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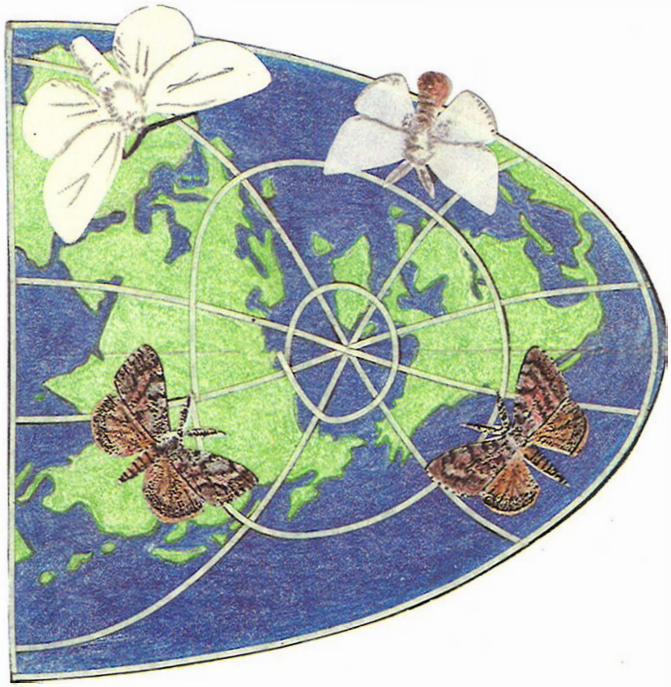
PROCEEDINGS

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



FOREWORD

Tussock moths constitute the major forest pest throughout the world. While similarities in ecology, behavior, natural enemies, and means of control may be similar for different 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.

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

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

Technical Coordinators:

William E. Wallner and Katherine A. McManus
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Sponsored jointly by the
Northeastern Forest Experiment Station and
The International Union of Forest Research Organizations

Welcoming Address

International cooperation on scientific issues
of common interest

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

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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

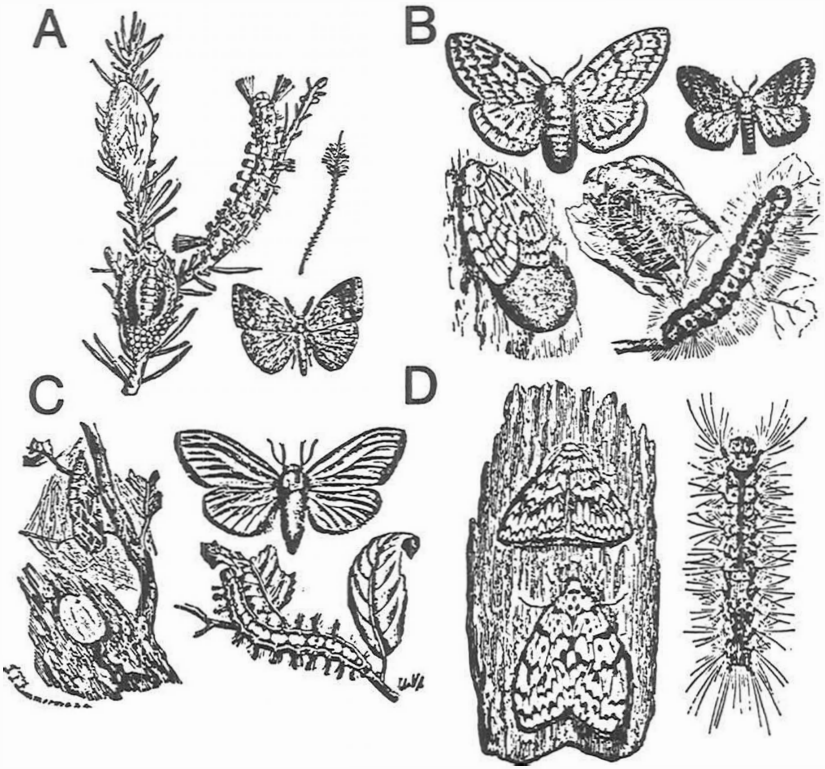

Figure 1: Representative Lymantriidae showing life stages.

A. Rusty Tussock Moth or Vapourer, Orgyia 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 Nusslin (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 Numenoides) 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 intrepretations 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 Dasychiricae Packard 1864, which both had precedence over Lymantriicae, 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 Orgyidae). 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 Ocneria).

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 (Beeson 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 Lymantica (which contain many species previously considered Lymantria) and Mpanjaka (Griveaud 1977). However, some of these genera must be viewed in light of different nomenclatural intrepretation 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[a]	46[a]	Ferguson 1978[b]
Brazil	4	9	d'Araugo e Silva, et al., 1968
Neotropics	8	132	D. Ferguson (pers comm.)[c]
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[d]
East Africa	18	67	LePelley 1959[d]
Madagascar	53	258	Griveaud 1977
Southern Africa	30	57	Pinhey 1979[d]
Japan	14[a]	45[a]	Inoue 1956-57[b]
Korea	14	37	Nam & Kim 1981
China	26	235	Chao 1978[b]
	30	270	Sun (these Proceedings)
Thailand	11	30	Anonymous 1965[d]
U.S.S.R.	16[e]	65[e]	Kozhanchikov 1950
India	11	47	Beeson 1941
Southeast Asia	17	29	Barlow 1982[c]
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, *Lymantria dispar* (L.)	1868	Medford, Mass. USA	France/ Belgium	Forbush, 1896
Satin moth, *Leucoma salicis* (L.)	1920	Malden, Mass. USA	Europe?	Burgess & Crossman,
	1920	Vancouver, British Columbia	?	1927
	1922	Bellingham, Washington, USA	Canada?	same
Browntail moth, *Euproctis chrysorrhoea* (L.)	1897	Somerville, Mass, USA	France/ Holland	Marlatt, 1911
Rusty tussock moth, *Orgyia antiqua* (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
Aroa Walker 1855	62	*Leucoma* Hubner 1822 (including *Stilpnotia*)	90
Calliteara Butler 1881	55	*Lymantica* Collenette 1936	27
Collenettema Griveaud 1977	22	*Lymantria* Hubner 1819	158
Dasychira Hubner 1809	432	*Mpanjaka* Griveaud 1976	37
Eloria Walker 1855	54	*Olapa* Walker 1855	21
Euproctis Hubner 1819 (including *Porthesia*)	796	*Orgyia* Ochsenheimer 1810	52
Eudasychira Moschler 1887	30	*Pantana* Walker 1855	25
Idalia Hubner (1819) 1816 (including *Caviria*, per Ferguson, pers. comm. 6/1988)	20	*Rahona* Griveaud 1976	22
		Redoa Walker 1855	38
		Rhypopteryx Aurivillius 1879	27
Lacipa Walker 1885	25	*Thagona* Moschler 1883	39
Laelia Stephens 1828	127		
(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 compliled 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 (Herrich-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 exclamationis 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 (Lorenthaceae) 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 Kukal & Kevan 1987; Kevan et al. 1982; Schaefer & Castrovillo 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. obfuscata 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	
Apina callisto Doubleday	Australia	Froggatt 1907
Aroa biformis Holloway	Borneo	Holloway 1976
Aroa cinerea Holloway	Borneo	Holloway 1976
Aroa transflava Holloway	Borneo	Holloway 1976
Birnara bicolor Walker	Borneo	Holloway 1976
Bracharoa dregei Herrick-Schaffer	South Africa	Watson et al. 1975
Eloria noyesi Schaus	Peru, Bolivia	Collenette 1950
Euproctis seximacula Swinhoe	Borneo	Holloway 1976
Euproctis sinuinigra Holloway	Borneo	Holloway 1976
Gynaephora groenlandica (Wocke)	Arctic Canada	Kukal & Kevan 1987
Lymantria mae ora (=Byrdia) rossi Curtis	Japan	Inoue et al. 1959
	Maine, USA	Schaefer & C. 1979
Ivela auripes Butler	Japan	Inoue et al. 1959,
Leucoma wiltshirei Collenette	Iraq	Wiltshire 1957
Lymantria dispar (L.)	North America	Ferguson 1978
Lymantria dispar japonica Motsch.	Japan	Inoue et al. 1959
Ocnerogyia amanda Stgr.	Iraq	Wiltshire 1957
Orgyia antiqua (L.)	North America	Ferguson 1978
	Eurasia	Gillanders 1908
Orgyia pseudotsugata (McDunnough)	North America	Ferguson 1978
Orgyia recens approximans Hubner	Japan	Inoue et al. 1959
Orgyia thyellina Butler	Japan	Inoue et al. 1959
	ADDITIONAL UNCONFIRMED SPECIES BASED ON COMPOUND EYE SIZE	
Aroa socrus Geyer	Taiwan	Schaefer unp.data
Aroa substrigosa Walker	Taiwan	Schaefer unp.data
Dasychira nachiensis Marumo	Japan, Taiwan	Schaefer unp.data
Dura alba Moore	Taiwan	Schaefer unp.data
Lymantica suarezia Mabille	Madagascar	Schaefer unp.data
Lymantria ampla Walker	India	Schaefer unp.data
Lymantria apicebrunnea Gaede	China	Schaefer unp.data
Lymantria marginata Walker	China	Schaefer unp.data
Lymantria obfuscata Walker	India	Schaefer unp.data
Lymantria tacita Hering	East Africa	Schaefer unp.data
Medama diplaga Hampson	Taiwan	Schaefer unp.data
Medama basimaculata Matsumura	Taiwan	Schaefer unp.data
Numenes takamukui Matsumura	Taiwan	Schaefer unp.data
Orgyia triangularis Butler	Japan	Schaefer unp.data
Pantana albipes Matsumura	Taiwan	Schaefer unp.data
Pantana infuscata Matsumura	Taiwan	Schaefer unp.data
Pantana simplex Leech	Taiwan	Schaefer unp.data
Perina nuda Fabricius	Hongkong	Schaefer unp.data
Pida nipponis Butler	Korea	Schaefer unp.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 pseudoconspersa 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 Oecura goodii Holland in tropical West Afr , 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, pseudoconspersa).

(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 marval 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.

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OVERVIEW OF RESEARCH ON LYMANTRIDS IN EASTERN AND WESTERN EUROPE

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SUMMARY

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) pudibunda (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.

Gypsy Moth
Lymantria dispar (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

conferous 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 (Entwistle, 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, Thelohania disparis and Pleistophora schubergi) during a GM outbreak, concluded that apart from killing the larvae, the infections also lowered the fecundity and mating capacity of adults. Streptoccccus 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) (Currado & 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 out- break of GM, resulted in 60% higher egg parasitization than in con- trol 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, Glyptapantales 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 SO2) 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. Klimitzek 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 (Klimitzek, 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).

Browntail Moth
Euproctis chrysorrhoea (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 Mediterrean 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 nudioculata, Masicera sphingivora (Sisojevic et al.,1976), Carcelia lucorum and Lydella nigripes are considered most important. In Sardinia, Pales pavida 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 kovacevici) 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^3. 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 (Lappland) 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 Hexamermis 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 (Ziemnicka, 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 unindentified 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 sibericus 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).

Rusty tussock moth
Orgyia antiqua (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; parazitization 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 Compsilura 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).

Pale tussock moth
Calliteara (Dasychira) pudibunda (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, Gregopimpla 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 (Zwolfer, 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	300.0 d	-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	0.3	-	-
Poland	-b	6,300.4d	-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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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
Dura	1
Medama	2
Heracula	1
Parakanchia	1
Cispia	6
Imaida	2
	Total 270

Pine lymantriid, Dasychira axutha Collenette

Host: Pinus massoniana, P. tabulaeformis, P. elliotti, P. taeda.

Distribution: Guangxi, Guangdong, Hunan, Jiangxi, Zhejing, 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 gererations 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; Casinaria 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 yunnanesis, 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 infestion:

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 infestion:

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 xylina Swinhoe

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

Distribution: Fujian, Guangdong, Taiwan.

Biology and infestion:

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.

Stilpnotia 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.

Stilpnotia 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 orienta 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 yunnanesis 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 than those in the North, so is the seriousness. The fauna of Lymantriidae in China is quite clear. The research on forest lymantriids stressed mainly on biology and control, lacking of deepened research in various other respects. More efforts are needed for better understanding and control.

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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.

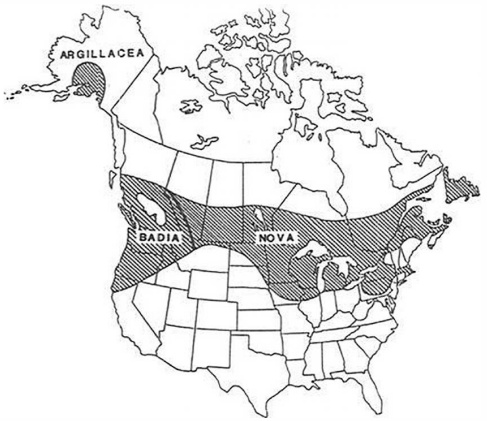
Research emphasis has been related directly to those lymantriids that present the most serious threat; support funding traditionally has been correlated with hectares of defoliation. The gypsy moth, Lymantria dispar (L.), and Douglas-fir tussock moth, Orgyia pseudotsugata (J.E. Smith), received accelerated 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

Rusty Tussock Moth
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 argillacae; nova closely approximates European nominate subspecies (Ferguson, 1978).



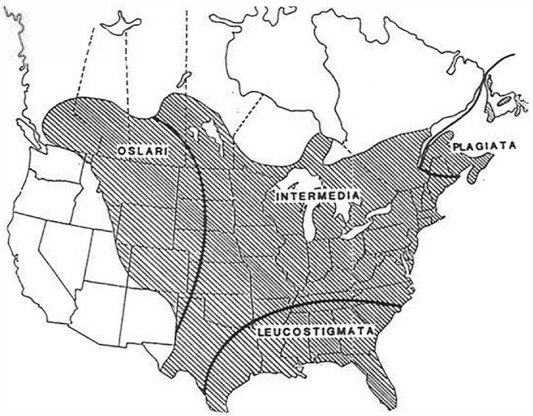
Distribution of the rusty tussock moth, Orgyia antiqua, and its subspecies in North America

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 Entomopthora 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.

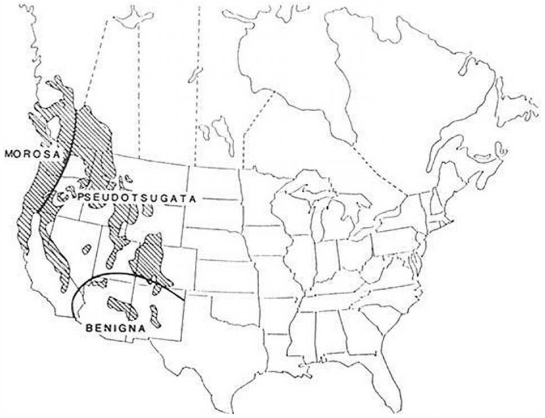
In efforts to establish parasites from Sicily for gypsy moth control in the United States, Schaffner (1934) found that Cotesia (Apanteles) melanoscelus survived solely on WMTM. Verly likely, other shared natural enemies exist. Damage by WMTM is so limited and sporadic that it has received little research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

Satin Moth
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 gigantica) 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

introduced parasites Compsilura concinnata and Apanteles solitarius are most important, but Cotesia melanoscelus, Coccygomimus pedalis, and Meteorus versicolor also cause mortality. Egg parasitism by Telenomus californicus and Trichogramma minutum occur but their impact is unknown. In fact, T. californicus ex DFTM would not parasitize SM eggs in laboratory tests in Europe (Grijpma, personal communication). Likewise, larval and pupal predation by the black-billed cuckoo and Calasoma frigidum, and adult predation by the hermit thrush and pentatomid bugs have been noted but their impact was not quantified (Jones et al., 1938; Reeks & Smith 1956; Wagner & Leonard 1980). While a number of mortality factors exist for SM, they do not prevent periodic outbreaks. The lack of rapid spread experienced by SM in contrast to such pests as gypsy moth suggests it is not likely to become a widespread pest in the near future.

Browntail Moth
Euproctis chrysorrhoea (L.)

Believed to have been accidently introduced into the U.S. on roses imported from Holland or France in 1890, the browntail moth (BTM) was found established in Sommerville, Massachusetts, in 1897. From the time of its discovery, BTM spread rapidly throughout eastern New England and parts of New Brunswick and Nova Scotia, and by 1915 reached a maximum distribution of 150,000 km^2. Population and range of BTM then declined rapidly and by the late 1960's could be found only in coastal dune habitats on three islands in Casco Bay off Portland, Maine, and the extreme end of Cape Cod, Massachusetts. By 1973, the distribution was only 4.8 km^2 (Schaefer, 1974). In the initial stages of its rapid spread BTM, which has hosts within 36 plant families, caused widespread defoliation of fruit trees, ornamental shrubs, and trees. Most preferred hosts were in the families Roseacae and Fagaceae. By the early 1980's, only beach plum, salt spray rose, and black cherry were attacked. However, starting in 1982, BTM began to expand dramatically in number and range on Cape Cod, Massachusetts (Snowden, 1986). Recent studies by Leonard (in press) indicate that not only has BTM significantly increased its range on Cape Cod, but by moving inland, attacks a wider range of hosts including bear oak and shadbush; beach plum is still the primary host and scrub pine growing in admixture with preferred hosts are not attacked.

The rapid expansion and equally rapid contraction of range by BTM is not easily explained. In the most recent comprehensive study of BTM, Schaefer (1974) concluded that winter temperatures (-25 C or lower), destruction of winter webs by man, and natural enemies caused this rapid decline. He found mortality for the fall feeding period was 45% and winter 20%. Egg parasitism was consistently less than 1%, and early larval mortality by Cotesia (Apanteles) lacticolor and Townsendiellemyia nidicola was 4%. Late larval parasitism averaged 13.5% by T. nidicola and Compsilura concinnata; predators and pathogens caused only minor mortality.

BTM population quality varies by host type and condition, which also influence the rate of winter mortality. Until recently the availability of suitable host plants in coastal regions moderated by winter weather has limited BTM. However, evidence of population increases and range expansion could be illustrative of genetic adaptation reported for other introduced insect pests (Simmonds & Greathead, 1977). If so, BTM damage can be expected to increase above the current restriction to coastal dune plant species. Furthermore, the probability of human encounters with the highly urticating larval hairs will exacerbate its pest status. Following a period of some 85 years of relative modest pest status, the future spread and increase in populations must be viewed with considerable apprehension.

Distribution of the browntail moth, Euproctis chrysorrhoea, in North America

G y p s y M o t h
Lymantria dispar (L.)

Purposely brought to the United States from France for developing more vigorous silkworm colonies, the gypsy moth (GM) escaped in 1869 and established readily in Medford, Massachusetts. Within 20 years, populations exploded dramatically to an area of 900 km^2 and efforts to eliminate it failed. Since then it has spread northward probably to the limits of its range but continues to spread south and west. Natural spread is approximately 10-15 km per year; long distance infestations continue to occur by human activities that inadvertently transport life stages.

In North America, oak and poplar are consistently most preferred, but gypsy moth has an exceptionally broad range of hosts. Over 250 hosts are known for North America, but interestingly, some

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 Pennsyvlania, 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 beeen 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.

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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 Pfalzer 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 reafforestation areas of the Maritime Alps, having migrated to them from surrounding patches of Sarothannus 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.[1]

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

[1] 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.

Larvae/pupae examined	Parasitized larvae/pupae	% parasitism in larvae	pupae	total
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.

Locality	Larval population per 100 trees	Pupal population per 100 tree basis
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 Euprocits spp. in 1982.

Forest division	Locality	Larval population per 100 trees	Pupal population 100 tree basis
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

Compartment	Plants observed	Larvae collected
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.

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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, Operophthera 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).[1] 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.

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[1] 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	
	N1	max.	mean	N2	mean	mean	max.
Kehl							
Communal forest of Neuried VI	16	5.1	1.8	22	164	294	834
Rheinau XXIII/XXV	14	3.9	2.3*	24	200	460	781
Rheinau XVII	33	3.5	2.0**	4	179	357	625
Offenburg							
Communal forest of Offenburg	25	10.7	4.7				
Subdistrict Spitalhof				32	180	938	2254
Subdistrict West				60	118	616	1480

N_1 = Number of plots with 10 trees in each; N_2 = 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 Operophthera 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 (Mesnil) 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
Parasetigena silvestris	202	2.5. - 1.7.
Blepharipa schineri	52	2.5. - 17.6.
Blepharipa pratensis	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 superparastizied. 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.

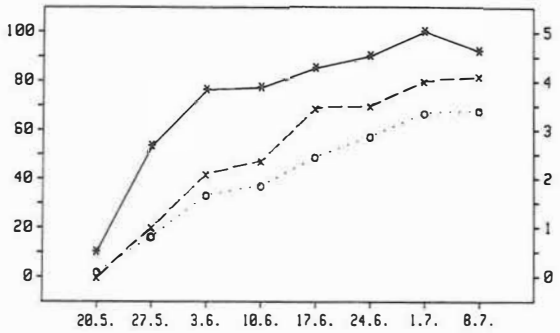

Fig. 1. Parasetigena silvestris: Percent parasitism and superparasitism of Lymantria dispar and number of maggots per host in the communal forest of Offenburg in 1986 (determined by larval dissection).

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.

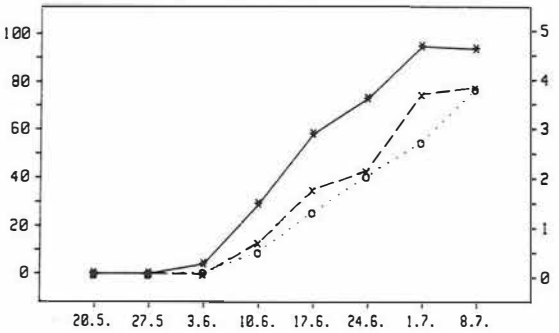

Fig. 2. Blepharipa schineri: Percent parasitism and superparasitism of Lymantria dispar and number of maggots per host in the communal forest of Offenburg in 1986 (determined by larval dissection).

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.

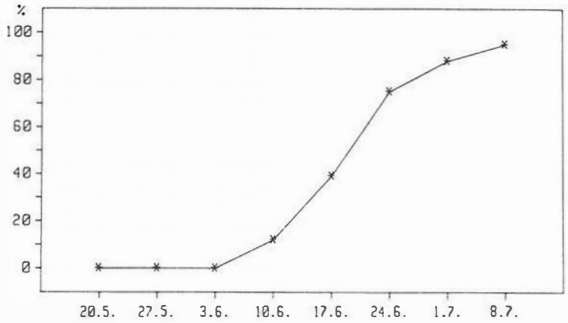

Fig. 3. Percent multiparasitism in Lymantria dispar larvae by Parasetigena silvestris and Blepharipa schineri (determined by dissection of host larvae.

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[2]

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.

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[2] 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 2.7×10^7 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 preparate 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.

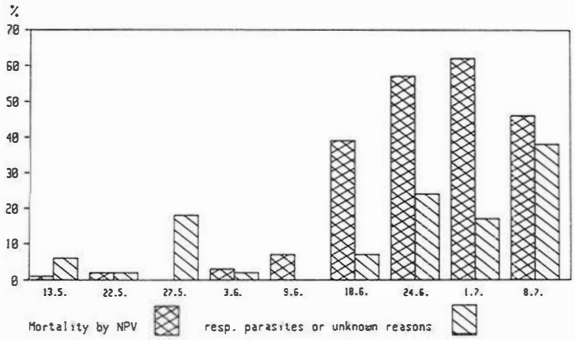

Fig. 4. Mortality rate of Lymantria dispar larvae in the plot treated with Gypchek (10^7 PIB's per ml).

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 10^8 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.

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NATURAL DISEASE OF GYPSY MOTH IN VARIOUS GRADATION PHASES

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INTRODUCTION

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.

METHODS

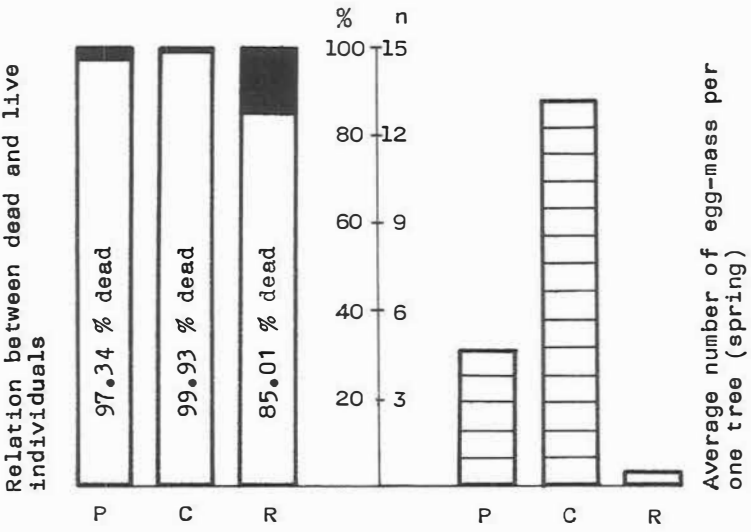
In 1985-1987 we monitored population dynamics of Lymantria dispar in the primary focus of its outbreak (locality Čifáre). Samples of pupae, larvae (by 100) were taken larval instar L_{1-2}, L_{3-4}, L_{5-6} from field population. We observed material in laboratory up to hatching of imagos. Dead individuals 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)

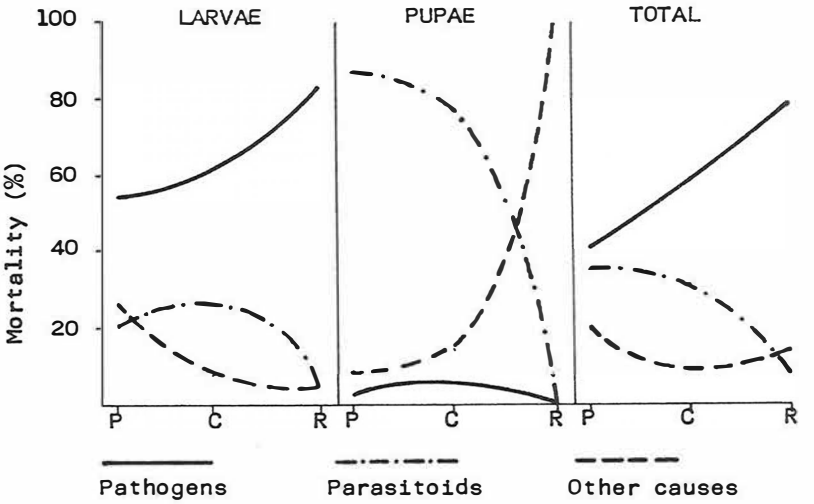


The situation is characterized vividly by autoregulative coefficient A_k (Table 1) which expresses on the basis of ratic of population weakening coefficient (N_k) and resistance coefficient (R_k) the state of conditions making possible the activation of bioregulative complex. Increasing A_k marks improving 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	1.39×10^{-1}
Culmination	14.28	0.07	2.04×10^{2}
Regression	0.06	17.63	3.40×10^{-3}

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



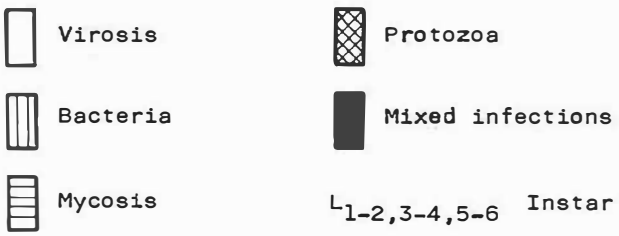
At whole the complex of pathogens was the most active bioregulator in all gradation phases. Parasitoids and other causes had significantly smaller share in the mortality. Importance of bioregulator group in larval stage was similar. But it difered basically from previous two causes in the stage of pupa (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.

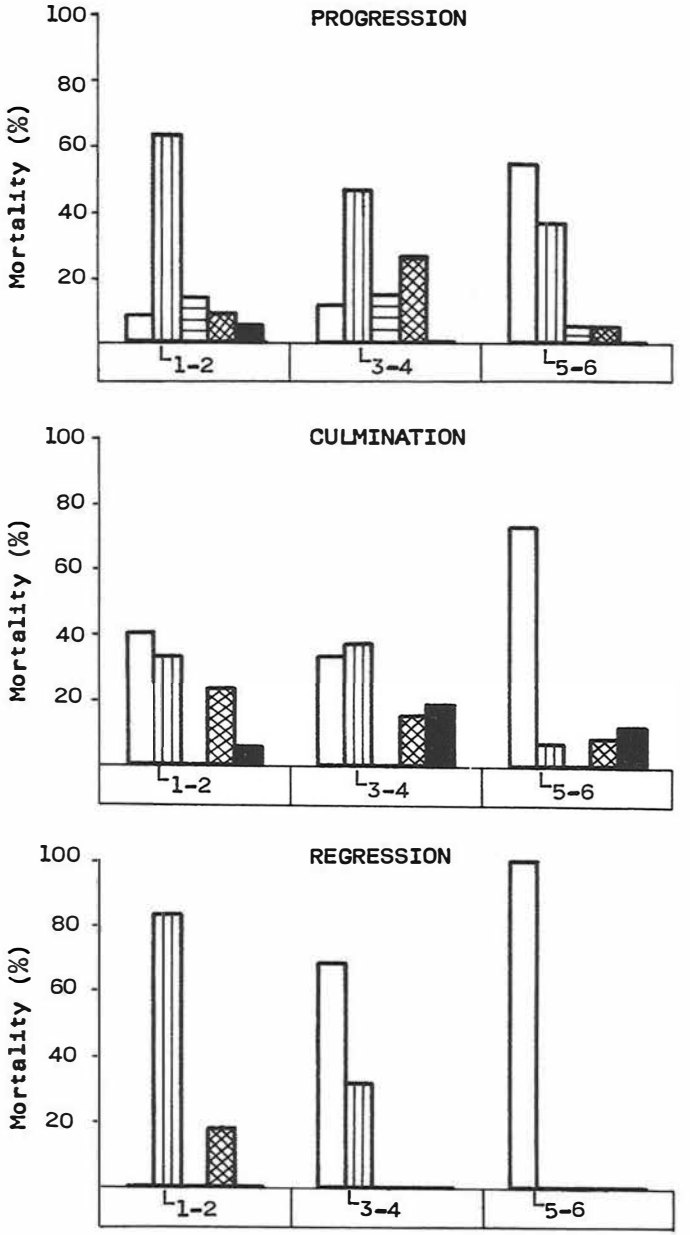
Table 2. Participation of pathogens in mortality of gypsy moth larvae.

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



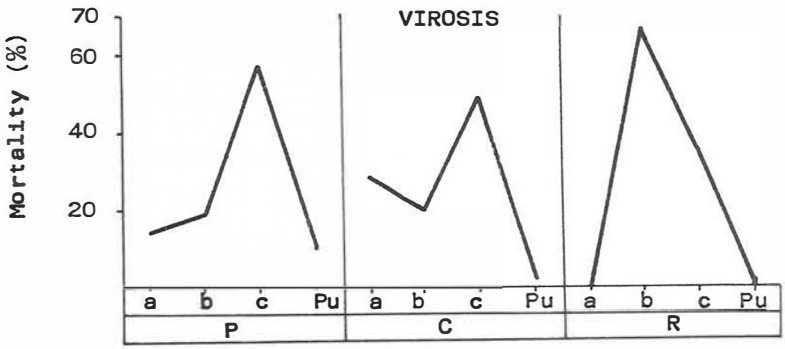

PROGRESSION
Mortality (%)
100
80
60
40
20
L1-2
L3-4
L5-6
CULMINATION
Mortality (%)
100
80
60
40
20
L1-2
L3-4
L5-6
REGRESSION
Mortality (%)
100
80
60
40
20
L1-2
L3-4
L5-6

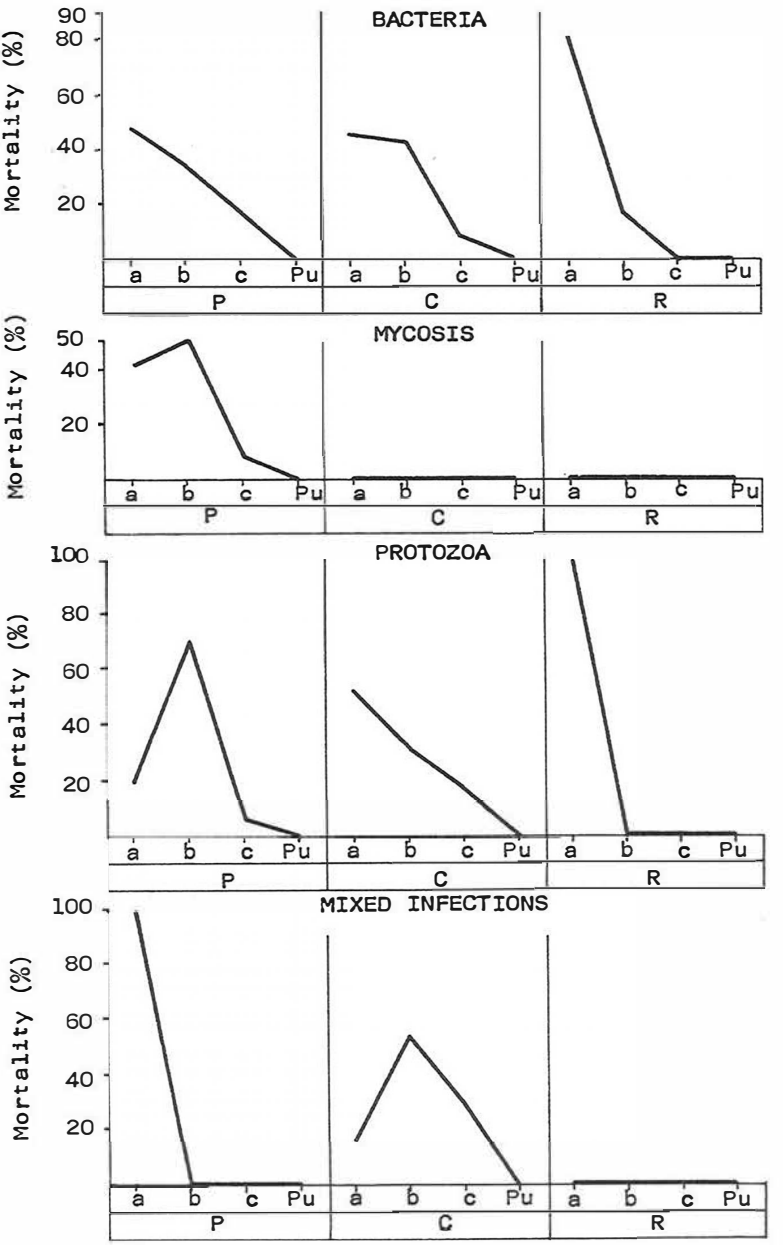
Figures 4 show the affinity of the groups of pathogens to instars of caterpillars, developmental stages of pest respectively.

