic microorganisms and developmental stages of pest or gradation phases. The observations of some authors (Podgwaite 1981, Glowacka 1983) suggest this fact.

We used the outbreak of *Lymantria dispar* on the territory of Slovakia in the years 1985-1987 for the study of some dependancies in the relation of entomopathogenic microorganisms and pest.

M E T H O D S

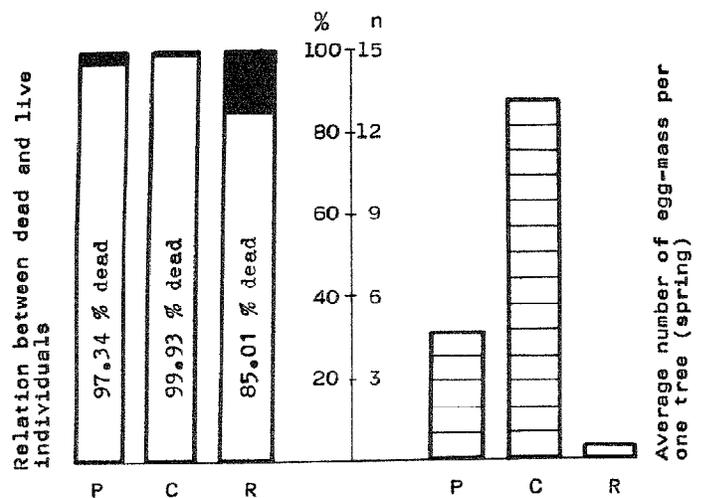
In 1985-1987 we monitored population dynamics of *Lymantria dispar* in the primary focus of its outbreak (locality Čifáre). Samples of pupae, larvae (by 100) were taken larval instar L<sub>1-2</sub>, L<sub>3-4</sub>, L<sub>5-6</sub> from field population. We observed material in laboratory up to hatching of imagos. Dead individuals were differentiated after examination into three groups according to fact whether pathogens, parasitoids or other causes (physiological and unknown reasons of dying) were the originator of mortality. Caterpi-

llars died due to pathogens were examined with the help of microscope and the pathogen was determined: virus, bacterium, protozoan, fungus, mixed infections. Then individual species of pathogens were specified. The determination was made in the cooperation with Dr. Jaroslav Weiser, DrSc. (ČSAV, Patologia hmyzu, Praha) corresponding member of the Czechoslovak Academy of Sciences who determined major part of material, revised previous determination respectively. Experimental material was taken from one primary focus (locality Čifáre) during whole three-year period where separate years were uniform for following gradation phases: 1985 - progression, 1986 - culmination, 1987 - regression. Gained data were worked out statistically and evaluated according to own mathematic formulas - coefficients.

## RESULTS

Abundant characteristics of population (Fig. 1) proves of significant dependancy among gradation phase, number of pest and mortality. In the dependance on the number of pest his disposability to bioregulators has been changing.

Figure 1: Abundance characteristics of *Lymantria dispar* population (P-progression, C-culmination, R-regression)

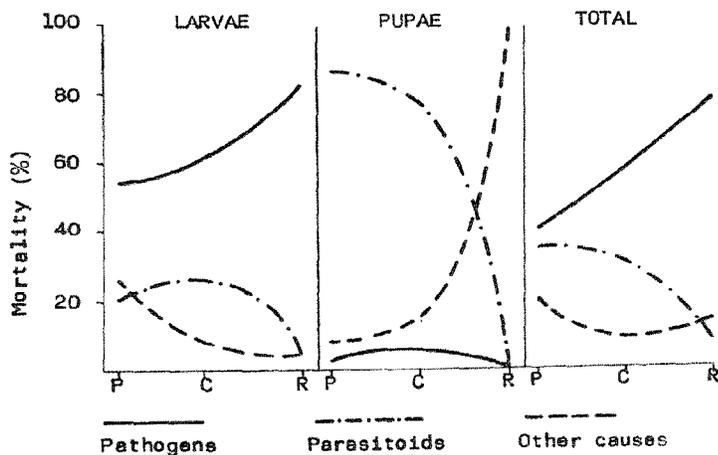


The situation is characterized vividly by autoregulative coefficient  $A_k$  (Table 1) which expresses on the basis of ratio of population weakening coefficient ( $N_k$ ) and resistance coefficient ( $R_k$ ) the state of conditions making possible the activation of bioregulative complex. Increasing  $A_k$  marks improving conditions for bioregulators effect and vice versa. In our trials  $A_k$  is of highest value in culmination phase because conditions for mass appearance of bioregulators ripened here. Then their spontaneous treatment to pest population changed the conditions for their effect significantly. As a result the lowest  $A_k$  in regression followed.

Table 1. Bioregulation characteristic of gypsy moth population.

Gradation phases	Population weakening coefficient ( $N_k$ )	Population resistance coefficient ( $R_k$ )	Autoregulative coefficient of ecosystem ( $A_k$ )
Progression	0.37	2.67	$1.39 \times 10^{-1}$
Culmination	14.28	0.07	$2.04 \times 10^2$
Regression	0.06	17.63	$3.40 \times 10^{-3}$

Figure 2: Share of bioregulators in mortality (P-progression, C-culmination, R-regression)



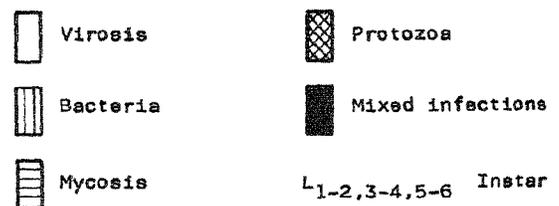
At whole the complex of pathogens was the most active bioregulator in all gradation phases. Parasitoids and other causes had significantly smaller share in the mortality. Importance of bioregulator group in larval stage was similar. But it differed basically from previous two causes in the stage of pupa (Fig. 2). With the comparing of the effect of individual pathogens we found that bacteria had the greatest effect in progression phase (49,5%), viruses in culmination (49,2%) and bacteria again in regression phase (60,0%). Similar pathogens were dominant also in larval stage. (Table 2). In the stage of pupa only viruses had mortal effect.

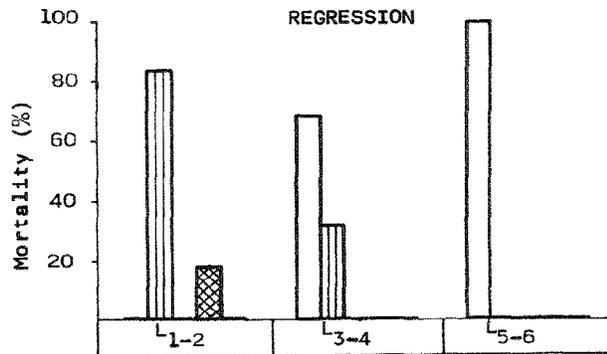
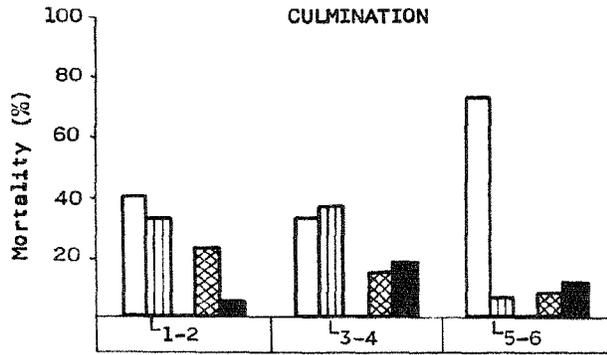
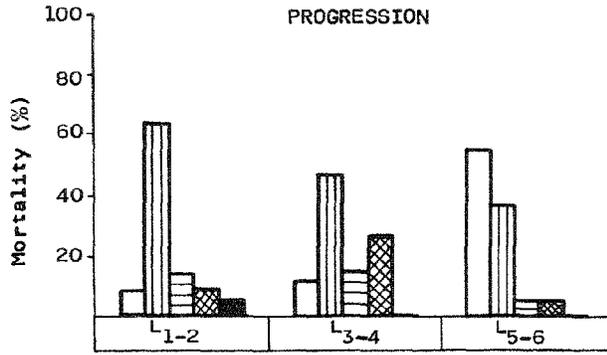
Table 2. Participation of pathogens in mortality of gypsy moth larvae.

Pathogen	Progression	Culmination	Regression
Virosis	20.0	48.6	30.0
Bacteria	50.6	24.9	60.0
Mycosis	12.6	0.0	0.0
Protozoa	14.7	16.0	10.0
Mixed infections	2.1	10.5	0.0

Also the presence of pathogens in the dependance on caterpillars instar was differentiated basically. With the youngest caterpillars bacteria prevailed during progression (69,9%), viruses during culmination (40,0%) and again bacteria in regression phase (83,3%). Representation of pathogens in the group of caterpillar  $L_{3-4}$  was different. Bacteria were the most abundant in the first and second period (45,9% and 34,5%), viruses in the third one (66,7%). With mature caterpillars viruses prevailed in all phases (54,6%, 74,2%, 100%) (Fig. 3).

Figure 3: Representation of groups of pathogens in different gradation phases



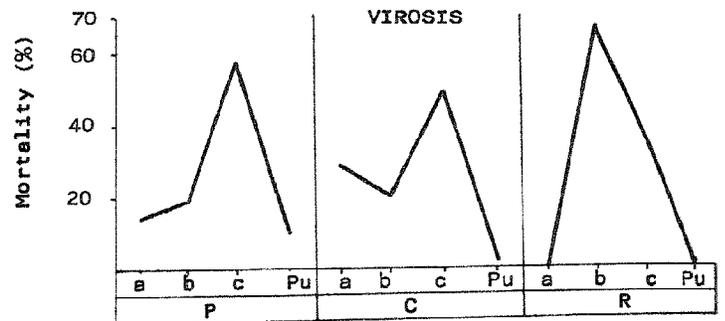


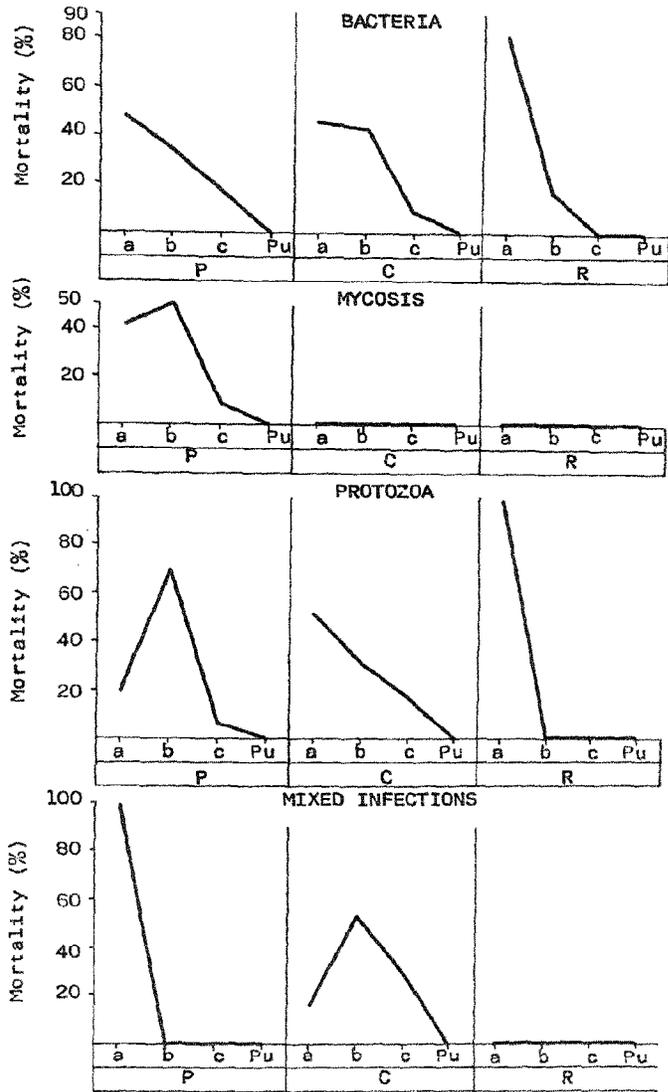
Figures 4 show the affinity of the groups of pathogens to instars of caterpillars, developmental stages of pest respectively.

Viruses had expressive effect in all gradation phases, in the most effective against mid-aged and mature caterpillars while dying ended also in the stage of pupa. Also bacteria had expressive course of their effect in all phases. They infested the youngest caterpillars intensively and their effect was sharply decreasing with the increasing of the age of caterpillars. It was equal to zero in the stage of pupa. We recorded the presence of fungi only in the progression phase. These pathogens were missing in culmination and regression.

Protozoal infections in the period of progression appeared expressively with caterpillars of middle age, with the increasing from the youngest instar and decreasing with the oldest instar. The effect upon pupae was not found. In culmination and regression phase was maximum equally in the period of the youngest caterpillars and it has decreasing trend in following instars. We found mixed infections in the progression phase only with the youngest caterpillars (bacteria + viruses). They were more frequent during culmination and their maximum was concentrated on caterpillars L<sub>3-4</sub>. In this period we found combination viruses + protozoa, viruses + bacteria, viruses + fungi, with caterpillars L<sub>1-2</sub> combinations viruses + protozoa, protozoa + bacteria, viruses + bacteria, viruses + fungi, viruses + protozoa + bacteria with caterpillars L<sub>3-4</sub>. The oldest caterpillars infested combinations of pathogens as viruses + protozoa, viruses + bacteria, viruses + fungi. Mixed infections did not occur in regression (Fig. 4).

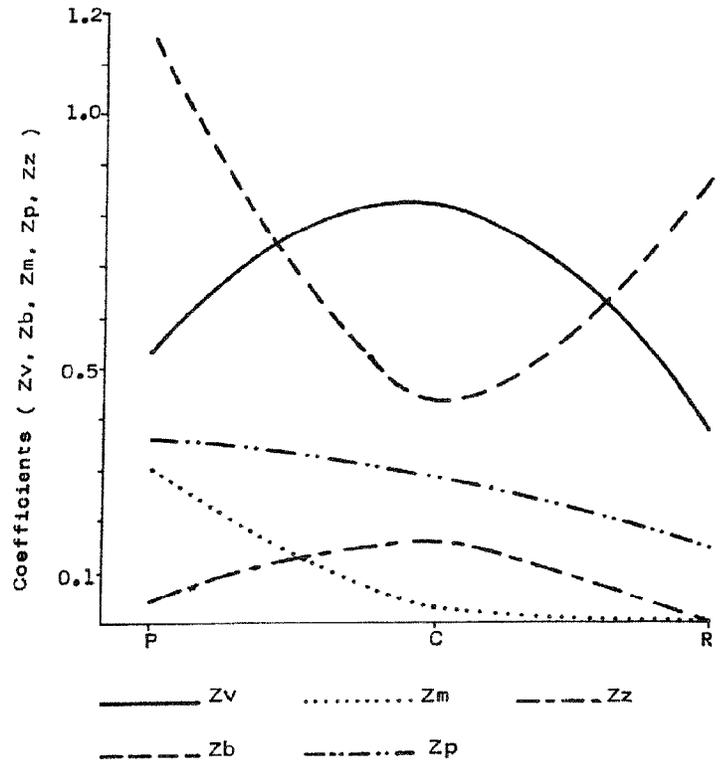
Figure 4: Binding of pathogens to instar, pest developmental stages resp. ( a- L<sub>1-2</sub>, b- L<sub>3-4</sub>, c- L<sub>5-6</sub>, Pu-pupae, P-progression, C-culmination, R-regression)





Coefficients of pathogen activation ( $Z_{v-z}$ ) give the survey on pathogen ability to be successful in control against pest in different gradation phases, as data giving relation between pathogen representation in pest population and total mortality induced by diseases. It can be seen from the comparing of the curves of the coefficients of individual pathogens activation (Fig. 5) that the order of pathogens activation in the progression phase is following. Bacteria are the most active, then follow protozoa, fungi and mixed infection.

Figure 5: Curves of activation coefficients of single pathogens (Coefficient  $Z_v$ -virosis,  $Z_b$ -bacteria,  $Z_m$ -mycosis,  $Z_p$ -protozoa diseases,  $Z_z$ -mixed infections; P-progression, C-culmination, R-regression)



The order is changing in culmination: viruses - bacteria - protozoa - mixed infections, fungi were not active. The order during regression was following: bacteria, viruses, protozoa, fungi; mixed infections were not active. The determination of pathogens asserted specific diversity of entomopathogenic microorganisms accompanying gypsy moth gradation. Nuclear polyhedrosis was represented the most often among viruses (94,74%). We recorded also cytoplasmic polyhedrosis (1,75 %) but also rare incidence of granulosis (3,51%) in examined sample. From bacilli systems of spores and stamens of septicemic bacteria (88,89%) prevailed, then cocci followed (9,10%) and *Bacillus thuringiensis* had only symbolic representation. Systems of spores of fungal pathogens (58,33%) and *Beauveria bassiana* (41,67%) represented mycoses.

With protozoa represented by microsporidia species *Nosema lymantriae* (38,64%), *Nosema serbica* (54,55%) and *Nosema* sp. (6,81%) were determined.

#### DISCUSSION

The role, structure and specific diversity of pathogens in our observations differ from data given by other authors. Nuclear polyhedrosis predominates in general in American populations of pest, bacteria are less represented and fungi only slightly. Protozoal infections are missing fully (Podgwaite 1981). According to other authors (Glowacka 1983) viruses - nuclear polyhedrosis always prevails in Europe and it is accompanied by microsporidia. Next year the presence of two given pathogens is increasing and also fungal infections have significant share in the mortality. Our experiments indicate that each pathogen, excluding fungi, has its own dynamics and place in the complex of bioregulators in the dependance on developmental stages of pest and its population density. Activation and pathogenicity of viroses was the most expressive with older and mature caterpillars with the peak in the culmination phase of gradation. This period is optimal for mass development of disease. Solid infectious base of pathogen which is transferred and multiplied by previous populations has been already existing in the biotope of pest. This one is increased by the effect of pest maximal abundance. It is activated by physiological weakening of caterpillars resulting from advanced phase of gradation.

Pathogen infests not only larval stage but we observed also the ending of mortality in the pupa stage.

Bacteria had expressive affinity to the youngest caterpillars without regard to gradation phase. Their direct pathogenicity is questionable in several cases. Pathogens excluding obligatory pathogens are activated for infections effect with helpful factor (climatic, physiological,

etc.) (Weiser 1966). Mass presence of bacteria in the most sensitive period of pest development ( $L_{1-2}$ ) indicates that the portion of detected mortality need not have primary reason in bacteriosis.

The presence of mycoses was expressively irregular. It occurred only in season when unsteady, heavily rainy weather prevailed in the spring. Their effect can be connected rather with climatic conditions as with pest development and its population density.

Infections induced by microsporidia have own special mechanism. The speed and mortality of infection depends on the importance of organ which was infested by pathogen (Weiser 1976). Therefore it may happen that some part of individuals infested by pathogen survives but usually also pathogen survives and it is transported to following population by special mechanism.

The representation of pathogen in separate instars does not indicate more significant dependence on the pest development and did not induce pupae mortality at all. The mechanism of effect can be connected with gradation phase. The formation of infections base started by accumulation of pathogen in ecotype during initial periods of gradation. Pathogenicity appeared in progression through mass dying of larvae of middle age. Other individuals infested but not died finished their development to imagoes hatching. But females transported pathogen with their bodies' surface to egg layings. Then the youngest caterpillars were infested in hatching and mortality appeared in first instars. The mechanism was repeated also in regression. But important part of infections induced by microsporidia cannot be recorded statistically. In more advanced phases of gradation viroses are strongly activated with individuals also in the case when the individual is infested by microsporidium. Viroses have speed course and induce host mortality before microsporidia are able to develop into full form. Therefore also viruses with microsporidia are the most frequent components of mixed infections. With mixed infections incidence their unspecificity to developmental stages of pest can be observed but evident binding to its population density. It is logical that with rising abundance of pest and its weakening the supposition for mass presence of several pathogens is increasing. So the probability of their meeting in the body of one host is increasing too.

#### SUMMARY

On the basis of the observation of pathogens abundance and structure in the population of gypsy moth (*Lymantria dispar* L.) under the conditions of Central Europe during 3 - year period we can conclude that individual patho-

gens acting as bioregulators of this pest have their specific relations to instars of caterpillar, to developmental stage of pest or its population density in different gradation phases resp. Fungal infections are exclusion since with them this dependance was not asserted unanimously. Gained knowledge are basic source of information for the study of complex problems of the artificial control of pest population density through the introduction of entomopathogenic microorganisms.

#### ACKNOWLEDGEMENT

I thank Dr. Jaroslav Weiser, DrSc. for his help in determination of pathogens.

#### LITERATURE CITED

- Głowačka, B., 1983: Rola patogenow w przebiegu gradacji brudnicy nieparki (*Lymantria dispar* L.) na bagnach biebrzańskich w latach 1976-1978. Prace Instytutu Badawczego Lesnictwa, Poland No. 608/612, 29-42.
- Guliy, V.V.-Golosova, M.A., 1975: Virusy v zaščite lesa ot vrednych nasekomych. Moskva, Lesnaja promyšlennost', 166 p.
- Mihalache, G.-Pirvescu, D., 1980: Microorganismele in combaterea biologica a daunatorilor forestieri. Bucures-ti, Editura Cereres, 270 p.
- Novotný, J., 1986: Nový charakter kalamity mnišky veľko-hlavej (*Lymantria dispar* L.) v lesoch Slovenska. Zprávy lesníckého výzkumu, 31, 3, p. 26-29.
- Podgwaite, J.D., 1981: Natural disease within dense gypsy moth populations. In: Doane, C.C.-McManus, M.L. : The gypsy moth: research toward integrated pest management. US Dep. of Agric., Science and Education Agency APHIS, Technical Bulletin 1584, 757 p.
- Weiser, J., 1966: Nemoci hmyzu. Praha, Academia, 554 p.
- Weiser, J., 1976: Contribution to the classification of microsporidia. Věstník čs. společnosti zoologické 41, p. 308-320.
- Zelinskaja, L.M., 1980: Rol mikrosporidij v dinamike čislennosti neparného šelkoprvjada (*Portethria dispar* L.) v lesonasazdenjach nižnego pridneprovja. Vestnik zoologii 1, p. 57-62.

MATE-FINDING BEHAVIORS AND  
CHEMICAL COMMUNICATION IN THE  
LYMANTRIIDAE

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Mate finding among moths incorporates displacement movements which result in one sex flying or walking toward a signal emitted by the other sex. This communication routinely occurs over distances of several to perhaps hundreds of meters and it is mediated principally by airborne chemical signals. As yet no species of moth has been documented to rely solely on non-pheromonal cues in these 'long-distance' displacement activities, although in many examples either visual or in a few species auditory cues augment the chemical stimulus, particularly after the responding sex arrives within a range wherein these latter signals can be utilized.

In examining the organization of the pheromone communication systems of lymantriids and its probable selective value it will be instructive to compare the known cases in this family with the diversity of communication habits described in other moth groups. This approach allows us to consider explanations of how the reproductive biology and generally arboreal habitat of the lymantriids may have shaped their use of the chemical communication channel for mate location and recognition.

WHY ARE FEMALES THE EMITTERS AND MALES THE RESPONDERS?

In moths the 'resource-limited' sex is the female: beyond fertilization a male generally contributes nothing to his offspring, although in some species nutrient transfer to the female via the spermatophore can occur (Greenfield 1982), and in some species improve her fecundity (Goss 1979). Generally a female's reproductive success is related to the number of eggs produced, whereas the male's is tied to the number of matings procured and how many of his sperm are successful in fertilizing eggs. Males must therefore

vie for the available females. A male able to detect and orient to volatiles from a female would enhance his reproductive fitness by being able to find females more readily. This proposal was originally offered by Thornhill (1979) to explain the origin of male-produced pheromones in scorpionflies: in this group the males provide nutrients as saliva balls or prey which they proffer to their prospective mates. Such abilities, once acquired, could be improved by enhancing both sensitivity to pheromone and skill in maneuvering to its source. The same reasoning has been used to explain why in the preponderance of moth species it is the female, the resource-limited sex, that perches and emits pheromone (Cardé and Baker 1984), whereas the male assumes the energetically more expensive task of 'ranging' and pheromone-mediated flight with its attendant risk of predation.

While this rule seems to be satisfied amongst most moth species, remarkable and presumably more recently evolved exceptions are found. In the pyralid, the lesser wax moth (*Achroia grisella*), males attract females with sound created by wing vibration augmented by pheromone emitted from costal glands on the forewings (Spangler et al. 1984). A possible resource offered by the male is that he may be situated near or in bee's nests, wherein host food is to be found. Several arctiid moths have a dual strategy of attraction (Boppré 1986). Early in the evening, males of *Estigmene acrea* inflate immense coremata at the tip of their abdomens. The released pheromone attracts additional males which settle and also evert their coremata. These congregations also lure females who will mate with one of the displaying males. Later in the night the roles are reversed and, as is typical in most moths, males are attracted to pheromone-emitting females (Willis and Birch 1982). The males of these species may provide a nutritive contribution to egg production through the spermatophore, but this remains to be established.

These cases serve to illustrate some of the diversity of mate finding strategies among the more than 120,000 described species of moths. What is then somewhat surprising is the evident uniformity of the communication systems used by lymantriids, which are comprised of 2160 species worldwide (Holloway et al. 1987). To date all the described cases involve the presumed ancestral state of long-distance male attraction to females. It is possible that systems which diverge from this plan remain to be uncovered. But the fact that females of many species in the Lymantriidae are wingless or winged but flightless (e.g. certain gypsy moth, *Lymantria dispar*, populations) (Ferguson 1978) argues that in this family there is a pronounced history of female investment in eggs rather than flight. An emphasis on females as the resource-limited sex predicts male attraction to the female and of course in the species lacking female flight, male flight to the female is the only possible solution for long-range attraction. A possible

contribution of the male to female fecundity through a nutritive donation contained in the spermatophore is not verified in this family. Indeed, adult lymantriids lack functional mouthparts, and the females generally mate soon after eclosion and immediately lay their full complement of eggs, so that such a donation would be unexpected.

#### WHY DO LYMANTRIID MALES LACK COURTSHIP PHEROMONE?

None of the lymantriid species studied appear to utilize a male-produced pheromone to facilitate any aspect of courtship, although such signals are widely distributed throughout other moth groups. There is a diversity of morphologically divergent and therefore independently evolved scent-disseminating structures used by male moths in courtship (Birch 1974) and the lack of such structures in lymantriids is unexpected.