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_{3-4}. In this period we found combination viruses + protozoa, viruses + bacteria, viruses + fungi, with caterpillars L_{1-2} combinations viruses + protozoa, protozoa + bacteria, viruses + bacteria, viruses + fungi, viruses + protozoa + bacteria with caterpillars L_{3-4}. The oldest caterpillars infested combinations of pathogens as viruses + protozoa, viruses + bacteria, viruses + fungi. Mixed infections did not occur in regression (Fig. 4).

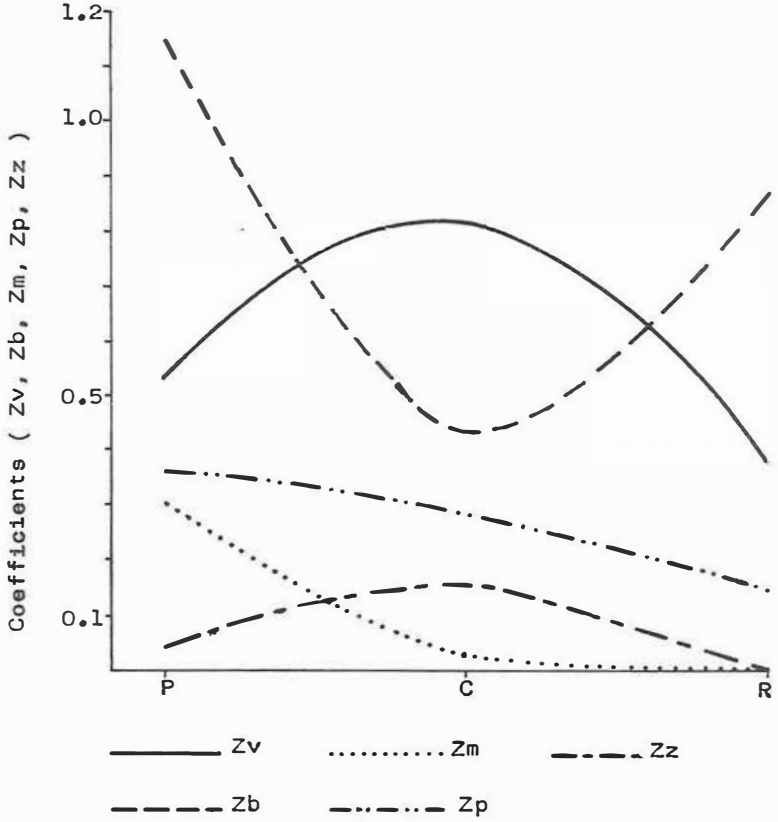
Figure 4: Binding of pathogens to instar, pest developmental stages resp. (a- L_{1-2}, b- L_{3-4}, c- L_{5-6}, Pu-pupae, P-progression, C-culmination, R-regression)




BACTERIA
MYCOSIS
PROTOZOA
MIXED INFECTIONS
Mortality (%)
90
80
60
40
20
50
100
a b c Pu
P
C
R

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 Zv-virosis, Zb-bacteria, Zm-mycosis, Zp-protozoa diseas, Zz-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 dependance on the pest development and did not induce pupae mortality et 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 imagos 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 unspecifity 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.

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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 nutritrive contribution to his offspring or a females'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
Orgyia			
pseudotsugata	P	Z6-21-11Ketone	Smith et al. 1975.
leucostigma	A	Z6-21-11Ketone	Grant 1977.
antiqua	A		Daterman et al. 1976.
cana	A		Daterman et al. 1976.
Dasychira			
grisefacta ella	A	Z6-21-11Ketone	Daterman et al. 1976.
vagans grisea	A		Daterman et al. 1976.
plagiata	A		Grant 1977.
Lymantria			
dispar	P	(+)cis7-8epoxy2Me-18Hy	Bierl et al. 1970 & Cardé et al. 1977.
dispar japonica	A	(±)cis7-8epoxy2Me-18Hy	Beroza et al. 1973a.
monacha	P	(+)cis7-8epoxy2Me-18Hy:10% (-)cis7-8epoxy2Me-18Hy:90%	Bierl et al. 1975 & Hansen 1984.
fumida	A	(±)cis7-8epoxy2Me-18Hy	Beroza et al. 1973a.
obfuscata	A		Beroza et al. 1973b.
Euproctis			
similis xanthocampa	P	Z7-18isovalerate	Tan et al. 1984.
Gynaephora			
ginghainensis	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.

HOW ARE PHEROMONE COMMUNICATION CHANNELS PARTITIONED?

The exclusivity of pheromone channels is not defined solely by specificity of production and response. The timing of daily and seasonal patterns of mating and habitat preferences each can provide sufficient separation to allow more than a single species to rely on the same pheromone (Roelofs and Cardé 1974). Differing diel periodicities of mating in particular have received emphasis as an effective partitioning mechanism in moths (e.g.,Cardé and Baker 1984, Cardé 1986). However, such rhythms are influenced by many other factors, including flight energetics and daily fluctuations in temperature, and the timing of avian and chiropteran predation (Cardé 1986).

The lymantriids that have been examined have comparatively broad female calling or pheromone emission periodicities and broad or multiple male response intervals. Schaefer (1974) demonstrated by hourly hand netting of flying male browntail moths, *Euproctis chrysorrhoea*, that there is a trimodal distribution of male flight: one hour after sunset, another close to midnight, and a final bout near dawn. Males were lured to female-baited sticky traps only during the latter two activity periods. The female satin moth, *Leucoma salicis*, initiates calling after sunset, with 50% calling by 22:30 hr (EST), and females continuing to call until dawn (Wagner and Leonard 1979). Male attraction and mating begins after sunset with 50% of matings occurring by 22:40.

Differing rhythms of calling are characteristic of some of the *Orgyia* species. These rhythms, however, are broad and they overlap considerably (Grant et al. 1975). Male *O. antiqua* are mainly attracted in the afternoon and male *O. leucostigma* mainly in the morning, but it is not yet clear how fully these differences isolate these tussock moths under natural conditions (Grant 1977).

Similarly, the sexual activity rhythms of *L. dispar* and *L. monacha* overlap to some extent (Schröter and Lange 1975) and thus may provide only a partial barrier to cross attraction. Habitat preferences and, to a lesser extent, seasonal flight periods of these two widely sympatric congeners also differ somewhat (Schröter 1981), but again a considerable overlap should allow cross attraction. Nevertheless, some isolation is achieved by differing rhythms of daily, seasonal activity and by habitat preference.

The extent to which specificity in the chemical message imparts isolation must be inferred from a few examples. In the gypsy moth the female emits (Hansen 1984) and the males respond optimally (Iwaki et al. 1974, Miller et al. 1977) to (7R,8S)-*cis*-epoxy-2-methyloctadecane [(+)-disparlure]. Its antipode (7S,8R-*cis*-epoxy-2-methyloctadecane) [(-)-disparlure] greatly diminishes attractivity when the two optical forms are admixed: a 1:1 blend evokes about one-

tenth the trap catch of (+)-disparlure. The nun moth has been estimated to emit roughly 10% of the (+)-enantiomer and 90% of the antipode (Hansen 1984). Male nun moths are optimally attracted to a wide range of mixtures of the two antipodes, and (+)-disparlure alone, but evidently not to the (-)-enantiomer (Klimetzek et al. 1976). Thus, a good degree of specificity between these two congeners is achieved by differences in the blend released and the reactions of the male, particularly the gypsy moth being 'inhibited' by the nun moths' release of (-)-disparlure.

Studies by several workers have suggested (*Z*)-6-heneicosen-11-one as a (or the only) pheromone component of 4 species of *Orgyia* tussock moths and very likely involved in the communication system of 3 species of *Dasychira* (ref. in Table 1). A variety of behavioral bioassays in the laboratory, electroantennograms, field trapping comparisons and hybridization tests have pointed toward the involvement of this chemical, but also support specificity being conferred by additional and as-yet-unidentified components (see review by Grant 1977). Thus the extent to which lymantriids employ multiple-component blends remains unclear.

WHAT ORIENTATION MANEUVERS ARE USED IN MATE LOCATION?

Male moths have been used extensively as a model system to examine and describe the mechanisms and maneuvers utilized by insects to orient to and successfully locate a point-source of odor over long distances (tens to hundreds of meters). Most of our knowledge of these orientation mechanisms pertains to those involved in orientation to pheromone plumes because these behaviors are so predictable and amenable to experimental manipulation in sustained-flight tunnels, and even in the field. In turn, virtually all of our knowledge of the orientation maneuvers used by lymantriids stems from studies of the gypsy moth, due in large part to its status as a pest species, and because most of these behaviors are relatively conspicuous since they are expressed during daylight.

At the initial stage of this process, it is not known if resting gypsy moth males are enveloped by a pheromone plume and then become 'activated' or if males initiate flight without pre-exposure to pheromone and then 'search' for pheromone plumes. Possibly both strategies come into play under natural conditions. Activation of quiescent gypsy moth males has been studied extensively in the laboratory. A resting male stimulated by pheromone can react by antennal movements, walking, and most noticeably and diagnostically, by initiation of wing fanning; wing fanning can occur while the male is stationary or walking. The latency of wing fanning varies inversely with pheromone

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

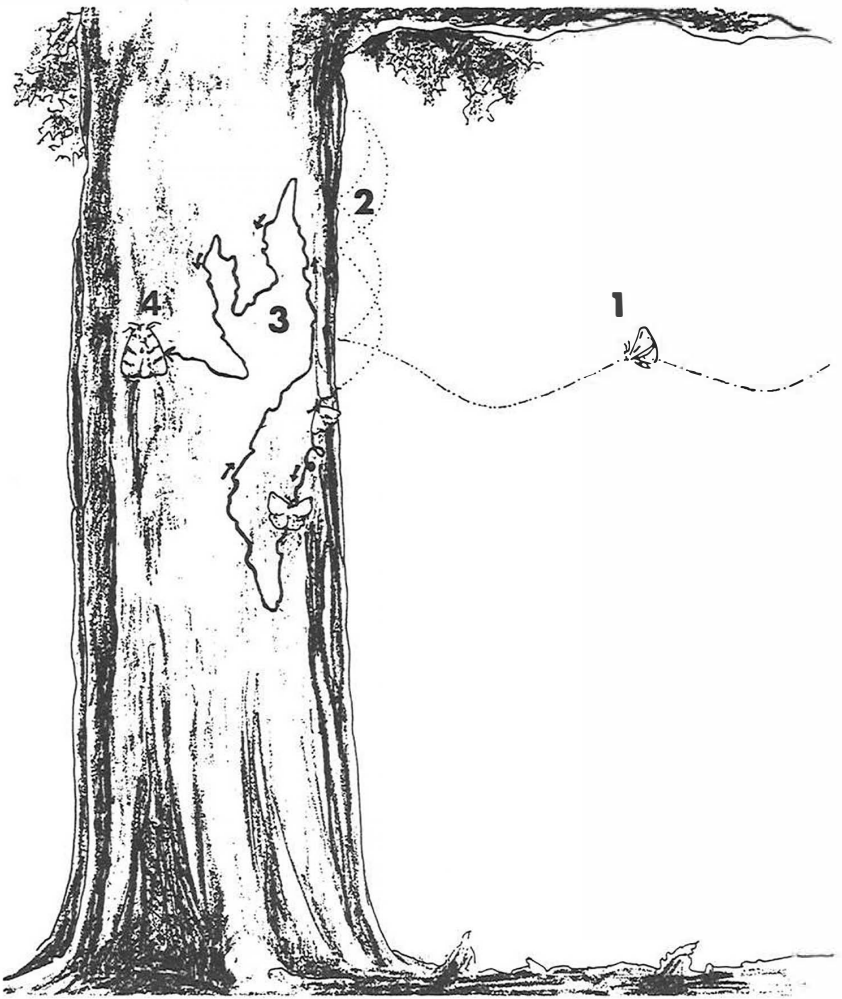

Fig. 1. Generalized sequence of male gypsy moth mate-seeking behaviors: (1) pheromone-modulated anemotactic flight toward the pheromone source; (2) vertical flight in the immediate vicinity of the tree bole harboring the calling female, whereby the male intermittently makes tarsal contact with the bark; (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

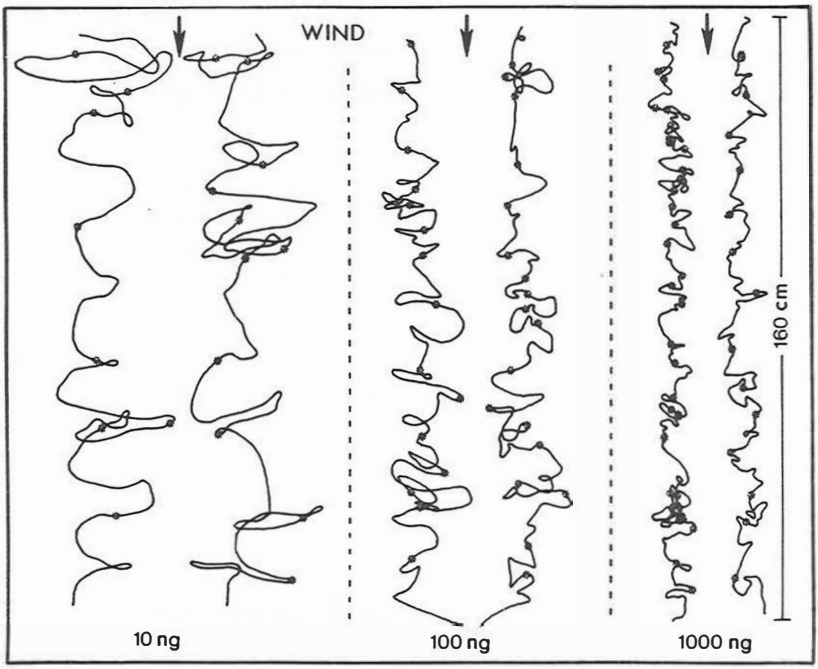

Fig. 2. Representative flight tracks of gypsy moth males flying to three different pheromone concentrations. Flight tracks were recorded in the plan view with the moth progressing from bottom to top (from Charlton et al. 1989e).

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 lingustri*) 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 then 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 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

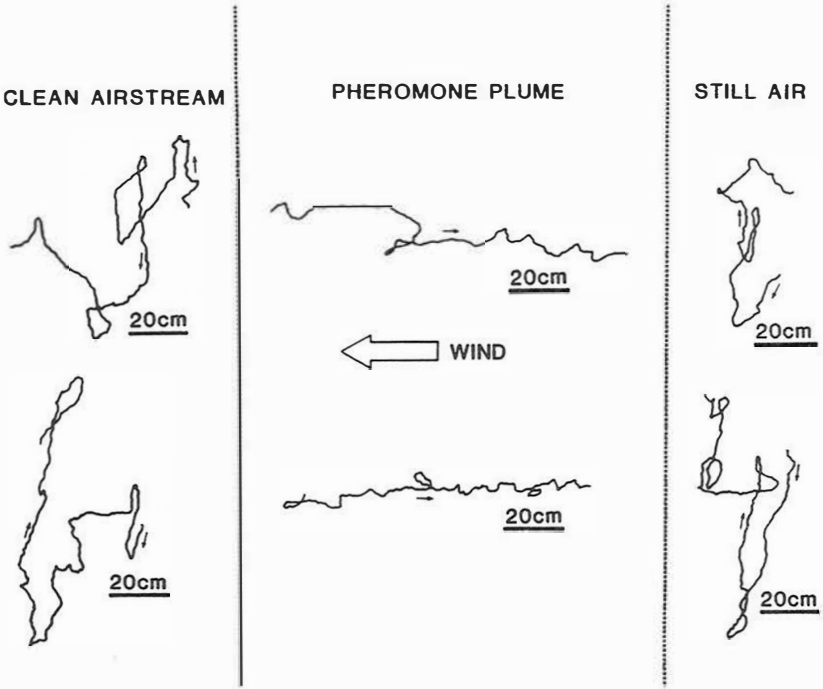

Fig. 3. Typical tracks of walking male gypsy moths in response to a pheromone plume (100 ng (+)-disparlure) or still air or a clean (pheromone-free) airstream following interruption of pheromone stimulation. Pathways were recorded on a vertical surface using a locomotion compensator (from Charlton et 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 ofttimes 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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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 occassionally 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 Srinigar in the Vale of Kashmir between 1968 and 1971. These sites were

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

Life stage	lx	dxF	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 sallow 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 $L_{5/6}$ ($0.05 > P > 0.01$) 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_{EF}, 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_{EF}, the discrepency 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_{EF}

The difference between the number of adult females emerging and egg-masses oviposited (k_{EF}) 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 obfuscata. *** P < 0.001 for departure from unity.

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

Table 3. Key factor and density dependence analysis of individual mortality factors acting on the $L_{5/6}$ and pupal stages of Lymantria obfuscata. *** P < 0.001 for departure from unity.

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

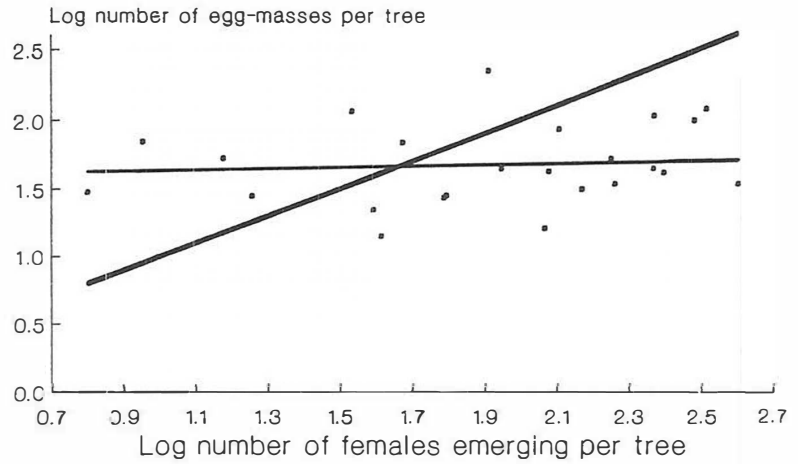

Fig. 1. Density dependent loss of oviposition in L. obfuscata, showing line of equality (thick) and regression line (thin) Y=a+bX, a=1.59±.30, b=0.04±.14, r^2=0.004, P > 0.05. Egg-mass density is therefore constant.

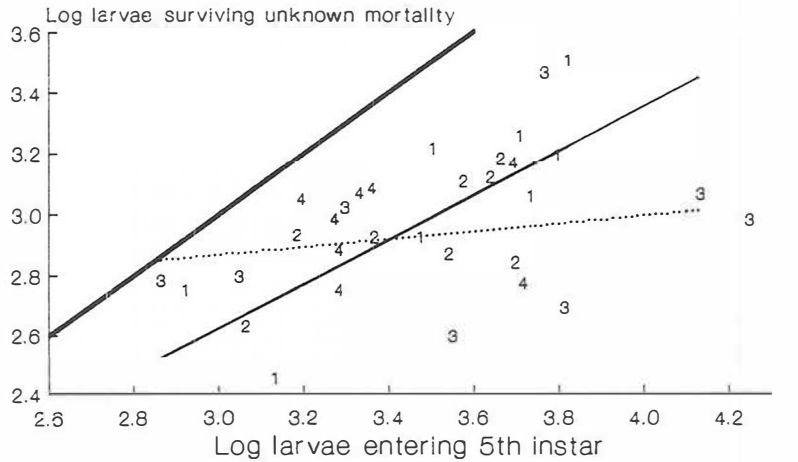

Fig. 2. Density dependent 5th instar larval mortality of L. obfuscata from unknown factors. Data plotted by locality, (1) Pinglain, (2) Pampore, (3) Athwajan and (4) Zainakoot, showing line of equality (thick) and regression lines Y=a+bX for localities 1+2 (a=0.44±.17, b=0.73±.16, r^2=0.59, P < 0.001, solid line) and 3+4 (a=2.49±.22, b=0.13±.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_{1-3}). 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 vertabrate 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).

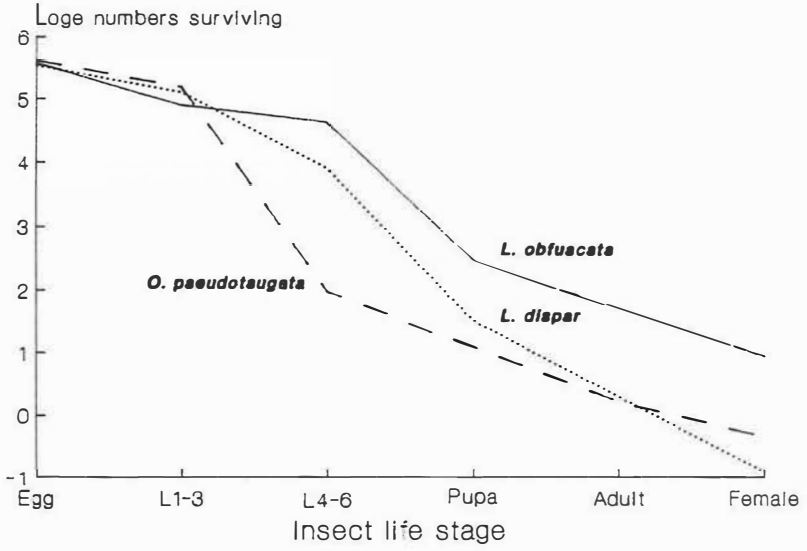

Fig. 3. Survival rate from egg to adult female of a single egg-mass during the outbreak phase of three lymantriid populations.

In summary, the lymantriid populations show similarity in their levels of fecundity and the prominance 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 O. 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 O. 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 O. 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. 1985, 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 precation. In contrast, Orgyia pseudotsucata 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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LATENCY CHARACTERISTICS OF TUSSOCK MOTHS (LEPIDOPTERA: LYMANTRIIDAE

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INTRODUCTION

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

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

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

Species

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

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

INITIAL POPULATION DENSITY

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

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

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

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

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

Site characteristics

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

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

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

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

Weather

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

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

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

DISPERSAL AND MIGRATION

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

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

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

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

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

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

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

LIFE STAGE MORTALITY IN LATENCY POPULATIONS

Egg Mortality

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

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

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

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

Host-Induced Larval Mortality

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

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

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

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

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

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

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

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

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

Predation, Disease and Parasitism

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

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

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

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

Pupal Mortality

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

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

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

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

Mortality of Imagoes

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

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

LATENCY FECUNDITY

Density-dependency

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

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

Sex Ratio

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

Number of Generations

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

Host Plant Relations

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

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

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

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

RELEASE OF LATENCY POPULATIONS

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

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

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

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

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

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

SUMMARY

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

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O U T B R E A K C H A R A C T E R I S T I C S

OF L Y M A N T R I I D S

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INTRODUCTION

The Lymantriids, known as Tussock moths, are a small family of very destructive defoliators. They feed on conifers as well as broad-leaved trees (FURNISS and CAROLIN, 1977). The species shown in Table 1 have reached high economic importance.

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

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

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

PRINCIPLES of POPULATION DYNAMICS of LYMANTRIIDS

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

Table 1: Lymantriids of economical importance

Genera	Species	common name	Distribution
Lymantria (Porthetria)	monacha	Nun moth	Europe/Asia
"	dispar	Gypsy moth	Europe/N-America
Orgyia	recens (=antiqua)	Rusty tussock moth	Europe/N-America
"	pseudotsugata	Douglas fir tussock moth	
"	leucostigma	Whitemarked tussock moth	N-America
"	vetusta	Western tussock moth	
Dasychira (Parorgyia)	pudipunda	Buchenrotschwanz	Europe
"	grisefacta	Pine tussock moth	N-America
Leucoma (Stilpnotia)	salicis	Satin moth	Europe/N-America
Euproctis	chrysorrhoea	Brown-tail moth	Europe

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

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

BERRYMAN (1986) formulates this as follows:

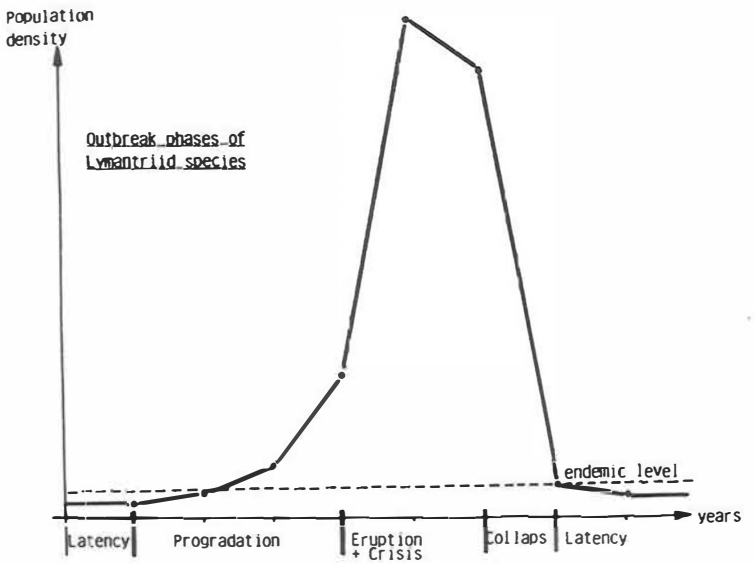
$$\text{Population change} = \text{birth rate} - \text{death rate} + \text{immigration rate} - \text{emigration rate}$$

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

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

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

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



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

DENSITY-DEPENDENT and INDEPENDENT FACTORS

Fertility

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

- female rate and
- number of eggs per female

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

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

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

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

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

for the 1st year: F = 0.65 x 220 = 143

for the 3rd year: F = 0.3 x 80 = 24

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

Mortality

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

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

Constitution

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

Food supply

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

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

Abiotic influences of environment

Temperature

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

Humidity

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

Climate

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

Weather

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

Biotic environmental factors

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

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

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

DEVELOPMENT and DURATION of NUN MOTH OUTBREAKS

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Population Phase		Number of Years	
		Pine Forest	Spruce Forest
progradation (increase)		2	4
eruption	(outbreak)	1	2
collaps		1	1

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

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

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

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

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

larger, more predictable supply in spruce stands.

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

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

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

CONCLUSIONS

The nun moth provides a prototype of the principle pattern of outbreaks of the tussock moth species shown in Table 1. Differences among the Lymantriids result essentially from species specific behaviour, such as host tree preference and climatic requirements and on the volume and effectiveness of their antagonists. Gypsy moth, for instance, prefers warmer and dryer habitats than nun moth. For that reason, the traditional European outbreak areas of the gypsy moth are in southern and southeastern Europe.

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

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MONITORING POPULATION CHANGE IN THE LYMANTRIIDAE

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INTRODUCTION

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

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

COMMON TECHNIQUES OF MONITORING

D e f o l i a t i o n

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

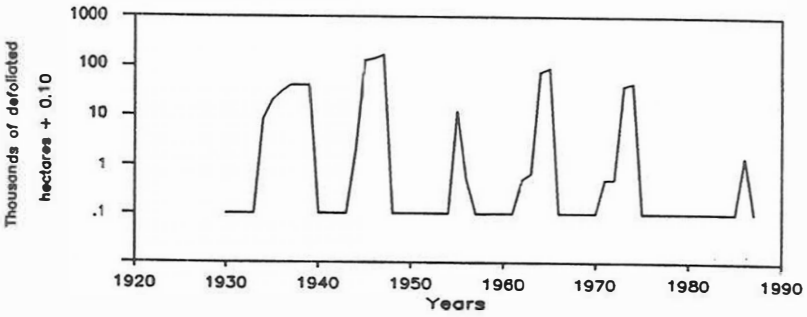

Figure 1. Trend of visible defoliation by Orgyia pseudotsugata in northern Idaho, 1930-87 (modified from Livingston, 1984).

Eggs

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

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

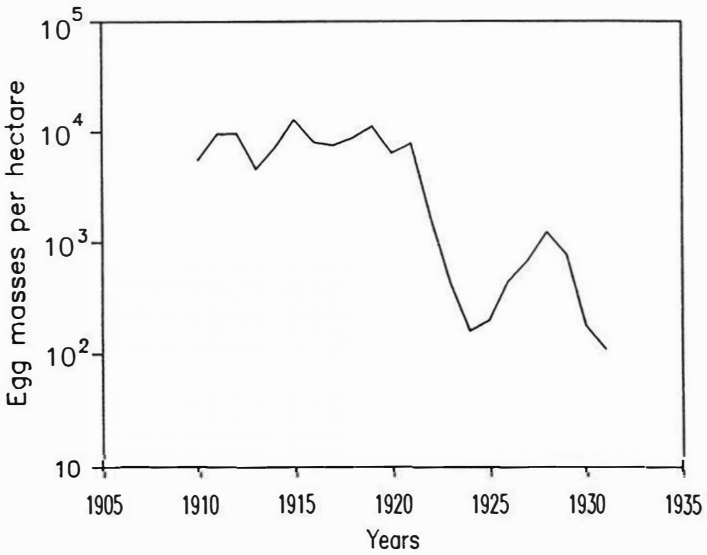

Figure 2. Trend of egg mass densities of Lymantria dispar in eastern New England, 1911-31 (modified from Campbell, 1967).

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

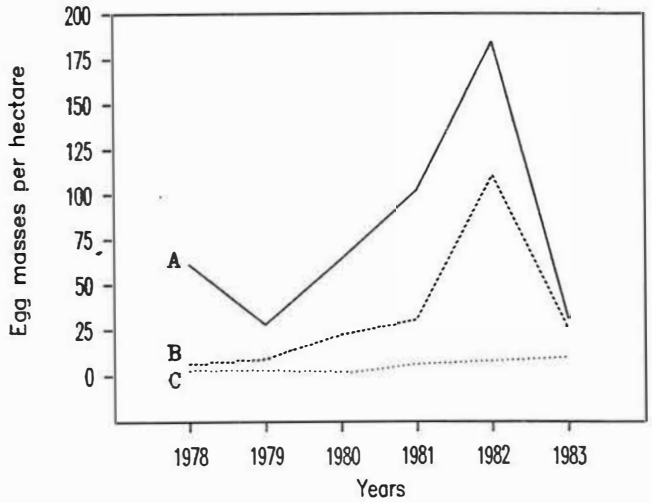

Figure 3. Trend of egg mass densities of Lymantria dispar in three study areas in Yugoslavia: A. Check area, B. Egg masses added, and C. Egg masses added (from Maksimović and Sivčev, 1984).

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

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

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

L a r v a e

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

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

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

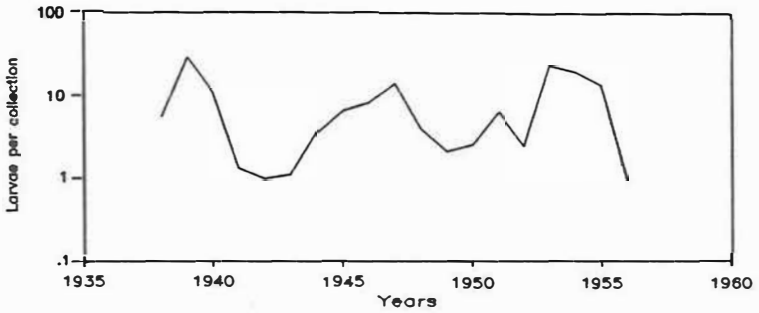

Figure 4. Trend of larval collections of Orgyia leucostigma in Canada, 1938-56. Data collected by the Forest Insect and Disease Survey of the Canadian Forestry Service (calculated from Prentice, 1962).

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

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

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

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

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

where M is midcrown density per m^2 of branch area, d is the average number of days since egg hatch, and p is the proportion of sample units with larvae. Because of the cost efficiency of the method we have been able to monitor low-density populations of O. pseudotsugata continuously over a longer period of time than would be possible by other more expensive methods (Fig. 5). Lower crown

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

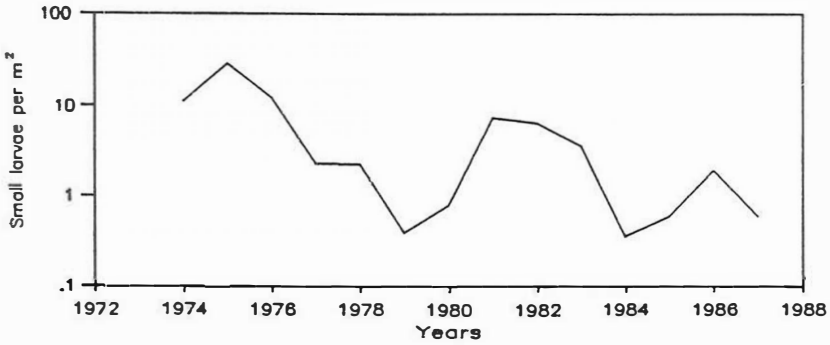

Figure 5. Trend of larval densities of Orgyia pseudotsugata in a nonoutbreak population in southern Oregon, 1974-87. Plotted data are means of eight sample plots (from Mason and Torgersen, 1987).

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

P u p a e

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

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

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

A d u l t s

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

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

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

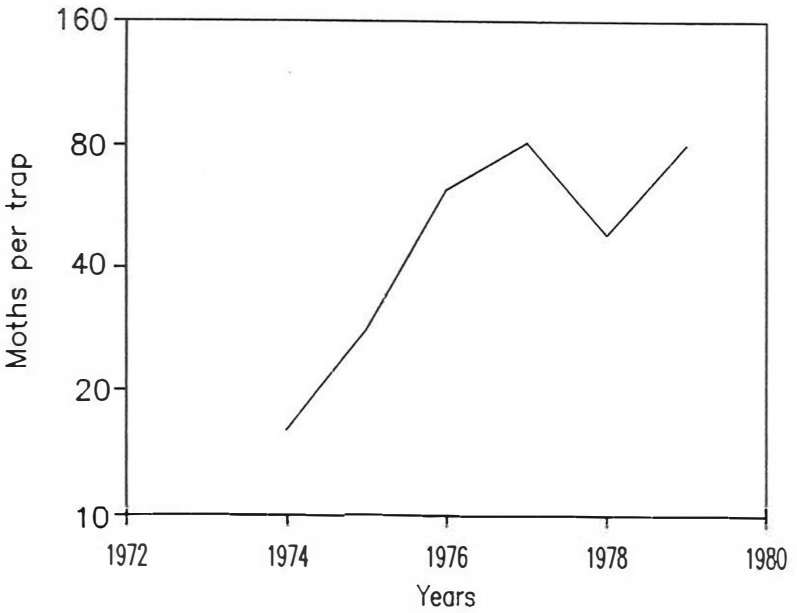

Figure 6. Trend of trapped adults of Lymantria monacha in a nonoutbreak population in southwest Germany, 1974-79. Plotted data are means of 130 traps in four forest districts (modified from Bogenschütz, 1979).