One explanation for the widespread occurrence of such male-produced courtship signals in moths is female-choice sexual selection (Baker and Cardé 1979, Phelan and Baker 1987). There remains some debate about how such signals originate, but one scenario posits females selecting males with 'better' behavioral traits for 'seduction.' In the ensuing generation this trait, which might be linked to some other aspect of inclusive fitness (Thornhill 1979) such as a male's nutritive contribution to his offspring or a female's fecundity, confers an advantage to her sons in courting 'choosy' females. Runaway sexual selection (O'Donald 1962) then rapidly fixes these characters in the species. There is no reason to suppose that male courtship pheromones cannot occur among the Lymantriidae, but if they do occur, their origin via this behavioral feature being linked initially to a male's nutritive contribution to his offspring or female fecundity seems unlikely. This disparity in sexual investment may explain the evident absence of male courtship pheromones in lymantriids, and suggests this factor as an explanation for their appearance in other moth groups.

The gypsy moth under natural conditions generally mates once (Doane 1968), although in dense populations remating may occur (Cardé and Hagaman 1984, see also Richerson et al. 1976). In general, multiple mating among lymantriids apparently occurs less frequently than among most Lepidoptera. Multiple mating has also been viewed as contributory to rapid sexual selection by female choice (Eberhard 1985).

## WHY ARE ATTRACTANTS FOR LYMANTRIIDS NOT COMPLEX BLENDS?

The known chemicals for male attraction and those that have been confirmed as being present in the female are given in Table 1 (after Arn et al. 1987). The compounds are unique in the sense that they do not appear to occur outside the Lymantriidae. Further, none of the many chemicals identified as attractant pheromones in other moth families have been found to lure male lymantriids (Arn et al. 1987). Finally, most of the pheromones identified appear to consist of only one or two components. In contrast, in other families of moths there is a paucity of such simple systems; blends typically consist of several to as many as 7 components, and component ratio is often crucial to attractivity.

Part of the explanation for the comparative simplicity of lymantriid pheromones may lie in the evident exclusivity of the chemicals employed by the relatively moderate number of species (2160) in this group. In contrast, blends of 12, 14, or 16 carbon chain-length acetates, alcohols or aldehydes with one or two double bonds generally characterize (Arn et al. 1987) the attractants of the species that have been investigated among the noctuids (340 of 21,000 species), tortricids (360 of 5,000 species) and pyralids (59 of 20,000 species) (tabulations of species by family in Holloway et al. 1987). Given the number of species in these latter three families using a relatively small number of compounds, exclusive communication channels would seem to necessitate complex blends.

A quite different explanation for the seeming simplicity of lymantriid pheromones, however, may lie in the methods used to characterize their chemistry and biological activity. Many of the species in the Noctuidae, Tortricidae and other families now accepted to utilize complex blends originally were characterized as having uncomplicated single or dual component systems. As the sophistication of analytical and bioassay techniques has advanced over the past 20 years, so too has the number of compounds attributed to their attractant pheromones.

In contrast, the pheromones of few lymantriid species have been characterized, and fewer still have been subjected to the scrutiny applied to several of the noctuids and tortricids. Thus the simplicity of the former systems may be deceptive. A final sampling problem is that the species so far examined are from temperate regions where this family is not rich in species. Such species assemblages would be less apt to have tightly-packed chemical communication channels characterized by complex blends (Cardé 1986).

Table 1. Sex pheromones (P)\* and attractants (A)\*\* of the Lymantriidae.

SPECIES	STATUS	STRUCTURE	REFERENCE
<i>Orgyia</i>			
<i>pseudotsugata</i>	P	Z6-21-11Ketone	Smith et al. 1975.
<i>leucostigma</i>	A	Z6-21-11Ketone	Grant 1977.
<i>antiqua</i>	A		Daterman et al. 1976.
<i>cana</i>	A		Daterman et al. 1976.
<i>Dasychira</i>			
<i>griseifacta ella</i>	A	Z6-21-11Ketone	Daterman et al. 1976.
<i>vagans grisea</i>	A		Daterman et al. 1976.
<i>plagiata</i>	A		Grant 1977.
<i>Lymantria</i>			
<i>dispar</i>	P	(+)cis7-8epoxy2Me-18Hy	Bierl et al. 1970 & Cardé et al. 1977.
<i>dispar japonica</i>	A	(±)cis7-8epoxy2Me-18Hy	Beroza et al. 1973a.
<i>monacha</i>	P	(+)cis7-8epoxy2Me-18Hy:10% (-)cis7-8epoxy2Me-18Hy:90%	Bierl et al. 1975 & Hansen 1984.
<i>fumida</i>	A	(±)cis7-8epoxy2Me-18Hy	Beroza et al. 1973a.
<i>obfuscata</i>	A		Beroza et al. 1973b.
<i>Euproctis</i>			
<i>similis xanthocampa</i>	P	Z7-18isovalerate	Tan et al. 1984.
<i>Gynsephora</i>			
<i>ginghainensis</i>	P	Z3, Z6, Z9-21Hy Z3, Z6, Z9-20Hy	Chen 1980.

From Arn et al. 1986.

\* Pheromones are defined here as sex attractants that have been verified as being produced by the female.

\*\* Attractants are defined solely by their ability to lure males.

concentration (Cardé and Hagaman 1979, Hagaman and Cardé 1984) and temperature (Cardé and Hagaman 1983).

Following exposure to the pheromone plume, male gypsy moths demonstrate four basic behavioral patterns that culminate in mating (Fig. 1): (1) pheromone-modulated anemotactic flight toward the odor source; (2) vertical flight in the immediate vicinity of the tree bole harboring the calling female, whereby the male intermittently contacts the bark with his tarsi; (3) landing on the trunk after which the male walks while wing fanning until he arrives at the female and; (4) contact with and recognition of the female with attendant expression of courtship behaviors that climax in copulation. Even though it is convenient to subdivide *L. dispar* precopulatory behaviors into such broad categories, it must be emphasized that these behaviors can cycle and some behaviors of the sequence may be omitted.

The most extensively studied orientation maneuvers in moths are those exhibited by males as they fly toward a pheromone source. Most current evidence supports a model which relies on the integration of two main mechanisms: (1) a chemically (pheromone) triggered and modulated, internally generated program of counterturns which cause the male to turn back and forth across the windline (Baker et al. 1984); and (2) an optomotor anemotaxis which once triggered by pheromone contact enables the male to judge wind direction and velocity by the visual perception of wind-induced drift, and steer his course accordingly (Kennedy and Marsh 1978, Marsh et al. 1976, David 1986). The integration of these mechanisms usually results in the generation of the typical zigzagging upwind flight track that is characteristic of the gypsy moth and most male moths observed to date (Baker 1985, Kennedy 1983). A more detailed examination of these mechanisms is presented in the next section of this chapter.

Although the in-flight maneuvers of male moths responding to plumes of female pheromone have been reasonably well studied, other aspects of orientation and mating behavior have received far less attention. For gypsy moth males, walking behavior constitutes another important element of the mate location process. Several studies have documented that once male gypsy moths land on trees, they navigate the intervening distance to the calling female or synthetic pheromone source by walking while wing fanning (Doane 1968, Richerson 1977, Cardé and Hagaman 1984). The resultant walking paths are characteristically convoluted, predominantly vertically directed, and may require several minutes to complete (Fig. 1).

Among the mechanisms which could enable the male to locate a calling female once he has landed are a pheromone-modulated anemotactic walk analogous to that used by flying males, a walk whose path is governed by a pre-programmed (central nervous system) search pattern, or a combination of these mechanisms. A more detailed examination of the behaviors and orientation mechanisms utilized by males

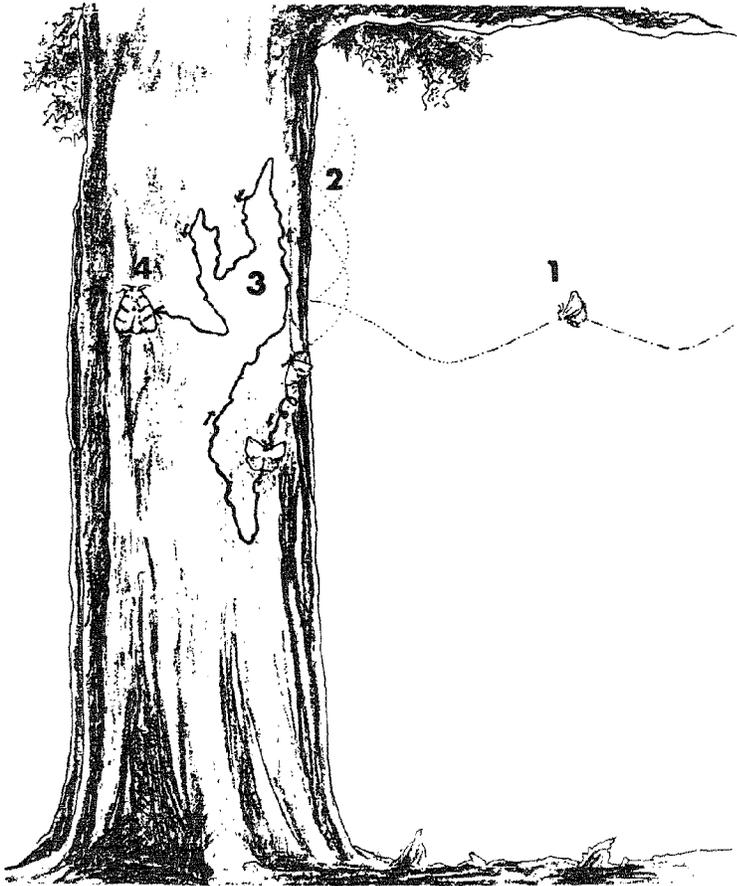


Fig. 1. Generalized sequence of male gypsy moth mate-seeking behaviors: (1) pheromone-modulated anemotactic flight toward the pheromone source; (2) vertical flight in the immediate vicinity of the tree bole harboring the calling female, whereby the male intermittently makes tarsal contact with the bark; (3) landing on the trunk after which the male walks while wing fanning until he arrives at the female and; (4) contact with and recognition of the female followed by mating (from Charlton 1988).

walking to a pheromone source will be presented in a following section of this chapter.

#### HOW DOES A FLYING MALE NAVIGATE A COURSE TO THE PHEROMONE SOURCE?

The orientation mechanisms utilized by male moths to locate sources of female pheromone have been the subject of research for many years, and recently have given rise to a number of contentious hypotheses to explain odor source location in moths. Currently the most accepted model for upwind flight to a female pheromone source involves the integration of two main mechanisms. The first is an internally generated (central nervous system) program of counterturns which is triggered by perception of the female pheromone and modulated by the quantity (concentration), quality (ratio of blend components), and the spatial and temporal nature of these chemical stimuli. The second major mechanism is an optomotor anemotaxis, that is, once the male has encountered female pheromone he turns into the wind and begins to displace upwind toward the source. The male judges wind velocity and direction visually by watching the ground pattern moving beneath him and compensating for wind-induced drift away from his steered course (Kennedy and Marsh 1974, Marsh et al. 1978, David 1986). The integration of these two main mechanisms yields the zigzagging flight track characteristic of male moths flying upwind to pheromone sources (Fig. 2).

Attempts to explain the adaptive value of the cross-wind counterturning resulted in a hypothesis (Kennedy 1983, Cardé 1984, Baker 1985) which proposes that the regular zigzagging typical of in-flight orientation is a mechanism whereby the males gain enhanced sensitivity to visually perceived, wind-induced drift. That is, by moving back-and-forth across the wind, the male makes himself more susceptible to being blown off course by the wind (like a sailboat tacking across the wind), thus enabling him to better see the wind-induced deviation and steer the appropriate maneuver to correct for wind direction and velocity. The ability to closely track the wind velocity and direction is extremely important in maintaining contact with a pheromone plume or regaining contact once the plume is lost in the constantly shifting winds experienced by flying male moths in nature.

Previously a pheromone plume had been envisaged to be aligned with the wind direction, such that in the field, an upwind heading would aim a flying organism toward the chemical source (e.g., Bossert and Wilson 1963). David et al. (1982, 1983) demonstrated that 'puffs' of pheromone-containing air emanating from a point source in an open, grassy field travel over 20 m in straight paths. As the

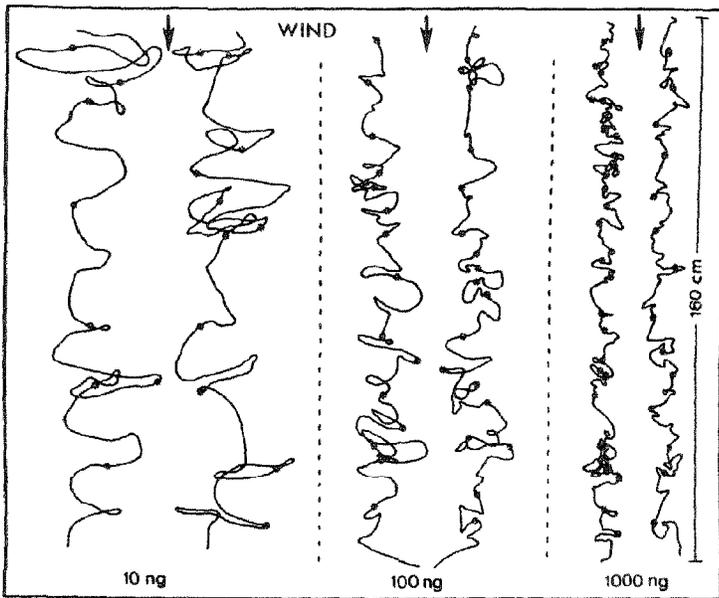


Fig. 2. Representative flight tracks of gypsy moth males flying to three different pheromone concentrations. Flight tracks were recorded in the plan view with the moth progressing from bottom to top (from Charlton et al. 1989e)

wind direction shifts the plume meanders, and the directions upwind and along the plume's centerline are no longer coincident. Gypsy moth males are able to successfully locate sources of female pheromone in this situation by initiating cross-wind casting behavior immediately following loss of pheromone. In fact, David et al. (1983) reported that the wide cross-wind counterturning, characteristic of casting behavior, enabled the males to relocate the pheromone plume closer to the source than where they had lost contact with it. In the forest habitat of the gypsy moth, however, the trajectory of pheromone puffs is non-linear, with a mean change of over 100 degrees within 20 m (Elkinton et al. 1987). The generally sinuous path of pheromone in a forest implies that a male in such habitats flying directly upwind often will be aimed away from the source, even though the mean direction of the wind tends toward the source.