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

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

Frass and Exuviae

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

DISCUSSION

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

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

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

SUMMARY

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

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SPATIAL ASPECTS OF GYPSY MOTH POPULATION DYNAMICS

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INTRODUCTION

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

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

WITHIN-STAND PROCESSES

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

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

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

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

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

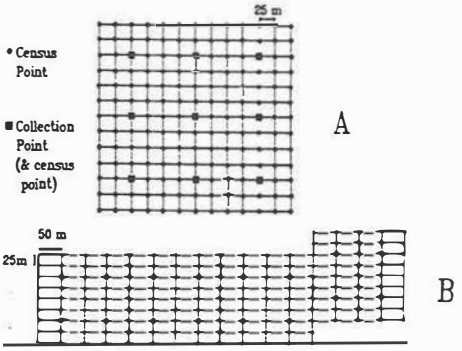

Figure 1. Location of density estimation census points and larval collection points. A. 9-ha site (site 1). B. 16-ha site (site 2).

Sampling Methodology

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

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

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

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

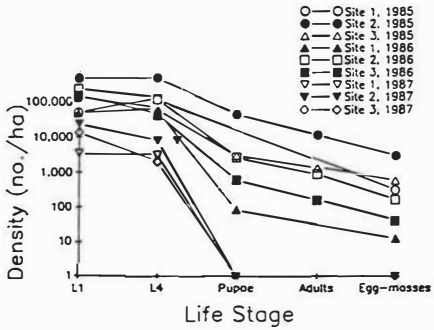

Figure 2. Densities of successive gypsy moth life stages at each site from 1985-1987. Site 3 was an additional 9 ha plot at which detailed spatial data was not collected.

Results

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

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

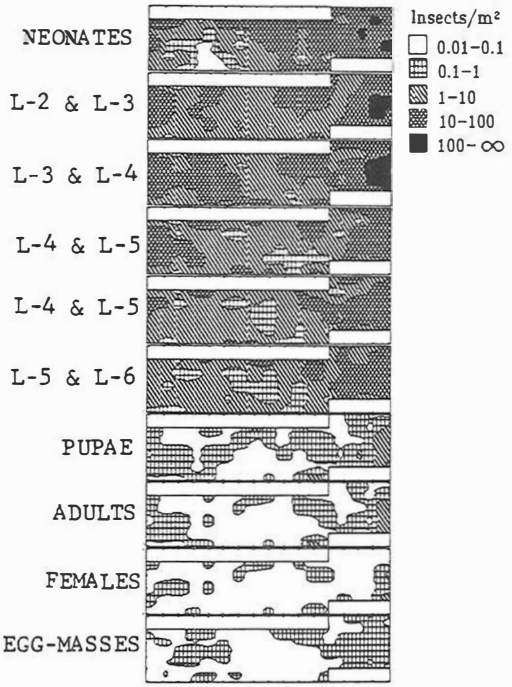

Figure 3. Spatial distribution of successive gypsy moth life stages at site 2, 1985. Data interpolated from 86 grid-point estimates using a Bessel interpolation.

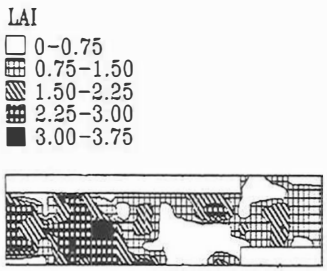

Figure 4. Spatial distribution of oak leaf-area (expressed as leaf area index [LAI]) at site 2. Data from 86 canopy photographs (Liebhold et al. 1988).

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

Mortality	Site 1 1985	Site 1 1986	Site 2 1985	Site 2 1986
k_1	/	.	/	/
C. melanoscelus	\	.	.	.
Unknown	.	.	.	.
NPV	.	.	/	.
k_2	.	.	.	.
C. melanoscelus	\	.	\	.
P. sylvestris	.	.	/	.
Unknown	.	.	.	.
NPV	.	.	.	.
k_3	.	.	/	.
k_4	\	.	/	/

K_1 was the most consistently density-dependent mortality (Table 1). Rearing of larval samples indicated relatively little mortality due to parasitoids and disease during this period. Thus, it is likely that the density-dependence observed during this period is due to predation or dispersal. The finding that mortality due to parasitization by *C. melanoscelus* tended to be inversely density-dependent is in agreement with findings from a similar study (Weseloh 1973). In general, specific density-dependent relationships did not remain constant across all plots and years. Hassell et al. (1987) found this to be true in their study of the spatial density-dependence of viburnum whitefly mortality. Thus, conclusions about density-dependence derived from spatial data are unique to the generation under observation.

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

REGIONAL PROCESSES

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

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

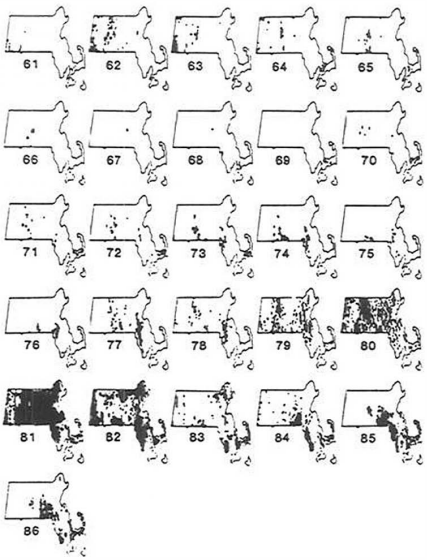

Figure 5. Defoliation incidence for each 1.9 x 1.9 km cell in Massachusetts, 1961-86.

Description of the Data

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

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

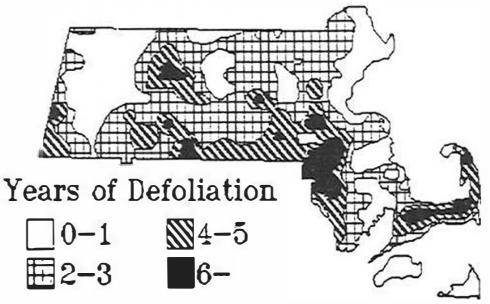

Figure 6. Spatial contour of defoliation frequency in Massachusetts from 1961-86.

Cluster Analysis

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

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

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

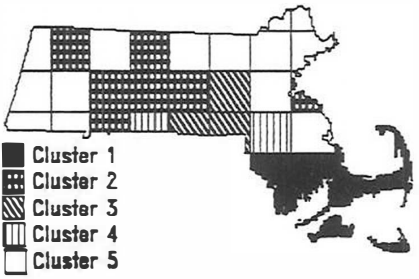

Figure 7. Map of clusters generated using Ward's algorithm.

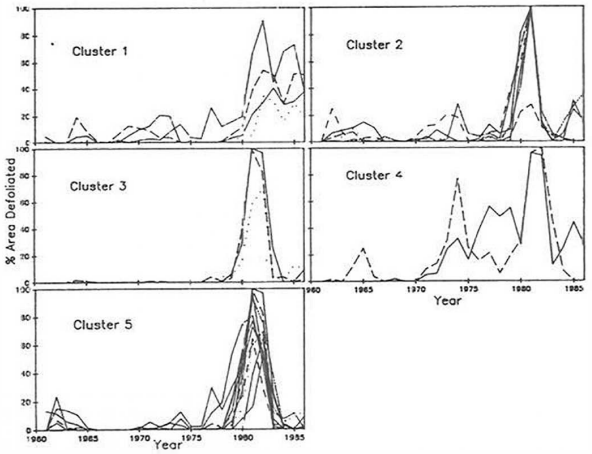

Figure 8. Yearly defoliation frequencies in each of 30 regions.

Transition Models

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

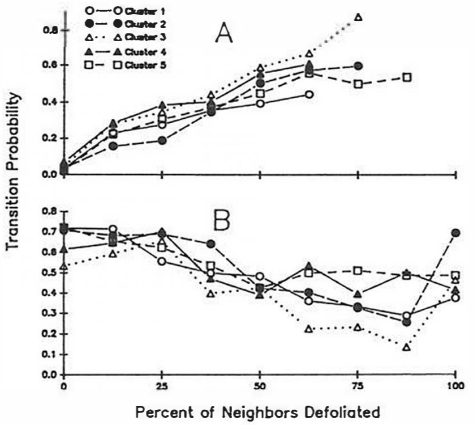

Figure 9. Probabilities of transition to a different defoliation state with varying numbers of defoliated neighbors: A. Transition from nondefoliated to defoliated; B. Transition from defoliated to nondefoliated.

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

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

Autocorrelation Analysis

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

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

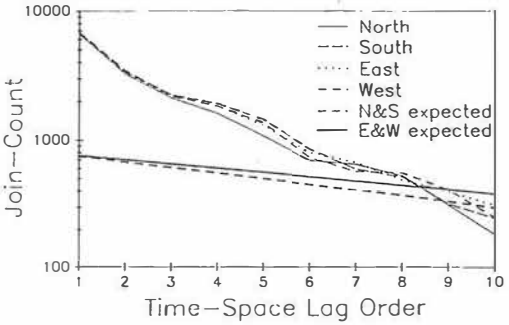

Figure 10. Directional spatio-temporal autocorrealation correlograms (Reynolds 1988; Oden and Sokal 1986) based on defoliation join-counts from 1961-86. Join-counts expected under a random distribution through time and space were the same for both North-South and East-West adjacency definitions.

SUMMARY

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

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

ACKNOWLEDGMENTS

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IMPACTS, SILVICULTURE, AND THE GYPSY MOTH

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INTRODUCTION

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

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

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

ASSESSING POTENTIAL STAND DEFOLIATION (SUSCEPTIBILITY)

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

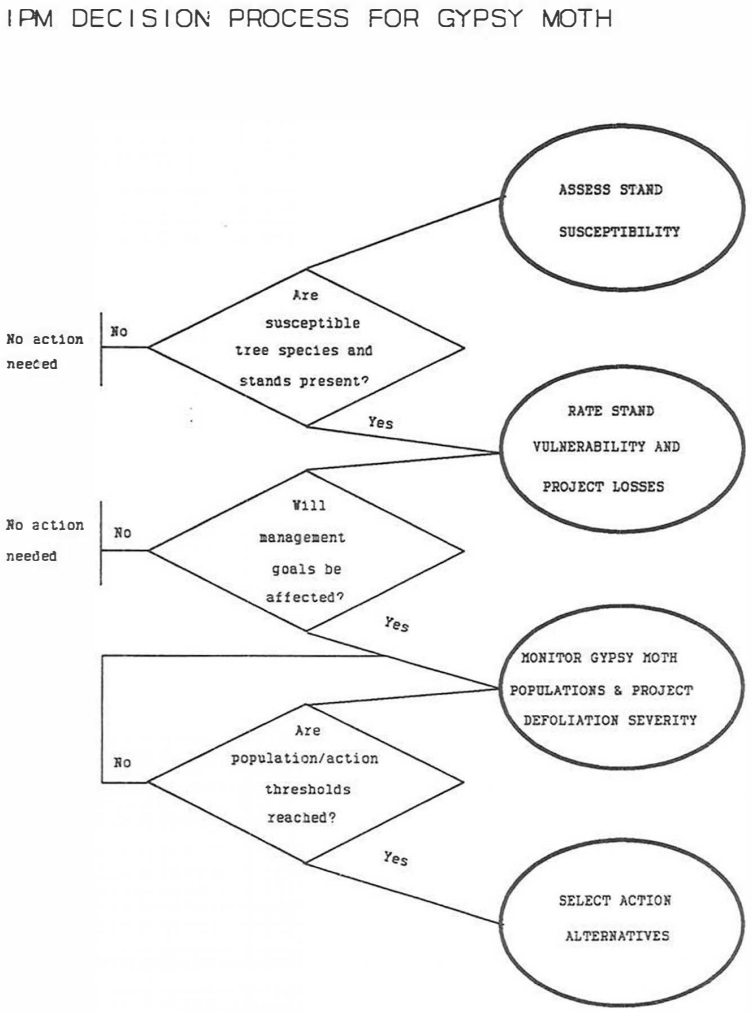

Figure 1. Integrated pest management (IPM) decision chart to help forest managers cope with the gypsy moth.

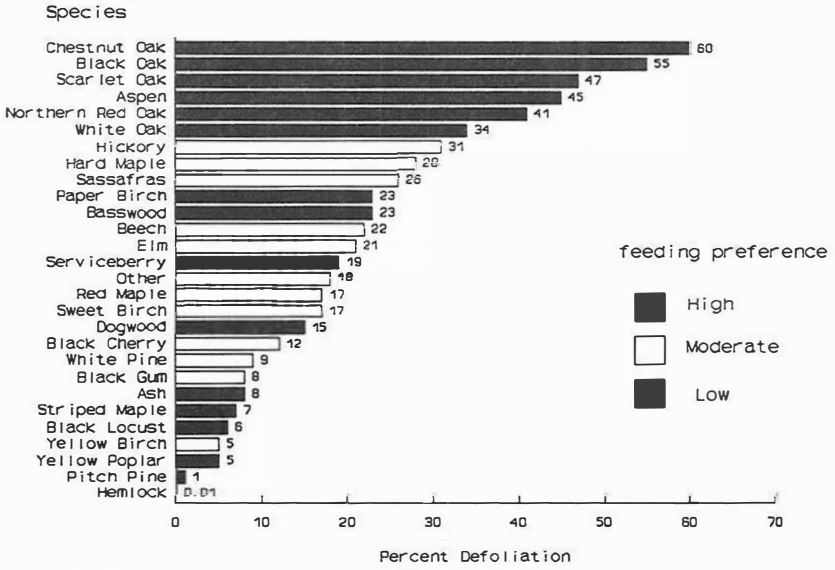

Figure 2. Average species defoliation on 600 plots in central Pennsylvania in 1981 (Gansner and Herrick 1985).

Rating Stand Susceptibility

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

Table 1. Host preferences of the gypsy moth.

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

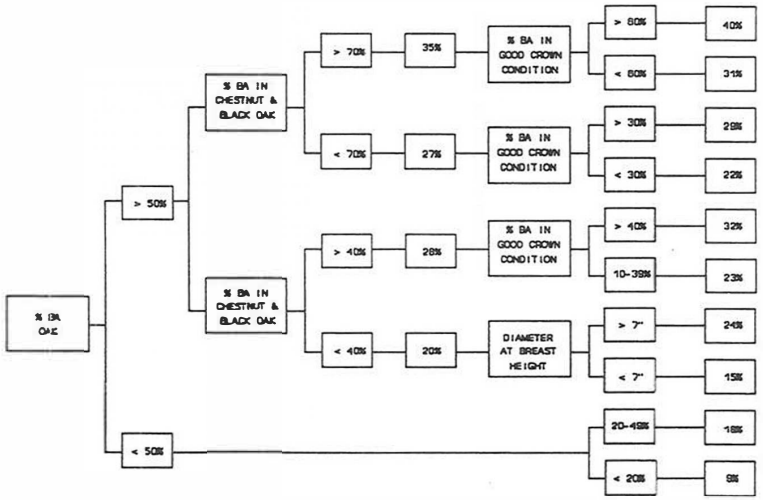

Figure 3. Guide for estimating gypsy moth defoliation potential in newly infested areas (Herrick and Gansner 1986).

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

ASSESSING POTENTIAL TREE MORTALITY (VULNERABILITY)

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

Defoliation Intensity, Distribution, and Frequency

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

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

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

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

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

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

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

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

Tree Condition

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

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

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

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

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

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

Site and Stand Conditions

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

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

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

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

Rating Stand Vulnerability

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

percentage of trees in the white oak group (found to be particularly vulnerable) and the percentage of trees with poor crowns (more than 50% dead branches, very thin foliage, reduced leaf size, poor color, or heavy

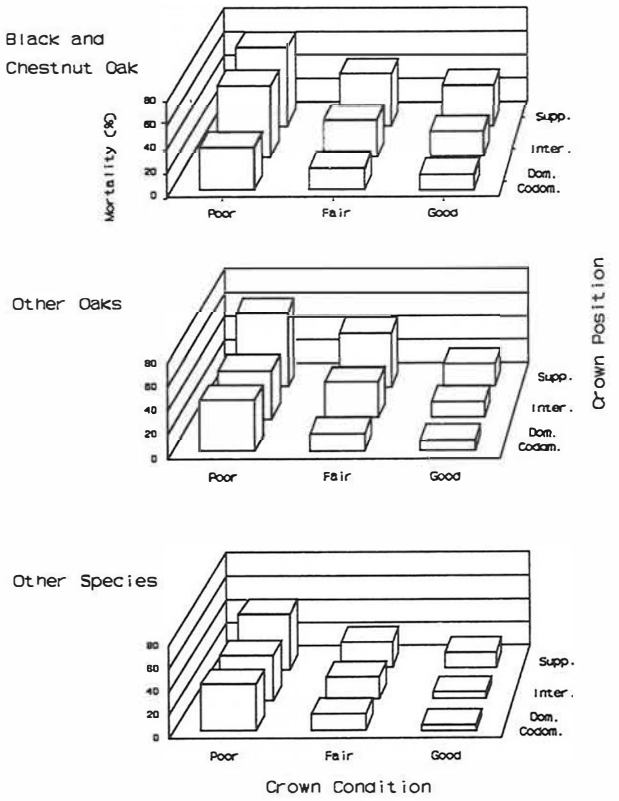

Figure 4. Individual tree mortality probabilities based on 600 central Pennsylvania plots (Herrick and Gansner 1987b).

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

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

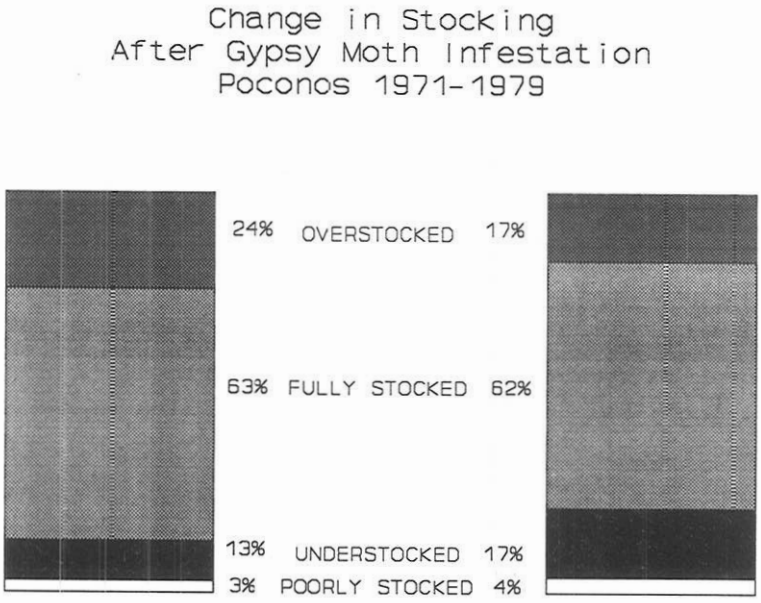

Figure 5. Change in stand stocking in Poconos Mountains region of Pennsylvania following gypsy moth related mortality (Gansner and Herrick 1984).

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

CONSIDERING IMPACT ON MANAGEMENT OBJECTIVES

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

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

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

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

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

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

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

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

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

MONITORING GYPSY MOTH POPULATIONS

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

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

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

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

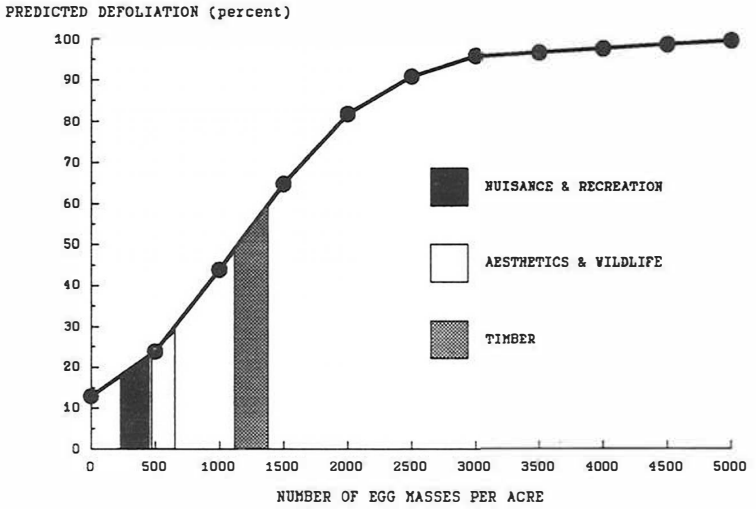

Figure 7. Egg-mass to defoliation prediction curve and thresholds for gypsy moth control treatments for different management objectives (altered from Gansner et al. 1985).

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

SELECTING ACTION ALTERNATIVES

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

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

Silvicultural Treatments

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

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

Alteration of stand susceptibility:
Maximizing tree growth and vigor
Manipulating gypsy moth habitat
Increasing forest diversity
Alteration of stand vulnerability:
Maximizing tree growth and vigor
Removing high risk trees and stands
Manipulating secondary organism habitat

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

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

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

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

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

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

Pesticide Applications

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

No Action

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

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

SUMMARY

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

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ARE GYPSY MOTH POPULATIONS IN NORTH AMERICA REGULATED AT LOW DENSITY?

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INTRODUCTION

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

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

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

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

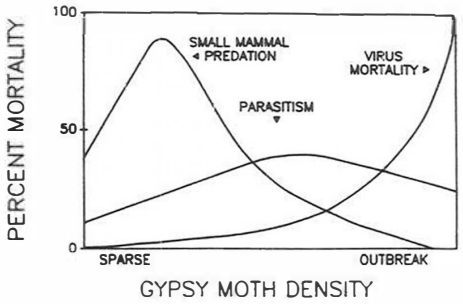

Fig. 1. Hypothetical percent mortality caused by the principal mortality agents maintaining bimodal stability in gypsy moth populations in North America (redrawn from Campbell 1975, Berryman et al. 1987)

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

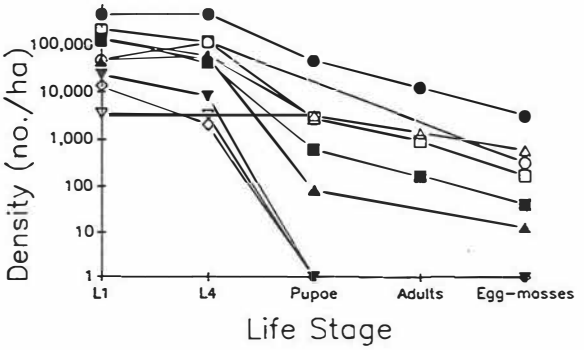

Figure 2. Survivorship curves for gypsy moth at three sites on Cape Cod, MA 1985-1987.

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

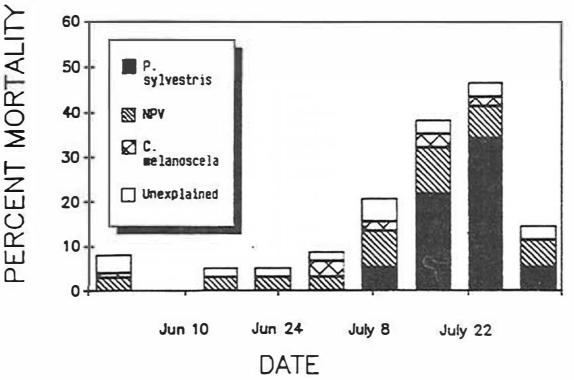

Figure 3. Proportion of gypsy moth larvae dying each week from various parasitoid spp. and disease in a low density population on Cape Cod, 1985.

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

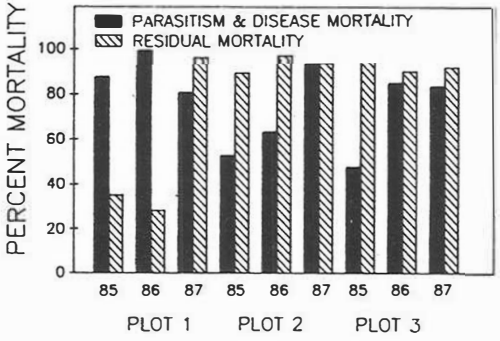

Fig. 4 Comparison of mortality of gypsy moths occurring between the fourth instar larva and pupal stages caused by parasitism plus disease versus residual mortality (which includes predation) at 3 sites on Cape Cod 1984 - 1987.

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

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

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

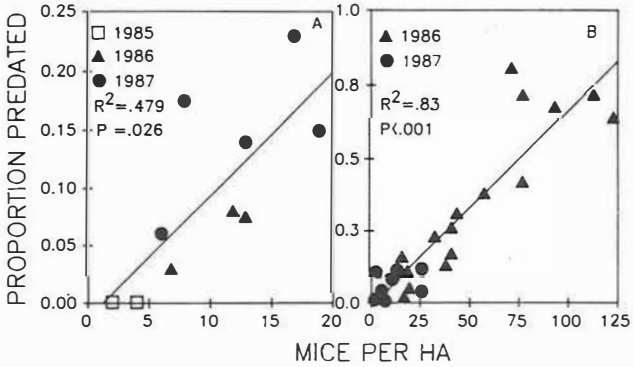

Fig. 5. Daily proportion of gypsy moth pupae consumed by vertebrate predators versus density of P. leucopus on A) 3 sites on Cape Cod and B) 16 sites in western Massachusetts.

EXPERIMENTAL MANIPULATION OF POPULATIONS

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

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

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

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

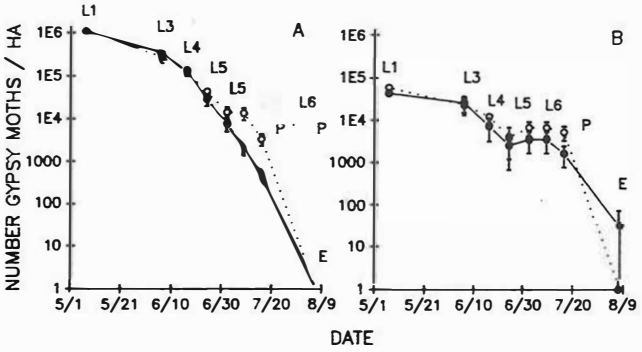

Figure 6. Survivorship curves obtained from A) two high density and B) two low density gypsy moth populations created on 1 ha plots in western Massachusetts by releasing field collected egg masses. Four other plots of intermediate initial densities showed similar patterns of survivorship that were intermediate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

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

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

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

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

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

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

IS SMALL MAMMAL PREDATION DENSITY DEPENDENT?

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

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

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

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

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

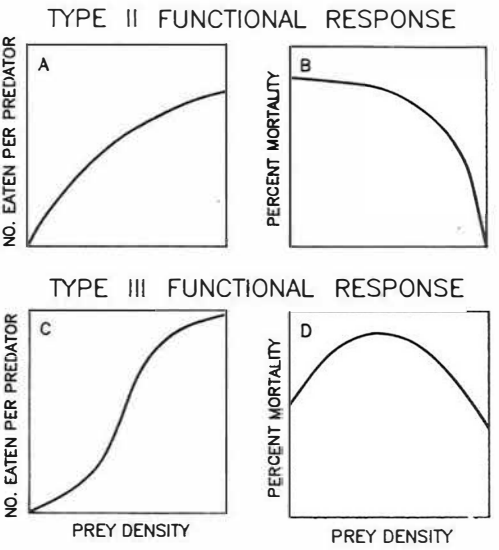

Figure 7. Hypothetical number and corresponding percentage of prey consumed as a function of prey density in Holling's (1959) Type II (A,B) and Type III (C,D) functional responses.

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

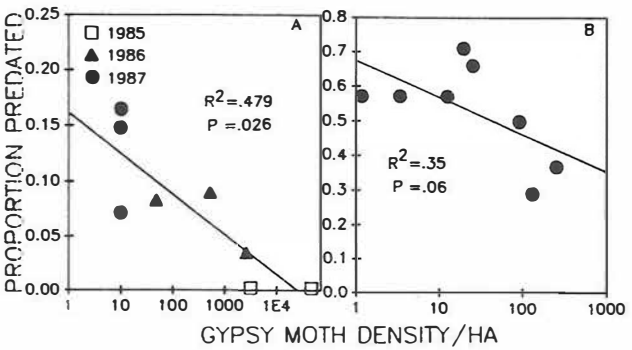

Figure 8. Proportion of pupae predated by vertebrate predators versus density of naturally occurring pupae on A) 3 sites on Cape Cod 1985-1987 and B) on the eight experimentally created populations in western Massachusetts, 1987.

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

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

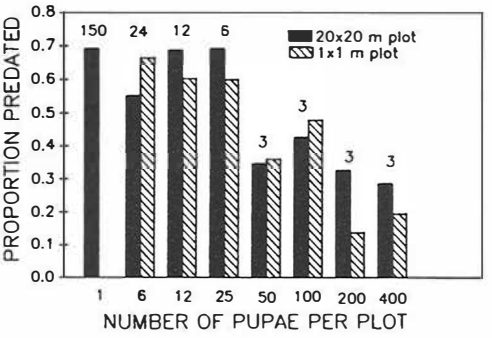

Figure 9. Proportion of gypsy moth pupae deployed in 1 X 1 m and 20 X 20 m plots that were consumed by vertebrate predators over three day test periods. Numbers above each bar indicate number of replicates conducted at each density.

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

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

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

SUMMARY

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

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

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THE CONTROL OF *Lymantria dispar*: SOME GENETIC AND BEHAVIOURAL CONSIDERATIONS

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Ernst Mayr wrote to me recently and told me that some years ago a new outbreak of *dispar* totally devastated the vegetation around his country house in New Hampshire. The massiveness of the infestation had been unbelievable - he counted 140 egg masses on the trunk of a single cherry tree. It was the first outbreak in his area for some twenty years, and he pointed out that the first instar larvae can apparently be carried by strong winds for hundreds of miles. When they land, at considerable densities, in an area free of parasites and pathogens, they multiply explosively. His outbreak soon subsided, as a result of viruses, bacteria and Braconid wasps. However, from this information I draw the conclusion that the only way to suppress *dispar* is by concentrating on areas where it is known to be endemic, since geographical "anticipation" is unreliable.

Let us now consider some methods of attacking the insect.

a) *Manipulation of the sex ratio.*

It is well known that in the USA and Canada there are no distinctive *dispar* races, probably because of the founder principle, which meant that the original genetic stocks were very small in number (see Wood and Way, 1988). In Japan on the other hand racial differences are marked. Sterile intersexes may therefore occur when races are hybridised and Goldschmidt (1931, 1934) made a special study of these. As a result, attempts have been made to suppress *dispar* in the USA by introducing sterile males (Mastro *et al.*, 1981).

E. B. Ford and I thought it was worth repeating some of Goldschmidt's crosses and re-evaluating the results using a modern technique. We came to an entirely different conclusion, particularly regarding Goldschmidt's most striking cross, that between the race in Hokkaido and the one in the Aichi region of Japan (Clarke and Ford, 1980, 1982, 1983 and 1984).

The new technique consisted of testing somatic cells for the presence or absence of a heteropyknotic body which Smith (1945) had shown to be present in females of the spruce budworm (*Archips fumiferans*) whereas the males lacked it. The same was found to be true in most species of Lepidoptera (Traut and Mosbacher, 1968) (Fig.1).

The procedure is as follows: using sharp dissecting scissors, an abdominal proleg from the larva (Fig.2) is removed, and enough tissue can be scraped from the inside of the proleg to make one good preparation, the material being teased out and spread as thinly as possible. After amputation each larva is kept separately and cotton wool applied to the wound. The larvae recover, and there is no deformity in the perfect insect. In the adult, gut or Malpighian tubule cells are used, from freshly killed insects (see appendix for staining technique).

In the cross female Hokkaido X male Aichi we confirmed Goldschmidt's finding of a big excess of males, but Table 1 shows that, as judged by Smith testing, they were normal males and not transformed females. The moths selected were taken at random, as were the larvae, which we usually tested in the 4th or 5th instar, sometimes earlier. As a control the pure races were also tested and here the overall sex ratio was near unity, and the larval Smith testing tallied with the sex of the moth. In Table 1 on only one occasion (brood 16510) was an individual scored as positive and yet developed into a completely male-like insect; this was Smith negative as an adult. We have occasionally found similar discrepancies in testing pure races, the Smith test not being entirely free from error.

From our broods there seems no doubt that Goldschmidt was wrong and that the excess of males was the result of the Haldane (1922) effect (see appendix) the female embryos or tiny larvae dying because of genic imbalance.

Our F1 males and the two F1 females were fertile and further evidence comes from the F2 and back cross broods, where there was a much more normal sex ratio, supporting Haldane's 'rule'. The details of these F2 and back cross broods are given by Clarke and Ford (1983) and in the same paper the sex ratio in some reciprocal crosses showed an excess of males, arguing against Goldschmidt.

b) Juvenile growth hormone as a possible suppressor of L. dispar.

Since the discovery of the juvenile hormones there has been much interest in the synthesis of analogues for use as insect control agents, but I do not know whether they have enjoyed any commercial success as far as dispar is concerned. But I believe that none of the synthetic compounds has closely resembled in chemical structure the natural juvenile hormone. However, with the recent discovery of juvenile hormone III in the Malaysian plant Cyperus iria there may be more hope (Toong et al., 1988). A summary of their Nature paper follows:

Third stadium grasshopper nymphs fed on the Malaysian plant Cyperus iria ate normally and continued to grow and moult just like control insects during their two subsequent instars. Following the final moult, however, 90% of the adults were abnormal compared to control animals reared on wheat seedlings. Typical transposition effects were observed, including twisted wings and colour changes reminiscent of treatment with excess juvenile hormone. In addition, the ovaries of females raised on C. iria contained markedly under-developed eggs com-

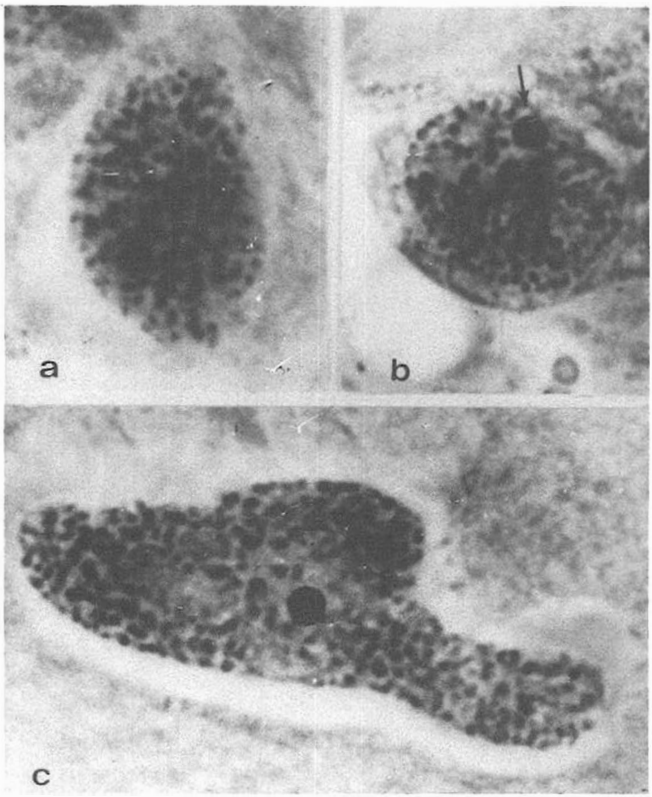


Figure 1. Cells from the proleg of L. dispar stained to show the absence a, (male) or presence b, c (female) of the heteropyknotic body.

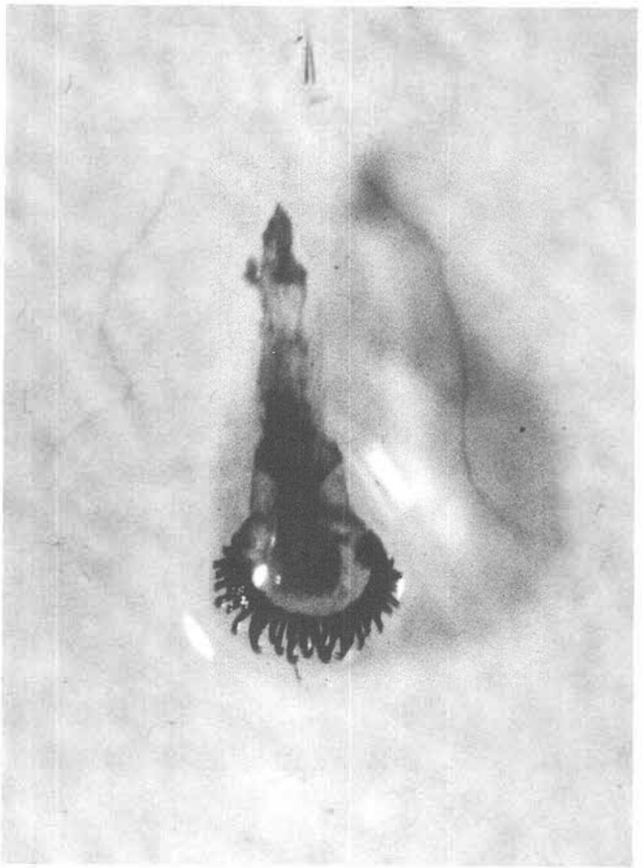


Figure 2. Proleg of L. dispar larva.

TABLE 1.

OUR BROODS OF THE CROSS FEMALE HOKKAIDO X MALE AICHI
(GOLDSCHMIDT'S MOST CRITICAL CROSS)

Our brood no:	Offspring	No. of adults Smith-tested as moths	results of Smith-testing of adults	No. of adults Smith-tested prospectively as larvae	results of Smith-testing as larvae. (In dead larvae information about the gonads is given where known.)
16508	45 ♂♂	25 ♂♂	25 neg.	4 ♂♂	4 neg.
16509	33 ♂♂	21 ♂♂	21 neg.	2 ♂♂	2 neg.
16510	42 ♂♂	25 ♂♂	25 neg.	13 ♂♂	12 neg. 1 pos. as larva but neg. in both gut and Malpighian tubules as adult. 5 larvae died, all neg. (all had testes)
	2 ♀♀ †	1 ♀ †	1 pos.	1 ♀	1 pos.
16513	11 ♂♂	7 ♂♂	7 neg.	0	2 larvae died, both neg.
16514	31 ♂♂	15 ♂♂	15 neg.	2 ♂♂	2 neg. 2 died as larvae, both neg. 1 died as larva, unscorable. In addition four small 16514 larvae were killed. All had testes and were Smith-negative in the cells of the gut.
16519	18 ♂♂	13 ♂♂	13 neg.	0	2 larvae died; 2 killed and dissected, both had testes; all 4 neg.

† The two females appeared normal except that they were intermediate as regards colour between Aichi females (dark) and Hokkaido females (white). One female was mated to a sib and the other was back-crossed to a Hokkaido male. Both females were fertile and produced no intersexes.

pared with controls, and these famales laid no egg cases.

The detection of very high levels of JH III in the leaves of C. iria and the demonstration of clear morphological effects on insects raise some intriguing ecological implications for these plants in their native habitat. Furthermore, it is clear that C. iria and other species represent a valuable source of JH III for research purposes.

Whether juvenile hormone specific for dispar could be synthesised and used as a spray I do not know, but if this could be done and the expense were not excessive it might be useful in areas where dispar is endemic, and it would have no effect on other insect life. See also addendum, p.13 and 14.

c) "Phototherapy"

Less specific at present is the work of a research team at the University of Illinois which has developed a pesticide that kills insects in a few seconds when they are exposed to light. The pesticide is applied at night as a spray or as a bait for insects to eat. When the sun comes up a chain reaction is initiated which converts delta aminolevulinic acid into proto-porphyrin, which destroys cell membranes. The insects affected spin round, vomit and die within ten seconds. The team is now attempting to provide insecticides on the above lines which are specific for particular pests but otherwise harmless (New Scientist, 1988).

d) Clean air and the lack of genetic polymorphism in L. dispar.

It is first important to remember the proper definition of polymorphism. It is a type of variation in which individuals with clearly distinct qualities exist together in a freely interbreeding single population, for example, the different forms of female in the mimetic butterfly Papilio dardanus, or the human blood groups. The definition excludes several familiar types of variation, for example racial variation as occurs in L. dispar in Japan. This can be made clearer by considering the Caucasian, Mongolian and Negroid races in Man. These do not constitute a polymorphism since when interbreeding occurs the hybrid populations are intermediate and variable. Seasonal forms too, as in Araschnia levana, are excluded from the definition, since all members of a generation are alike. Finally, continuous variation, as in human height, is not an example of polymorphism. Here, as in racial differences, many genes are at work and the variation is brought about by the cumulative effects of segregation taking place at many loci, and not by 'switch' genes giving rise to distinct alternative forms. Genetic polymorphism is therefore not a characteristic of L. dispar, anyhow for visual characters, although some isozymes conform to the definition (Harrison et al., 1983; Bevegovoy and Gill, 1986). The lack of polymorphism in dispar might lead to its undoing. For instance, I read with interest that one way of subduing the pest was to improve the quality of the trees so that they could better withstand defoliation. A more concentrated attack on pollution might therefore help since lightening of the bark would make male dispar more conspicuous to predators. This is what we think has happened in England in the poly-

morphic Peppered Moth, Biston betularia, which we have surveyed at my home for the past 27 years (Clarke et al., 1985). The graph (Fig.3) shows how the proportion of the pale form of the insect has greatly increased and the likelihood is that as a result of cleaner air there has been a new critical level of background lightness at which birds fail to see f. typica. This form would then rapidly increase. In this case the polymorphism saves the moth, but the lack of it could be disastrous for dispar.

e) Molecular genetics (genetic engineering).

The essential feature of this new discipline is that DNA fragments from two different organisms can be combined to produce functioning DNA molecules. In this way one is bypassing the barriers normally imposed by sexual incompatibility. To do this, donor DNA - for example from a patient - or any organism - is incorporated with the recipient DNA of a virus which can infect bacteria. The hybrid DNA is therefore inserted into a bacterium so that replication can take place and many copies of the hybrid DNA can be produced. Theoretically therefore it is possible to exchange a bad gene for a good one or vice versa.

I have thought a good deal about applying this principle to eradicating L. dispar, but I could not see daylight, and neither could several experts whom I consulted. It seems that only an individual moth could be 'engineered' and how any damage could spread to the whole population of the moth unless it had compensating advantages (which would probably be undesirable) is hard to see. On the plant side, however, the genetic engineers have given the tobacco plant a pesticide gene (Hilder et al., 1987) but this is non-specific. An important new angle is set out in the addendum, p.13 and 14.

f) Hybrid dysgenesis.(Eggleston & Kearsey 1980; Bregliano et al.1980)

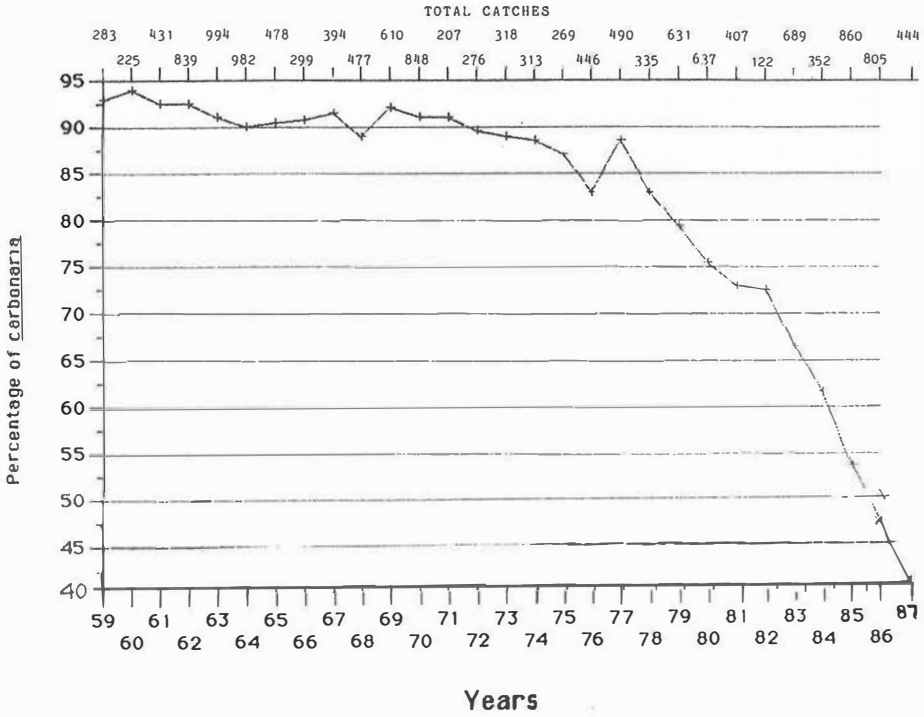
This might be thought of as a naturally occurring example of genetic engineering. It was much written about a few years ago and concerned Drosophila. When strains derived from wild males are crossed with long-established laboratory female flies, dysgenic (i.e. undesirable) traits occurred, e.g. enhanced mutation rates, chromosome aberration, distorted segregation and sterility. The mechanism appears to involve an interaction between the paternal genome and the maternal cytoplasm, and results in genes changing places - "transposable elements".

Hybrid dysgenesis sounds most promising in relation to dispar, but as far as I can make out it has never got further than the fruit fly, and even there less is heard of it than formerly. Nevertheless, it is worth remembering as there may be new developments.

g) Inbreeding.

This is often suggested without much thought having been given to it. Consanguineous matings certainly lead to the appearance of deleterious genes in double dose, but the argument can be turned so that if the population is big enough the deleterious traits are got rid of and

Fig.3. The effect of the Clean Air Acts on Biston betularia.



the species prospers. The Japanese nation is the best example of this in modern times! Also, in dispar I cannot see how in practice one could encourage inbreeding.

h) An attack via pheromones.

We have some observations here on the genus Orgyia. In England bred Japanese O. thyellina females assembled O. antiqua males to a far greater number than did antiqua females (Clarke 1979) - previously we only knew that we had an occasional antiqua in our locality. Again, O. recens and antiqua fly together but neither assembles the other, and of particular interest is the fact that thyellina does not assemble O. recens (Greenberg et al., 1982). Lastly, on the Great Wall of China I could not assemble any species of Orgyia using thyellina female virgins that I had brought with me as pupae from UK. However I found, adjacent to the Wall, a full-grown Vapourer-like caterpillar which produced (in China) a wingless female which looked very like antiqua, but no males were attracted to it.

These results are puzzling, remembering that it is stated that all species in the genus Orgyia have similar pheromones, but whether measured by electroantennograms or by chemical means I am not certain.

In the case of dispar might it be possible to make some super-attractant, perhaps from a combination of the pheromones of dispar and monacha (see Leonard, 1981) which would parallel what happens with thyellina and antiqua?

Conclusions (see also addendum, p.13 and 14)

My view is that the best way to deal with dispar is to alter the moth's natural surroundings rather than employ ever more elaborate pesticides which may cause other biological damage and in any case engender antagonism. Although never a pest in England, in 1820 dispar was quite abundant in some of the Fens and also in the Norfolk Broads. However, Richard South, writing in 1892, states that somewhere about the fourth decade the species began to decrease in numbers and towards the end of the fifties it had practically ceased to exist as a wildling. What was the reason for its failure to survive in some of its former localities which still seemed suitable? Ford (1955) thinks there are two main reasons; one is that the area they could inhabit would be a minute fraction of that of the past, and small populations are in great danger if subject to fluctuation in numbers. The other was that the drainage of the Fens must have had a great effect on the areas that remained causing local climatic changes, so that Fenland is now probably drier in winter, hotter in summer, and less subject to mist than it was a century ago. Land reclamation has also caused an alteration in the bird population, concentrating the true Fenland bird species into very small areas and causing those normally found along hedgerows and in agricultural land to colonise the Fens, so adding to the hazards experienced by the insects which inhabit them. Such changes may well prove fatal to species which are rather accurately adjusted to this specialised environment.

SUMMARY

The use of sterile males to upset the mating habits of L. dispar is discussed and evidence produced to show that the "Goldschmidt phenomenon" is untrue; in his most critical cross the excess males are fertile and the result of the Haldane effect, not intersexuality. This was discovered by sexing the moth in its early stages and staining for the heteropyknotic body which is present in female cells but not in those of the male. The larva is undamaged by this technique.

Other means of controlling L. dispar are discussed, among them the use of juvenile hormone, which would have possibilities if it could be made specific. Inbreeding is dismissed as impracticable, but the lack of a phenotypic polymorphism in the species might be exploited by reducing atmospheric pollution and thus rendering all male dispar more visible on tree trunks, as well as improving the nutrition of the trees. A comparison with the polymorphic Biston betularia in UK is made.

In general the author feels that natural means rather than the widespread use of pesticides should be used to control the moth, since sudden geographical spread is difficult or impossible to anticipate. If specific measures are used they should be employed in areas where the species is endemic and not necessarily a pest. See also addendum on pages 13 and 14 and for new hope in genetic engineering.

APPENDIX

Definitions, and staining technique.

Intersexes: These are predisposed to by crossing races or species, the effect being that an insect develops for a time as one sex and then changes to the other, though the chromosomal sex remains that of the original zygote. If the change takes place early enough in development, e.g. at the formation of the gonads, the whole insect appears to be sexually converted, whereas if it occurs later only those structures formed during the end of development, e.g. the wings, will be affected. Intersexes are commonly regarded as being sterile.

Haldane's "rule": Haldane (1922) stated that 'when in the F1 of a cross between two animal species or races one sex is absent, rare or sterile, that sex is always the heterozygous sex'. The rule holds well in the Lepidoptera and here, when there is an upset in the sex ratio, it is nearly always in the direction of a marked deficiency of the heterogametic sex, i.e. females; nevertheless, F1 females do occasionally 'get through'.

Haldane's explanation of the deficiency of females in the F1 was that it is the result of genic imbalance either between the X and the Y chromosomes or between the autosomes and the sex chromosomes or a combination of both. Thus there will be an intermediate effect between the action of the complete set of genes for each race (or species) of a cross in the homogametic sex, so that the sex balance is not impaired. In the heterogametic sex, however, this holds good but only for the

autosomes. The single X in the female is aligned with the Y, but part of the Y is non-pairing and in this section the genes are non-allelic with those on the X, and selection may cause them to be different in the two races. The normal XY balance may therefore be upset and it is assumed that this has pathological effects in the female.

F1 hybrids may, like intersexes, be sterile, but they are often normally fertile or may have hybrid vigour. Thus they differ from intersexes.

The sex chromatin staining technique: The cells are not fixed before staining. Two drops of 2% orcein in 45% acetic acid are placed over the tissue and a coverslip added. After 10 to 15 minutes the coverslip is firmly pressed to make a 'squash' preparation. The 'Smith' body, when present, can be clearly seen under a X 40 objective, as well as under a X 90 (oil immersion) (see Cross and Gill, 1979).

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ADDENDUM

Since writing this paper I have come across two other pieces of information which I think are worth mentioning.

A) Juvenile hormone and the gypsy moth (see p.3)

Professor R.P. Dales, Professor of Zoology at the Royal Holloway and Bedford New College, University of London, asked the entomologist in his Department, Dr. Peter Credland, for his views. He did so as follows:-

"Juvenile hormone (JH) is a term now used to include a number of native compounds found in insects. At least three forms are known to occur, sometimes in combination, in different species. There are also a number of factors with JH-like activity which have been isolated from plants, the first being the 'paper factor' discovered by Slama in Canadian fir balsam in 1961. There is a rapidly increasing number of synthetic analogues of which methoprene has been registered for several uses, notably the control of some dipterous pests.

The major problem with the use of JH analogues is that they are all fairly unstable and degrade rapidly under field conditions. Since their action is effective only at certain critical stages in the life histories of their targets, application times are most important. Therefore for species with several generations in each year and imperfect synchrony in life histories, they are expensive both in financial and in 'time' terms.

Chitin synthesis inhibitors are sometimes more stable and diflubenzuron has been registered for gypsy moth control purposes. These compounds are not hormones or their analogues but disrupt the deposition of cuticle following and during a moult. As such, they are known, with JH and its analogues, as Insect Growth Regulators (IGRs).

For what it may be worth, I do not see the current generation of JH analogues as serious contenders for the gypsy moth control programme. Compounds with greater stability are required but then, of course, effects on non-target insect species become a potential difficulty."

B) Genetic engineering (see p.7)

In the British Medical Journal of the 18th June 1988 there was a leader entitled "Release of genetically altered viruses into the environment", by D.H.L. Bishop, Professor of Virology in the Institute of Virology in Oxford. In it he refers to an earlier paper (Bishop 1986) describing how a baculovirus (baculus = rod), Autographia californica, well known for producing nuclear polyhedrosis in caterpillars, can be modified by genetic engineering to become

more efficient and specific, by adding, replacing or deleting a particular sequence of genetic information. For example, an insect hormone gene can be inserted into the genetic make-up of the virus so that early during a caterpillar infection the pest becomes physiologically deregulated, causing it to stop eating. Baculoviruses are good subjects for genetic engineering as they can be restricted in their host ranges to particular insect species and do not infect or affect other invertebrates, plants or vertebrates.

Dr P. Entwistle, who is a colleague of Professor Bishop and who is a participant in this symposium, can give more details and tell us whether or not this particular form of genetic engineering has been used in the control of L. dispar. It sounds a promising treatment for endemic areas.

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MITOCHONDRIAL DNA AS A TRACER OF GYPSY MOTH ORIGINS

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INTRODUCTION

The dynamics of gypsy moth populations have been a subject of considerable interest to entomologists, primarily because of the periodic outbreaks of this serious forest pest. A variety of empirical and theoretical approaches have been used in an attempt to elucidate the factors responsible for the dramatic changes in population density. In contrast, relatively little attention has been focused on patterns of genetic variation within gypsy moth populations and on the genetic consequences of population fluctuations. Furthermore, despite intense interest in the moth not only in North America, but also in Europe and Asia, there has been remarkably little effort devoted to documenting genetic variation among gypsy moth populations and to deciphering its recent evolutionary history. Here we discuss the use of mitochondrial DNA (mtDNA) as a genetic marker for gypsy moth - its utility as a tool for documenting patterns of genetic relatedness among populations worldwide and for studying local population outbreaks. We focus attention on two issues: (1) Can mtDNA comparisons provide information on the source of the North American introduction, relationships of European and Asian moths, and patterns of geographic variation within east Asia? (2) Can mtDNA be used as a genetic marker within North America to distinguish among persistent low density populations and to provide a tracer of the origins of outbreaks?

Goldschmidt (1934) suggested that the origins of the genus *Lymantria* were in southeast Asia and that this was also the original home of the gypsy moth. *Lymantria dispar* is now found across central Asia, throughout Europe and in North Africa (Giese and Schneider 1979). Its presence in the United States is clearly a result of an accidental introduction in 1869 (Forbush and Fernald 1896). Goldschmidt (1934) documented patterns of geographic variation, using a variety of morphological and life history characters. He argued that the gypsy moth is extremely variable in Japan and eastern Asia, but relatively homogeneous throughtout much of the rest of its range. Such a pattern of variation is consistent with east Asian origins and with a relatively recent spread of the moth across Eurasia. However, characters examined by Goldschmidt and others (Pintereau 1980) do not vary concordantly, and patterns of morphological and developmental variation may reflect local adaptation (rather than common ancestry). Moreover, Goldschmidt's interpretation of his data on

intersexuality (which served as an important component in his classification of "races" of gypsy moths) has recently been challenged (Clarke and Ford 1980, 1982). Clearly, more reliable genetic markers are needed to document patterns of genetic relationships and to resolve the evolutionary history of the gypsy moth.

Allozyme data (Harrison et al. 1983) revealed significant differences in frequencies between a Japanese population and populations across Europe. European populations have lower levels of genetic variation and are relatively homogeneous across a broad geographic area. The allozyme data also suggest that European populations may be derived relatively recently from an east Asian ancestor. North American populations exhibit virtually no allozyme variation (observed heterozygosities ranged from 0.000 to 0.008), presumably a consequence of the severe population bottleneck that accompanied the introduction.

According to records of gypsy moth population outbreaks, which span several decades in New England, certain discrete (2-10 ha in area) forest sites are historically "first to be defoliated" (Bess et al. 1947; Houston and Valentine 1977). These sites have a reputation for always having detectable gypsy moth populations. It has been hypothesized that gypsy moths disperse from these susceptible forests, which serve as reservoirs from which area-wide outbreaks emanate when abiotic or biotic conditions change in adjacent stands. If these susceptible/focal sites are the sources for periodic outbreaks and if genetic markers can be found that distinguish among populations from these sites, such markers could be used to trace the origin and spread of outbreaks.

Methods for assessing DNA sequence similarity or difference have recently become important tools in population and evolutionary biology. Sequence variation provides reliable markers for distinguishing populations and species, and sequence comparisons can be used for estimating genetic relationships and inferring evolutionary history. Data on DNA variation in natural populations have come principally from comparisons of restriction endonuclease fragment patterns and site maps. Restriction endonucleases are enzymes that cleave double-stranded DNA at specific recognition sequences. Digestion of a length of DNA with a restriction enzyme yields a series of fragments, the number and sizes of which will vary depending on where within the DNA the recognition sequence occurs. Differences in fragment patterns following digestion of homologous sequences from two or more individuals must reflect DNA sequence divergence. Therefore, fragment pattern differences can conveniently serve as markers of genetically distinct lineages. Moreover, comparisons of restriction fragment patterns or restriction site maps can be used to derive measures of genetic distance among individuals or populations and can provide data sets appropriate for phylogenetic analysis.

We have used comparisons of restriction fragment patterns and site maps to examine sequence variation of gypsy moth mitochondrial DNA. MtDNA has a number of properties that make it particularly attractive as a genetic marker in population and evolutionary biology (Avise 1986; Avise et al. 1987; Moritz et al. 1987). First, it is relatively easy to isolate and purify. Second, there is no ambiguity about the homology of the sequences being compared. Third, mtDNA is a small DNA molecule (15-30 kilobases), a size convenient for restriction site mapping. Fourth, mtDNA is maternally inherited and therefore provides direct information about matriarchal genealogies. This property makes mtDNA especially useful in tracing patterns of colonization. Fifth, there is no recombination between mtDNA molecules, so that a series of restriction site differences form a completely linked set. This provides exceptionally high resolution for discriminating common ancestry (e.g. in identifying the source of a colonization event or an introduction).

MATERIALS AND METHODS

Gypsy moths were collected from a series of sites in eastern North America (Table 1). Four of these sites (ONT, MA, CT, PA) were selected to provide individuals from geographically diverse populations. The other three North American sites (VT1, VT2, RI) are localities that have been identified as possible "focal sites" by Houston and Valentine (1977). Moths from Japan and France were collected by personnel at the USDA Agricultural Research Service's Asian and European Parasite Laboratories, respectively, and shipped as pupae to the USDA Forest Service Laboratory in Hamden, CT. Adults were frozen as they emerged and have been stored at -80° since that time. These samples correspond to the France-2 and Japan populations for which we have published data on allozyme variation (Harrison et al. 1983). Gypsy moths from China were brought back by one of us (TMO) following visits to China in 1983 and 1987. Again, adults from each of these collections were frozen as they emerged.

Table 1. Geographic origins of samples used for mtDNA analyses.

Region/Population	n[1]
NORTH AMERICA (NA)	
Ontario (ONT)	2
Vermont 1 (VT1)	6
Vermont 2 (VT2)	3
Massachusetts (MA)	2
Rhode Island (RI)	7
Connecticut (CT)	2
Pennsylvania (PA)	2
FRANCE (FR)	
Provence	6
CHINA (CH)	
Heilongjiang Province (CH1)	4
Beijing (CH2)	2
JAPAN (JN)	
Hokkaido	6

1 n is the number of individuals for which mtDNA data are available.

For a majority of the collections, total DNA was prepared from individual frozen moths following standard procedures (e.g. see Harrison et al. 1987). For the

three "focal sites", isofemale lines (lines derived from single females) were reared and pure mtDNA prepared from eggs taken from female progeny. Since mtDNA is maternally inherited (Avise 1986; Wilson et al. 1985), all progeny of a single female will have identical mtDNA genotypes. In addition, we prepared pure mtDNA from eggs of females from a standard laboratory strain (NJSS - Forest Service, see ODell et al. 1985). Details of procedures for preparing pure mtDNA from gypsy moth eggs will be described elsewhere.

In order to characterize variation in mtDNA restriction fragment patterns, total DNA from each individual was digested with an array of restriction enzymes. The resulting fragments were separated on 0.7% agarose gels, transferred to nitrocellulose filters or nylon membranes and hybridized with a ^{32}P-labeled pure mtDNA probe (for details of this whole genome Southern blot technique see Maniatis et al. 1982). Fragment patterns were visualized by autoradiography, and fragment sizes estimated by comparison with a series of known standards.

Having characterized restriction fragment patterns, we proceeded to construct restriction site maps for each of the observed mtDNA genotypes. Maps were constructed using information obtained from double-digests (Maniatis et al. 1982). The restriction site maps (which will be presented elsewhere) enabled us to estimate the proportion of restriction sites shared between different mtDNA genotypes and to estimate the percent nucleotide difference between these genotypes.

The techniques described above are suitable for analysis of restriction fragment patterns produced by cutting the mtDNA molecule into relatively few large fragments. In order to obtain higher resolution, it is necessary to use restriction enzymes that cut the mtDNA molecule into many (small) fragments. By so doing, we are able to examine a much larger number of fragments (sites) and therefore assay a much larger proportion of the mtDNA genome. Pure mtDNA from the isofemale lines derived from moths collected at VT1, VT2 and RI was digested with enzymes that cut gypsy moth mtDNA many times, i.e. enzymes that have recognition sequences that occur many times within the mtDNA molecule. Following digestion, the resulting fragments were end-labeled, using ^{32}P-labeled nucleotides (dNTPs) and the Klenow fragment of *E. coli* DNA polymerase. Labeled fragments were separated on 5% or 7% acrylamide gels and visualized by autoradiography. Note that this approach requires preparation of pure mtDNA from each individual or isofemale line and will not work on total DNA preparations. Pure mtDNA is difficult to obtain from frozen material, and therefore, we did not attempt to use this approach on material obtained from abroad.

RESULTS

Using the whole genome Southern blot technique, we characterized mtDNA fragment patterns for moths from North America (ONT, MA, CT, PA), France (FR), China (CH1 and CH2) and Japan (JN). Our survey included fifteen different restriction enzymes, each of which produced 1-5 fragments. For most enzymes, the survey included 26 moths (at least two individuals from each site - see Table 1), but due to partial digestion and/or weak hybridization, data are missing for some individuals for six of the enzymes. However, we have characterized fragment patterns for the entire set of enzymes for individuals from each of the four major collecting areas (NA, FR, CH, JN). Furthermore, we have mapped all restriction sites for the fifteen enzymes - a total of 39-44 sites for each composite mtDNA genotype.

Except for a single restriction site polymorphism in the CH1 population, we found no variation in mtDNA composite genotype within any of the populations or even within any of the four major areas. The observed polymorphism involved the absence of a single MspI restriction site in one moth.

Although separated by 1000 km, the two Chinese populations had identical mtDNA genotypes. They shared 39 restriction sites, with no unique sites found in either population. The mtDNA genotypes of North American moths were identical to those of moths collected in south France; these moths had 44 restriction sites in common.

Despite the remarkable homogeneity within populations and regions, mtDNA genotypes of moths from different regions exhibit substantial amounts of divergence. In all of our samples (ignoring the single polymorphic site in the CH1 populations), we observed only three composite mtDNA genotypes - one characteristic of both North American moths and the single French population, a second characteristic of the Chinese populations, and a third found in Hokkaido, Japan. The NA/FR genotype differs from the CH genotype by nine restiction site gains or losses and from the JN genotype by eleven site changes (Table 2). The two Asian genotypes differ in the presence/absence of fourteen restriction sites, i.e. they are more different from each other than either is from the NA/FR genotype. The number of restriction sites shared between mtDNA genotypes (and the total number mapped for each genotype) are summarized in Table 2.

Table 2. Number of mtDNA restriction sites mapped for each population or region (on the diagonal) and number of restriction sites shared between pairs of populations

	NA	FR	CH1	CH2	JN
North America	44	44	37	37	36
France		44	37	37	36
China 1			39	39	32
China 2				39	32
Japan					39

We used the method of Nei and Tajima (1983) to estimate genetic distances among the three genotypes - in terms of the percent nucleotide difference (Table 3). Nucleotide sequence divergence between gypsy moth mtDNA genotypes ranges from 2.1-3.6%. If gypsy moth mtDNA sequences are evolving at about the same rate as those in vertebrates, the differences among the three genotypes reflect divergence times of 1-2 million years (the rate of mtDNA sequence divergence between lineages is generally estimated to be 2-4% per million years in vertebrates- see Brown 1985, Wilson et al. 1985).

Table 3. Estimates of the percent nucleotide sequence divergence between gypsy moth mitochondrial genotypes.

	NA	FR	CH	JN
North America	0.0	0.0	2.1	2.6
France		0.0	2.1	2.6
China			0.0	3.6
Japan				0.0

If useful genetic markers are to be found within North American gypsy moth populations, we clearly must resort to higher resolution techniques. That is, we must assay a larger proportion of the mtDNA genome. We have recently initiated a survey using restriction enzymes that cut gypsy moth mtDNA into many (40-60) fragments. Gel banding patterns of such complexity are difficult to interpret, but our intitial goal is simply to discover whether any mtDNA polymorphism exists within North America and whether individual morphs are unique to specific localities. The preliminary data involve comparisons of moths from three "focal sites" within New England - two sites in Vermont (VT1 and VT2) and one in Rhode Island (RI). There are clearly polymorphisms, i.e. differences in gel banding patterns. At this point, however, we have not discovered any restriction fragment patterns that are characteristic of only one site.

DISCUSSION

Mitochondrial DNA composite genotypes, defined by the presence and absence of restriction endonuclease recognition sites, provide high resolution markers which clearly define maternal lineages. The utility of mtDNA as a marker in both inter- and intra-specific comparisons has been clearly demonstrated for a variety of animal species (Avise et al 1987; Moritz et al 1987). Our preliminary data on mtDNA genotypes in worldwide gypsy moth populations indicate that this molecule will be of considerable value as a tracer of gypsy moth origins.

The existing mtDNA diversity within North American gypsy moth populations is a function of the original diversity of genotypes that escaped in Medford, Massachusetts in 1869. Because mtDNA is both maternally inherited and effectively haploid, the effective population size for mtDNA is only one-fourth that for nuclear gene markers. Hence mtDNA genotype diversity is particularly sensitive to population bottlenecks and founder events. If more than one mtDNA genotype were present immediately after the introduction, the chance extinction of certain maternal lineages may have led to a subsequent decrease in diversity. This would be opposed by an increase in variation due to the accumulation of mutations in *L. dispar* populations in the 120 years since the introduction. The extremely low level of mtDNA diversity observed within North American gypsy moth populations suggests that the original founder event involved very few moths.

However, the absence of mtDNA restriction site differences between moths collected in North America and those collected in France (Provence) suggests that French populations may also exhibit very low levels of variation (in which case the amount of variation within North American populations also refects the absence of

variation in the source population). It is thought that French moths were the source of the North American introduction (Forbush and Fernald 1896; Burgess 1944), but the exact site from which they came is not known. If significant mtDNA variability is present within French populations, then we have fortuitously sampled a population that has a mtDNA genotype identical to that introduced into North America. It seems far more likely that French populations of *L. dispar* represent a single mtDNA genotype (with respect to the restriction sites that we have mapped). If true, this would suggest that French (and perhaps all European) gypsy moths are relatively recent arrivals or that recent population bottlenecks have reduced mtDNA diversity. Data from other characters (e.g. morphology and development (Goldschmidt 1934), allozymes (Harrison et al. 1983)) also suggest homogeneity of gypsy moth populations across Europe. Indeed, Goldschmidt (1934) went so far as to say that across much of Eurasia the gypsy moth "behaved practically as a unit". We find significant differences in mtDNA genotype between French and Chinese populations, but no differences between two Chinese populations that are separated by at least 1000 km.

Although Goldschmidt (1934) argues for an east Asian origin of the gypsy moth, there is little direct evidence for deciphering the evolutionary history of this important insect pest. Our data suggest that mtDNA may be a good marker for tracing the Asian origins of European (and North American) gypsy moth populations. The marked differences among the French, Chinese and Japanese mtDNA genotypes reflect a relatively ancient divergence. It is probable that several (many) other distinct genotypes will be found upon further sampling of Asian moths. It is possible that a genotype very similar to that found in Europe and North America may be present in east Asia. Given that mtDNA is a set of completely linked markers, it provides excellent discrimination between common ancestry and convergence and will allow us to trace phylogeographic patterns with considerable confidence. With only three distinct genotypes, we cannot yet draw any conclusions about the population phylogeny of the gypsy moth. Based on mtDNA comparisons, French moths are more similar to Chinese moths than they are to those collected in Hokkaido, but the differences in genetic distance are not signficant. The observed divergence between French and Japanese gypsy moths is consistent with earlier observations based on allozymes (Harrison et al. 1983).

Obviously, additional sampling of east Asian populations should be a high priority. Recently, we have discovered that satisfactory total DNA preparations can be made from ethanol preserved specimens. This may allow us to circumvent the obvious problems associated with importing live Asian material into North America.