One explanation for successful gypsy moth flight to pheromone over many meters is that progress toward the source occurs when the long axis of the pheromone plume and the wind are closely parallel. A moth encountering a plume aligned across the instantaneous wind and flying upwind would exit the plume. However, the wind direction is often consistent for intervals of several seconds or more (David et al. 1983, Elkinton et al. 1987), and it is during these episodes when plume segments are aligned with wind direction that substantial progress toward the source presumably occurs. In this view it is the consistency of wind direction and not the linearity of puff trajectory that determines the success of moth navigation (Elkinton et al. 1987).

Results of recent studies lend further support for the existence of an internal counterturn generator (Charlton et al. 1989e) and suggest that its function may be as hypothesized (Kennedy 1983, Cardé 1984, Baker 1985)--to enhance visual perception of wind-induced drift (Willis and Baker 1987). By comparing the maneuvers used by male *Grapholita molesta* (Tortricidae) to fly and walk to the same pheromone sources, Willis and Baker (1987) demonstrated that males walking upwind in a pheromone plume apparently did not zigzag along their tracks as flying males do. Not only were the angles steered by the walking males inconsistent with the zigzags of the flying male, there was no temporal regularity of intervals between turns as there is in flying males. Since walking males can perceive wind speed and direction via mechanoreceptors and steer directly upwind, they have no need of the hypothetical increase in sensitivity to visual cues provided to the flying males by counterturning across the windline. Charlton et al. (1989e) have demonstrated, using the gypsy moth, that the temporal regularity of counterturning in flying males is unaffected by variation in temperature. The turning frequency (a measure of the output of the counterturning program) is

likewise unaffected by the concentration of the pheromone plume.

The spatial and temporal nature of the chemical stimuli is also important for a male to make prolonged upwind progress toward, and to eventually locate the source. The necessity for intermittent, or pulsed pheromone stimulation for male moths to maintain prolonged upwind flight to the source, implied from earlier work (Kennedy et al. 1980, 1981, Willis and Baker 1984), has recently been verified (Baker et al. 1985). When *G. molesta* males were released in either a homogeneous cloud of pheromone or clean air, they were unable to make sustained upwind progress. However, when they were released into an airstream composed of alternating slices (spanning the tunnel from floor-to-ceiling and from side-to-side) of homogeneous pheromone and clean air they became activated, took flight and flew upwind in the zigzagging flight path typical of a *G. molesta* male orienting upwind to a point-source plume of pheromone. This illustrates the necessity for intermittent pheromone stimulation for prolonged upwind orientation to an odor source.

The ability of male gypsy moths and male moths in general to respond to an intermittent pheromone stimulus has recently been demonstrated at the central nervous system level. Olberg, Willis, and Cardé (in preparation) have shown that the nervous system of gypsy moth males is very responsive to an intermittent pheromone stimulus, continuing to show elevated firing rates for as long as intermittent pheromone stimuli were presented to the insect. Continuous stimulation with homogeneous pheromone elicited an initial increase in firing rate followed by a return to base line activity, even though the pheromone was still being presented to the preparation. Increased responsiveness to intermittent pheromone stimulation was observed from the antennae, the ventral nerve cord, and the thoracic ganglia, using both intracellular and extracellular recording techniques. A detailed examination of the ability of the central nervous system to respond to and encode intermittent stimulation has been undertaken with *Manduca sexta* (Christensen and Hildebrand, 1987). Interneurons in the deutocerebrum responded by firing bursts of spikes 1:1 with pheromone pulses at pulse rates as high as 10 Hz, and when pheromone was presented as random pulses. These findings indicate that the pheromone-specific areas of male moth brains are exquisitely sensitive to the intermittent pheromone stimulation that is characteristic of the typical point-source pheromone plume.

Sex attractant pheromones of moths commonly consist of multicomponent blends and are often composed of geometric isomers (Tamaki 1985). The specificity of the female emission and male response to these blends is often thought to be responsible for species specificity in communication. As noted previously, blends of geometric isomers have not been encountered in the Lymantriidae, although many of the

known pheromone compounds possess a chiral center and thus exist in two enantiomeric forms.

After it was discovered that the (+)-enantiomer of disparlure was far more effective as an attractant than the previously employed (±)-disparlure, the effect of the (-)-enantiomer on male orientation behavior has been explored. Field trapping studies using synthetic pheromone sources with differing ratios of (+)- to (-)-disparlure showed that increased amounts of the (-)-enantiomer resulted in decreased trap catch (Cardé et al. 1977). Behavioral observations indicated that fewer males approached the traps and those that did exhibited rapid and disorganized zigzagging flight with relatively little landing and wing fanning on the traps (Cardé et al. 1977). Later wind tunnel studies showed that gypsy moth males did not persist as long in their upwind flight in plumes with higher proportions [up to 90:10 (-):(+)] of the (-)-enantiomer as they did in plumes of pure (+)-disparlure (Miller and Roelofs 1978), and that males flew significantly slower in pheromone plumes with high ratios [up to 50:50 of (-):(+)] (Cardé and Hagaman 1979). In testing the ability of tethered gypsy moths to respond to visual patterns and maintain altitude, Preiss and Kramer (1983) found that when a male being stimulated by (+)-disparlure was also exposed to the (-)-enantiomer, the latter blocked the male's ability to stabilize his altitude using optomotor cues. Another way to interpret these results would be to suggest that Preiss and Kramer (1983) were recording the males' attempts to leave a plume with the wrong pheromone component blend.

It seems probable that the high proportion of (-)-disparlure present in the pheromone glands of *L. monacha* females could be important in maintaining species isolation where these species are sympatric. Detailed studies are necessary to determine how increased proportions of the (-) enantiomer of disparlure affect the flight maneuvers of free-flying gypsy moth males.

Although its importance to source location has fluctuated from irrelevance (Farkas and Shorey 1972) to omnipotence (Kennedy and Marsh 1974), the necessity of the optomotor response to detect the moth's movement in relation to the visual field is now known to be of primary importance to successful upwind orientation to an odor plume (Kennedy 1983, 1986, Baker 1986). Even though its importance is widely recognized, few studies have concentrated solely on experimentally determining the significant stimulus parameters (spatial wave length of the pattern, velocity of pattern movement, most sensitive region within the visual field), and their effects on flight behavior.

It is not known precisely what areas of moths eyes are most sensitive to optomotor stimulation. Collett and Blest (1966) recorded extracellular activity in the optic lobe of a sphinx moth (*Sphinx linguistri*) brain as they manipulated the visual field, and found that the receptive fields subtended most of the eye and that all parts of the field

were directionally selective. In experiments using tethered gypsy moths, Preiss and Kramer (1983) have, by restricting the area of a visual pattern visible to the moth, demonstrated that the tethered moths movements to adjust altitude were made in response to movement in the lateral parts of the visual field. Tethered gypsy moths attempted to adjust their flight speed when the frontal part of their visual field was stimulated by pattern movement (Preiss and Kramer 1983). As in other experiments with tethered or restrained insects, these results need to be verified with free-flying moths. Sanders et al. (1981) found that males of the spruce budworm moth (*Christoneura fumiferana*) were relatively unresponsive to a moving floor pattern, but were extremely sensitive to a moving visual pattern on the ceiling.

Thus the information available for optomotor response in flying moths indicates that (1) the entire eye may be sensitive to optomotor stimuli (Collett and Blest 1966); (2) separate sub-sections of the eye in tethered gypsy moths are sensitive to different movements (Preiss and Kramer 1983); and (3) in another moth inhabiting a forest environment (which has ample visual stimulation available on all sides), the males are more sensitive to optomotor stimulation from above than from below (Sanders et al. 1981).

#### WHAT LIMITS THE DISTANCE OF PHEROMONE COMMUNICATION?

The renowned sensitivity of male moths to pheromone has been based largely upon accounts of males being lured to females over many kilometers (Bossert and Wilson 1963), although careful scrutiny of the procedures involved and the times between release and arrival at the female offer tenuous support to the notion that the males detected and oriented upwind to pheromone at the distance at which they were released. Two of the experiments sometimes cited as examples of long-distance signalling involve the gypsy moth (Forbush and Fernald 1896, Collins and Potts 1932). But the time intervals between release and arrival are far longer than direct flight to the source would suggest and in the Collins and Potts experiments in which males were lured to females on coastal islands, anemotactic flight over open sea would seem impossible because there would be few of the visual cues so necessary to the optomotor navigation, as described previously.

In recent experiments in a forest, released male gypsy moths rarely flew directly to the pheromone source 20 m or more away and but a small proportion of males reached the pheromone source when released at distances of 120 m, even though they could routinely detect the presence of pheromone at such distances as verified by the wing-fanning bioassay (Elkinton et al. 1987). The disparity between detection of

and ability to navigate a course to the pheromone source has been explained by the fact that the wind direction shifts frequently in the forest and the direction upwind and the direction toward the pheromone source are rarely congruous even within 5-10 m of the origin of the pheromone. Thus the major restriction to mate finding over long distances is meteorological and not readily circumvented by enhancing the rate of pheromone emission or diminishing the threshold of response (Elkinton et al. 1987).

#### HOW DOES A LANDED MALE LOCATE A FEMALE?

After a male alights on a tree trunk or branch upon which the female is calling, he negotiates the intervening distance to the female through an elaborate and often prolonged array of walking maneuvers (Fig. 1). Field observations indicate that several lymantriids including *L. monacha* (Schröter 1976), and *L. dispar* (Richerson 1977; Cardé and Hagaman 1984) display these walking behaviors but the cues and mechanisms inherent to this process have been systematically evaluated only in the case of the gypsy moth. Studies on *L. dispar* (Preiss and Kramer 1986) and several moth species in other families (Shorey and Farkas 1973, Kramer 1975, Willis and Baker 1987) have shown that males walking on horizontal surfaces orient anemotactically upwind in predominantly straight-line paths when stimulated by pheromone. Under natural conditions, however, gypsy moth, nun moth, and possibly other lymantriid males walk primarily on vertical objects such as tree trunks where the calling females are generally found. In addition, the variable wind field and attendant pheromone dispersion patterns prevalent in a forest mean that a walking male probably experiences frequent or lengthy intervals out of the pheromone plume.

Charlton et al. (1989d) used a locomotion compensator (servosphere) to decipher the behavioral responses of male gypsy moths exposed to various temporal pheromone stimulation patterns while walking on a vertical surface. The results indicated that even on a vertical surface, males displayed positive anemotaxis when they were in a pheromone plume (Fig. 3). When pheromone stimulation was interrupted either by still air or a clean (pheromone-free) airstream, males exhibited an area-restricted local search characterized by primarily vertical or oblique movements with frequent reversals in direction (Fig. 3). During these movements, the males wing fan almost constantly and the body axis is aligned vertically with the head upward; downward movements are accomplished by the male backing down.

The behavioral reactions elicited by loss of pheromone may serve at least a dual function. First, walking in a vertical plane should enhance the likelihood of recontacting

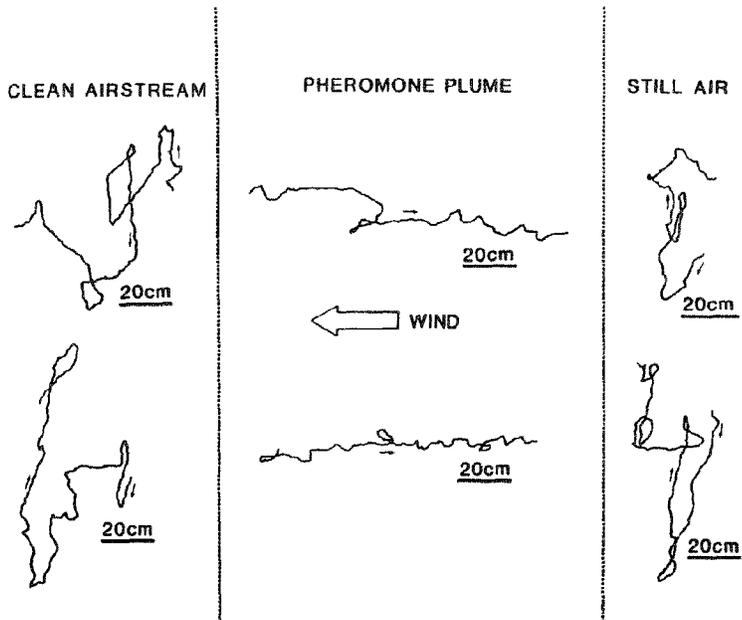


Fig. 3. Typical tracks of walking male gypsy moths in response to a pheromone plume (100 ng (+)-disparlure) or still air or a clean (pheromone-free) airstream following interruption of pheromone stimulation. Pathways were recorded on a vertical surface using a locomotion compensator (from Charlton et al. 1989d).

the plume since, for the most part, wind in the forest flows parallel to the ground. This response may therefore be functionally analogous to the across-wind casting maneuvers displayed by flying moths when they lose the odor plume. Second, during the course of these movements, males can encounter a female by accident: once a male contacts a female with his tarsi, copulatory behavior is released by structural attributes of the scales and mating quickly follows (see next section).

Although never explored experimentally in lymantriids, the wing fanning may abet the orientation process by actively sampling the odor plume. Investigations on other moths have shown that wing fanning serves to draw air over the antennae (Obara 1979). It is possible that within a few centimeters of the female, wing fanning could redirect the pheromone plume, provided that the force generated by the wings exceeds that of the wind.

Because the white female gypsy moths contrast markedly with the typically dark background of their calling sites, it is tempting to assume that the males would rely on vision to orient to the female. At least for the gypsy moth, however, the evidence indicates that visual stimuli presented by the female do not influence the male's choice of landing site nor do they facilitate more efficient walking orientation to the female (Charlton and Cardé 1989a). Since male gypsy moths possess well developed tympana sensitive to ultrasound (Baker and Cardé 1978; Cardone and Fullard 1988) and superposition compound eyes (Brown et al. 1977), it has been proposed (Charlton and Cardé 1989a) that gypsy moths were originally nocturnal and that mate location strategies tailored to a dark environment were retained when they shifted to their present diurnal habit, thus explaining the lack of visual response. An alternate hypothesis (R. Webb, personal communication) suggests that the reason for not relying on visual orientation is that in dense populations there are numerous mated females (as many as hundreds per tree) but perhaps only a few are virgins emitting pheromone. In such outbreak populations dependence on visual cues could be quite ineffective.

#### HOW DO MALES RECOGNIZE FEMALES AT CLOSE RANGE?

A male that has arrived in the vicinity of a female must still successfully execute courtship behaviors, thereby recognizing and gaining acceptance by the female in order to initiate copulation. Based on studies examining several lymantriid species (Doane 1968, Schröter 1976, Grant 1981, Swaby et al. 1987, Charlton and Cardé 1989b), the generalized sequence of male precopulatory behaviors can be summarized as follows. After nearing the calling female,

the male approaches while wing fanning and walking and contacts the female usually first with the tarsi, followed by the antennae. Almost immediately following this initial contact, the male moves alongside the female and begins to flex his abdomen at almost a right angle toward the female while exposing his claspers as he attempts to copulate. Mating quickly ensues and, interestingly, copulating lymantriids remain facing in the same direction rather than assuming the end-to-end or opposed position characteristic of many other moths.

The factors associated with the female that elicit male copulatory behaviors have been explored in detail in two lymantriids, *L. dispar* and *O. leucostigma*. By applying various attributes of female gypsy moths to surrogate models (supplemented with pheromone) and assaying male response, Charlton and Cardé (1989c) found that abdominal and forewing scales evoked male copulatory behavior, as has been reported for other moths (Ono 1977, 1981, Shimizu and Tamaki 1980, Grant 1987). Extracting the scales with various organic solvents did not diminish the male response, whereas pulverizing the scales to destroy their structural characteristics eliminated their activity. Thus, tactile cues from the scales perceived via the tarsi provide the recognition cues needed to initiate the copulatory attempt. Copulatory behavior can occur in the absence of the attractant pheromone, provided the male is stimulated by pheromone in an earlier stage of behavior, such as flight or walking, before he contacts the females' scales (Charlton and Cardé 1989c).

The scales of the female whitemarked tussock moth also release the copulatory attempt of the male (Grant 1981). This response is mediated in part by structural attributes of the scales, but the scales also provide a chemical stimulus which releases male copulatory behavior: four straight-chain alkanes extracted from the scales, n-tricosane, n-tetracosane, n-pentacosane, and n-heptacosane, evoke copulatory attempts when presented on a substrate that has a suboptimal tactile surface (Grant et al. 1987). This represents the first report in moths of chemicals (other than those released from the pheromone gland) that function as a copulation-releaser pheromone.

The question arises whether these recognition cues are effective in maintaining reproductive isolation between species? Schröter (1976) observed courtship between *L. dispar* and *L. monacha* and found that these congeners readily attempted to mate with each other, although matings were never successful; Schröter and other authors have attributed the failure to mate to genitalic incompatibility. Indeed, male moths of several species have been shown to respond with copulatory behavior when offered the scales of other, often distantly related species (Ono 1977, Shimizu and Tamaki 1980), suggesting that the response is quite ubiquitous and non-specific and probably not sufficient to effect reproductive isolation.

The factors beyond attractant pheromone that induce copulation are of particular interest because of the unexplored possibility that they play a role in reproductive isolation and because of their potential contribution to mate finding when long-distance communication is thwarted due to the omnipresence of synthetic pheromone applied as a mating disruptant.

#### CONCLUSION

The family-level characteristics of the pheromone signalling system used by lymantriids appear to have undergone no divergence from the presumed ancestral plan: a female-emitted pheromone to lure the male. Further there is no evidence yet in any species of a male-produced courtship pheromone. These features seem explicable in terms of the females' status as the resource-limited sex and the females' tendency to mate once. However, as the number of species examined increases, these trends may prove to have been deceptively simplistic.

Our diagnosis of the structure of the pheromone communication systems in lymantriids and the probable selective forces promoting this plan have been based upon detailed studies of but a small fraction of the species in this family. Chemical verification of the female-produced pheromone has been accomplished in fewer than 1% of the described species. These have been generally temperate in distribution and possessing few potential 'competitors' for their pheromone communication channel. A verification of these trends among the lymantriids of the Old World tropics, where this group is supposed to have originated and where species diversity is high, would provide convincing support for these suppositions or, alternatively, new paradigms to be tested.

Our comprehension of the orientation maneuvers used by moths to fly to the vicinity of a pheromone source, land and then navigate the last decimeters to the chemical's source have relied heavily on one lymantriid, the gypsy moth, as an experimental resource. The notion that some male moths, with the gypsy moth oftentimes cited as an exemplar, are attracted to females over distances of kilometers is not substantiated by direct experimentation.

When the male is engulfed by an above threshold concentration of pheromone, the principal orientation maneuver involved in flying to a female includes upwind anemotaxis. Because in a forest environment the directions upwind and toward the pheromone source are only infrequently aligned, especially as the distance from the source increases, this orientation strategy must be coupled with crosswind casting or other flight maneuvers that have the

effect of allowing a male to recontact the pheromone plume following shifts in wind direction.

The walking maneuvers that follow landing near the pheromone source have been studied in detail only in the gypsy moth. Because of the variable wind direction of a pheromone source on a tree bole, a male cannot routinely use walking anemotaxis; instead he employs a 'preprogrammed' path and recognizes the female by tactile cues following tarsal contact. Mate recognition by the whitemarked tussock moth is released by a combination of tactile and contact chemical cues from the female's scales.

The typically arboreal habitat of lymantriids has created formidable meteorological constraints to an organism either flying or walking continuously upwind to a pheromone source. Evolution of strategies to contend with the vagaries of wind shifts in such a turbulent environment have dictated maneuvers that allow males to recontact a lost scent, or in the case of a landed male at close range, to find a female in the absence of pheromone. It thus may be that a male's ability to contend with these stochastic and variable wind shifts is the limiting factor in an optimal strategy of mate finding.

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## LITERATURE CITED

- Arn, H., M. Tóth and E. Priesner. 1986. *List of sex pheromones of Lepidoptera and related attractants*. International Organization Biological Control, Paris.
- Baker, T.C. 1985. Chemical control of behavior. In, *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. (G.A. Kerkut and L.I. Gilbert, eds.) pp. 621-672. Pergamon Press, Oxford.
- Baker, T.C. 1986. Pheromone-modulated movements of flying moths. In, *Mechanisms in Insect Olfaction* (T.L. Payne, M.C. Birch and C.J.E. Kennedy, eds.) pp. 39-48. Clarendon Press, Oxford.
- Baker, T.C. and R.T. Cardé. 1978. Disruption of gypsy moth male sex pheromone behavior by high frequency sound. *Environ. Entomol.* 7: 45-52.
- Baker, T. C. and R.T. Cardé. 1979. Courtship behavior of the oriental fruit moth (*Grapholitha molesta*): experimental analysis and consideration of the role of sexual selection in the evolution of courtship pheromones in the Lepidoptera. *Ann. Entomol. Soc. Am.* 72: 173-188.
- Baker, T.C., M.A. Willis and P.L. Phelan. 1984. Optomotor anemotaxis polarizes self-steered zigzagging in flying moths. *Physiol. Entomol.* 9: 365-376.
- Baker, T.C., M.A. Willis, K.F. Haynes, and P.L. Phelan. 1985. A pulsed cloud of sex pheromone elicits upwind flight in male moths. *Physiol. Entomol.* 10: 257-265.
- Beroza, M., K. Katagiri, Z. Iwata, H. Ishizuka, S. Suzuki and B.A. Bierl. 1973a. Disparlure and analogues as attractants for two Japanese lymantriid moths. *Environ. Entomol.* 2: 966.
- Beroza, M., A.A. Punjabi and B.A. Bierl. 1973b. Disparlure and analogues as attractants for *Lymantria obfuscata*. *J. Econ. Entomol.* 66: 1215-1216.
- Bierl, B.A., M. Beroza and C.W. Collier. 1970. Potent sex attractant of the gypsy moth: its isolation, identification and synthesis. *Science.* 170: 87-89.
- Bierl, B.A., M. Beroza, V.E. Adler, G. Kasang, H. Schröter and D. Schneider. 1975. The presence of disparlure, the sex pheromone of the gypsy moth, in the female nun moth. *Z. Naturforsch.* 30c: 672-675.

- Birch, M.C. 1974. Aphrodisiac pheromones in insects. In, *Pheromones* (M.C. Birch, ed.). pp. 115-134. North Holland, Amsterdam
- Boppré, M. 1986. Insects pharmacophagously utilizing defensive plant chemicals (pyrrolizidine alkaloids). *Naturwissenschaften*.
- Bossert, W.H. and E.O. Wilson. 1963 The analysis of olfactory communication among animals. *J. Theo. Biol.* 5:443-469.
- Brown, E.A. and E.A. Cameron. 1977. Studies of the compound eye of *Lymantria dispar* (Lepidoptera: Lymantriidae) males, and behavioral implications. *Can. Entomol.* 109: 255-260.
- Cardé, R.T. 1984. Chemo-orientation in flying insects. In *Chemical Ecology of Insects*. (W.J. Bell and R.T. Cardé, eds.). pp. 111-124. Chapman and Hall, London.
- Cardé, R.T. 1986. The role of pheromones in reproductive isolation and speciation in insects. In, *Evolutionary genetics of invertebrate behavior* (M.D. Huettel, ed.). pp. 303-317. Plenum, New York.
- Cardé, R.T. and T.E. Hagaman. 1979. Behavioral responses of the gypsy moth in a wind tunnel to air-borne enantiomers of disparlure. *Environ. Entomol.* 8: 475-484.
- Cardé, R.T. and T.E. Hagaman. 1983. Influence of ambient and thoracic temperatures upon sexual behavior of the gypsy moth, *Lymantria dispar*. *Physiol. Entomol.* 8:7-14.
- Cardé, R. T. and T.C. Baker. 1984. Sexual communication with pheromones. In, *Chemical Ecology of Insects* (W.J. Bell and R.T. Cardé, eds.). pp. 355-383. Chapman and Hall, London.
- Cardé, R.T. and T.E. Hagaman. 1984. Mate location strategies of gypsy moths in dense populations. *J. Chem. Ecol.* 10: 25-31.
- Cardé, R.T., C.C. Doane, T.C. Baker, S. Iwaki and S. Marumo. 1977. Attractancy of optically active pheromone for male gypsy moths. *Environ. Entomol.* 6: 768-772.
- Cardone, B. and J.H. Fullard. 1988. Auditory characteristics and sexual dimorphism in the gypsy moth. *Physiol. Entomol.* 13: 9-14.

- Charlton, R.E. 1988. Pheromone-mediated flying and walking orientation and factors promoting mate recognition in the gypsy moth, *Lymantria dispar* (L.). Ph.D. Dissertation. University of Massachusetts, Amherst, Massachusetts.
- Charlton, R.E. and R.T. Cardé. 1989a. Orientation of male gypsy moths, *Lymantria dispar* (L.) to pheromone sources: the role of olfactory and visual cues. *J. Insect Behav* (submitted).
- Charlton, R.E. and R.T. Cardé. 1989b. Behavioral interactions in the courtship of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). *Ann. Entomol. Soc. Am.* (submitted).
- Charlton, R.E. and R.T. Cardé. 1989c. Factors mediating mate recognition and copulatory behavior in the male gypsy moth, *Lymantria dispar* (L.). *Physiol. Entomol.* (submitted).
- Charlton, R.E., W.J. Bell, and R.T. Cardé. 1989d. Effect of temporal pheromone stimulation patterns on vertical and horizontal walking orientation in male gypsy moths, *Lymantria dispar* (L.). *Physiol. Entomol.* (submitted).
- Charlton, R.E., H. Kanno, R.D. Collins and R.T. Cardé. 1989e. Influence of pheromone concentration and ambient temperature on flight of the gypsy moth, *Lymantria dispar*, in a sustained-flight wind tunnel. *Physiol. Entomol.* (in press).
- Chen, T.M. 1980. Present status of insect pheromones in China. *XVI Int. Cong. Entomol.* Kyoto. (structures not in abstract).
- Christensen, T.A. and J.G. Hildebrand. 1987. Frequency dependent responses to pulsed sex pheromone stimulation in central olfactory neurons of *Manduca sexta*. *Soc. Neurosci. Abstr.* 13: 139.
- Collett, T.S. and A.D. Blest. 1966. Binocular, directionally selective neurones, possibly involved in the optomotor response of insects. *Nature.* 212: 1330-1333.
- Collins, C.W. and S.F. Potts. 1932. Attractants for the flying gypsy moths as an aid in locating new infestations. *U.S.D.A. Tech. Bull.* 336. 43 p.
- Daterman, G.E., L.J. Peterson, R.G. Robbins, L.L. Sower, G.D. Daves, Jr. and R.G. Smith. 1976. Laboratory and field bioassay of the Douglas-fir tussock moth pheromone, (Z)-6-heneicosen-11-one. *Environ. Entomol.* 5: 1187-1190.