One advantage of the approach we are taking is that it allows us to gain a very high level of resolution in distinguishing lineages. Our ongoing studies of mtDNA variation in North American gypsy moth populations have not yet provided any markers that distinguish among the sites we have sampled. However, we can clearly identify mtDNA restriction fragment pattern variants within populations. At this point we are not sure whether these reflect variation in presence/absence of restriction sites or size variation of the gypsy moth mtDNA (i.e. small insertions or deletions). In either case, these mtDNA variants may prove useful either in continuing attempts to document the genetic structure of North American populations or in release experiments in which it is important to have a presumably neutral genetic marker.

SUMMARY

We have initiated a study of mitochondrial DNA restriction site variation within and among gypsy moth populations from North America, Europe and Asia. MtDNA is an excellent marker for determining the history of colonization and introduction. One objective is to use mtDNA comparisons to decipher the recent evolutionary history of the gypsy moth. For the small set of populations sampled to date, we find no restriction site differences between North American and French moths (and no variation within North America for the 44 mapped sites). However, there are many site differences between these moths and those from China and Japan and even greater differences between the two Asian localities. These results suggest a relatively ancient divergence among existing gypsy moth lineages. The approach used here would seem to hold great promise for determining the source of European populations. Additional sampling of east Asian populations is a high priority. Our second objective is to develop high resolution techniques that will provide us with mtDNA markers within North America for tracing the origin of local outbreaks and perhaps for use in sterile male releases.

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GENETIC CONTROL OF LYMANTRIIDAE: PROSPECTS FOR GYPSY MOTH MANAGEMENT

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SUMMARY

Progress in the current program to develop the sterile insect technique for control of gypsy moth, Lymantria dispar L., is reviewed. The discussion includes a synopsis of radiation biology studies, competitiveness evaluation of sterile adults, and field testing of three application techniques. A field test involving the release of fully sterile male gypsy moths was successful in eradicating an isolated population, but labor demands were high and execution was logistically difficult. Releases of partially sterile males in another isolated population was equally successful in that their F_1 progeny were observed the year after release and eradication was achieved. But again, this approach was logistically and economically costly. The current method of releasing F_1 eggs (progeny of irradiated males and normal females) is described. These egg masses can be produced and stockpiled in the laboratory in large numbers. Release of F_1 egg masses prior to native egg eclosion establishes a population of sterile insects that ultimately mate with the native population, imparting a suppressive effect. Treatment of a sparse, isolated infestation using this technique resulted in population eradication and other results indicate promise for use in control of low density, isolated populations. Problems associated with estimating native population densities, determining the impact of treatment, and evaluation of competitiveness of immature and adult stages are discussed.

INTRODUCTION

Investigations into the use of the sterile insect technique (SIT) for gypsy moth, Lymantria dispar, control were initiated over thirty years ago (Godwin et al., 1964). Godwin's work and studies by other investigators using gamma radiation and chemosterilants to induce sterility were reviewed by Mastro et al., (1981). Although this early work laid the basis for establishing the radiation biology of the gypsy moth and resulted in some early field trials, there were practical barriers to the successful demonstration of SIT as a control technique. Some technological problems that prevented progress in this approach included lack of: 1) adequate rearing techniques, 2) evaluation criteria and techniques for measuring insect competitiveness and 3) techniques for monitoring densities of wild populations and the subsequent impact of a sterile insect release.

However, even if the technical problems confronting development of the SIT were overcome, the inconsistent management policies and objectives that have persisted almost since the gypsy moth's introduction into North America (Dunlap, 1980; McManus & McIntyre 1981; Ravlin et al., 1987) may have proven a greater barrier. In the 1960's and 1970's, no overall management strategy prevailed within the area generally infested by the gypsy moth. Objectives of management programs ranged from prevention of defoliation, abatement of nuisance, protection of esthetics, protection of high value timber and watershed protection to no action when defoliation threatened. Control programs tended to be defensive and were reactions to outbreak or near outbreak insect population densities. Use of the sterile insect technique would have been of little practical value in this type of reactionary situation. Because of the inherent density-dependency of the technique, it would not be practical or economical to rear sterile insects in large enough numbers to overflood these types of defoliating populations. However, techniques such as SIT can theoretically be used in area-wide IPM programs where the emphasis is on population maintenance at densities well below defoliating levels.

Despite quarantine measures, introductions of the gypsy moth occur yearly outside of the generally infested area, largely through the movement of outdoor household articles. The United States Department of Agriculture, Animal and Plant Health Inspection Service, in cooperation with individual states, maintains a survey and detection program for identifying these introduced populations (Ravlin et al., 1987; Schwalbe, 1981). The policy for introduced populations has been clear: to eradicate populations as quickly as possible. In the past, these eradication programs mainly utilized applications of chemical insecticides. These introduced populations are isolated from the generally infested area and are usually detected when they are sparse and of limited size (usually less than 200 ha). The sterile insect technique can theoretically be used economically in these circumstances. Enhancing the SIT's value in these situations is

the public's increasing resistance to broadcast insecticide applications in residential areas where, because of the mode of transport, these infestations are usually detected.

The area generally infested by the gypsy moth is also increasing through natural spread. Along this expanding edge, no uniform management strategy prevails. Currently, there is an ongoing dialogue about the feasibility of containment or a slowing of the rate of natural spread of gypsy moth. A stated objective of the Appalachian Integrated Pest Management (AIPM) Project, a large demonstration program along a portion of the leading edge, is to "minimize the spread and adverse effects of the gypsy moth within the project area". This objective implies treatment of newly established and numerically sparse populations along the expanding edge of the currently infested area. Theoretically, this is an ideal place for the application of SIT, when applied in combination with other management tools. If populations are carefully monitored in an IPM program, intervention measures could be initiated when populations are sufficiently sparse for sterile release to be biologically and economically feasible.

How the SIT will ultimately fit into the varied management strategies for gypsy moth is the subject of much discussion. If the strategy involves suppression or eradication of sparse populations, then the potential for use of SIT is promising. The challenges are greater to develop the technology for management of large infested areas in the Eastern States. Reevaluation of the SIT technique for gypsy moth control was undertaken in 1977 because of developments in mass rearing techniques (Bell et al., 1981), a broader understanding of the insect's biology and behavior, and the recognized need for alternatives to chemical control.

EVALUATION OF CLASSIC STERILE INSECT TECHNIQUE

Our initial approach evaluated the use of the sterile insect technique in the "classical" way: large numbers of fully sterile adult insects are released to "overflood" a wild population. In this approach, as the overflooding ratio of sterile:fertile (wild) insects increases, the probability of successful mating between wild adults decreases, which results in population suppression. The first major success using this technique was a small eradication trial for the screwworm fly, Cochliomyia hominivorax (Coquerel), over thirty years ago (Baumhover et al., 1955). Since that time, the technique has been successfully applied to a number of pest species. Perhaps the most widely known are extensive programs for the control of the Mediterranean fruit fly, Ceratitis capitata (Wiedemann) (Patton, 1982; Rode, 1970; Steiner et al., 1962).

Initially, we investigated the radiation biology of the gypsy moth and the competitiveness of laboratory reared males. Irradiation studies demonstrated that near total sterility was

induced when males were exposed to 15 krads of gamma radiation (Cobalt 60) as pupae or adults, and somatic damage was minimized when pupae were treated 8 days or more after pupation. Evaluation of laboratory reared male moths (irradiated and untreated) indicated that they were competitive with their wild counterparts. Laboratory and field tests evaluated male longevity, flight behavior, pheromone response, mating periodicity and frequency and other competitive indices. Table 1 summarizes competitiveness traits examined (see Lance et al., 1988; Mastro, 1980; Waldevogel et al., 1982).

Table 1. Behavioral traits examined for competitiveness comparisons of adult male gypsy moths.

Field comparisons using mark-release-recapture techniques

- Pupal eclosion periodicity
- Adult dispersal periodicity
- Response to pheromone sources and periodicity of response
- Response to pheromone sources as a function of male age
- Horizontal and vertical distribution in the forest canopy

Field cage comparisons

- Frequency of mating of males of various ages
- Periodicity of mating
- Length of mating

Laboratory comparisons

- Response to pheromone (flight tunnel)
- Periodicity of activity (actograph)
- Propensity to fly (actograph)

Pilot Test of Sterile Insect Technique

In 1980, an isolated population in Berrien Co., Michigan, was selected for a field evaluation of the impact of release of sterile males. Males were irradiated (15 k) as pupae 8-11 days after the pupal ecdysis. To facilitate release, pupal release containers were positioned systematically throughout the infested area on a 50m grid in consideration of the relatively short dispersal distances of male gypsy moths (Elkinton & Carde, 1980; Schwalbe, 1981; Schwalbe & Paszek, 1978). Male loss from a population is rapid (Mastro & ODell, unpublished) and one or two-day old males comprise the largest proportion of a male population which is actively mating. To maintain high overflooding rates throughout the wild flight period, sterile male pupae were placed at the

release sites daily. Released sterile males were internally marked with calco oil red dye. Sterile:fertile overflooding ratios were carefully monitored by examining the abdomen of males recovered at pheromone-baited traps for presence of dye. In addition, females were placed daily throughout the release area to monitor mating success. Egg masses produced by monitor females were evaluated for hatch to determine the type of male parent (sterile male matings resulted in no hatch). After three years of sterile male release, the native population was eradicated. Based on analysis of the observed sterile:fertile overflooding ratios, the native population was reduced in a systematic and predictable manner (Table 2). Released sterile males appeared to be highly competitive with the target population.

Table 2. Results of treating an isolated gypsy moth population in Berrien County, Michigan, with sterile[1/] male gypsy moths.

Year	No. of sterile males released/day	No. of wild males trapped	Observed sterile:fertile ratios	
			Trapping method[2/]	Female mating ratios
1979	0	90	-	-
1980	10,000	274	14.4:1	5.9:1
1981	10,000	50	128.6:1	29.8:1
1982	6,000	1	5842:1	287:0
1983-86	0	0	-	-

1/ Males irradiated as 8-12 day-old pupae with 15 krads.
2/ Mean male trapping ratios were computed from daily ratios of sterile and fertile males captured in traps during peak native flight - 1979 (7/31-8/11), 1980 (8/1-8/10) and 1981 est. (8/1-8/10).

This pilot study also identified difficulties in the operational use of the technique. Male pupae are large (approximately 0.5g) and somewhat fragile, necessitating special packing and shipping provisions to minimize damage and prevent eclosion during transit. The release cages, which were designed to eliminate predators but allow exit of eclosed moths, were costly and difficult to maintain. Broadcasting pupae was considered as a release strategy but rejected because of projected losses caused by predators. However, as already mentioned, the major impediment was the need to release males frequently throughout the flight period to maintain desired overflooding ratios. The expense of

maintaining personnel at the release site throughout the adult flight period added appreciably to the cost of applying the technique. On the relatively small scale of this test (approximately 2.59 km^2), the technical and logistic problems were overcome. However, applying the technique on a larger scale was judged to be impractical.

EVALUATION OF INDUCED INHERITED STERILITY

Our initial irradiation studies suggested that sterility was induced in the F_1 generation when the radiation dose was approximately halved. Indeed, earlier investigators had induced F_1 sterility in the gypsy moth using low doses of radiation [reviewed by Mastro (1981)]. The mechanism of inducing sterility in the F_1 generation has been investigated by Bauer (1967) and North & Holt (1968). It is now generally believed that F_1 sterility can be induced in any lepidopteran species, and has been demonstrated for a number of species and was reviewed by North (1975) and La Chance (1985). Our interest in F_1 sterility stemmed from the theoretical advantages of using it as opposed to releasing totally sterile males (Knipling, 1969, 1970; Brower, 1980; Nielsen & Brister, 1980; Carpenter et al., 1983).

Radiation Biology

To explore the feasibility of using the induced-inherited sterility technique (F_1 technique) for gypsy moth, we initiated a study of the radiation biology in 1980. Male gypsy moths were (P_1) irradiated at different pupal ages (6 groups) with seven levels of radiation, i.e. 42 dose/age treatments. Irradiated laboratory-reared males were mated with untreated laboratory-reared females (50 pairs per treatment) and the resulting F_1 progeny were evaluated in the egg, larval, pupal and adult stages. Egg masses were evaluated for number of eggs, degree of embryonation and percent hatch. Length of development and survival of other stages were also observed and any abnormalities were noted. Resulting F_1 adults were incrossed within their own treatment group and outcrossed to normal insects. In the F_2 generation, insects were evaluated in the egg, larval and pupal stages in the same manner as their parents and again outcrossed to untreated insects and incrossed within their treatment groups. All treatments were evaluated through the F_3 egg stage and some selected treatments were evaluated through the F_4 egg stage. All insects used in this study were from a colony maintained by the Otis Methods Development Center for twenty generations (NJS-G_{20}) [see ODell et al., (1984)] and were reared under standard laboratory conditions as outlined by Bell (1981). Because of the quantity of data generated, only a synopsis of this study will be presented.

Effects on P_1 Generation

The results of our irradiation studies closely parallel those of studies with other Lepidoptera species (Brower, 1979, 1980; Carpenter et al., 1983, 1987). Debilitating effects of irradiation on P_1 males are most pronounced in youngest pupal age classes at the higher radiation doses. When males were exposed to only 4 krads 0-1 days after pupation, only 44% of the females produced an egg mass vs. 98% in a control group. This effect was not observed in the next older pupal age class (2-3 day old) until the dose was increased to 8 krads, and not pronounced until the dose was increased to 10 krads (i.e., respectively 78% and 36% of the pairs produced egg masses). Also, when paired with males irradiated in younger age classes, those females that did oviposit produced fewer eggs. Other effects noted were incomplete eclosion and wing deformities of irradiated P_1 males. Matings with males irradiated in older age classes resulted in F_1 egg masses with high levels of embryonation. Pairs with males irradiated with 15 krads greater than 1 day old averaged 84.4% embryonation vs. 96.6% for control matings.

Hatch from F_1 egg masses produced by the various male irradiation treatments is summarized in Figure 1. The degree of sterility increased (i.e. the proportion of eggs which hatched decreased) as the radiation dose increased from 2 to 15 krads. Also, as the pupal age at irradiation increased, generally the degree of sterility decreased. However, males irradiated in the oldest age class (10-11 days old) were more sterile than the next younger age class (8-9 days old).

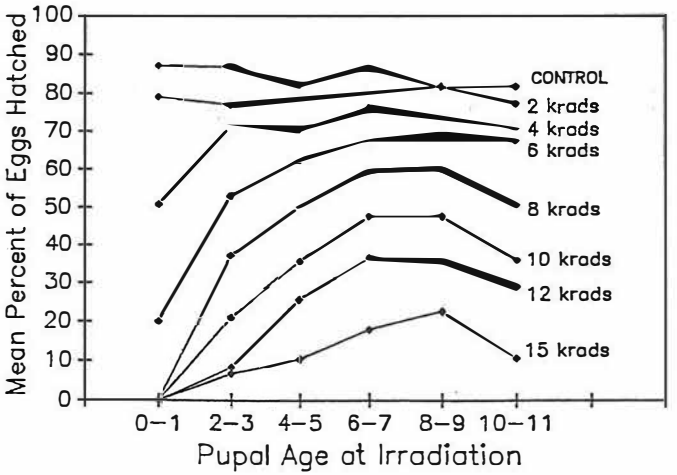

Figure 1. Mean percent hatch from F_1 egg masses which resulted from mating males (treated at various ages with different doses of radiation) with untreated females.

Effects on F_1 Generation

Survival of F_1 immatures from all treatment groups was generally high (60-98%). The proportion surviving, however, was dose dependent; F_1 larval survival decreased as the radiation dose of the P_1 male increased (Figure 2). At lower radiation doses between age classes, survival rates were nearly constant. For example, survival of progeny of males irradiated with 10 krads ranged from 82% to 91%, respectively, for the 2-3 and 8-9 day-old age classes. Larval developmental time from eclosion to pupation increased as dose increased. Mean larval developmental times (all age classes) for F_1 male larvae for the 2 and 15 krad treatment groups were, respectively, 30.5 days and 35 days. Developmental times of female larvae were similarly dose dependent (i.e. respectively 32 and 37 days in the 2 and 15 krad treatment groups). LaChance (1985) states that delayed development of F_1 progeny may be a common phenomenon. Also, as in studies with other Lepidoptera, there was a male-biased sex ratio shift in the F_1 generation which resulted in an approximately 2:1 ratio at the 10 krad level of P_1 treatment.

Characteristics of F_2 egg masses produced by incrossing and outcrossing F_1 adults from selected treatments are summarized in Table 3. Generally, F_1 insects whose male parents received higher radiation doses were more sterile than those whose parents were irradiated with lower doses.

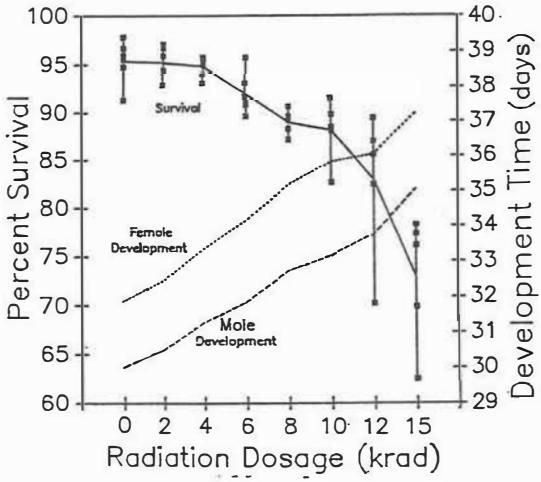

Figure 2. Survival and developmental times of F_1 larvae that hatched from egg masses produced by untreated females mated to irradiated males. Data presented are mean development times for all age classes at each dosage. Mean percent survival for individual age classes are represented by ■.

Table 3. Viability and size of F_2 egg masses resulting from incrossing (within treatment groups) and outcrossing F_1 adults (progeny of an irradiated male and an untreated female).

Treatment of P_1		Mating type			
Dose	Age	♂ x ♀	No. successful mating pairs (n=25)	Mean no. of total eggs produced	Mean percent of eggs embryonated	Mean percent of total eggs which hatched
6	8-9	F_1 x C	24	809.5	43.9	6.5
		C x F_1	21	747.5	74.7	13.0
		F_1 x F_1	20	572.2	44.1	1.3
6	10-11	F_1 x C	21	673.0	46.1	13.0
		C x F_1	26	823.3	77.2	13.6
		F_1 x F_1	24	659.4	31.8	1.2
8	8-9	F_1 x C	21	612.4	22.1	1.2
		C x F_1	12	495.2	13.6	0.0
		F_1 x F_1	12	495.2	13.6	0.0
8	10-11	F_1 x C	19	624.4	23.5	1.9
		C x F_1	22	920.4	79.3	4.5
		F_1 x F_1	18	505.4	13.7	0.1
10	8-9	F_1 x C	17	607.0	39.8	7.4
		C x F_1	25	661.4	74.1	0.5
		F_1 x F_1	20	548.6	9.7	0.1
10	10-11	F_1 x C	19	460.1	16.8	0.1
		C x F_1	22	622.8	66.8	0.9
		F_1 x F_1	16	584.3	10.9	0.1
Control		C x C	145 (n=150)	947.3	93.7	76.5

Egg masses produced by crosses of F_1 males and untreated females characteristically contained less than half the proportion of embryonated eggs that normal crosses produced. Abnormal sperm and poor eupyrene sperm transfer are possible explanations (Ashrafi & Roppel, 1973; North, 1975; Brower, 1979; LaChance et al., 1979; LaChance, 1985). At radiation doses of 6 krads or greater, the degree of sterility induced in the F_1 parents, as measured by percent hatch of F_2 egg masses, was relatively high for all age groups and mating types. Generally, F_1 sterility increased as the P_1 male parent's radiation dose increased. At lower doses, F_1 females outcrossed to untreated males produced more highly embryonated F_2 egg masses and more progeny than the reciprocal cross. At higher radiation levels, and as total sterility is approached, differences between the fertility of F_1 males and females disappears (Fig. 3).

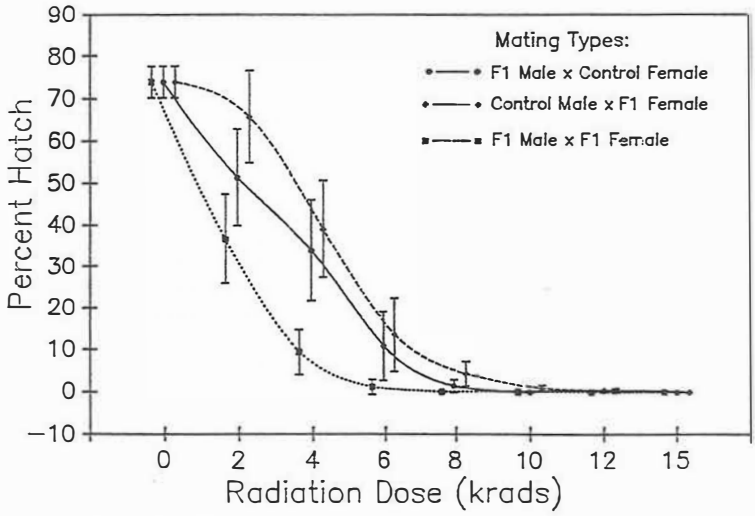

Figure 3. Mean percent hatch and 95% confidence intervals for F_2 egg masses, progeny of F_1s whose P_1 male parent was irradiated as 10-11 day-old pupae.

Effect on the F_2 Generation

Survival and developmental characteristics of F_2 progeny are summarized in Table 4. Survival of F_2 progeny resulting from outcrossing either F_1 males or females from the 6 krad treatment group was high (i.e. respectively 59.7 and 60.7%) vs 76.6% for control insects. Length of larval development for both F_2 males and females from these same treatment groups also averaged only 1 and 2 days longer than control insects. Data from F_2 groups originating from radiation treatments above 6 krads are limited because F_1 sterility is high and few F_2 neonates were available for

rearing. The limited amount of observations, however, indicate a general trend of longer larval development times with increasing dose.

Effects of radiation on fertility are apparently carried into at least the F_2 adult stage. F_3 egg masses produced by outcrossing F_2 adults were less embryonated than control matings and had lower proportions of eggs which hatched. Egg masses produced by incrossing F_2 adults generally contain the smallest proportions of eggs which were embryonated and which hatched. When progeny of males irradiated with a dose as low as 2 krads were inbred for two generations, reduced viability was noted (data not shown).

Effects on the F_3 Generation

Survival and development of F_3 progeny, regardless of the parentage, approximates the control group better than the F2 generation. Survival of first instars to the pupal stage was similar to control insects for nearly all treatment groups. Male and female larval development times, however, were longer than those of control insects. This difference, however, was not as pronounced as in the F_2 generation. Although the radiation effects are not as pronounced in the F_3 larval stage, they still are apparent. Incrossing and outcrossing F_3 adults resulted in egg hatch rates only slightly lower than control matings.

Competitiveness of F_1s

Results of radiation biology studies defined potential fitness deficiencies of F_1 progeny, e.g., longer larval developmental times, decreased survival and possible poor sperm transfer of F_1 males. How these and other characteristics would be effected by natural conditions was our next area of investigation.

In preliminary studies we found that when F_1 larvae were reared on excised oak foliage in an insectary or on caged oak foliage, survival to the adult stage was significantly lower than the survival rate of wild insects reared in the same manner (Lance et al., 1983; 1984). Untreated insects from the laboratory colony (NJS), from which F_1s were derived, developed faster than wild insects. Mean F_1 male larval developmental rate was approximately 1 to 2 days longer than wild immatures. Also, when unfed first instar F_1s were placed on branches of a host, they tended to establish in a manner similar to wild first instars. However, a larger proportion of first instars from the untreated laboratory strain dispersed (Lance et al., 1982). We found that when late instar larvae of three strains (NJS, wild and F_1) were released on trees, patterns of activity were similar. However, F_1 larvae tended to leave the tree more often than the untreated laboratory reared NJS or a strain reared from field collected eggs (Mastro & Schwalbe, 1986).

Adult F_1 male progeny paternally treated with three levels of

Table 4. Survival and development of F_2 larval progeny of incrossed and outcrossed F_1 adults from families in which P_1 males in two age classes were variously irradiated.

Treatment of P_1									
Dose	Age	Mating type of F_1 parent ♂ x ♀	No. of neonates infested	Percent survival	No. of male pupae	Mean male larval develop-ment time	No. of female pupae	Mean female larval development time	Sex ratio M:F[2/]
6	8-9	F_1 x C	216	59.7	63	29.5	66	32.6	0.95
		C x F_1	244	60.7	73	29.8	75	32.7	0.97
		F_1 x F_1	9	88.9	3	35.0	5	38.8	0.60
6	10-11	F_1 x C	264	75.8	115	30.2	85	32.8	1.35
		C x F_1	260	70.4	113	30.6	70	32.0	1.61
		F_1 x F_1	52	76.9	20	29.7	20	32.4	1.00
8	8-9	F_1 x C	18	55.6	2	32.0	8	37.2	0.25
		C x F_1	74	68.9	26	29.5	25	33.9	1.04
		F_1 x F_1	None [1/]	-	-	-	-	-	-
8	10-11	F_1 x C	26	53.9	6	34.4	8	35.9	0.75
		C x F_1	77	71.4	31	30.5	24	34.1	1.29
		F_1 x F_1	None [1/]	-	-	-	-	-	-
10	8-9	F_1 x C	136	60.3	54	30.0	28	34.6	1.93
		C x F_1	6	33.3	1	34.0	1	38.0	1.00
		F_1 x F_1	None [1/]	-	-	-	-	-	-
10	10-11	F_1 x C	None [1/]	-	-	-	-	-	-
		C x F_1	10	40.0	3	30.5	1	32.0	3.00
		F_1 x F_1	None [1/]	-	-	-	-	-	-
Control Group			3118	76.6	1382	28.6	1007	30.5	1.37

1/ Treatments where no F_2 neonates were available for rearing.
2/ Sex ratios computed on the basis of the females' proportion equaling one.

radiation (6, 8 and 10 krads as 8-11 day-old pupae) were compared in field trials. Pupal eclosion, adult dispersal and response to pheromone sources located at various distances from the eclosion site were monitored. In the parameters measured, there were not significant differences between F_1s and wild or untreated laboratory reared insects. In field cage studies designed to evaluate mating propensity, F_1 males mated an initial time with lab-reared females as frequently as did wild males, however, fewer F_1 males mated a second time on the same day, e.g., F_1s mated 1.8 times vs. 3.4 and 2.5 respectively for wild and untreated laboratory reared males (ODell & Mastro, unpublished). The impact of this competitiveness shortcoming is still to be determined in field tests. F_1 females generally attracted males and mated in patterns similar to wild females (Mastro et al., 1987). Competitiveness testing related to the areas just described is ongoing in order to define more precisely, potential impact on the overall competitiveness of sterile F_1 progeny.

When considering a particular management objective (e.g. eradication vs. suppression), the characteristics of F_1 progeny of the various dose/age treatments must be considered carefully. Treating P_1 males with 10 krads in either the 8-9 or 10-11 day age groups provides F_1 progeny which are very sterile (see Table 3). However, the proportion of F_1 eggs which hatch is small (approximately 34-40%, Figure 1), and mean larval developmental times are approximately three days longer than that of control insects and survival is reduced. Only a small number of F_2 larvae result from outcrossing F_1 adults from this treatment group (Table 3) perhaps making it the best irradiation treatment for eradication programs. The fertility of the F_1 female and the survival of any of her F_2 progeny should be closely scrutinized when making a selection (Tables 3 & 4). Selection of a lower treatment dose (6 krad) provides F_1 larvae with a faster development time and a greater number of F_1 adults (e.g. higher proportions of F_1 eggs hatch and survive); these adults, however, are more fertile than F_1 progeny of males receiving higher radiation treatments and the outcrossed F_1 female is more fertile than the reciprocal cross. Although 6 krads may not be considered as a suitable treatment dose when the objective is eradication, it may be a better choice for population suppression purposes. Simulation modeling is essential to accurately predict the consequences of various treatments and release options.

Pilot study of F_1 technique

The information compiled from radiation and competitiveness studies and the theoretical advantages of F_1 sterility prompted us to initiate a field trial. In 1982 an isolated, low-density population in Horry Co., South Carolina, was selected. Irradiated (10 krads) males treated as pupae (8-12 days old) were released throughout the flight period. Release procedures were similar to the fully sterile male release described previously. The site was intensively monitored in 1982, and in the following year.

Interaction with the native population was demonstrated, and the population was declared eradicated in 1985 after two years of negative pheromone-baited trap survey (traps deployed on a 268m grid). Although the outcome of the trial was positive, the technique was nearly as difficult and costly as releasing fully sterile insects. The theoretical advantage is that a greater suppressive effect results from releasing partially sterilized males because the F_1 progeny of released males which mate with wild females are available in the next generation for continued suppression. In 1983 we began to consider the release of F_1 egg masses (progeny of males treated with a substerilizing dose and mated with untreated females). Since F_1 eggs can be easily produced and held for months in diapause, large numbers could be stockpiled either in the laboratory or at the release site under field conditions. Just prior to native egg hatch, F_1 egg masses could then be distributed throughout the target population. Release rates, theoretically, can be adjusted to result in the desired overflooding F_1:wild adult ratio, provided that the native density is known, F_1 and native eggs hatch in synchrony, and comparative survival and synchrony information on immature stages is accounted for.

Reasonably accurate estimates of the native egg mass density are essential to establish the desired sterile:fertile overflooding ratios. However, in sparse insect populations where application of this control technique should be considered, current techniques for estimating egg mass densities are not sensitive (Wilson & Fontaine, 1978). Studies with grids of pheromone traps, have demonstrated a relationship between the proportion of males captured and actual male density (Schwalbe & Paszek, 1978; Elkinton & Carde, 1980). Currently, we use a technique based on pheromone trap information for estimating densities in isolated populations. The applicability of using trap information for monitoring densities within areas that are continually infested is under investigation (Ravlin et al., 1987).

F_1 Egg Mass Release Pilot Study

To date, nine isolated gypsy moth infestations have been treated using releases of paternally irradiated F_1 eggs whose male parent was irradiated. In addition, approximately 400 ha. of infestation have been treated with F_1 eggs at sites within the endemic area (plot size ranged from 7.5 to 225 ha.) Generally, the release and monitoring techniques described below are similar to those used at all release sites.

To describe the details and effectiveness of the F_1 egg release technique, the treatment of one isolated population in Bellingham, Washington, is summarized below. The infestation was detected in a residential area in 1983 through the use of pheromone-baited traps. More intensive trapping in 1984 succeeded in delimiting the boundaries of the infestation and capturing more male moths (n=82). Also egg masses and larval and pupal exuviae

were found. Based on the previously described relationship between trap density and proportion of males captured, we estimated that approximately 20 percent of the males were captured in 1984 resulting in a population estimate of 400 wild males. To arrive at an estimate of the overwintering egg mass density, we assumed that there was a 1:1 adult sex ratio during the 1984 flight period and that all females mated and produced viable egg masses that survived and hatched in the spring of 1985. The resulting estimate of 400 native egg masses may have been too high. Campbell et al., (1976a) and others have shown that skewed sex ratios occur in sparse populations. We assumed that the residential nature of the area and the abundance of man-made objects would foster female larval and pupal survival (Campbell et al., 1976b). At worst we believed our native egg mass estimate would be too high and we would err only in overflooding at a higher than projected rate.

The desirability of establishing a very high overflooding ratio had to be balanced against other factors. Because we would be releasing a feeding stage in a residential area with limited numbers of ornamental and fruit trees, we did not want to release numbers of gypsy moths which would produce objectionable defoliation. We circumvented this problem by releasing numbers which would provide the desired overflooding ratios and produce the desired outcome, eradication, over a two-year period. Also, in 1985, the release area was thoroughly inventoried for numbers and size of host trees in order to estimate the number of insects which could be released without causing objectionable damage. Thirty-four thousand F_1 egg masses were released in the initial year. We calculated that this was equivalent to 13,600 "wild" egg masses (wild egg mass equivalents = W.E.M.E.) in terms of the numbers of adult males produced. The factors that were used to compute the W.E.M.E. are the number of eggs per mass, reduced F_1 egg hatch, a skewed 2:1 male:female sex ratio, reduced F_1 larval survival and asynchronous development. Egg masses were distributed in 1985 according to location and size of host trees. Based on all of the previously mentioned assumptions, the 1985 release density should, theoretically, have produced a 34:1 F_1 sterile male:wild male overflooding ratio. Based on the preliminary results of the initial release, an additional 12,769 egg masses (5,108 W.E.M.E.) were released in the spring of 1986, which should have produced an overflooding ratio high enough to effect eradication. The distribution of wild, immature insects located through sampling in 1985 was also used as an additional weighting factor in the 1986 release, i.e. more F_1 egg masses were placed at these sites in 1986.

The impact of the release was monitored using a variety of techniques. To compare the proportions and synchrony of F_1 and wild egg mass hatch, samples of both were held within the release area in a screened enclosure designed to prevent escape, but which maintained ambient temperature conditions. Larval hatch from individual egg masses was generally monitored daily. Theoretically, successful establishment and survival of F_1 neonates would be reduced if hatch of F_1s was out of synchrony with host

development (Hough & Pimentel, 1978; Raupp et al., 1988).

Daily random samples of larvae and pupae were collected throughout the release area to provide material for monitoring developmental synchrony, survival, and overflooding ratios. Collected larvae were placed individually in 44.4 ml cups provisioned with artificial diet (Bell et al., 1981) and held in the laboratory until type (i.e., F_1 sterile or wild) could be determined. Male larval type was determined using two techniques: chromosome analysis and mating-egg mass evaluation.

A portion of the male larvae collected as first through fourth-instars was typed by the examination of sperm cells. Type was determined by scoring early metaphase cells for number of normal pairs of chromosomes (normally n=31) and presence or absence of translocations. Males were typed as wild if two cells were found with the normal numbers and appearance of chromosome pairs. To type a male as an F_1 required observing translocations in two cells.

Type of the second group of males (approximately half of all larvae collected as first through fourth-instars and all fifth-instar and male pupae) was determined by using a mating-egg mass evaluation technique. Field collected insects were reared in the laboratory until adult emergence. On the following day, one-day-old adult males were mated to similarly aged virgin laboratory-reared females. Resulting egg masses were held 30 days (25° C, 50%-60% RH) for embryonation and type determinations were based on the proportion of eggs which were embryonated. The proportion of embryonated eggs in each mass was compared using Chi-square techniques with mean values for mating type 2 and type 4 (Table 5) (Mastro et al., 1984).