- David, C.T. 1986. Mechanisms of directional flight in wind. In, *Mechanisms in Insect Olfaction* (T.L. Payne, M.C. Birch and C.J.E. Kennedy, eds. pp. 49-57. Clarendon Press, Oxford
- David, C.T., J.S. Kennedy, A.R. Ludlow, J.N. Perry and C. Wall. 1982. A reappraisal of insect flight towards a distant point source of wind-borne odor. *J. Chem. Ecol.* 8: 1207-1215.
- David, C.T., J.S. Kennedy and A.R. Ludlow. 1983. Finding of a sex pheromone source by gypsy moths released in the field. *Nature* 303: 804-806.
- Doane, C.C. 1968. Aspects of mating behavior of the gypsy moth. *Ann. Entomol. Soc. Am.* 61: 768-773.
- Eberhard, W.G. 1985. *Sexual selection and animal genitalia*. Harvard, Cambridge. 244 p.
- Elkinton, J.S., C. Schal, T. Ono and R.T. Cardé. 1987. Pheromone puff trajectory and upwind flight of male gypsy moths in a forest. *Physiol. Entomol.* 12: 399-406.
- Farkas, S. R. and H.H. Shorey. 1972. Chemical trail following by flying insects: a mechanism for orientation to a distant odor source. *Science*. 178: 67-68.
- Ferguson, D.C. 1978. In, *Lymantriidae, Fasc. 22.2, The Moths of America North of Mexico*. E.W. Classey, Faringdon, England.
- Forbush, E.H. and C.H. Fernald. 1896. *The gypsy moth*. Wright and Potter, Boston.
- Goss G.J. 1979. The interaction between moths and plants containing pyrrolizidine alkaloids. *Environ. Entomol.* 8: 487-493.
- Grant, G.G. 1977. Interspecific pheromone responses of tussock moths and some isolating mechanisms of eastern species. *Environ. Entomol.* 6: 739-742.
- Grant, G.G. 1981. Mating behavior of the whitemarked tussock moth and role of female scales in releasing male copulatory attempts. *Ann. Entomol. Soc. Am.* 74: 100-105.

- Grant, G.G. 1987. Copulatory behavior of spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae): experimental analysis of the role of the sex pheromone and associated stimuli. *Ann. Entomol. Soc. Am.* 80: 78-88.
- Grant, G.G., D. Frech and D. Grisdale. 1975. Tussock moths: pheromone cross stimulation, calling behavior, and effect of hybridization. *Ann. Entomol. Soc. Am.* 68: 519-524.
- Grant, G.G., D. Frech, L. MacDonald, K.N. Slessor, and G.G.S. King. 1987. Copulatory releaser pheromone in body scales of female whitemarked tussock moth, *Orgyia leucostigma* (Lepidoptera: Lymantriidae): identification and behavioral role. *J. Chem. Ecol.* 13: 345-356.
- Greenfield, M.D. 1982. The question of paternal investment in Lepidoptera: male-contributed proteins in *Plodia interpunctella*. *Int. J. Insect Reprod.* 5: 323-330.
- Hagaman, T.E. and R.T. Cardé, 1984. Effect of pheromone concentration on organization of preflight behaviors of male gypsy moth, *Lymantria dispar*. *J. Chem. Ecol.* 10: 17-23.
- Hansen, K. 1984. Discrimination and production of disparlure enantiomers by the gypsy moth and the nun moth. *Physiol. Entomol.* 9: 9-18.
- Holloway, J.D., J.D. Bradley and D.J. Carter. 1987. *CIE Guides to Insects of Importance to Man. 1. Lepidoptera.* CAB International Inst. Entomol., London. 262 p.
- Iwaki, S., S. Marumo, T. Saito, M. Yamada and K. Katagiri 1974. Synthesis and activity of optically active disparlure. *J. Am. Chem Soc.* 96: 7842-7846.
- Kennedy, J.S. 1983. Zigzagging and casting as a programmed response to wind-borne odour: a review. *Physiol. Entomol.* 8: 109-120.
- Kennedy, J.S. 1986. Some current issues in orientation to odour sources. In, *Mechanisms in Insect Olfaction* (T.L. Payne, M.C. Birch and C.J.E. Kennedy, eds.) pp. 12-25. Clarendon Press, Oxford.
- Kennedy, J.S. and D. Marsh. 1974. Pheromone-regulated anemotaxis in flying moths. *Science.* 184: 999-1001.
- Kennedy, J.S., A.R. Ludlow and C.J. Sanders. 1980. Guidance system used in moth sex attraction. *Nature.* 288: 475-477.

- Kennedy, J.S., A.R. Ludlow and C.J. Sanders. 1981. Guidance of flying male moths by wind-borne sex pheromone. *Physiol. Entomol.* 6: 395-412.
- Klimetzek, D., G. Loskant, J.P. Vité and K. Mori. 1976. Disparlure: differences in pheromone perception between gypsy moth and nun moth. *Naturwissenschaften* 63: 581-582.
- Kramer, E. 1975. The orientation of the male silkmoth to the sex attractant bombykol. In, *Olfaction and Taste*, Vol. V. (D.A. Denton and J.P. Coghlan, eds.) pp. 329-335. Academic Press, New York.
- Marsh, D., J.S. Kennedy and A.R. Ludlow. 1978. An analysis of anemotactic zigzagging flight in male moths stimulated by pheromone. *Physiol. Entomol.* 3: 221-240.
- Miller, J.R., and W.L. Roelofs. 1978. Gypsy moth responses to pheromone enantiomers as evaluated in a sustained-flight tunnel. *Environ. Entomol.* 7: 42-44.
- Miller, J.R., K. Mori and W.L. Roelofs. 1977. Gypsy moth field trapping and electroantennogram studies with pheromone enantiomers. *J. Insect Physiol.* 23: 1447-1453.
- Obara, Y. 1979. *Bombyx mori* mating dance: an essential in locating the female. *Appl. Entomol. Zool.* 14: 130-132.
- O'Donald, P. 1962. The theory of sexual selection. *Heredity.* 17: 541-552.
- Ono, T. 1977. The scales as a releaser of the copulatory attempt in Lepidoptera. *Naturwissenschaften* 64: 388.
- Ono, T. 1981. Factors releasing the copulatory attempt in three species of Phycitidae (Lepidoptera: Phycitidae). *Appl. Entomol. Zool.* 16: 24-28.
- Phelan, P.L. and T.C. Baker 1987. Evolution of male pheromones in moths: reproductive isolation through sexual selection. *Science.* 235: 205-207.
- Preiss, R. and E. Kramer. 1983. Stabilization of altitude and speed in tethered flying gypsy moth males: influence of (+) and (-)-disparlure. *Physiol. Entomol.* 8: 55-68.
- Preiss, R. and E. Kramer. 1986. Anemotactic orientation of gypsy moth males and its modification by the attractant pheromone (+)-disparlure during walking. *Physiol. Entomol.* 11: 185-198.

- Richerson, J.V. 1977 Pheromone-mediated behavior of the gypsy moth. *J. Chem. Ecol.* 3: 291-308.
- Richerson, J.V., E.A. Cameron and E.A. Brown. 1976. Sexual activity of the gypsy moth. *Am. Midl. Nat.* 95: 299-312.
- Roelofs, W.L. and R. T. Cardé. 1974. Sex pheromones in the reproductive isolation of lepidopterous species. In, *Pheromones*. (M.C. Birch, ed.) pp. 96-114. North Holland, Amsterdam.
- Sanders, C.J., G.S. Lucuik and R.M. Fletcher. 1981. Responses of male spruce budworm (Lepidoptera: Tortricidae) to different concentrations of sex pheromone as measured in a sustained-flight wind tunnel. *Can. Entomol.* 113: 943-948.
- Schaefer, P.W. 1974. Population ecology of the browntail moth (*Euproctis chrysorrhoea* L.) (Lepidoptera: Lymantriidae) in North America. Ph.D. Dissertation, University of Maine, Orono, Maine.
- Schröter, H.-J. 1976. *Lymantria* (*Porthetria*): Isolationmechanismen im Paarungsverhalten von Nonne und Schwammspinner. Inaugural dissertation, University of Freiburg.
- Schröter, H.-J. 1981. Untersuchungen zur Tagesperiodik der Bewegungsaktivität von *Lymantria monacha* L.- und *Lymantria dispar* L.-Männchen. *Mitt. Deut. Gesell. Allg. Angew. Entomol.* 3: 268-274.
- Schröter, H.-J. and R. Lange. 1975. Untersuchungen über Einfluss des weiblichen Sexualpheromons auf die Flugaktivität der Männchen von *Lymantria monacha* L. im Freiland. *Z. Angew. Entomol.* 77: 337-341.
- Shorey, H.H. and S.R. Farkas. 1973. Sex pheromones of Lepidoptera. 42. Terrestrial odor-trail following by pheromone-stimulated males of *Trichoplusia ni*. *Ann. Entomol. Soc. Am.* 66: 1213-1214.
- Shimizu, K. and Y. Tamaki. 1980. Releasers of the male copulatory attempt in the smaller tea tortrix moth (Lepidoptera: Tortricidae). *Appl. Entomol. Zool.* 15: 140-150.
- Smith, R.C., G.E. Daterman and G.D. Daves, Jr. 1975. Douglas-fir tussock moth: sex pheromone identification and synthesis. *Science.* 188: 63-64.

- Spangler, H.G., M.D. Greenfield and A. Takessian. 1984. Ultrasonic mate calling in the lesser wax moth. *Physiol. Entomol.* 9: 87-95.
- Swaby, J.A., G.E. Daterman, and L.L. Sower. 1987. Mating behavior of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae), with special reference to effects of female age. *Ann. Entomol. Soc. Am.* 80: 47-50.
- Tamaki, Y. 1985. Sex pheromones. In, *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. (G.A. Kerkut and L.I. Gilbert, eds.) pp. 145-189. Pergamon Press, Oxford.
- Tan Zhong-Xin, Wu Yun-Wei, Lin Guo-Qiang, Wu Bi-Chi, Liu Han-Quan, Xu Xiao-Yun, Zhou Wei-Schan, Pu Guan-Qin and Zhang Min-Shen. 1984. Study on identification and synthesis of insect pheromone. XVII. The sex pheromone of *Euproctis similis xanthocampa*. *Acta Chimica Sinica.* 42: 1178-1182.
- Thornhill, R. 1979. Male and female sexual selection and the evolution of mating strategies in insects. In, *Sexual Selection and Reproductive Competition in Insects*. (M. Blum and N. Blum, eds.) pp. 81-121. Academic Press, New York.
- Wagner, T.L. and D.L. Leonard. 1979. Aspects of mating, oviposition, and flight in the satin moth, *Leucoma salicis* (Lepidoptera: Lymantriidae). *Can. Entomol.* 111: 833-840.
- Willis, M.A. and M.C. Birch. 1982. Male lek formation and female calling in a population of the arctiid moth *Estigmene acraea*. *Science.* 218: 168-170.
- Willis, M.A. and T.C. Baker. 1984. Effects of intermittent and continuous pheromone stimulation on the flight behaviour of the oriental fruit moth, *Grapholita molesta*. *Physiol. Entomol.* 9: 341-358.
- Willis, M.A. and T.C. Baker. 1987. Comparison of manoeuvres used by walking versus flying *Grapholita molesta* males during pheromone-mediated upwind movement. *J. Insect Physiol.* 33: 875-883.

LIFE TABLES OF THE LYMANTRIIDAE WITH  
PARTICULAR REFERENCE TO LYMANTRIA  
OBFUSCATA IN KASHMIR

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INTRODUCTION

Our current understanding of the population dynamics of insects owes much to the development of quantitative sampling methods and the application of life tables to the study of numerical changes in insect populations pioneered by Morris and Miller (1954). Life table data provide a unique means of comparing the relative influence of mortality factors in shaping the observed fluctuations in insect numbers. In this paper I present an analysis of unpublished life table data on the Indian gypsy moth, Lymantria obfuscata Walk., collected in the late 1960's by the Indian Station of the CAB International Institute of Biological Control during exploration for natural enemies for use against L. dispar in North America (Rao 1972). The results are then considered in relation to life table data for other lymantriid species, and Lepidoptera in general, to assess whether certain population processes are common to this group of pests or whether populations of each species are influenced by unique factors.

L. obfuscata is a defoliator of poplars, willows and occasionally fruit trees in northern India and has a life-cycle comparable to that of L. dispar L. in Europe and North America (Roonwal 1977). Egg-masses are laid on the trunks of the trees in late June/early July and overwinter until hatching in early April. Dispersal occurs during the 1st larval instar and, in general, all larval stages feed at night and seek out shaded congregation sites during the day. Pupation occurs in June and the emerging, flightless, adult females oviposit their complement of eggs in a single egg-mass on the trunks of the host trees. Outbreaks have been reported from India (Beeson 1941, Roonwal 1977) and may persist for several years before collapsing.