Similar to the second group of males, all field collected female larvae and pupae were similarly held until adult eclosion and mated as one-day-old females to normal laboratory males. Resulting egg masses were held for the normal 30-day embryonation period and an additional 150 days (4-5° C) to satisfy diapause requirements. A determination of the female type was then based on percent hatch of the eggs. Characteristics of each egg mass were compared statistically to mean values for percent hatch for mating types 3 and 4 (Table 5). Holding egg masses produced by females of unknown type is necessary because F_1 females, when mated to normal males, produce highly embryonated egg masses often indistinguishable from egg masses produced by normal mating pairs.

Table 5. Characteristics of egg masses produced by incrossing and outcrossing F_1 adult gypsy moths progeny of males irradiated (10 krad) as 6-11 day-old pupae mated with normal females.

Type	Mating type (male x female)	n[1/]	Mean proportion of eggs embryonated	SE	Mean proportion of total eggs which hatched	SE
1	F_1 x F_1	50	0.0910	0.0155	0.0012	0.0006
2	F_1 x Normal	52	0.2630	0.0380	0.0277	0.0104
3	Normal x F_1	60	0.6711	0.0353	0.0088	0.0020
4	Normal x Normal	145	0.9374	0.0118	0.7653	0.0154

1/ Number of mating pairs producing an egg mass.

Sterile F_1:fertile wild male mating ratios were monitored by placing one-day-old, virgin F_1 females throughout the release area. In other studies, we found that normal laboratory-reared and F_1 females attract and mate with wild males with the same periodicity and frequency as wild females (Mastro et al., 1987). Egg masses oviposited by these females were evaluated for male parental type based on the proportion of eggs which were embryonated (Table 5, mating types 1 & 3).

After the adult flight season, egg masses from the release area were collected and evaluated for mating type. Evaluations were based on the proportions of embryonated eggs and the hatch of total eggs (Table 5). These field collected egg masses could potentially be the progeny of all four possible mating types.

A 23.3 sq. km. area centered over the release area was trapped throughout the adult flight period with USDA high capacity milk-carton pheromone baited traps during both years of treatment. Traps were placed on a grid at a rate of 13.9 traps/sq. km. Trapping information was used to determine if the treated area was adequately isolated from other infested areas, and to provide estimates of the total adult male density during both treatment years.

Results and discussion of treatment with F_1 eggs

Hatch from samples of wild-type and F_1 egg masses during the spring of 1985 was nearly synchronous. Wild egg masses were not available for monitoring in the spring of 1986 but samples of F_1 egg masses appeared to hatch in synchrony with bud break of host trees. Wild egg masses in 1985 produced a mean of 279 larvae per mass while F_1 egg masses produced a mean of 162 larvae.

Results of evaluation of 1985 male larval samples provided estimates of overflooding ratios close to those expected. Of the 466 male larvae that were typed using chromosome analysis, 458 were

F_1s and 8 wilds, resulting in a 57:1 F_1:wild ratio (Table 6). F_1 larval establishment and survival studies on host foliage have shown that most F_1 mortality occurs in the first stadium. Therefore, a better estimate of the eventual adult overflooding ratio would be based only on determinations of later stadia larvae. When only those insects collected after the first observation at the release site of a fourth stadium larva are considered, the F_1:wild ratio was approximately 32:1 (254 F_1s and 7 wilds).

In all, 693 field-collected males were reared to the adult stage and crossed with normal laboratory reared females for type determination. Evaluation of resulting egg masses disclosed that male parents of 677 of these samples were sterile F_1s and 11 were fertile wilds. In 5 cases, the proportion of eggs embryonated was not different than mean proportions of embryonated eggs for either mating type (Table 5). If only the later collections of late stadia larvae and pupae are considered, as in males typed using chromosome analysis, the estimate of the overflooding ratio becomes approximately 80 F_1:1 wild (n=483). Wild male larvae were found widely scattered throughout the release area, indicating that the native population distribution was well represented by trap captures the previous year.

Results from sampling and evaluating female larvae and pupae in the release site are consistent with results of male evaluations. Of the 372 field collected females reared to the adult stage and paired with normal laboratory-reared males, 309 produced egg masses which could be evaluated; 241 females produced egg masses characteristic of a fertile male x F_1 female mating, while 9 females produced egg masses characteristic of a fertile x fertile mating. Of the remainder, 49 egg masses contained all unembryonated eggs (i.e., possibly did not mate or had an F_1 male parent) and 12 females produced egg masses with characteristics which could not be distinguished from mean values of the two possible mating types. Computing a female overflooding ratio from these data results in an approximately 27 F_1:1 wild ratio. Theoretically, the F_1:wild female ratio in the field should be approximately half the male ratio because F_1 egg masses produce adults in an approximately 2:1 male to female ratio. The observed overall female F_1:wild ratio in 1985 of 27:1 was approximately half of the observed male ratios arrived at by chromosome analysis (57:1) and mating-egg mass evaluation (62:1). These female data have not been separated to exclude early stadia larvae.

In 1985 monitor F_1 females produced 93 egg masses which could be characterized as being the result of a mating with an F_1 male (n=88) or a wild type male (n=5). The calculated overflooding F_1:wild ratio is 17.6:1. An additional 734 egg masses could not be characterized because they contained all unembryonated eggs. Unembryonated egg masses can be the result of an F_1 male mating or no mating. Undoubtedly, some of these 734 egg masses were the result of an F_1 male mating, but it is impossible to separate these from egg masses produced by unmated females. In unpublished studies we have determined that mated females begin to oviposit

soon after mating (generally within an hour), while unmated females generally do not begin to oviposit until they are 3 days old or older. Unfortunately, we did not note when the monitor females had begun to oviposit in 1985. In 1986, we recorded if oviposition had commenced when the female was retrieved and if not, how soon afterward, in an attempt to separate females producing unembryonated egg masses into mated and unmated categories.

After the 1985 adult flight period, 63 egg masses were collected from within the release area. These egg masses could potentially be progeny of all four mating types. Of the 63 egg masses collected, 1 was determined to be from a (male x female) wild x wild mating, 7 from wild x F_1 matings, 19 from F_1 x F_1 matings and 17 from F_1 x unknown female matings. The computed mating ratios follow: sterile to fertile male 5.1:1 (n=43) and sterile:fertile female 26:1 (n=27). This female ratio agrees with the ratio from female larval and pupal collections. However, the male ratio is much lower than the predicted ratio or the ratios determined by larval sampling or monitor females. The difference between these male ratios is unexplained. Overall, the ratio of sterile egg masses (where at least one parent was an F_1) to fertile egg masses (both parents fertile wilds) was 62:1.

Pheromone traps in 1985 captured a total of 869 males and 745 of these were captured within the release area. The remaining males were captured within ca. 0.5 km of the release site.

It was only possible to collect a small number of immature male insects (n=39) during the 1986 larval and pupal sampling period. Of these, 30 males could be evaluated. Five of these were dissected for chromosome analysis and all were typed as F_1s. The remaining males were reared to the adult stage and mated with normal females. Twenty-four produced egg masses characteristic of an F_1 male parent and 1 produced an egg mass characteristic of a wild male parent. Based on all males, the F_1:wild ratio was calculated as 29:1.

Also, in 1986 twenty-six field collected immature females were reared to the adult stage. Mating of these females with normal laboratory males resulted in 14 egg masses on which a determination could be made. Thirteen of these egg masses were evaluated to be from F_1 females and 1 was determined to be from a wild female.

Of the monitor F_1 females placed in 1986, 116 of these produced egg masses determined to be the result of an F_1 male mating. No monitor females produced an egg mass which could be characterized as the result of mating with a fertile male.

Trapping in 1986 resulted in 209 males captured within the F_1 release area. This was approximately 28% of the males captured in the same area in 1985 (n=745). This roughly corresponds to the reduced numbers of F_1s released in 1986 (35% of the 1985 release). In all of the area trapped in 1986, 244 males were captured.

Based on 1986 results, no further release was made in 1987. Trapping in 1987 was carried out at the same trap density as in previous years, but the high-capacity USDA milk carton trap was replaced by the more efficient USDA delta trap. No males were trapped in 1987 or 1988.

A summary of monitoring this release site is presented on Table 6. Generally, the sterile F_1:fertile wild male ratios observed were near the expected 34:1 overflooding ratio in 1985. The observed ratios from male chromosome analysis (57:1) and male mating egg mass evaluation (62:1) are not different at the 5% level of significance (Chi-square analysis). Also, ratios calculated from reduced data sets (i.e., using only later stadia insects for chromosome analysis (32:1) and mating-egg mass evaluation (80:1)) are not significantly different from ratios derived from their parental data sets or each other. Both of the overall male ratios computed from larval sampling are significantly different (5% level) from the ratio computed using monitor female egg mass evaluation (17.6:1) and post season egg mass evaluation (5.1:1). Ratios derived from these two evaluation techniques are also significantly different (5% level) from each other.

Table 6. Expected and observed results of releasing F_1 progeny of irradiated males (10 krads) in an isolated gypsy moth population in Bellingham, Washington.

Method of Estimation	Year 1984	1985	1986	1987
Expected spring wild egg mass density	-	400	8	0
Numbers of F_1s released (W.E.M.E.)	0	13,600	5,108	0
Expected F_1:Wild male ratio (Range)		34:1	640:1 (189:1 to 2,2554:1)	
Observed F_1:Wild male ratios				
1) Chromosome analysis				
A) All instars		57.3:1	5:0	
B) Later instars		31.8:1		
2) Mating egg mass evaluation				
A) All samples		61.5:1	24:1	-
B) Later instar & pupae		79.5:1		
3) Monitor female mating ratio		17.6:1	116:0	-
4) Post season egg mass evaluation				
A) Male ratio		5.1:1	no data	-
B) Overall ratio		(62:1)		
Observed F_1:Wild female ratios				
1) Mating egg mass		27:1	13:1	-
2) Evaluation of post season egg masses female ratio		26:1	no data	-
No. of males trapped	82	869	244	0
Estimated male population	400	9,549	2,681	0

At the beginning of the 1986 field season, an estimate of the residual wild population was needed to determine the number of F_1 egg masses to be released to achieve eradication. From pheromone trap catches, we estimated that the 869 males trapped represented 9.1% of the total male population (i.e., 9,549). Only three estimates of male overflooding ratios in 1985 were available at the time of the 1986 egg release (i.e., male chromosome and mating-egg mass evaluations and monitor female-egg mass evaluation). Based on these ratios (ranging from 17.6:1 to 79.5:1), we calculated that the wild male population could have been between 119 and 513 males (i.e., 1.25 to 5.38 percent of 9,549 males). Again, we made the assumption of a 1:1 sex ratio in the wild population and that F_1 males were completely competitive. The number of successful wild mating pairs in 1985 was calculated to be from 2 to 27, respectively, for F_1:wild mating ratios of 17.6:1 and 79.5:1. We believed that the estimated mating ratio of 17.6:1 provided by monitor female data was too low for previously mentioned reasons and the true mating ratio was nearer 34:1 or higher. When the appropriate calculations are made using a 34:1 F_1:wild male ratio, wild egg density in the spring of 1986 was estimated at 8 wild egg masses. We released 5,108 F_1 W.E.M.E. which, if the wild egg mass population in the spring of 1986 consisted of 8 egg masses, would provide a male overflooding ratio on the order of 640 F_1:wild male.

In sparse gypsy moth populations immatures are difficult to locate and we were only successful in locating a small number in 1986. Based on all males collected as immatures and typed (both techniques) the male ratio was 29 F_1:1 wild. Monitor female data provided a much higher estimate of the sterile male overflooding ratio (116:0). It was mentioned earlier that in 1986 egg mass release was weighted at known sites of wild insects. Sampling was concentrated around these same sites because immatures could only be located at these sites. Monitor females, however, were distributed as in 1985 (i.e., generally throughout the area). A ratio based on assessment of immature males, because of our skewed sampling, could be biased. Monitor female data may provide a better estimate of the ratio throughout the release area.

We conclude that the F_1 egg mass release in Bellingham, WA. was successful in eradicating the native population. Two years of negative trap survey data is generally considered necessary for confirming the outcome of an eradication attempt. The evidence of successful interaction with, and suppression of the native population is apparent.

In other studies in isolated sites and within the generally infested area, we have not always achieved predicted overflooding ratios and results do not appear as clear cut. These results suggest that we need to develop better techniques for estimating native insect density and distribution. Several investigators are currently exploring the utility of pheromone-baited traps for monitoring populations in the generally infested area, as well as techniques for estimating densities of other life stages (Liebhold & Elkinton, 1980ab). We are also far from a clear understanding

of how, compared to wilds, F_1 immatures survive and develop in the field. Several ongoing studies are exploring the comparative behavior, relative egg viability, immature development and survival of F_1s. Also, the possible impacts of parasites and predators on F_1 egg releases are unknown. In some field release sites, we have noted rapid disappearance of late instar larvae and pupae, and although the overall population density was lowered, we do not know how this precisely affected the sterile:wild ratio. Propensity of F_1 males, as described earlier, to multiple mate on the same day has been shown to be lower than wild males. The impact of this competitive deficiency on the actual mating ratio under field conditions is still to be determined.

Studies have been initiated to explore the impact of female multiple mating on viability of resulting egg masses. It was generally believed that female gypsy moths are monandrous, however, in unpublished laboratory studies, we found 15% of the females mated twice. If mating with an F_1 male does not elicit the normal monocoitic response, or if there is sperm precedence in multiple-mated females, then the F_1 male competitiveness could be adversely affected. A better understanding of these areas of exploration should enable us to apply the technique more effectively and interpret our field results more clearly.

Results from the Bellingham site and other sites where F_1 eggs have been released have also posed several problems which must be addressed: 1) how to predict when native hatch will occur and how to time F_1 egg mass release so that hatch is synchronous, 2) what is the impact of dispersal (neonate and adult) on the overflooding ratios, and 3) how does egg distribution within a site affect survival.

Evaluation techniques used in this study and other similar studies are labor intensive and require that the insects be held for a period of time before a determination of type (F_1 or wild) can be made. A method to rapidly discriminate between F_1 and wild insects would allow a more intensive evaluation of releases, lower the cost of evaluation and provide a valuable tool for the ongoing research described previously. Some techniques under investigation which would provide for a rapid discrimination between wild and F_1 insects, have a genetic basis (i.e.larval setal patterns, morphometrics of adult male wing venation) and others, such as paternity assays may depend on identification of damage induced by radiation.

We believe that the F_1 technique is at present a viable technique that can be operationally useful for treating isolated gypsy moth infestations. Furthermore, we believe that the technique may be potentially useful for management of gypsy moth populations within the generally infested area. This possibility becomes more attractive when considering F_1s that are progeny of males receiving lower (6 or 8 krad) doses of radiation. Finally, all the investigations associated with the technique have led to a better understanding of the biology and behavior of the insect.

With a concentrated effort to resolve outstanding monitoring and competitiveness questions and additional efforts to improve laboratory colonization, the sterile egg technique can be operationally used within a short period of time.

An as yet unexplored potentially beneficial area for control of the gypsy moth is the use of other genetic control techniques reviewed by Whitten & Foster (1975). Downes (1959) suggested that, based on the work of Goldschmidt (1931, 1933) males from different geographic races of gypsy moth could be used in a control program. Both Downes and later Leonard (1974) recognized that the Japanese genome would enter the North American population, and potentially impart some factors which would make it more successful or destructive. However, no experimental work was initiated to explore the possibility of using this type of sterility.

An exciting possibility is the use of backcross sterility, which was originally described by Laster (1972), if it could be found in the gypsy moth. Although the genetic basis for backcross sterility is poorly understood, male sterility is associated with abnormal eupyrene sperm formation which is not transferred to females (Goodpasture et al., 1980; La Chance, 1984). This system offers a number of advantages over the F_1 sterile insect technique. Foremost, is that theoretically, once the sterility factor is introduced into a population it can persist indefinitely. Although this technique has not been explored for the gypsy moth, a number of closely related old world species, including Lymantria obfuscata, L. mathura, and L. monacha, offer potential candidates for investigation. Although it is impossible to predict if backcross sterility will be found with the gypsy moth, at least one of these species, L. obfuscata, will hybridize (Lenek, 1974). The advantages and potential benefits appear to be so great that the effort and expense of examining backcross sterility in gypsy moth appears well justified.

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OVIPOSITION SITE SELECTION BY JAPANESE LYMANTRIID MOTHS

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INTRODUCTION

Oviposition site selection is one of the most important habitat selection in insects. As for the oviposition of the gypsy moth, Lymantria dispar L., overwintering egg masses have been shown to be protected against avian predators (Higashiura, 1980; Schaefer 1981) and low winter temperatures (Leonard, 1972) by the insulative effect of snow. Thus, habitat suitability for oviposition is higher beneath the snow than above (Coulson & Witter, 1984). However, more egg masses are deposited above the eventual snow line than beneath (Leonard, 1972; Higashiura, 1980). To solve this puzzling distribution, I present a conceptual model of oviposition site selection by using the fitness set approach of Levins (1968). The prediction by the model is tested in comparison of oviposition sites by Japanese lymantriid moths.

Predation on lepidopteran eggs is thought to be small, and so relatively little is known about it (Torgersen & Mason, 1987). The egg masses of the gypsy moth is, however, known to be subject to high avian predation (Higashiura, 1980; Brawn & Cameron, 1982). During 1974-83, I estimated the bird predation on the egg mass to reveal the habitat suitability in oviposition of the gypsy moth in a snowy region, Hokkaido northern Japan.

Finally, I present a control method of gypsy moths utilizing the strategy of the oviposition site selection by the moths.

THE MOTH

Pintureau (1980) treated Japanese gypsy moths as two species, Lymantria dispar hokkaidoensis Goldschmidt for Hokkaido populations, and L. japonica Motschulsky for Honshu populations. Here, however, I treat the two species as the same, L. dispar L., in examination of their behavior in oviposition, because both females can fly during oviposition site selection as in other Asian populations (Goldschmidt, 1934).

Adults of the gypsy moth emerge between July and September. A female moth deposits only one egg mass. Larvae hatch during the following April and May. The eggs withstand the winter low temperatures and are rarely attacked by egg parasites in Japan (Schaefer, 1981).

METHODS

During 1974-83 I studied bird predation on gypsy moth egg masses in a birch, Betula platyphylla Sukatchev, forest at Bibai, Hokkaido, northern Japan (Fig. 9). Three study plots (Plots 1-3) neighboring each other were established in autumn 1974. The plots were 0.51 ha, 0.52 ha, and 0.52 ha. Plot 4 (0.63 ha) was added in autumn 1975. Plot 1 was reduced to 0.18 ha in May 1980 and disappeared in May 1982. The density of canopy layer trees was 1096/ha. The birch accounted for 57% of them. During the study period, almost all egg masses (1077) were deposited on bark of the birch as in the previous studies (Schaefer, 1978; Higashiura, 1987), only two egg masses being laid on Sorbus commixta Hedle.

The predator left characteristic scratches on the bark surface wherever egg masses had been removed (Higashiura, 1980). The scratches made it possible to distinguish egg masses eaten by birds from those physically damaged by the compression of accumulating snow.

Predation rate was visually estimated for a single egg mass to seven grades, i.e. 0, 10, 30, 50, 70, 90, and 100%, in early May just before larval hatching. The mean predation rate in each plot, or in each height class, was obtained by averaging these visually estimated predation rates of all egg masses. Because the mean predation rate hardly differed among egg-mass sizes (Higashiura, 1980), egg-mass size

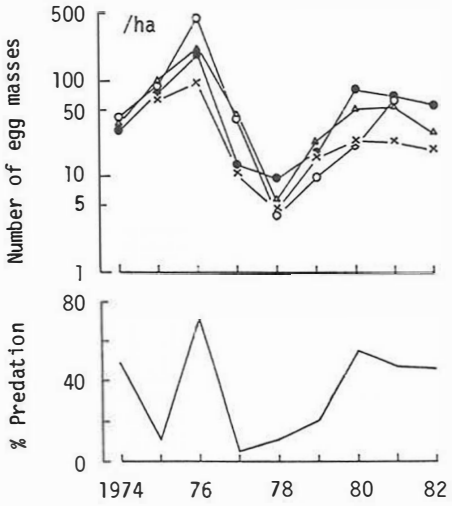

Figure 1. Population trends in egg masses in autumn (upper) and changes in predation rate on egg masses by birds (lower) at Bibai. Predation rate during the winter was plotted in the year of oviposition. ○: Plot 1, ●: Plot 2, △: Plot 3, ×: Plot 4.

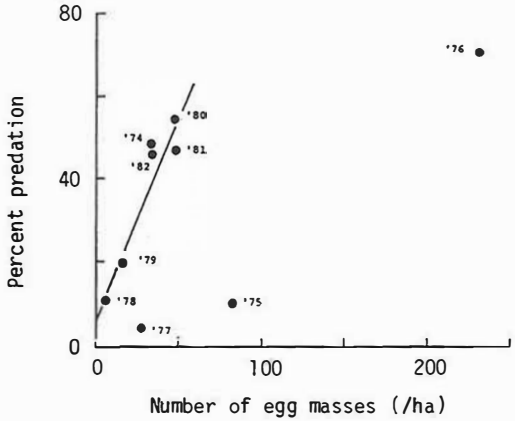

Figure 2. Predation rate in relation to initial egg mass density over the entire study area at Bibai. Suffix numbers denote the year of oviposition. The relationship was significantly density-dependent in the latter five winters, winters 1978-1983 ($y=5.80+0.98x$: $r=0.965$: $P<0.01$). The straight line shows this regression.

is not taken into account here. Sample sizes from winter 1974-83 were 56, 179, 503, 59, 13, 36, 88, 89, and 56 egg masses, respectively. During winter 1980-81, predation rates were estimated at intervals of one to four days to reveal the progression of bird predation. In each year, during September, the aboveground height of every egg mass in the study plots was recorded except in 1974. Additional studies of predation were carried out at Asahikawa, Hokkaido in winter 1982-83 using te same methods.

The aboveground heights of egg masses were measured in seven stands in five regions of Japan by January (Fig. 9). The hights of the tree and of the lowest branch were recorded for each tree having eggs. At Bibai and Asahikawa the two heights were measured for each of ten study trees.

RESULTS

Population trends in egg masses, or in ovipositing females were similar in the four plots, though there were considerable differences in the density among plots (Fig. 1). Mean density over all plots varied from 6 /ha in 1978 to 231 /ha in 1976.

Predation rate by birds in the plot also varied considerably, between 0% and 84%, the latter occurring in Plot 4 in winter 1976-77.

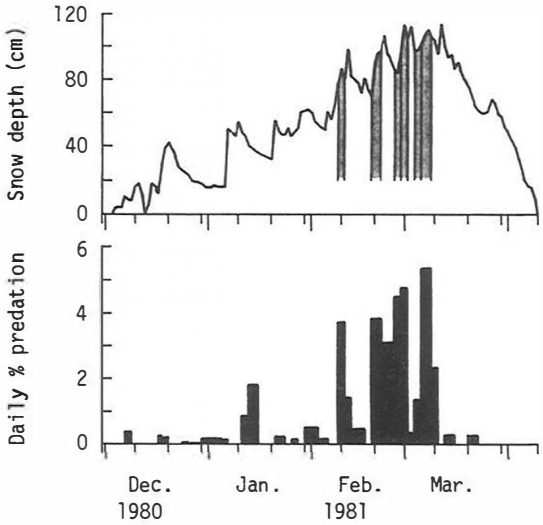

Figure 3. Snow depth (upper) and daily predation rate on egg masses above the snow (lower) in winter 1980-81 at Bibai. Stippled bars in the upper correspond to periods of increase in the daily predation rate between 9 February and 9 March 1981.

The most common predator was the nuthatch, Sitta europaea baicalensis Taczanowski, recognized from direct observations and from the characteristic scratches left from their beaks and claws. Other predatory species were Parus palustris hensoni Stejnege, P. major minor Temminck & Schlegel, and Garrulus glandarius pallidifrons Kuroda. The mean predation rate during the nine generations was 38.8% in the geometric mean. The percentage of egg masses physically damaged by the compression of accumulating snow was negligibly low; 8.8% in winter 1982-83 was the highest during the study period.

Figure 2 shows the relationship between egg mass density averaged over all plots (/ha) and predation rate by birds. There was no significant relationship during the nine years of the study ($r=0.589$: $P>0.05$). However, a highly significant relationship was observed through the latter five winters, winter 1978-79 to winter 1982-83 ($r=0.965$: $P<0.01$). During the other four winters 1974-78, there was no significant relationship ($r=0.706$: $P>0.2$).

The daily percentages of egg masses eaten by birds are shown in Figure 3 for winter 1980-81. Since attacking egg masses beneath the snow was impossible for any birds, I calculated the percentage only for egg masses above the snow. Moreover, I assume that birds maintain a constant predation rate during the interval.

Predation rate was 54.7% in the winter, the second highest during

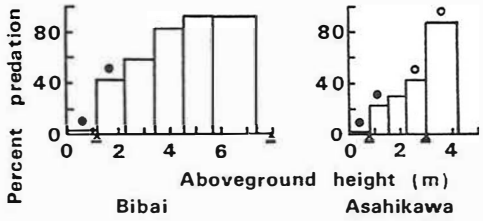

Figure 4. Vertical distributions of mean predation rate at Bibai in winter 1980-81 (left), and in a Larix forest at Asahikawa in winter 1982-83 (right). Open and closed triangles show heights of maximum snow depth in the winter and of the lowest branch, respectively. Open and closed circles indicate the significant difference between the adjacent two height classes at the 1 % and 5 % levels, respectively (the Tukey-Kramer method using the arcsine transformation).

the nine winters. In this winter of high predation, birds attacked egg masses mostly in February and March, when the snow depth was highest of the year, and never attacked any egg mass after March when the snow began to melt. Figure 3 also suggests that snow accumulation intensified predation in February and March.

Since predation was concentrated in snowy season, the height at which the egg mass was laid on a tree affected mortality from bird predation at Bibai and Asahikawa (Fig. 4). Predation rate beneath the snow was significantly lower than just above the snow (the Tukey-Kramer method, $P<0.05$: Sokal & Rohlf, 1981). Although percent predation gradually increased with height above the snow, the most intensive predation was concentrated above the lowest branch at Asahikawa even in the year of 23% predation (Fig. 4). At Bibai, females rarely oviposited above the branch.

Table 1. Maximum snow depth and mean height of egg masses at Bibai, Hokkaido.

Year of oviposition	1975	1976	1977	1978	1979	1980	1981	1982
Maximum snow depfth (cm)	116	156	99	129	90	114	92	99
Mean height of egg masses (cm: 95% C.L.)	187 ±16	249 ±15	265 ±56	233 ±90	248 ±68	298 ±41	271 ±37	229 ±35

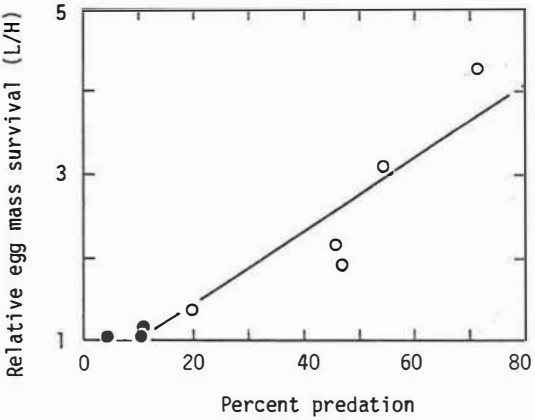

Figure 5. Correlation between relative egg mass survival and percent predation measured from overall egg masses at Bibai in winters 1975-83. Correlation was highly significant ($y=0.569+0.044x$: $r=0.939$: $P<0.001$). Relative egg mass survival (L/H) is expressed by dividing the proportion of egg masses surviving beneath the snow (L) by that above the snow (H) (snow height used was the average maximum through the eight winters, or 112 cm). Open and closed circles indicate that the difference of the proportion of egg masses surviving between the two height classes (L and H) was statistically significant ($P<0.01$) and insignificant ($P>0.1$), respectively (t-test using the arcsine transformation).

The insulative effect of snow can be demonstrated more obviously by the survival of the egg masses beneath the snow (L) relative to those above the snow (H). Throughout the eight winters at Bibai, relative survival (L/H) increased with average percent predation on egg masses (Fig. 5). Oviposition beneath the snow had the advantage of producing high egg mass survival in five of eight winters. However, survival approached equality in the year of low predation.

Since snowfalls at Bibai did not vary so much (Table 1: C.V. in maximum snow depth was 20%), inferences from mean snowfall values accurately indicated above or beneath the snow.

The population density in larval and egg stages is correlated with oviposition heights in Europe (Luciano & Prota, 1981). At Bibai, however, mean height of egg masses were not different among years during 1976-82 (Table 1: $P>0.25$), irrespective of egg density. Significant differences were observed only between the height in 1975 and others ($P<0.05$), except between 1975 and 1978 and between 1975 and 1979 ($P>0.1$).

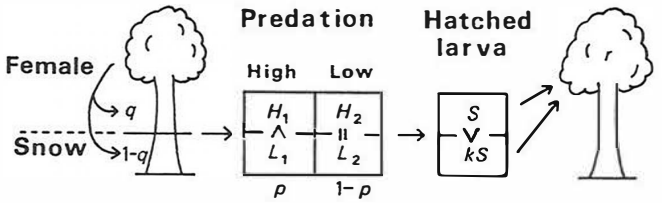

Figure 6. Two factors, winter predation and cost of larval dispersion, affect oviosition site selection by the gypsy moth as assumed by the model. q denotes the proportion, or probability of females ovipositing above the eventual snow line. Egg masses above the snow have much lower survival than those beneath the snow in the year of high predation. In the year of low predation, however, the proportion of surviving egg masses above the snow is almost the same as beneath the snow. Probability of high predation is p. Larvae hatched on the lower site experience lower survival (kS: $0<k<1$). The rate of increase (r) after larval dispersion is not affected by hatching sites.

Model of oviposition

The data presented above showed that oviposition beneath the snow was advantageous in snowy regions. In the year of low predation, however, egg mass survivals were almost the same above and beneath the snow. The question that arises is, why do not all females oviposit beneath the snow in snowy regions? In this section I present a conceptual model, based on the fitness set approach of Levins (1968), which suggests that a mixed strategy of ovipositing both above and beneath the snow is optimal in unpredictably changing environments.

Ovipositing in higher locations is thought to be advantageous for hatched larvae. Newly hatched larvae of the gypsy moth move up trees. As they move, they spin a thread of silk without feeding on any host leaves (Mason & McManus, 1981). Therefore, larvae from egg masses deposited lower must crawl longer distances and spin a longer thread to disperse or reach a food source. However, during years of high predation these larvae gain the benefit of high survival during the egg stage beneath the snow. In winters of low predation, the same proportion of egg masses survived beneath the snow as above the snow in three of the eight winters (Fig. 5). Natural selection favours ovipositing above the snow in this case, though ovipositing above the branch results in high predation on the egg masses even in the year of low predation in the snowy region (Fig. 4). Females should oviposit beneath the snow only in years of high predation, or in years when survival differs above vs. beneath the snow. However, since oviposition precedes predation, the predation stress makes the environment unpredictable and changing for the adult females. Our aim is to find the proportion, or probability, of oviposition above the snow, q, that

maximizes the long-term expectation of fitness, i.e., the optimal oviposition strategy.

I assume two types of temporally varying environments, environment 1 (in which predation is high) and environment 2 (low predation), and two sites for oviposition (above and beneath the snow) (Fig. 6).

Table 2. Definitions of symbols in the model: H and L denote the proportion of egg mass survivals above and beneath the snow, respectively.

Symbols	Definitions
H_1	H in the year of high predation (environment 1)
L_1	L in the year of high predation (environment 1)
H_2	H in the year of low predation (environment 2)
L_2	L in the year of low predation (environment 2)
S	Survival rate of larvae hatched from the higher site
kS	Survival rate of larvae hatched from the lower site ($0<k<1$)
r	Rate of increase after dispersion

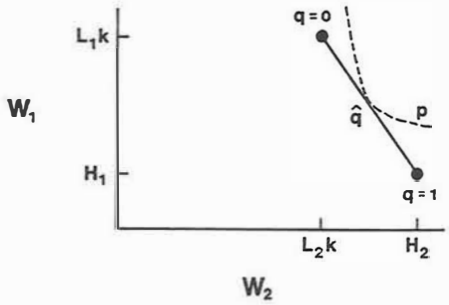

Figure 7. A fitness set analysis of the strategy of oviposition site selection by the gypsy moth. The point at q=1 represents females ovipositing above the eventual snow line. They have very different survival rates in the two environments. While the point at q=0 represents females ovipositing beneath the snow line. Survival rates are almost the same in these forms.

Definitions of symbols in the model are given in Table 2. Then the adaptive function in environment 1 (W_1) is

$$W_1=[qH_1S+(1-q)L_1kS]r,$$

and the adaptive function in environment 2 (W_2) is

$$W_2=[qH_2S+(1-q)L_2kS]r.$$

Since the moth is univoltine and of discrete generations, the alternative environments are "coarse-grained" (Levins, 1968), so that the average fitness ($\bar{W}$) can be estimated as the geometric mean of the fitness in each environment according to its probability (p for environment 1, and 1-p for environment 2) (Levins, 1968).

$$\log \bar{W} = p \log W_1 + (1-p) \log W_2$$

Setting $d\log \bar{W}/dq=0$, the optimum $\hat{q}$ is calculated as

$$\hat{q}= k \frac{L_1(H_2-L_2k)-p(H_2L_1-H_1L_2)}{(L_1k-H_1)(H_2-L_2k)} \qquad (1)$$

This fitness set analysis is shown in Figure 7. Since the value $\hat{q}$ must lie between 0 and 1, we must adjust it as follows.

$$\text{If } p \geq \frac{L_1(H_2-L_2k)}{H_2L_1-H_1L_2}, \text{ then } \hat{q}=0.$$

Thus, if there are many years of high predation, natural selection favours always ovipositing beneath the snow.

$$\text{If } p < \frac{H_1(H_2-L_2k)}{k(H_2L_1-H_1L_2)}, \text{ then } \hat{q}=1.$$

Thus, if there are many years of low predation, selection favours always ovipositing above the snow.

If p lies between those values mentioned above, then the optimum $\hat{q}$ equals the $\hat{q}$ calculated in eqn (1). Thus the mixed strategy is optimal. This strategy corresponds to the oviposition site selection at Bibai.