METHODS

All life stages of L. obfuscata were sampled from selected trees at four sites (Pampore, Pinglain, Athwajan and Zainakoot) in the region of Srinagar in the Vale of Kashmir between 1968 and 1971. These sites were

e 1. An example of a typical life table for *L. obfuscata* on poplar at Pinglain in 1969-1970.

Life stage	$l_x$	$dx_F$	$dx$	$k$ -value
Potential eggs	49,734	Loss of fecundity	0	$k_{PF}$ 0.0
Expected eggs	49,734	Loss of oviposition	36,226	$k_{EF}$ 0.566
Observed eggs	13,508	Eclosion failure	3,454	
		Predation	88	
		Parasitoids	814	
		Unknown	2,456	
		Subtotal	6,812	$k_E$ 0.304
$L_1$	6,696	Arthropod predation	113	
		Unknown	321	
		Subtotal	434	$k_{L1}$ 0.029
$L_2$	6,262	Arthropod predation	274	
		Parasitoids	114	
		Unknown	274	
		Subtotal	602	$k_{L2}$ 0.043
$L_3$	5,660	Arthropod predation	69	
		Parasitoids	185	
		Unknown	198	
		Subtotal	452	$k_{L3}$ 0.036
$L_4$	5,208	Arthropod predation	236	
		Parasitoids	373	
		Unknown	1,141	
		Subtotal	1,750	$k_{L4}$ 0.177
$L_{5/6}$	3,458	Arthropod predation	117	
		Parasitoids	92	
		Disease	514	
		Unknown	2,290	
		Subtotal	3,013	$k_{L5}$ 0.890
Pupa	445	Emergence failure	50	
		Parasitoids	320	
		Unknown	34	
		Subtotal	404	$k_P$ 1.035
Adult	41	Sex ratio (44% fem.)	5	$k_{SR}$ 0.056
				$K$ 3.140

chosen as representative of localities where populations of *L. obfuscata* were generally more abundant. A single poplar and a single willow tree were selected at each site so as to be on open ground with no nearby hiding places for larvae. Because all larvae congregate in sheltered resting sites on the trunk during the day, a total census of the number and life stage of the insects on each experimental tree could be made by examining individuals under strips of hessian cloth wrapped around various sections of the trunks. These censuses were made at two day intervals from before egg hatch until the end of adult emergence.

Parasitism and disease were estimated by rearing samples of 100 egg-masses, 200 larvae of stages  $L_2$ ,  $L_3$ ,  $L_4$  and  $L_5/L_6$  and from 100 pupae from each experimental tree. Predation of eggs was assessed directly from the sample of 100 egg-masses. Larval predation under the hessian cloth, by arthropod predators, was measured at each sample interval from the observed remains of predated individuals. Predation by vertebrate predators was not estimated and is combined with other causes of mortality such as dispersal in an "unknown" category.

This routine provided 4 consecutive sets of life tables for each of the two host trees at each of the 4 localities. In the analysis of the life table data, densities are expressed as numbers per tree and mortalities are expressed as  $k$ -values, the difference in log densities before and after the mortality. Regression analyses are used to identify key factors and responses to population density (Southwood 1978).

## RESULTS

An example of a typical generational life table for *L. obfuscata* is presented in Table 1, indicating the life stages and mortality factors examined. In addition, potential fecundity (the number of emerging females times 614, the maximum number of eggs observed in an egg-mass), expected fecundity (the number of emerging females times the mean number of eggs in an egg-mass observed on each tree at each locality) and sex ratio (the number of females in relation to adult emergence) are considered in the life table. During the 4 year period of investigation the mean number of egg-masses per experimental tree was 16,241 and fluctuated between 3,120 and 38,051. Thus *L. obfuscata* populations varied only 12 fold during the observation period but defoliated the selected trees when larval densities were high.

A generalised linear ANOVA model, based on maximum likelihood estimation and binomially distributed errors, was used to examine the effects of host tree and locality on the mortalities recorded in the 8 sets of life tables (2 host trees at each of the 4 localities). The resulting deviances indicate that while both host tree and the interaction of host tree and locality have no effect on mortality at any life stage ( $P > 0.05$  in all cases), the locality had a significant influence on egg mortality ( $0.01 > P > 0.001$ ), mortality of  $L_5/L_6$  ( $0.05 > P > 0.01$ ) and bias in sex ratio ( $0.01 > P > 0.001$ ). Taking note of this, the 8 sets of life tables

containing data over a 4 year period were combined to provide a more powerful analysis of the stage specific mortalities of L. obfuscata.

### Life Stage Analysis

An initial assessment of mortality in each life stage and its influence in contributing to the general trend of population abundance and regulation of the population was made using regression analysis to determine the key factors (Podoler and Rogers 1975) and mortalities responding to population density (e.g. Southwood 1978). Mean stage mortalities, expressed as  $k$ -values (Table 2), ranged from 0.02 (5%) for 1st instar larvae to 0.70 (80%) during the 5th and 6th instar. Thus mortality from dispersal of young larvae was not extensive but generally increased through the larval stages.

In a key factor regression analysis, the regression coefficients of individual stage mortalities in relation to the total generational mortality ( $K$ ) sum to unity and thus those with largest coefficients have greater predictive power of trends in population abundance. The key factors for L. obfuscata (Table 2) are  $k_{FF}$ , the difference between the number of adult females emerging and egg-masses oviposited, and  $k_{L5}$  and  $k_p$ , the late larval and pupal mortalities.

A mortality factor that increases in intensity with population density is density dependent and has the potential to regulate population levels. This type of regulation of populations can be detected from a logarithmic regression of population densities of successive life stages. A regression coefficient significantly less than unity indicates density dependent mortality. For L. obfuscata this analysis indicates that  $k_{FF}$ , the discrepancy between adult female emergence and the number of egg-masses oviposited, and  $k_{L5}$ , late larval mortality, exhibit direct density dependence.

#### Loss of oviposition, $k_{FF}$

The difference between the number of adult females emerging and egg-masses oviposited ( $k_{FF}$ ) on the selected sample trees was not always positive, with more egg-masses than females occurring on several sampling occasions (Fig. 1). Nonetheless, in total the data do indicate little correlation between adult female emergence per tree and the number of egg-masses that are subsequently oviposited. This density dependent key factor, then, is an example of a regulating factor for which the data are highly variable (Southwood 1967) and the response to population density is 'vague' (Strong 1984).

Possible explanations for the observed but highly variable density dependence are density related migration of the females, the production of more than one egg-mass per female at lower densities or density dependent mortality of females at higher densities by predation or

Table 2. Key factor and density dependence analysis of the life stage mortalities of *Lymantria obfusca*. \*\*\* P < 0.001 for departure from unity.

Mortality factor	Mean $\pm$ s.d.	Regression coefficients $\pm$ s.e.	
		key factor	density dependence
k <sub>PF</sub>	0.25 $\pm$ .22	-0.01 $\pm$ .05	1.11 $\pm$ .09
k <sub>EF</sub>	0.15 $\pm$ .45	0.44 $\pm$ .07	0.13 $\pm$ .10***
k <sub>E</sub>	0.33 $\pm$ .17	-0.10 $\pm$ .04	0.95 $\pm$ .12
k <sub>L1</sub>	0.02 $\pm$ .01	0.01 $\pm$ .01	0.99 $\pm$ .01
k <sub>L2</sub>	0.05 $\pm$ .04	0.03 $\pm$ .01	1.02 $\pm$ .02
k <sub>L3</sub>	0.06 $\pm$ .03	0.02 $\pm$ .01	1.02 $\pm$ .02
k <sub>L4</sub>	0.19 $\pm$ .01	0.06 $\pm$ .02	0.92 $\pm$ .06
k <sub>L5</sub>	0.70 $\pm$ .32	0.20 $\pm$ .07	0.28 $\pm$ .12***
k <sub>p</sub>	0.43 $\pm$ .36	0.28 $\pm$ .07	1.03 $\pm$ .28
k <sub>SR</sub>	0.04 $\pm$ .14	0.07 $\pm$ .03	1.00 $\pm$ .06
K	2.23 $\pm$ .76	1.00	

Table 3. Key factor and density dependence analysis of individual mortality factors acting on the L<sub>5/6</sub> and pupal stages of *Lymantria obfusca*. \*\*\* P < 0.001 for departure from unity.

Life stage	Mortality factor	Mean $\pm$ s.d.	Regression coefficients $\pm$ s.e.	
			key factor	density dependence
L <sub>5/6</sub>	Unknown	0.53 $\pm$ .30	0.14 $\pm$ .07	0.34 $\pm$ .12***
	Predation	0.02 $\pm$ .02	0.004 $\pm$ .005	1.01 $\pm$ .01
	Disease	0.07 $\pm$ .05	0.04 $\pm$ .01	0.97 $\pm$ .03
	<i>Drino discreta</i>	0.02 $\pm$ .02	0.005 $\pm$ .006	0.98 $\pm$ .01
	<i>Exorista rossica</i>	0.06 $\pm$ .06	0.01 $\pm$ .01	0.98 $\pm$ .03
	Subtotal	0.70 $\pm$ .32	0.20 $\pm$ .07	0.28 $\pm$ .12***
Pupa	Unknown	0.08 $\pm$ .08	0.07 $\pm$ .01	1.03 $\pm$ .06
	Failed emergence	0.08 $\pm$ .06	0.04 $\pm$ .01	1.02 $\pm$ .04
	<i>Brachymeria intermedia</i>	0.07 $\pm$ .07	0.04 $\pm$ .02	0.99 $\pm$ .06
	<i>Monodontomerus aereus</i>	0.07 $\pm$ .04	0.02 $\pm$ .01	0.97 $\pm$ .03
	<i>Pimpla</i> spp.	0.04 $\pm$ .05	0.04 $\pm$ .01	1.03 $\pm$ .04
	<i>Theronia atalantae</i>	0.01 $\pm$ .01	0.003 $\pm$ .003	0.98 $\pm$ .01
	<i>Exorista rossica</i>	0.08 $\pm$ .11	0.07 $\pm$ .02	0.98 $\pm$ .01
	Subtotal	0.43 $\pm$ .36	0.28 $\pm$ .07	1.03 $\pm$ .28

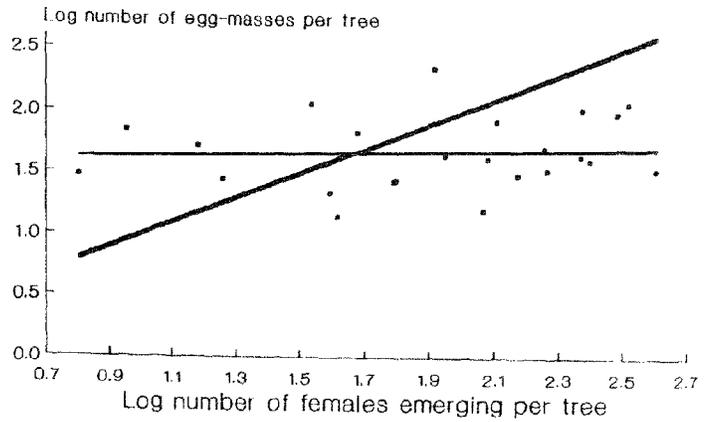


Fig. 1. Density dependent loss of oviposition in *L. obfuscata*, showing line of equality (thick) and regression line (thin)  $Y=a+bX$ ,  $a=1.59\pm.30$ ,  $b=0.04\pm.14$ ,  $r^2=0.004$ ,  $P>0.05$ . Egg-mass density is therefore constant.

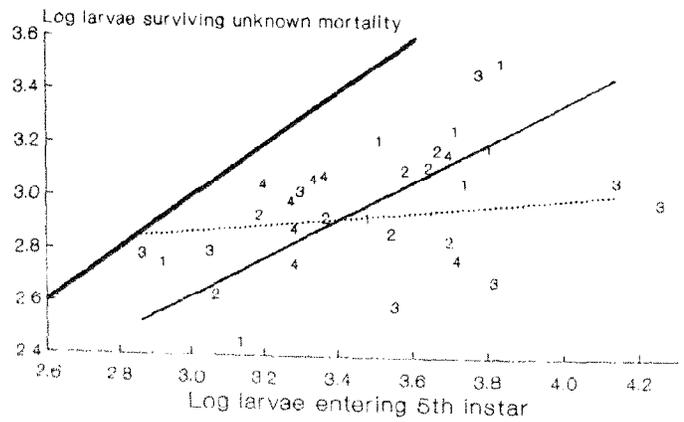


Fig. 2. Density dependent 5th instar larval mortality of *L. obfuscata* from unknown factors. Data plotted by locality, (1) Pinglain, (2) Paarpore, (3) Athwajan and (4) Zainakoot, showing line of equality (thick) and regression lines  $Y=a+bX$  for localities 1+2 ( $a=0.44\pm.17$ ,  $b=0.73\pm.16$ ,  $r^2=0.59$ ,  $P<0.001$ , solid line) and 3+4 ( $a=2.49\pm.22$ ,  $b=0.13\pm.15$ ,  $r^2=0.05$ ,  $P<0.001$ , dotted line).

competition for suitable oviposition sites. While the first two possibilities do not correspond well with the known biology of L. obfuscata they are the sole explanations for more egg-masses than emerging females other than poor census technique. In contrast, predation of adults or competition for oviposition sites more readily account for density dependent losses at higher densities and any differences between the selected trees or between the resident vertebrate predator populations in the various localities would add considerably to the variance of the response to population density. Since none of these factors were independently estimated, however, further field observations are required to identify the causes of their variable density dependent response.