Tests of the model

Costs for larvae hatched from lower egg masses, k in eqn (1), have been included in the model, because the larva must spin a longer thread of silk without feeding. The height of the lowest branch is

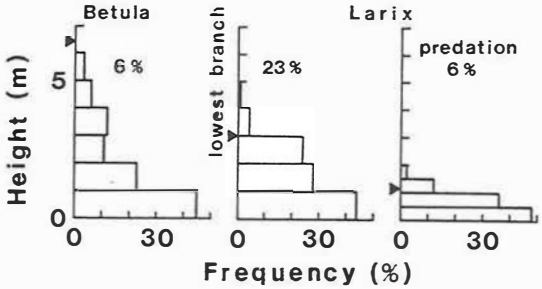

Figure 8. Oviposition sites by the gypsy moth in relation to the height of the lowest branch at Asahikawa, Hokkaido in autumn 1982. Triangles show the mean height of the lowest branch. Predation rates of egg masses in winter 1982-83 are also shown. Left: Betula plantation. The mean tree height was 16.0 m. Sample size was 97 egg masses. Middle and Right: Two forests were in the same Larix plantation. The mean tree height was 9.8 m. Branches below 3 m were pruned in the middle forest. Sample sizes in the middle and right were 177 and 86 egg masses, respectively.

important in this case. Since hatched larvae can easily reach a food source on trees branching out beneath the snow line, oviposition beneath the snow line should be suitable for both egg mass and larval survivals.

The gypsy moth at Asahikawa (snowy region) deposited her eggs beneath the branch, irrespective of the heights of branches (Fig. 8). Egg masses were distributed to higher sites on trees without lower branches than those on trees having lower branches. Predation rate was lower in the later forest because of snow protection. The maximum snow line was 83 cm in the winter. Predation rate was also low in the Betula forest. Some birds, even the nuthatch, slipped off the smooth surface of birch bark during predation, their claws leaving slip marks on the surface. Once they slipped down, they left the tree for an another.

Highest predation occurred during the snowy season, February and March; snowfalls accelerated predation (Fig. 3). Consequently, differences in both predation pressure and the insulative effect of snow against predation should be expected in southern populations where snowfall is lighter. Oviposition site selection in northern and southern Japanese populations should reflect these differences.

Oviposition sites were considerably different among geographical regions (Fig. 9). Egg mass distibution is represented by relative aboveground heights (letting the height of the lowest branch equal one, and the top of the tree equal two) in Figure 9. Using the relative height, we can compare the distributions above and beneath the lowest branch and also above and beneath the snow, irrespective the

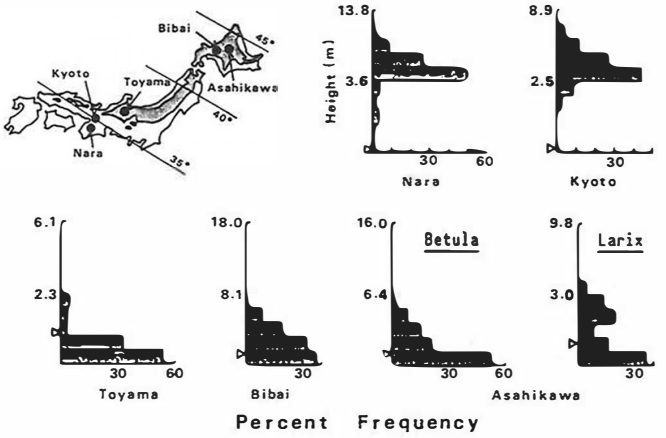

Figure 9. Geographical variation of the oviposition site in Japanese gypsy moth. The abscissa shows the frequency distribution of egg masses. The ordinate represents the aboveground height relative to the heights of the lowest branch and of the top of tree. Both average absolute heights are shown, each interval being divided into five classes. Stippled area in the map shows the region having snow depths over 1 m. The average maximum snow depths (1976-83) are shown by triangles. Snow is rare at Nara and Kyoto, where snow temporarily covers the ground for 5 and 11 days each year, respectively. In contrast, the other sites are characterized by heavy snow: snow lies for 64 days (Toyama), 132 days (Bibai), and 146 days (Asahikawa) through the year. Sample sizes were 75 egg masses on 20 trees (mainly Zelkova serrata and Sarix spp.) at Nara, 67 on 21 trees (Prunus spp. and Quercus glauca) at Kyoto, 54 on 33 trees (Magnolia obovata and Ilex macropoda) at Toyama, 503 on 288 trees (Betula platyphylla) at Bibai, 97 on 28 trees (B. platyphylla) at Asahikawa, and 177 on 81 trees (Larix leptolepis) at Asahikawa.

absolute heights of trees and branches. I compared frequency distributions of egg masses between the two forests in Figure 9 using the G-test (Sokal & Rohlf, 1981). Of the fifteen pairs, the distributions were significantly different in thirteen pairs ($P<0.05$), and were not significantly different in only two pairs (Kyoto and Nara, $G=1.105$, $d.f.=3$, $0.75<P<0.90$; Toyama and the Betula forest at Asahikawa, $G=5.366$, $d.f.=2$, $0.05<P<0.10$).

In the regions with light snow, Nara and Kyoto, almost all egg masses were deposited in tree canopies, frequently on undersides of branches. Low predation should be expected in these regions, or p is

small. In contrast, females oviposited mostly beneath the snow at Toyama, where snow depths reached 96 cm on an average and were most variable during each year. The largest p should be expected. Egg masses were deposited both above and beneath the snow at Bibai and Asahikawa, where predation rate considerably fluctuated between years (Figs. 1 & 5).

Oviposition sites in Japanese lymantriid moths are mainly divided into two sites (Table 3). Species overwintering in larvae oviposit on undersides of host leaves, except Leucoma candidum. In contrast, species overwintring in eggs oviposit on tree trunks, except E. pseudoconspersa. The most interesting selection for oviposition site is observed in Orgyia thyellina. Female moths, which are bivoltine, switch oviposition sites from undersides of host leaves for nondiapause eggs to tree trunks for diapause eggs (Kimura & Masaki, 1977).

DISCUSSION

In the present study, the mean predation rate on the egg mass was 38.8% during the nine years, although this fluctuated considerably. The highest predation (84%) was observed in Plot 4 in winter 1976-77. These high frequencies suggest that bird predation on the egg mass is as important a mortality factor as parasites are in the egg and larval stages. Although predation clearly showed a density-dependet trend in the later five winters, the trend was ambiguous during the nine study period. Thus females cannot predict predation pressure through their density.

Eggs of the moth are covered by a dense coating of hairs, sloughed from the female abdomen. The hair covering is believed to provide some protection against bird predation (Leonard, 1981). The behavior of birds attacking the egg mass suggests that it is unpalatable. Birds ate the egg mass not wholly at once, but bit by bit (Higashiura, 1980). Egg masses were eaten mainly during winters with heavy snowfalls (Fig. 3), which is when adult nuthatches experience the highest mortality from starvation (Nilsson, 1982). Nuthatches may be feeding on the egg mass simply to avoid starvation during the deep snow cover that prevents them from feeding on their favorable foods.

Dring the intensive predation period, egg masses deposited under the snow line survived from the predation. Thus, in snowy regions, habitat suitability for oviposition was higher beneath the snow than above. Egg mass survival beneath the snow was 1.9-4.3 times higher than above the snow in years of high predation, four out of eight years. However, survival was almost the same on both sites in the three years of low predation. Thus bird predation created unpredictably changing environments for ovipositing female gypsy moths. In contrast, height suitability was suggested to be different in regions with little snowfall: not only were egg masses rarely attacked by birds, but egg masses suffered predation at all heights. Egg mass distributions at Nara and Kyoto are thought to reflect these differences of predation pressure. There are three strategies for oviposition site selection shown in Figure 9: ovipositon in tree canopies (Nara & Kyoto), oviposition beneath the snow (Toyama), and oviposition

Table 3. Oviposition sites in Japanese lymantriid moths.

Species	Host	Stages in overwintering	Oviposition site: Diapause eggs	Oviposition site: Non-diapause eggs	References
Cifuna locuples Walker	D	Larva		L	Mutuura et al., 1965
Calliteara abietis (D. & S.)*	E	Larva		L	Matsushita, 1943
Euproctis similis (Fuessly)	D	Larva		L	Mutuura et al., 1965
E. subflava (Bremer)	D	Larva		L	Matsushita, 1943
E. pseudoconspersa (Strand)	E	Egg	B+L	B+L	Mutuura et al., 1965
Orgyia recens (Hübner)	D	Larva		L	Higashiura, unpublished
O. thyellina Butler	D	Egg	T	L	Kimura & Masaki, 1977
Leucoma candidum Staudinger	D	Larva		T	Sirota et al., 1976
L. salicis (L.)	D	Larva		T	Burgess & Crossman, 1927
Lymantria mathura Moore	D	Egg	T		Matsushita, 1943
L. fumida Butler	E	Egg	T		Matsushita, 1943
L. monacha (L.)	D+E	Egg	T		Matsushita, 1943
Ivela auripes (Butler)	D	Egg	T		Matsushita, 1943

Species: (D. & S.)*=(Denis & Schiffermüller) Host: E=Evergreen, D=Deciduous
Oviposition site: L=Leaf, B=Branch, T=Trunk

both above and beneath the snow (Hokkaido). Although the model is an oversimplification, it predicts these three strategies.

Japanese lymantriid moths mostly deposited nondiapause eggs on host leaves, but diapause eggs on tree trunks. Orgyia thyellina use the two site each for the egg. Tauber, Tauber & Masaki (1986) have regarded such the use of oviposition sites for diapause eggs as a strategy for depositing eggs on permanent sites. However, avoidance of winter predation on eggs accounts more precisely for the behavior, because the oviposition site is on considerably lower parts of tree trunks (never on twigs). Other members depositing diapause eggs also use the lower parts, except Euproctis pseudoconspersa and Lymantria fumida. Reversely, depositing nondiapause eggs on leaves is probably to avoid the cost of dispersion, because the egg stage of nondiapause eggs is too brief to be attacked. For univoltine species, such as the gypsy moth, females should select oviposition sites at once to balance both costs of predation and dispersion in long-term expectation.

In the argument mentioned above, the height of the lowest branch is most important for the gypsy moth. In forests having branches near the ground, oviposition near the ground should satisfy both egg and larval survivals. Outbreaks of the gypsy moth frequently occurs in young larch, Larix leptolepis (Sieb. et Zucc.), plantations, just after canopy closure. Shinohara & Higashiura (1982) reported that the outbreaks in larch plantations at Furano, near Asahikawa (Hokkaido), occurred only in 6-18 years old plantations. Egg masses were deposited in higher sites due to pruning of the lower branches (Fig. 8). The environment in the forest is changed to be like in the older by pruning, and reduces both egg and larval survivals.

Pests in man-made forests are selected through adaptations to the environment created in such forests. Control methods utilizing their life history strategies are one of the most powerful methods against these pests.

I am grateful to the late I. Hiura who suggested the study of this problem and helped me on the field work at Nara. I am indebted to my colleagues at Bibai and Shintoku, especially to S. Yamaguchi. I am also grateful to J.L. Bronstein for her helpful comments to improve early drafts and correct the English.

SUMMARY

Mean predation rate on gypsy moth egg masses by birds was estimated at 38.8% during nine years at Bibai, Hokkaido, Japan. The predator, mainly the nuthatch, attacked egg masses during a snowy season, February and March. Thus oviposition beneath the eventual snow line had the advantage of producing high egg mass survival only in the year of high predation. Since predation rate varied considerably, the predation created changing environments for females. The model of optimal oviposition strategy was presented by using the Levins model. The prediction of the model was consistent with the geographical variation of oviposition sites in Japanese gypsy moth and in Japanese lymantriid moths.

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ECOLOGICAL BASIS OF THE EVOLUTION OF HOST RELATIONSHIPS IN EURASIAN GYPSY MOTH POPULATIONS

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INTRODUCTION

Gypsy moth, Lymantria dispar L., is one of the most economically important pests of forests of boreal zones of the Holarctic. Despite numerous publications devoted to this species (Leonard, 1974; Vorontsov, 1977; Doane & McManus, 1981; Montgomery & Wallner, 1988) many aspects of its biology haven't been duly elucidated. Throughout its vast range, the gypsy moth inhabits many various biotopes whose ecological features have considerable influence on the biological properties of the species. One of the properties - intensity of gypsy moth migrations - has long been the focus of attention of forest entomologists.

In this work, I will summarize the literature data and our own observations on migrations in gypsy moth populations in northern Palearctic. There are many gypsy moth populations in this region where the females take flight (migrate) and populations where they do not fly. Thus, this is an excellent opportunity to make experimental comparisons of trophic adaptations of gypsy moth populations that differ in migration activity.

GYPSY MOTH MIGRATION ACTIVITY AND PREDICTABILITY OF HABITATS

There is disagreement in the entomological literature on the flying abilities of gypsy moth females. Numerous records on forest entomology unambiguously state that the gypsy moth females are not capable of active flight. But there are quite opposite statements as well. For example, Yu. P. Kondakov (1963) disagrees with the statement of Ya. V. Chugunin (1949) about the flight passiveness of gypsy moth females. A.I. Vorontsov (1977) thinks that A.I. Ilyinsky (1954) also underestimated the flying abilities of this species. Those who believe that the females do not fly are located in Western, Central, or Southwestern Europe (Schedl, 1936; Chugunin, 1949; Ilyinsky, 1959; and others) while researchers in Siberia state that the females have active flight (Meinhardt, 1912; Kondakov, 1963; Zemkova, 1963, Terskov & Kolomiets, 1966; and others). The data, as a whole, show that as we move from eastern to western boundaries of the species range, the females gradually lose their flight ability (Fig. 1). In the centre of

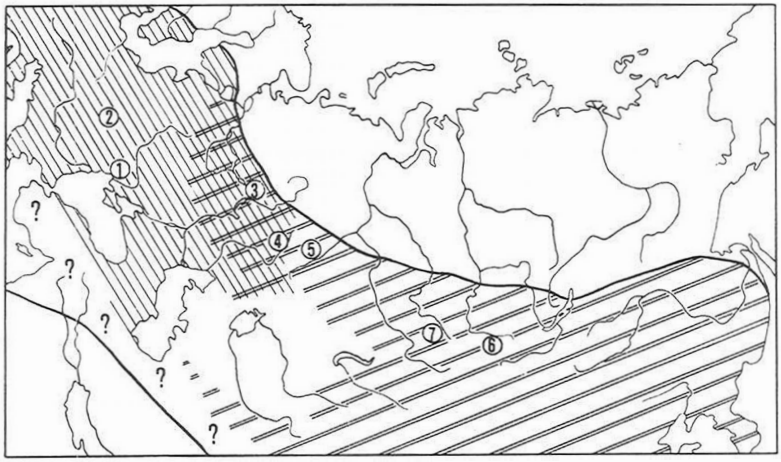

Figure 1. Zones of gypsy moth female flight ability in Eurasia. Double cross-hatching = zones of flying females; cross-hathcing = zone of flightless females; overlapping = transition zone. Local gypsy moth populations: 1 - Ukraine-acacia; 2 - Karpats; 3- Tataria; 4 - Baskhiria; 5 - Zauralje; 6 - Tuva; 7 - Altai. (See text.)

the species range, southeast Asia (Kozhanchikov, 1950), the gypsy moth females cover long distances on their wings. According to Yu. P. Kondakov (1963) their flights in Khakass region (southern part of Krasnoyarsk Territory) may be 4-7 km long. In our experiments in the Buryat Republik, marked females travel to light traps from a distance of 3.5 km. In the Krasnoyarsk and Amour regions (Terskov & Kolomiets, 1966), in the mountainous forests of the Western Sayan ridge (Zemkova, 1963), in Mongolian People's Republik (our unpublished observations), in Altai Mountains and in Northern Kasahstan (Gninenko, 1986), the females actively fly to ultraviolet light. There are reports of good flying performance of Chinese populations (Goldschmidt, 1934; Schaefer et al., 1984).

The transition zone of occasional female flights is situated in Eastern Europe (Fig. 1). The female moth here can fly well (Khanislamov et al., 1958; Benkevich, 1959; Andrianova, 1970), but active flights are relatively short and insects travel considerable distances only with moving air masses (Khanislamov et al., 1958; Mikkola, 1971).

In Western, Central, and South-Eastern Europe gypsy moth females don't fly (Schedl, 1938, Fig. 1). Nor do they fly in North America (Friend, 1945; Campbell, 1967; Beroza & Knipling, 1972). However, there are five cases of gypsy moth females gliding from trees in the USA that are described in detail (Forbush & Fernald, 1896; Sandquist et al., 1973). Inability of gypsy moth females from North American populations to fly is very demonstrative - the species was brought to

the USA in 1869 from France which was the western edge of its range (Goldschmidt, 1934).

The "east-west" reduction of the flying ability of the gypsy moth female is an example in favour of the rather poorly reasoned assumption of I.V. Kozhanchikov (1950) on eastern-Asian provenance of Lymantria dispar L. species. If we agree with the statement that in telomorphosis function is first lost and then the organ (Schmalhausen, 1969), it is evident that inability of the European females to fly is a secondary phenomenon due to selection under new environmental conditions.

Peculiarities in migration activity of gypsy moth imagoes affect the role of the adult insects in the distribution strategy of individual populations. In Siberia the species spreads both by the flying females and by caterpillars of the first instar carried by the air streams (Kondakov, 1961, 1963). In the European part of the USSR, migrations are due mainly to the caterpillars (Ilyinsky, 1959), massive movements of the adult moths is a rare phenomenon there (Vorontsov, 1958; Mikkola, 1971). On the American continent, the species migrates only by the larvae carried in spring by the winds (Cameron et al., 1979).

There is a large body of literature on the ability of the species to distribute at the phase of the first instar caterpillar. Impressive figures are presented for the distance migrated - from 10 to 40 km (Collins, 1915; Chugunin, 1958; Kondakov, 1963) to 150 km (Ilyinsky, 1959). But verification of such migration abilities in the natural larval populations of the species was an enigma. Research carried out within a USA federal program in the 1970's showed that even in the knob topography with complicated air mass motion, as for example in the mountainous ridges in Pennsylvania, the caterpillars taken by the convection air stream from the trees on the tops of the hills are carried by the wind for only several kilometers (Mason & McManus, 1981). Recently, aerial sampling with airplane tow nets above ridge-valley terrain showed that caterpillars theoretically can be carried up to 16 km by air currents, but this would be only a very small percentage of the total population (Taylor & Reling, 1986). In the valley forests, caterpillars actually don't intensively spread with the air streams. In oak and hickory stands where trees are 9-12 m high on the average, no more than 0.3% of the caterpillars of the first instar hatched on a tree were found more than 30 m from the trunk of this tree (Cameron et al., 1979; Mason & McManus, 1981). If the stand density decreases the possibility of distribution is higher, though it remains in rather modest limits. So, nearly 80% of the caterpillars taken by the wind do not fly farther than 75 m from the edge of the forest (Minott, 1922).

It is understood that migration abilities of European and Asian populations of gypsy moth differ considerably. These differences must affect substantially the rate and trends of the microevolution in the gypsy moth populations of these regions. In Siberia the migration process involves imago and larvae of the local populations. In the piedmont and mountainous landscape in the south of Siberia, these processes are of large scale. Each season there are two waves of migrations: in spring the caterpillars hatched in the rocky outcroppings of river valleys are carried away by the winds, and in summer when the females fly from the flood plain forests to the rocky

outcroppings to lay eggs. Although there is evidence of mass flights of females covering up to 100 km (Rozhkov & Vasilyeva, 1982) usually the movement of imagoes is limited by the topographic peculiarities of intermontane basins and seldom exceed 3-5 km. Because each gypsy moth micropopulation in Siberia annually changes its habitat two times, the possibility of the caterpillars of the filial generation feeding on the host species of the parents and the possibility of successive generations of gypsy moth developing in the same microhabitat is practically ruled out.

The females of most European populations of gypsy moth, on the contrary, usually lay eggs on or near the trunk of its food tree and the caterpillar, after hatching, goes up into the crown and starts feeding making attempts to leave the "native" tree only when the density of infestation is rather high (Semevsky, 1971). But in the valley forests, airborne dispersal by the caterpillars can result, at best, only in changing one tree for another, which in a one-species stand does not affect the course of trophic specilization of individuals. In contrast to many other species of Lepidoptera, gypsy moth chooses the food plant only at the larval stage. The ovipositing female isn't involved in it. Practically every regional record on the biology of gypsy moth has evidenced this, but to the best of my knowledge the evolutionary consequences of this on host relationships has never been considered in this respect.

Lack of rocky outcroppings in the habitats of Asian populations of gypsy moth has no effect on the pattern of laying eggs by the females. According to a number of authors (Kondakov, 1961; Alekseyeva, 1969; and others) and our own experience in the valley forests in Southcentral Siberia and in the Baikal region, the gypsy moth females, when in flight, concentrate at forest edges and on the periphery of single groups of trees giving preference to thicker trunks. Concentration of egg clusters has no relevance to the nutritional value of the plant for the gypsy moth caterpillars. Crucial in choosing the ovipositional site are the surface structure of the substrate and its temperature condition. Baranchikov & Kravtsov (1981) noted that the flight of gypsy moth females into the rocks in the habitats with mountainous topography is due to the temperature condition of the rocky outcroppings during the hours of migration activity of the moths. There is no reason to think that in the absence of rocky outcroppings there are other reasons for the females to choose large trunks but the peculiarities of their temperature condition. Our viewpoint is supported by the vertical distribution of egg clusters on pine trunks (Kondakov, 1963) in relation to the trunk temperature at various heights from the soil surface (Zyubina, 1965).

Migration of two life stages in Asian populations of gypsy moth is associated with the necessity to overcome insufficiency of total positive temperature required to complete egg embryogenesis during summer and autumn period (Baranchikov et al., 1987). This insufficiency is overcome by behavioural adaptation when eggs are placed in the optimal temperature conditions. Since climatic conditions in the European part of the species area are more favourable, migrations have little adaptive value and are not sustained by selection. This ecologically conditioned behaviour of imago is the primary reason for the differentiation of geographical populations of

gypsy moth which becomes crucial in forming the properties of their trophic adaptations.

The landscape and climatic properties of Central and Eastern Asia has fostered a double-stage migration biotype. The result is that the gypsy moth population mixes intensively over vast areas while the host plant relations of the populations are totally unpredictable. Migration of females into sites where the distribution of young caterpillars is most intense augments the unpredictability of the habitat of each sequential generation of gypsy moth. This reduces the possibility of the gypsy moth forming a specific relationship with one or even a few host plant species. Instead, these conditions seem to have brought about a superpolyphagous species inhabiting more than 600 species of plants.

Reduced migration abilities of the species in the forests of European valleys considerably increases the level of predictability of environment for the next generation of gypsy moth. With a less cold climate, the need to disperse from the host to better thermal substrates for oviposition is reduced; thus, regional host plant specialization is possible. Under such conditions, the phytophage can adapt more fully both to chemical and phenological properties of a limited range of food objects. The data available in literature support this assumption and one can see how European populations of gypsy moth, in the absence of migrations, trend to local trophic specilization, and time caterpillar hatching to the beginning of vegetation of the major food plant in the given habitat and how this results in chronological isolation of divergent groups (Kolybin & Zelinskaya, 1975; Kireyeva, 1983; Mamontova et al., 1983; Baranchikov, 1985).

HOST-PLANT ACCEPTABILITY AND SUITABILITY BY DIFFERENT POPULATIONS OF NEWLY ECLOSED FIRST INSTAR GYPSY MOTH LARVAE

There is numerous evidence of the peculiarities of gypsy moth larval development when feeding on a spectrum of food species. The host range of this species has been recorded for several regions in Europe (Kelus, 1939; Kurir, 1953; Edelman, 1956; Khanislamov et al., 1958; Zhigunova, 1967; Heskova, 1978), in Asia (Bey-Bienko, 1924; Kondakov, 1963, 1979), and in North America (Mosher, 1915). These and more recent reports (Vshivkova, 1983, 1984; Hough & Pimentel, 1978; Barbosa & Greenblatt, 1979; Rozkov & Vasilyeva 1982) support Vorontsov's (1963) statement that there is considerable variability of gypsy moth development (growth rate, mortality, weight of the pupae) in different regions feeding on the same host species. These differences are usually related to the diversity of feeding conditions and to biochemical and anatomical features of the peculiar species of plants in various parts of their areas (Vorontsov, 1963). These assumptions are supported repeatedly by experiments (Radkevich, 1980). We will first examine in detail regional distinctions in the ability of the individuals of some gypsy moth populations to feed on the foliage of one species of woody plant.

Methods

Gypsy Moth Populations

In our experiments we used caterpillars from geographically different gypsy moth populations. These populations are named below along with its location and the characteristics of its trophic relations citing the literary references. Populations are numbered as in Figure 1.

"Ukraine" (1) - insects were collected in three habitats along the Dnieper River in the Kherson region of the Ukrainian SSR: "Ukraine oak"- in the oak forests of the Black Sea Preserve; food species - oak, Quercus robur L.; "Ukraine-willow" in the Salix alba L. forests, and "Ukraine-acacia" in Robinia pseudoacacia L. plantations near Golaya Pristan settlement (Kireyeva, 1983; Mamontova et al., 1983).

"Karpats" (2) - near the city of Mukachevo of the Transkarpat region of the Ukrainian SSR. Food species - oak (Baganich, 1981).

"Tataria" (3) - the city of Zelenodolsk of Tatar, ASSR; the major food species - birch (Kondorsky, 1983, 1984).

"Bashkiria" (4) - the city of Blagoveschensk of Bashkirean ASSR; birch and oak (Idrisova, 1977).

"Zauralje" (5) - Chebarkul settlement of the Chelyabinsk region; birch (Rafes, 1980).

"Tuva" (6) - near Ishtii-Hem settlement of the Tuva ASSR. Food species: larch, birch, elm (Mashanov et al., 1981).

"Altai" (7) - near Chemal settlement of the Mountainous Altai Autonomous District of the Altai region. Food species: birch, elm, bird-cherry, willow (Benkevich, 1959).

Gypsy moths from the nine populations from the seven regions were collected as eggs and maintained in the laboratory for 1-2 generations on leaves of birch, Betula pendula Roth. Mating took place exclusively within the population groups. Eggs were collected in the years when all populations were latent.

Acceptability and Suitability of Food Plants

To compare the initial preference of food species we used newly hatched first instar larvae from "Ukraine-acacia," "Transkarpat," "Bashkiria," and "Tuva" populations. The larvae, kept solitary in small petri dishes, were offered small (5 mm) circular pieces (leaf disks) cut from the leaves at the beginning of blossom of willow (Salix viminalis L.), birch (Betula pendula Roth.), bird-cherry (Padus asiatica Kont.), and several needles of larch (Larix sibirica Ledeb.). We carried out two test combinations of food: willow-birch-bird-cherry and willow-birch-larch. Each population was represented in every test by 50 larvae selected randomly from 15-20 egg clusters beginning to hatch. The dishes were observed daily and individuals starting to feed were removed. The remaining dishes were filled with fresh leaf disks. Experiments were observed in the red light.

Mortality of larvae from seven of the populations (Ukraine-acacia, Transkarpat, Tatatia, Bashkiria, Zauralje, Tuva and Altai) was estimated by placing 250-350 newly hatched larvae of each population

into chambers with leaves or needles of the following food species: birch, bird-cherry, elm (Ulmus pumila L.), haw-thorn (Crataegus sanguinea Pall.), mountain ash tree (Sorbus sibirica Hedl.), larch, lime-tree (Tilia sibirica Fisch.) and acacia (Caragana arborescens Lam.). The leaves and needles were collected from the same trees near Krasnoyarsk. Each day the food was changed and dead insects removed. The number of molted second instar larvae was recorded.

Results

Irrespective of the main food plant of the local population - acacia, oak, birch or larch - the larvae of the Ukrainian, Transkarpatian, Bashkirian or Tuva population in the first variant of the experiment preferred, in decreasing order, willow-birch-bird cherry and in the second varient willow-birch-larch (Fig. 2). Distributions of larvae within each test showed difference in species selectivity: the value of Kolmogorov-Smirnov criterion λ in no case exceeded 0.85 ($P>0.2$). Only Ukrainian and Tuva populations differed in the number of larvae feeding and rejecting the food (lamba = 1.5; $P<0.05$), for the rest $P>0.05$.

These results cast doubt upon the view of some authors that regional oligophagy owes its formation to conveyance of maternal effect on food acceptability of phytophagous insects (Konikov, 1978). They agree with other work (Fox & Morrow, 1981) disproving the so-called "Hopkins host selection principle" which connects the trophic selectivity of herbivore with the food plant of its parents.

The larvae of several European and Asian gypsy moth populations similar in trophic selectivity differ substantially in the ability to develop successfully on individual host species. Figure 3 compares the levels of mortality of the first instar larvae among seven gypsy moth populations grown en masse on the leaves and needles of nine plant species each of which is a potential host for this phytophage. To make it more vivid, the results of each experiment are normalized relative to the mortality of the Ukrainian population.

Despite considerable variability in mortality within populations from each continent, the European populations of gypsy moth (Ukraine, Transkarpats, Tataria) are clearly distinct from the Asian ones (Zauralje, Tuva, Altai). Elevated survival of the Asian populations is most obvious when the larvae are grown on the species of Sorbus, Larix, Pinus, Tilia, and Caragana which are, by Kozhanchikov (1950), not the most suitable host species for Lymantria dispar. In the preceeding experiment the preference of the newly hatched larvae to representatives of Rosacea and Pinacea families was the least (Fig. 2). It is important to point out that the ancestors of the larvae participating in the experiment were fed birch leaves only for 1-2 generations. Thus, the revealed properties are related to the hereditary preadaptation level of European and Asian gypsy moth populations.

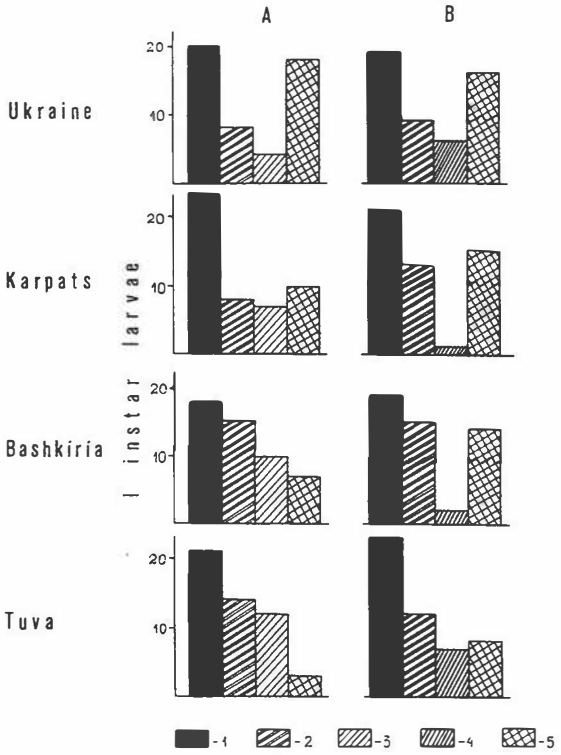

Figure 2. Distribution of newly eclosed larvae from four geographical gypsy moth populations on food plants. Tests: A - willow-birch-bird cherry; B - willow-larch-birch. Food selected: 1 - willow; 2 - birch; 3 - bird cherry; 4 - larch; 5 - the larvae weren't feeding.

FOOD UTILIZATION EFFICIENCY AND FEEDING BEHAVIOUR OF LARVAE FROM EUROPEAN AND ASIAN GYPSY MOTH POPULATIONS

The literature indicates that wherever Larix species coexist sympatrically with gypsy moth they are usually a major food plant of the insect. This statement is valid not only for Western, Middle and Eastern Siberia, but for Eastern Asia - China (McFadden et al., 1981) and Japan (Furuta, 1982) as well. Feeding experiments show that larch needles are a superior food species for Transbaikal and Middle Siberian gypsy moth populations (Kondakov, 1963, 1979; Kondakov et al., 1967). Similar results were found in Tuva (Vshivkova, 1978) and South Baikal (Rozkov & Vasilyeva, 1982) populations. Larvae from the populations in

no-larch localities such as Voronezh region and Southern Urals, however, grew poorly and died when fed larch (Kelus, 1939; Amirkhanova, 1962). When grown in the laboratory on larch needles, the larvae of a number of West European and North American populations of gypsy moth were brought to imago (Mosher, 1915; Schedl, 1936; Jankovic, 1958), but these researchers never featured larch among the species most favourable for the gypsy moth.

The following experiment compares the growth, development, food utilization efficiency and feeding behaviour of the larvae from European and Asian gypsy moth populations on larch and on willow.

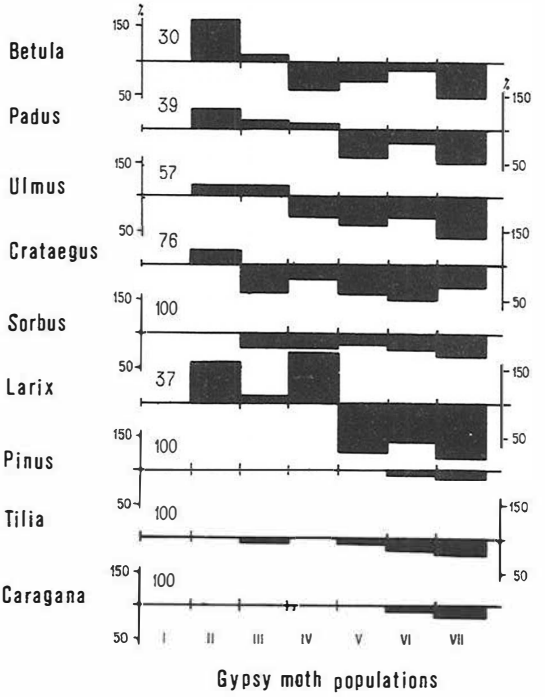

Figure 3. Relative indice of mortality of gypsy moth first instar larvae when growing on a number of food species. Gypsy moth populations: I - Ukraine; II - Karpats; III - Tataria; IV - Bashkiria; V - Zauralje; VI - Tuva; VII - Altai. Mortality of the "Ukraine" population is taken as 100%; the figures denote true indice of mortality, %.

Methods

Growth and Development

Larvae from the egg clusters of "Ukraine-oak," "Ukraine-willow," and "Ukraine-acacia" as well as Altai populations were used. We took 10 egg clusters from each locality. When about 70% of the eggs hatched, 10 larvae from each egg-cluster were placed into a glass chamber where they were grown to pupation, food was changed daily, mortality, number of instars, pupation time and weight of pupae were recorded. On the whole, 400 larvae were used in the experiment, 100 larvae (10 chambers) from each population. The larvae were fed needles of Siberian larch from five 20-year-old open-grown trees. Before feeding, the needles were thoroughly mixed.

Simultaneous to the start of the above experiment, 50 first instar larvae from the Altai and Ukraine-oak populations were placed into larger glass chambers in three replicates each. These larvae were fed with the leaves of willow (Salix viminalis L.). The food was changed every day, pupation time and weight of the pupae were recorded.