#### Late larval, $k_{L5}$ , and pupal, $k_p$ , mortality

During the 5th and 6th instars and pupal period, L. obfuscata is killed by a range of parasitoids, by arthropod predation (mainly spiders and ants), by disease (nuclear polyhedrosis virus) and by additional unknown mortality including vertebrate predation, starvation and larval emigration. These life stages experience considerable mortality which is both predictive of population change and density dependent in action (Table 3). This breakdown of the complete stage  $k$ -values to those for individual mortality factors clearly indicates that it is the unknown losses of the larger larvae that is most significant. As with loss of oviposition, these losses are not only key components for the prediction of population change but are also density dependent. Late larval mortality also varies significantly with locality due to a significantly lower larval mortality at Pinglain and Pampore as compared to Athwajan and Zainakoot (Fig. 2). The latter two localities are on marshy ground and show a greater intensity of larval mortality in relation to larval density.

The cause of these unknown losses is unclear but may be due to larval starvation, emigration or vertebrate predation. If starvation was the main factor, then the sex ratio of emerging adults would become more biased towards males, which require less food to complete their development, as larval density increases. However, there is no correlation between the  $k$ -value for unknown losses of larger larvae and the  $k$ -value for changes in sex ratio of emerging adults ( $r=0.09$ ,  $P>0.05$ ). Thus larval emigration or vertebrate predation would appear to be the more probable cause of the density dependent losses. The lower populations of small mammals supported by marshy habitats would suggest that these predators are not responsible for the greater intensity of predation but further experimental observations are required to more adequately assess the true cause of this mortality.

A comparison of Tables 2 and 3 indicates that mortality of late larvae and pupae due to the tachinid Exorista rossica is the most significant mortality caused by a parasitoid. It is also of some significance as a key factor for predicting population change but shows no response to the density of large larvae, the life stage that is attacked ( $r=0.01$ ,  $P>0.5$ ).

## DISCUSSION AND CONCLUSIONS

The within generation survivorship curve for *L. obfuscata* can be compared to that of outbreak populations of *Lymantria dispar* and *Orgyia pseudotsugata* (McDunnough) (Fig. 3), the only other Lymantriids for which life table data are available. These three lymantriid pests have a similar fecundity and mortality rate of eggs but significant differences occur in the mortality rates of young larvae (L<sub>1-3</sub>). For *O. pseudotsugata* the dramatic mortality rate at this stage, caused by viral disease (Mason 1976) and larval dispersal (Mason et al. 1983), appears to be a density dependent key factor (Mason 1976, Mason and Overton 1983). This early instar loss, however, is not significant in the *Lymantria* species, although losses in *L. dispar* (Campbell 1981) are greater than observed for *L. obfuscata*. Rates of mortality of larger larvae are typically lower in outbreak populations of *O. pseudotsugata* and appear to be independent of density (Mason 1976), although high rates of parasitism have been observed in moderate populations (Dahlsten et al. 1977). In contrast, mortality in the late larval stages of both *Lymantria* species is high and evidently density dependent, due to viral disease in *L. dispar* (Campbell 1981) and to vertebrate predation or larval migration in *L. obfuscata*. Pupal and sex ratio losses in *O. pseudotsugata* and *L. obfuscata* are similar, while that of *L. dispar* is greater, perhaps reflecting a greater incidence of viral disease and vertebrate predation during the pupal stage and a stronger influence of larval history on adult sex ratios (Campbell 1981).

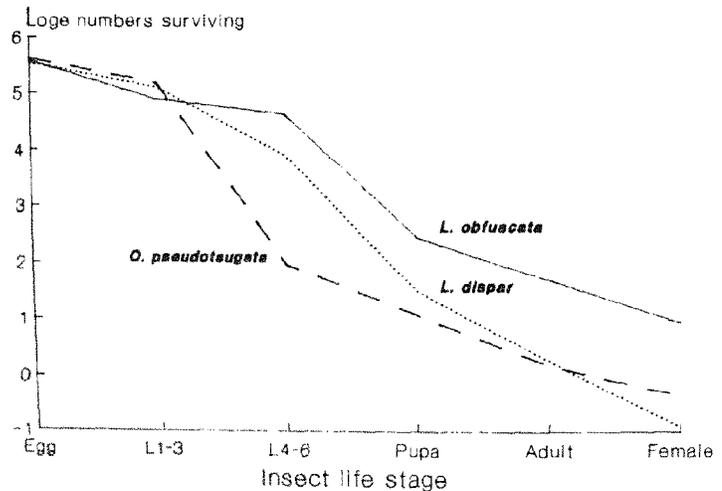


Fig. 3. Survival rate from egg to adult female of a single egg-mass during the outbreak phase of three lymantriid populations.

In summary, the lymantriid populations show similarity in their levels of fecundity and the prominence of viral disease at high population densities. Mortality from parasitism tends to be of greatest significance in the pupal stage, although L. dispar differs in that it does not suffer as much pupal mortality from parasitism by a macro-type egg-laying tachinid, a feature that is quite characteristic of the Lymantriidae (e.g. Mills and Schönberg 1985). Vertebrate predation may also have considerable influence on this group of forest insects. Differences occur between Q. pseudotsugata and the Lymantria species in the significance of mortality from young larval dispersal and the life stages at which there is density dependent regulation and a significant impact of viral disease. While no life table data exist for Lymantria monacha (L.) and Orgyia antiqua (L.) in Europe, these species also appear to fit the general characteristics of their respective genera (Mills, unpublished observations).

In comparison to other Lepidoptera, the lymantriid populations also show certain similarities. Dempster (1983) reviewed life table data for a range of 14 lepidopteran species and noted that vertebrate predation of larger larvae and pupae and loss of fecundity through dispersal, variation in fecundity and adult mortality are the two most frequent key factors. The lymantriid life tables suggest the same key factors, accepting that lymantriid dispersal occurs in the young larval instars rather than the adult stage. However, the adoption of the early instars as the dispersive life stage may confer advantages in the relative resistance of these larvae to lack of synchronisation between bud burst and egg hatch. The Lymantria species show minimal losses at this stage which is often the key factor for non-dispersive Lepidoptera. Density relationships are often difficult to determine from life table data (e.g. Hassell, 1985) and Dempster (1983) found no consistent patterns for the lepidopteran life tables that he reviewed. However, he suggested that reduced fecundity and dispersal resulting from food shortage are the most prominent causes of density regulation and these factors also appear to be important in the Lymantriidae.

Lymantriid populations tend to exhibit cyclical trends in population fluctuations. Cyclical behaviour can result from time delayed density dependent mortality such as may occur through an increase in natural enemy populations (Anderson and May 1980, Berryman 1986) or of host plant defenses (Fischlin and Baltensweiler 1979). To determine these time delayed effects it is necessary to compare the relative rates of population increase in relation to current and previous year population densities (Royama 1977, Berryman 1986). This requires a long enough series of population estimates and was not possible for the 4 year data set of L. obfuscata. However, Montgomery and Wallner (1988) have demonstrated this effect for a Yugoslavian population of L. dispar and Berryman (1978) has produced a model to show that a one-year time delay in density dependence could predict the population cycles seen in Q. pseudotsugata. The biotic factors that are responsible for the delayed density dependence remain untested and while natural enemies, including viruses, are perhaps the most obvious candidates for a one year delayed action, larval starvation and induced host tree defenses may also be involved, particularly in the case of Q. pseudotsugata.

While life tables developed during population outbreaks provide a very useful means of describing the stage specific survivorship of insect populations, experimental manipulations are essential to test hypotheses generated from such investigations. The cause and effect nature of various mortality factors can only be adequately assessed by manipulation of population densities either of the selected insect or of its biotic mortality factors. While some effort has been made to do this with the Lymantriidae (Furuta 1982, Maksimovic and Sivcev 1987, Mills et al. 1986, Weseloh 1982 for L. dispar and Mason and Torgersen 1983 for O. pseudotsugata), this group of forest pests offers the greatest potential for ease of such experimental treatments and could be profitably exploited in the development of more effective management of these pest species.

#### SUMMARY

An analysis of life table data collected for Lymantria obfuscata in Kashmir between 1968 and 1971 is presented. This analysis indicates that loss of oviposition and late larval mortality are the key factors determining changes in population abundance and that these mortalities also respond to population density. A comparative analysis of life table data from three lymantriid species suggests that their populations exhibit common features such as level of fecundity and the influence of viral epizootics, late larval parasitism and vertebrate predation. In contrast, Orgyia pseudotsugata differs from the Lymantria species in the dramatic losses occurring during the young larval instars. The cyclical nature of numerical changes in lymantriid populations is considered and the need for an experimental approach to population studies is emphasised.

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#### LITERATURE CITED

- ANDERSON, D.J. and MAY, R.M. 1980. Infectious diseases and population cycles of forest insects. *Science* 210: 658-661.
- BEESON, C.F.C. 1941. The ecology and control of the forest insects of

India and the neighbouring countries. Dehra Dun.

- BERRYMAN, A.A. 1978. Population cycles of the Douglas-fir tussock moth (Lepidoptera: Lymantriidae): the time-delay hypothesis. *Can. Ent.* 110: 513-518.
- BERRYMAN, A.A. 1986. On the dynamics of blackheaded budworm populations. *Can. Ent.* 118: 775-779.
- CAMPBELL, R.W. 1981. Population dynamics. pp. 65-86 In: Doane C.C., McManus, M.L. (eds.). *The gypsy moth: research toward integrated pest management.* USDA Tech. Bull. 1584.
- DAHLSTEN, D.L., LUCK, R.F., SCHLINGER, E.I., WENZ, J.M., COPPER, W.A. 1977. Parasitoids and predators of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae), in low to moderate populations in central California. *Can. Ent.* 109: 727-746.
- DEMPSTER, J.P. 1983. The natural control of populations of butterflies and moths. *Biol. Rev.* 58: 461-481.
- FISCHLIN, A. and BALTENSWEILER, W. 1979. Systems analysis of the larch bud moth system. Part 1: The larch-larch bud moth relationship. *Mitt. Schweiz. Entomol. Ges.* 52: 273-289.
- FURUTA, K. 1982. Natural control of *Lymantria dispar* L. (Lep., Lymantriidae) population at low density levels in Hokkaido (Japan). *Z. ang. Ent.* 93: 513-522.
- HASSELL, M.P. 1985. Insect natural enemies as regulating factors. *J. Anim. Ecol.* 54: 323-334.
- MAKSIMOVIC, M. and SIVCEV, I. 1987. A contribution to the biological control of the gypsy moth. *Zast. bilja* 38: 197-205.
- MASON, R.R. 1976. Life tables for a declining population of the Douglas-fir tussock moth in northeastern Oregon. *Ann. ent. Soc. Am.* 69: 948-958.
- MASON, R.R. and TORGERSEN, T.R. 1983. Mortality of larvae in stocked cohorts of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae). *Can. Ent.* 115: 1119-1127.
- MASON, R.R. and OVERTON, W.S. 1983. Predicting size and change in nonoutbreak populations of the Douglas-fir tussock moth (Lepidoptera: Lymantriidae). *Environ. Entomol.* 12: 799-803.
- MASON, R.R., TORGERSEN, T.R., WICKMAN, B.E. and PAUL, H.G. 1983. Natural regulation of a Douglas-fir tussock moth (Lepidoptera: Lymantriidae) population in the Sierra Nevada. *Environ. Entomol.* 12: 587-594.
- MILLS, N.J. and SCHOENBERG, F. 1985. Possibilities for the biological

- control of the Douglas-fir tussock moth, Orgyia pseudotsugata (Lymantriidae), in Canada, using natural enemies from Europe. Biocontr. News & Info, 6: 7-18.
- MILLS, N.J., FISCHER, P. and GLANZ, W.-D. 1986. Host exposure: a technique for the study of gypsy moth larval parasitoids under non-outbreak conditions. Proc. IUFRO World Congr., Div. 2, Vol. 2, pp. 777-785.
- MONTGOMERY, M.E. and WALLNER, W.E. 1988. The gypsy moth, a westward migrant. In Berryman, A.A. (ed.). Insects in forest ecosystems: enquiries into the causes of outbreaks. (In press)
- MORRIS, R.F. and MILLER, C.A. 1954. The development of life tables for the spruce budworm. Can. J. Zool. 32: 283-301.
- PODOLER, H. and ROGERS, D.J. 1975. A new method for the identification of key factors from life-table data. J. Anim. Ecol. 44: 85-114.
- RAO, V.P. 1972. Evaluation of hymenopterous parasites of the gypsy moth and study of the behaviour of promising species. Unpubl. Final Techn. Rpt., CIBC, Bangalore.
- ROONWAL, M.L. 1977. Life-history and control of the Kashmir willow defoliator Lymantria obfusca (Lepidoptera: Lymantriidae). J. Ind. Acad. Wood Sci. 8: 97-104.
- ROYAMA, T. 1977. Population persistence and density dependence. Ecol. Monogr. 47: 1-35.
- ROYAMA, T. 1981. Evaluation of mortality factors in insect life table analysis. Ecol. Monogr. 51: 495-505.
- SOUTHWOOD, T.R.E. 1967. The interpretation of population change. J. Anim. Ecol. 36: 519-529.
- SOUTHWOOD, T.R.E. 1978. Ecological methods with particular reference to the study of insect populations. Chapman and Hall, London.
- STRONG, D.R. 1984. Density-vague ecology and liberal population regulation in insects, pp. 313-327 In: Price, P.R., Slobodchikoff, C.N. and Gaud, W.S. (eds.). A new ecology, novel approaches to interactive systems. Wiley, New York.
- WESELOH, R.M. 1982. Implications of tree microhabitat preferences of Compsilura concinnata (Diptera: Tachinidae) for its effectiveness as a gypsy moth parasitoid. Can. Ent. 114: 617-622.