Consumption and Utilization of Food

The feeding experiments were performed on fourth instar larvae from the Altai and Ukraine-oak populations that had been fed in the laboratory on larch needles from the first instar. Food consumption and utilization was estimated by a standard gravimetric technique (Waldbauer, 1968). Nutritional indices were calculated on the basis of the weight of leaves consumed (C), feces dropped (F) and larva body biomass gained (P):

AD (approximate digestibility) = $(C-F)\cdot C^{-1}\cdot 100$, %;
ECD (efficiency of conversion of digested food) = $P\cdot(C-F)^{-1}\cdot 100$, %;
ECI (efficiency of conversion of ingested food) = $P\cdot C^{-1}\cdot 100$, %;
RCR (relative consumption rate) = mg consumed · (mg mean larval biomass)$^{-1}$ (day)$^{-1}$.
RGR (relative growth rate) = mg biomass gained · (mean larval biomass)$^{-1}$ · (day)$^{-1}$.

Induced Feeding Preferences

Ability to induce feeding preference for first instar larvae of the Altai and Ukrainian populations was compared for larch. The preference tests were carried out immediately after hatching and after three and eight days of feeding on larch. Individual larvae were offered disks from leaves of Salix viminalis L. and larch needles. Feeding on each food or rejection were recorded for a day and the distribution of feeding on each food was analyzed between the populations by chi-square test. Each test had 100 larvae, 10 replications of 10 larvae each. Each larva was used only in one experiment.

Results

The experiment showed remarkable difference of the Altai population from the Ukrainian in the major parameters of growing and developing on larch trees. The results in Tables 1 and 2 are based on the data from 30 out of 40 chambers, because in four chambers with the "Ukraine-acacia" population and in six with "Ukraine-oak" population, most of the insects died from disease. As sex identification of the living larvae was not reliable, males and females in the data of Tables 1 and 2 are not differentiated.

Table 1. Development time and mortality of the gypsy moth I-V instar larvae from different geographical populations when feeding on Larix sibirica Ledeb.

Population	Development time, days		Mortality, %	
Ukraine:				
Willow	38.4 ± 1.1	(34)+	66.0 ± 3.2	(10)++
Acacia	35.9 ± 1.0	(36)	40.0 ± 13.4	(6)
Oak	33.5 ± 0.6	(31)	22.5 ± 8.5	(4)
Altai	25.8 ± 0.4	(85)	14.0 ± 8.3	(10)

Note: in brackets + = number of larvae; ++ = number of chambers, 10 larvae in each.

Analysis of the material obtained shows that the Altai larvae are different from the Ukraine populations in the development time (Table 1, in all variants $P<0.05$). Mortality recorded in the Altai insects and the larvae from the "Ukraine-oak" and "Ukraine-acacia" populations were similar (Table 1, $P>0.05$); mortality differed most in "Altai" and "Ukraine-willow" populations (Table 1, $P<0.01$). The development time of all four populations coincided only in the first instar, the majority of other larval instars of the Ukrainian populations had a markedly prolonged time of development. The development of the Altai population was more synchronous.

The weight of the male and female pupae (Table 2) from the Altai was much greater ($P<0.05$) than any of the Ukraine populations which did not differ from each other ($P>0.05$). Since the moths of Asian gypsy moth populations are known to be larger than European ones (Vnukolsky, 1926), the superior growth of individuals from the Altai populations fed larch needles may be due to an inherited property of larger individual size rather than these larvae being better adapted to larch than larvae from the Ukraine. However, when larvae from Altai and "Ukraine-oak" populations were fed willow, the weights of the male and female pupae from the two populations were statistically insignificant (Table 3). Thus, the greater weight of Altai compared to Ukraine larvae fed larch is due to better adaptation to larch of the former.

There is evidence similar to these data in the literature. Amirkhanova (1962) and Idrisova (1983) both showed the mortality of the gypsy moth in the Bashkir ASSR (Europe) to be elevated when feeding on larch. When grown simultaneously on the leaves of Betula pendula Roth., the Bashkir gypsy moth differed little from the larvae of the Tuva population (Asia) in the rate of consumption and growth, time of development and the weight of the larvae and pupae (Vshivkova, 1982). Derevyanko et al. (1985), at my request, grew larvae of the Ukrainian and Siberian gypsy moth populations on oak leaves under the natural conditions in the Black Sea preserve in the Kherson region. The weight of the pupae from these populations did not differ (for males 359.5 ± 17.0 mg, and 969.8 ± 26.5 mg for females).

Table 2. Weight (mg) of the pupae of different gypsy moth populations grown on Larix sibirica Ledeb.

Population	Males	Females
Ukraine:		
Willow	387.7 ± 28.9 (19)	911.9 ± 46.6 (11)
Acacia	378.8 ± 24.8 (21)	918.8 ± 29.9 (15)
Oak	362.8 ± 45.8 (11)	936.5 ± 89.4 (13)
Altai	521.6 ± 35.1 (32)	1454.3 ± 89.4 (13)

Note: in brackets = number of larvae.

Thus, we find that all of the European and Asian gypsy moth populations feeding on different food species have similar success in developing on the species of Betula, Quercus, Salix, and Padus. These are hosts which I.V. Kozhanchikov (1950) regards as a sort of trophic standard for Lymantria dispar L. species. However, when gypsy moth larvae are exposed to food species that are somewhat outside the scope of the trophic standard, clear differences arise, usually with the more polytrophic Asian populations performing better.

The results of the experiment on comparing the efficiency of feeding of the larvae from the Altai population to that of the "Ukraine-oak" are given in Table 4. They enable us to argue that the earlier observed differences in the weight of the pupae from Ukrainian and Siberian gypsy moth populations are based on the significantly lower rate of growth of the Ukrainian larvae. The growth rate is, in its turn, limited by the lower consumption rate. The larvae of the Ukrainian and Altai gypsy moth populations had little difference in digestibility and efficiency of food conversion. This prompts us to

Table 3. Weight (mg) of pupae of different gypsy moth populations grown on Salix viminalis L.

Population	Males		Females	
Ukraine	670.0 ± 21.5	(25)	1453.4 ± 83.9	(24)
Altai	687.6 ± 14.5	(51)	1666.1 ± 53.2	(27)
Difference:	P > 0.6		P = 0.05	

Table 4. Indice of gypsy moth fourth instar larvae from different geographical populations feeding on Larix sibirica Ledeb.

Feeding indice	Populations		Significance of differences
	Altai	Ukraine	
AD, %	41.2 ± 4.4	33.6 ± 2.6	0.1 < P < 0.2
ECI, %	9.1 ± 0.7	8.2 ± 0.4	0.2 < P < 0.4
ECD, %	18.8 ± 1.7	26.8 ± 3.4	0.2 < P < 0.4
RCR mg/mg/day	2.56 ± 0.25	1.40 ± 0.08	P < 0.01
RGR mg/mg/day	0.25 ± 0.05	0.11 ± 0.003	P < 0.01

suspect the reason for differences in consumption rate is in differences in sensory system perception. Gypsy moths from the two geographical populations likely differ in their perception of food plants falling outside the scope of the trophic standard of the species.

As we are now unable to study directly the differences of the sensory input of the gypsy moth larvae, we attempted to do it indirectly - analyzing the features of their trophic behaviour. This was done by comparing the ability of first instar larvae from the Ukraine and Altai to develop induced feeding preference when growing on larch needles. This comparison (Table 5) showed no cardinal differences in the initial response of the caterpillars from the Altai and Ukraine to willow and larch. Though the ratio of the larvae from two populations feeding on willow and larch during the experiment differed (χ^2 = 4.9; P<0.05), willow enjoyed significant preference in both cases. However, after three days of feeding on larch needles, the larvae from the Altai showed some induction of larch preference (χ^2 = 2.6; P = 0.1) and this was increased on the eighth day (χ^2 = 10.1;

P<0.01). The larvae from the Ukraine, on the contrary, decreased larch preference significantly after 3 and 8 days ($\chi^2 = 9.6$; $P < 0.01$). Thus, the larvae of the Altai population showed clear induction preference for larch needles, while those from the Ukraine showed a learned aversion to larch.

The induction of preference for previously eaten food is known to come into action in the insects by lowering the sensitivity of the deterrent receptors by repeated feeding on a species of food plant(Schoonhoven, 1969). This results in increased intensity of feeding on previously consumed food. The sensory mechanism of the induction of aversion to previously eaten food isn't clear so far. This is to a great extent due to our poor knowledge of the modification mechanisms of the deterrent receptors.

The long-duration of larvae from the Ukrainian population on one host plant - oak - seems to have lowered the threshold of their

Table 5. Food selection by first instar larvae from the Ukrainian and Altai gypsy moth populations fed first on larch needles and then given a choice between larch (L) needles and willow (W) leaves

Percentage selecting	Days previous feeding on larch needles		
	0	3	8
	Altai population		
L only	11.0 ± 3.1	24.0 ± 3.7	32.0 ± 3.3
L + W	22.0 ± 4.4	27.0 ± 4.2	36.0 ± 6.0
W only	53.0 ± 6.0	47.0 ± 3.7	30.0 ± 4.7
No feeding	12.7 ± 4.0	5.0 ± 2.2	2.0 ± 1.3
	Ukrainian population		
L only	4.0 ± 1.6	0	0
L + W	12.0 ± 2.5	2.0 ± 1.9	5.0 ± 2.2
W only	65.0 ± 3.4	74.0 ± 4.0	90.0 ± 3.0
No feeding	19.0 ± 3.8	24.0 ± 7.6	5.0 ± 2.2

deterrent receptors, making them more sensitive to the biochemical features of new biologically active food - larch needles. The terpenoids of the conifers are known to lower the consumption rate of the larvae from a number of the European gypsy moth populations (Meisner & Skatulla, 1975). Inadequate sensory input information of the larvae from the Ukrainian gypsy moth population seems to lower the insect's consumption (and growth) rate and affect the direction of its feeding preference. Therefore, the local oligophages - the larvae from

the Ukrainian population - fed previously on larch needles lowered its consumption on subsequent days, while the considerably more polytrophic larvae of the Altai population showed increased preference for larch.

The material obtained proves that the intraspecific trophic differentiation of polyphagous Lepidoptera at the level of ecologically isolated populations does not affect an insect's ability to learn, but affects the ability of the larval sensory periphery to perceive or code information coming from the food plant. The ability to activate detoxications system gives any gypsy moth population the potential to be polyphagous. Long-duration feeding on one species of the food plant ensues in adapting the insect's physiological systems to more complete utilization of food (Kolybin & Zelinskaya, 1975), but simultaneously can reduce the possibility of successful development on other host-species. The latter can take place both owing to induced preference to the host-plant and to lowering the deterrent threshold of the sensory systems, affecting the intensity of feeding on new food.

CONCLUSION

This work has illustrated differences in the evolution strategy of European and Asian (Siberian) gypsy moth populations. Adaptations to climatic properties of the region caused the European populations to lose double-stage migration, resulting in intensive parapatric divergence of local phytophage populations. In Europe, selection results in the forming of local trophic specializations where larval hatching is timed to the beginning of bud-burst of the major host plant for the given locality and, hence, chronological isolation of the diverging groups.

Parapatric divergence is observed both in European and Asian populations of gypsy moth (Baranchikov, 1987), but with the latter it is hampered by high migration activity of the moths and larvae. The flight ability of the Asian gyspy moth females determines the majority of the specific properties of pest populations in the northeastern Palearctic. Unpredictable conditions of these localities are responsible for their high ecological elasticity: frost resistance of eggs, preadaptation to a wide range of food plants, morphologic, colour and physiological polymorphism. High variability of these characteristics is associated with elevated genetic polymorphism of the Asian populations compared to European and American ones (Harrison et al., 1983; Derevyanko et al., 1985).

Comparative study of geographical gypsy moth populations in northern Eurasia is just beginning. These investigations can be a fruitful foundation for revealing the role of ecological mechanisms in evolutional transformations of herbivorous insect populations. The results of these studies can and will be applied to developing regional programmes of forest protection from gypsy moth.

SUMMARY

Comparison of ecological properties of a number of geographical gypsy moth populations in Eurasia revealed differences in evolutionary strategy of European and Asian (mainly Siberian) populations of the species.

Adaptations to the milder climatic conditions of the region made European populations lose the double-stage migration habit, resulting in parapatric divergence of local polyphage populations, connected, in particular, to the local trophic specialization. Elevated polyphagy of Siberian populations was demonstrated by experiment. This is a consequence of adaptation to unpredictable conditions of habitats of this species in continental Asia. Local trophic specialization reduces successful development of gypsy moth larvae on a number of plant species, especially those falling out of the scope of the trophic standard of this phytophage species.

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RELATIONSHIPS BETWEEN FOLIAR CHEMISTRY AND SUSCEPTIBILITY TO *LYMANTRIA DISPAR*

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INTRODUCTION

An outstanding characteristic of the gypsy moth is its very broad host range and ability to adapt to novel hosts. The gypsy moth is by far the most polyphagous of the 40+ species of Lymantriidae in North America. It can utilize more than 60 host species, which exceeds by a factor of five the maximum diet breadth of 28 other major forest defoliators in North America (Northnagle & Schultz, 1987). In Europe, the gypsy moth attacks about half of the 185 native tree species (Kurir, 1953). Jankovic (1958) reported that 45 species of forest trees, 11 species of fruit trees, and 24 species of shrubs were completely defoliated during an outbreak in Yugoslavia. Although the gypsy moth has adapted to several novel tree genera in North America, e.g., *Hamamelis, Liquidambar, Sassafras,* and *Carya* (Lechowicz & Mauffette, 1986), it may be less polyphagous on that continent than in Europe. There are genera common to both continents (e.g., *Juglans, Cornus, Celtis,* and *Ulmus*) that do not seem to be to the gypsy moth's liking in North America, but are readily fed on in Europe. In North America, the native *Robinia pseudoacacia* is a poor host (Mosher, 1915), but in Europe it is fed on heavily by gypsy moth (Jankovic, 1958) and colonies may persist in robinia thickets for several successive years (Sidor & Jodal, 1983).

The more restricted host range and host adaptability of North American compared to European gypsy moth would be expected since the gypsy moth in North America apparently was derived from a single, small introduction from Western Europe 120 years ago (Forbush & Fernald, 1896). While some genetic variation in diet breadth has been reported for North American gypsy moth (Rossiter, 1987), this is not as striking as in Europe. For example, oak, willow, and robinia forests in the Ukraine each have distinctively colored gypsy moth biotypes (Kireeva, 1986). The greatest diversity in gypsy moth life history and color patterns, however, is in Eastern Asia (Goldschmidt, 1934). Baranchikov (this proceedings) presents strong evidence that the gypsy moth in Asia, where females fly, is more polyphagous than in Europe.

Although the gypsy moth has a broad host range and the ability to adapt to novel hosts, it generally avoids plants with a well-developed qualitative chemical defense such as alkaloids (Barbosa & Krischik, 1987). Plant families on which the gypsy moth prospers, such as Fagaceae and Betulaceae, seem to depend largely on quantitative defenses such as tannins. Quantitative defenses are not very toxic in small dosages and act by reducing digestion efficiency (Feeny, 1976).

These defenses may not present much of an evolutionary barrier to colonization, but they nevertheless may have considerable impact on an insect's population dynamics.

Tannins are widely distributed in vascular plants and can be divided into two major groups: the condensed tannins (proanthocyanidins), which are flavanol derivatives, and the hydrolyzable tannins, which are esters of glucose, usually with one or more gallic or hexahydroxydiphenic acids. The former are ubiquitous in woody plants while the hydrolyzable tannins are absent in some gypsy moth hosts such as Populus deltoides (Meyer & Montgomery, 1987) and Acer macrophyllum (Swain, 1979).

The significance of tannins in defense of plants against insect herbivores has been questioned from both an ecological (Bernays, 1981; Martin & Martin, 1983) and evolutionary (Beart et al. 1985; Scalbert and Haslam, 1987) perspective. Many Lepidoptera, including the gypsy moth, apparently are able to utilize leaves with high tannin content because they have surfactants and high pH in the midgut that inhibit tannin activity (Martin et al., 1985). However, to achieve a strongly alkaline midgut, considerable energy must be expended since leaves have pH values of 4.1-6.2 and are well buffered (Schultz & Lechowicz, 1986). Thus, the ecological activity of tannic acid could reside in its function as an organic acid rather than a protein precipitator. There also is evidence that the toxicity of tannins may not necessarily be due to the formation of insoluble protein complexes (Mole & Waterman, 1987; Blytt et al., 1988)

Regardless of the mode of action of tannins, it seems that any effect they have on the gypsy moth would be subtle and not the strong deterrent response that more species-specific defenses such as diterpenes (El Nager & Doskotch, 1980) have on the gypsy moth. Thus, in the following comparisons of foliar tannin content and insect performance, it is possible that a cause/effect relationship may be swamped by any of several other factors that determine the nutritional quality of foliage for gypsy moth. With this in mind, free sugar concentrations in the foliage will be examined with the larval performance variables.

Since there has been extensive research on the suitability of tree species as gypsy moth hosts, relationships will be examined between variation in foliar chemistry and larval performance for several species of trees. Variation in host chemistry and larval performance will be examined within a single species and within an individual tree. While larger differences in parameters are likely to be seen across species, the role of generally distributed secondary chemicals such as tannins may be detected more readily through intraspecific comparisons since qualitative variation in chemistry would be less and unidentified factors would be fewer.

Larval growth and feeding preference will be used to bioassay the quality of the foliage. Martinat & Barbosa (1987) found that the order of acceptability in choice tests was the same as the order of host suitability for gypsy moth growth. This implies that if tannins are deleterious, the gypsy moth should be able to directly taste or otherwise detect dietary tannin. Whether or not the gypsy moth can taste tannin is uncertain, however. Meisner & Skatulla (1975) reported that adding tannic acid at 0.2% dry weight to polystyrene lamellae containing ethanol extracts of Quercus robur did not reduce gypsy moth

feeding. The extract of Q. robur was highly phagostimulatory (it likely contained sugars and tannic acid). I have found that adding tannic acid or wattle condensed tannin at 0.1-5% to artificial diet has no effect on feeding rate, but adding 0.5% tannic acid to lettuce leaves increases feeding (unpublished). Feeding on several nonhosts, including potato, was increased if they were sprayed with tannic acid solutions (Gornitz, 1954). Dethier (1982) found that the gypsy moth does not have a receptor that fires in response to tannic acid, but that tannic acid does inhibit firing of sugar receptors. Thus, at the onset, it cannot be predicted whether tannin/growth relationships will complement tannin/preference relationships.

EXPERIMENTAL

Variation Between Species

Methods. Gypsy moth larvae were reared individually on excised foliage from fourth instar until pupation. Initial larval fresh weight (x 0.16 to convert to dry weight), development time, and dry pupal weight were recorded. The frass was collected and the nitrogen content of it and the larvae were determined by the Kjeldahl method and used to calculate nitrogen utilization efficiency (NUE) (Montgomery, 1982). Relative growth rates (RGR) were calculated as: $\ln(W_f/W_i)/t$, where W_f = weight final, W_i = weight initial, and t = days elapsed.

There were two series of tests, both of which were maintained at 21 $\pm$ 1°C and 90-100% relative humidity. In Series I, larvae and leaves were placed in petri dishes. In Series II, larvae and leaves were placed in 0.4-liter paperboard containers with the leaf petiole inserted in a vial of water. Foliage was collected and renewed three times per week.

For chemical analyses, a subsample from each foliage collection was immediately frozen and weekly samples were pooled, freeze-dried, and ground to pass through a 0.2-mm mesh. Weighed samples (60 $\pm$ 2 mg) were extracted by stirring with 10 ml of 50% methanol for 2 hr at room temperature. After centrifugation (2,400 RCF), aliquots of the supernatant were taken for these tests: Total phenolics, Folin-Denis reagent with tannic as a reference (Rosenblatt & Peluso, 1941); condensed tannins, heated for 2 hr at 95° in butanol-5% hydrochloric acid with purified red oak tannin as standard; free sugars, gas chromatography after converting the sugars to oximes and then trimethylsilylethers (Method 18, Handbook and Catalog 1986-1987, Pierce Chemical Co., Rockford, Ill.). Nitrogen was determined on 0.5-gm of leaf powder by the Kjeldahl method using Kjeltec equipment.

Results. Table 1 shows that growth of late-stage gypsy moth larvae was best on foliage from Salicaceae species. Growth was not necessarily similar within a family or even a genus. This is seen most clearly with the Betula; good growth occurred on B. populifolia and poor growth on B. lenta. In the Series II tests, growth was better than expected on Fagus grandifolia and Carya ovata, which generally are not thought of as primary gypsy moth hosts. The data from both series

are for the last half of larval life and do not show that establishment and growth of young larvae on many of these hosts was poor compared to growth on oak.

Association of RGR with the other factors listed in Table 1 was tested using Spearman's coefficient of rank correlation (r_s), which tests for monotonic functional relationships. This is more appropriate than Pearson's product-moment coefficient, which measures degree of linearity between two variables. Also, a nonparametric procedure should be used since species cannot be considered samples from a bivariate normal distribution. Within Series I, RGR was closely associated with NUE ($r_s = 0.91$). This implies that something that affects nitrogen utilization, such as protein being bound by tannin, may have occurred. However, the relationship of condensed tannin with RGR was 0.56 ($p < 0.05$) and with NUE was 0.30 ($p < 0.05$). Only total phenolics were negatively associated with RGR (-0.46), though this too was not significant. Free sugar and nitrogen were poorly associated with RGR, 0.13 and 0.14, respectively. Series II species are too few to draw statistical correlations. However, these data seem to exhibit the same relationships observed with Series I species. Thus, although gypsy moth growth seems closely related to nitrogen utilization, growth could not be linked to any of the four chemical variables that could perhaps affect nitrogen utilization.

Variation within a Tree

(Crown Position)

Methods. Q. velutina foliage was collected from outer branches located in the upper, middle, and lower thirds of the crown on two dates: 2 weeks and 6 weeks after bud opening. There were seven dominant trees ranging in height from 4-8 m in the test.

Part of each leaf sample (one from each tree/position on each date) was used for chemical and physical measurements. After freeze drying, the leaf lamina were weighed and area measured with a Li-Cor area meter. In addition to the chemicals reported for the species, hydrolyzable tannins were measured with Chinese gallotannin as a standard (Halsam, 1966).

Preferences for leaves were determined by giving larvae a choice between leaves from two areas within a tree crown. With 2-week-old leaves, whole leaves were used and with 6-week-old leaves, 2-cm-dia discs were cut and used. Both were placed in petri dishes on moistened filter paper and either five instar II larvae (2-week leaves) or a single instar IV larva (6-week leaves) were added and allowed to feed overnight. Leaf area consumed was measured and multiplied by the leaf specific weight to obtain dry weight consumed. Each choice-pair within a tree was replicated 8 times with differences in feeding on a choice-pair within a tree pooled. For statistical analysis, a randomized block design with trees as the blocking factor was used with each of the three choice-pairs for each leaf age tested against zero.

Results. Two weeks after bud opening, foliage in the lower part of the crown was preferred over foliage from higher levels in the crown (Table 2). This situation was reversed at 6 weeks after bud opening

Table 1. Relative growth rate (RGR) and nitrogen utilization (NUE) of female larvae reared from instar IV to pupation and the chemical contents of foliage used for rearing.

Host species	RGR (mg/mg/day)	NUE (%)	Total phenolics (%)	Condensed tannin (%)	Free sugar (%)	Total nitrogen (%)
Series I						
Quercus rubra	0.100d	27.0d	11.4bc	9.9c	3.1c	2.11de
Q. alba	0.104d	40.6bc	14.7ab	3.1e	3.8c	2.06e
Q. prinus	0.105d	35.5c	14.5ab	11.7b	3.5c	2.09e
Salix lucida	0.131ab	43.7b	12.8bc	15.2a	5.1b	3.06a
Populus deltoides	0.127bc	47.0ab	11.5bc	3.5e	3.7c	2.68b
P. grandidentata	0.142a	49.5ab	11.6bc	15.0a	3.8c	2.41c
P. tremuloides	0.142a	55.6a	11.6bc	13.8ab	5.2b	2.19b
Betula lenta	0.075e	17.7e	16.1a	3.0e	3.5c	2.34c
B. populifolia	0.119c	38.8bc	10.4c	11.0bc	3.0c	2.19d
Carpinus caroliniana	0.103d	24.8de	17.0a	15.2a	6.6ab	2.32c
Alnus serrulata	0.088e	30.4cd	16.5a	7.1d	8.0a	2.73b
Series II						
Quercus velutina	0.096b	24.2e	14.2a	4.0c	5.2b	NM
Fagus grandifolia	0.111a	39.9a	14.4a	6.5b	5.7b	NM
Carya ovata	0.103ab	33.0b	8.6c	3.7c	7.0a	NM
C. cordiformis	0.091b	28.8c	11.0b	1.2d	5.2b	NM
Robinia pseudoacacia	0.074c	23.2e	10.6b	9.8a	0.9c	NM
Tsuga canadensis	0.068c	26.2ce	8.6c	0.9d	NM	NM

NM = not measured.

Values in columns within a series not followed by the same letter are significantly different ($p < 0.05$), Bonferroni t-test was used for larval parameters because of unequal sizes (n = 3 to 10), and Tukey's hsd for chemicals (n = 4).

when upper crown foliage was preferred over lower crown foliage.

Table 2. Consumption by larvae given a choice between foliage from two crown strata of black oak.

Foliage age (weeks)	Crown strata choice-pair	Respective consumption mg dry wt/larva		Significance level[1]
Two	Top vs mid	0.70	1.16	0.006
Two	Mid vs low	0.96	1.45	0.008
Two	Top vs low	0.99	1.27	0.052
Six	Top vs mid	37.35	16.17	0.001
Six	Mid vs low	32.96	25.48	0.010
Six	Top vs low	37.50	20.01	0.001

[1] Analysis of variance on the difference in consumption for each pair tested against zero, df = 1, 12; see text for model.

Chemical composition of foliage from each third of the tree crown is given in Table 3. Total phenolics, hydrolyzable tannin, and condensed tannin were higher in lower canopy foliage at 2 weeks. At 6 weeks, however, total phenolics and condensed tannin were higher in the upper crown foliage. Free sugar also followed this pattern. Hydrolyzable tannin remained higher in the lower crown foliage. In this case, the gypsy moth chose to feed on leaves with the highest condensed tannin and free sugar contents.

Effects of Stress

(Defoliation)

Methods. Black oak foliage was collected during the last 2 weeks of June when natural gypsy moth populations were in the fourth and fifth larval instars. A heavily defoliated stand was paired with an undefoliated stand of similar species composition and structure. In one case the stands were fairly close, within 2 km of each other. In the other case, the stands were 100 km distant. All sample leaves selected from the defoliated stand, where overall more than 75% of the foliage had been consumed, had some damage, but usually less than one-third of the leaf lamina had been eaten. Sample leaves from undefoliated stands had no damage and were from trees similar to the defoliated sample trees in size and in amount of solar radiation received. There were 10 trees selected from each stand. Leaves from each tree were analyzed chemically as detailed in the preceding sections.

Choice tests were conducted with fourth- or fifth-instar larvae that had been reared on Q. rubra foliage prior to use in the assays. Two 2.3-cm-dia discs from a defoliated tree were paired with two discs

Table 3. Chemistry (% dry wt.) of black oak foliage from each third of the tree crown at 2 and 6 weeks after budbreak.[1]

Crown strata	Total phenolics	Hydrolyzable tannin	Condensed tannin	Free sugars
		Two-week foliage		
Upper	28.7a	15.5a	0.08a	0.68a
Middle	27.2a	15.7ab	0.19a	1.14a
Lower	34.2b	18.5b	1.03b	1.26a
		Six-week foliage		
Upper	27.7b	5.9a	38.4b	8.20b
Middle	25.4ab	5.9a	31.4b	7.70b
Lower	23.4a	8.7b	12.4a	6.44a

[1] Different letters after chemicals in an age group indicate that they are different statistically at $p < 0.05$, Tukey's hsd test.

from an undefoliated tree in a petri dish. Each defoliated tree was tested once against each undefoliated tree (100 tests for each pair of stands). One larva was added to each dish in early evening when the larvae naturally begin to feed. Leaf area consumed was measured when about 50% of the discs were consumed.

Results. The three measures of phenolics usually were higher in the defoliated stand foliage, although only total phenolics were significantly different in both pairings (Table 4). Free sugars were much lower in defoliated than in undefoliated foliage in both pairs of stands. For both the nearby and remote stand pairs, larvae ate more foliage from the undefoliated stands than from the defoliated stands. These data suggest low levels of free sugars and high levels of condensed tannin as the most likely reasons for the rejection of leaves from defoliated trees.

DISCUSSION

Comparison of larval performance and foliar chemical parameters across several tree species showed a positive relationship between growth rate (RGR) and nitrogen utilization (NUE). This implies that the ability of the gypsy moth to digest and utilize dietary protein may be growth limiting. Since tannins are ubiquitous in gypsy moth hosts and have the potential to reduce digestion of proteins, it is reasonable to presume that tannins would affect foliage suitability. On the basis of Feeny's (1969) pioneering research, we would expect the condensed tannins to be more active than the hydrolyzable tannins because they are more effective at reducing digestion of protein at the highly alkaline pH that prevails in the midgut of caterpillars.

However, a positive association was observed between gypsy moth growth and condensed tannin across tree species in this study.

Table 4. Chemistry and larval choice of foliage from naturally defoliated and undefoliated black oak forests.

Choice-pairs	Foliar content (% dry wt.) Total phenolics	Hydrol. tannin	Cond. tannin	Free sugar	Larval choice (No.)
Nearby stands					
Defoliated	12.9	15.3	21.0	3.0	32
Undefoliated	11.1	18.1	11.4	5.1	57
Prob. level[1]	0.007	0.30	0.017	0.001	0.01
Remote stands					
Defoliated	15.4	14.6	22.0	2.7	12
Undefoliated	12.5	8.6	19.0	7.4	52
Prob. level[1]	0.001	0.090	0.22	0.001	0.001

[1] Probability of incorrectly declaring that the defoliated and undefoliated stands are different, t-test for chemicals and chi-square for larval choice.

A study by Lechowicz (1983) examined the natural distribution of gypsy moth larvae and egg masses on several tree species in relation to foliar chemistry. Lechowicz's analysis suggested that gypsy moth larvae prefer trees with tough, dry leaves which also have high condensed tannin levels with preferences affected little by total phenolics or nitrogen. Similarly, levels of herbivory on tropical foliage were found by Coley (1983) to be most highly correlated with toughness, followed by fiber content. Phenolic measures were the least well correlated with herbivory. Feeny (1970), contrary to what the title of his paper implies, concluded that leaf toughness was the chief factor in deterring insect herbivores from feeding on mature oak foliage. The intimate association of condensed tannin with leaf toughness illustrates the difficulty in separating out which individual leaf traits are important determinants of foliage nutritional quality.

Another critical problem in attempting to establish the role of broadly distributed chemicals across several species of trees is that their role may be overshadowed by more potent species-specific secondary chemistry. Comparisons within a species or individual tree should better detect the influence of quantitative variation of a chemical because qualitative differences in foliar chemistry should be much less. Examination of foliage within a tree crown complimented the across-species findings, providing additional evidence of a positive relationship between gypsy moth host preferences and condensed tannin content. However, a similar relationship was found with free sugars, which were highly associated with condensed tannin (r_s = 0.88). This illustrates the difficulty in attributing variation in insect

performance to levels of a single specific chemical. The upper crown leaves in this study were primarily sun leaves and the lower crown leaves were primarily shade leaves. A similar positive relationship was reported (Montgomery, 1986) between growth and total phenolics, condensed tannin, and free sugar of gypsy moth reared from the fourth instar to pupation on sun and shade leaves of Q. rubra and Q. prinus. Within unstressed oak trees, foliage preferences seem to be related to high sugar and high condensed tannin levels.

Variation in foliar chemistry associated with tree species and location in the tree crown are examples of constitutive chemistry. This chemistry can be changed or induced by stress such as defoliation. Defoliation-induced changes in chemistry are thought to be an active defensive response to reduce foliage quality in order to negatively impact the population dynamics of the herbivore. The strong nonpreference reported here for foliage from heavily deloliated trees implies that this foliage was lower in quality. That leaves from defoliated trees consistently had lower levels of free sugars and higher levels of total phenolics supports the contention that defoliated leaves are lower in quality; however, neither hydrolyzable nor condensed tannins were consistently connected with nonpreference for defoliated leaves. Schultz and Baldwin (1982) examined leaf traits of Q. rubra that were 50% defoliated by a gypsy moth outbreak and compared this to values from undefoliated trees on the other side of a small ravine. Condensed and hydrolyzable tannins were not measured, but ability to precipitate protein (tanning) was higher in leaves from the defoliated trees (54 vs. 37%). Leaves from defoliated trees also were tougher and had a slightly higher content of total phenolics (7.6 vs. 6.1%) than leaves from undefoliated trees.

One problem with such studies of natural defoliation is the selection of a nondefoliated control. Protecting trees from defoliation in an outbreak area by cages or pesticides risks altering foliar chemistry or affecting palatability. Selecting trees on a different, undefoliated site has the risk that differences in chemistry are due to constituitive differences betweeen sites rather than to induction from defoliation. Conversely, in selecting leaves from a defoliated stand where most of the foliage already has been consumed, the remaining leaves that are selected for tests may not have been missed by the caterpillars due to chance, but may have been rejected because they were initially less palatable.

Studies that examine growth of gypsy moth on artifically defoliated trees remedy these ambiguities, though this technique also has inherent problems, such as how and when to defoliate artificially. Valentine et al. (1983) reported that artificial defoliation of Q. velutina reduced free-sugar levels in leaves and that this was correlated negatively with gypsy moth pupal weight. No relationship was found with several of the other factors measured (individual sugars, minerals, and amino acids), and no secondary chemicals were measured. The recent study by Rossiter et al. (1988) examined phenolics but not nutrients in artificially defoliated Q. velutina. Here, defoliation levels of 10-60% were correlated with total phenolics ($r = 0.42$), hydrolyzable tannin ($r = 0.43$), and tanning ($r = 0.44$), but not with condensed tannin. Female but not male pupal weights were negatively correlated with the phenolic measures and percent defoliation. When all the measured phenolics were placed in a

regression model along with defoliation, less than 50% of the variation in pupal weights was accounted for. Thus, nonphenolic components of foliage chemistry also may have affected pupal weight in this study.

Although considerable variation in the chemistry of the host foliage can be identified and it can be established that the gypsy moth responds to variation in foliage quality, the ecological significance of specific foliar chemicals is dificult to define because variation of the chemicals often is correlated. It is particularly difficult to identify the effect of phenolics because the gypsy moth's response is paradoxical; i. e., phenolics seem to be positively correlated with the quality of the foliage when the variation is constituative and negatively correlated when it is induced. Since all of the phenolic assays measure structural classes rather than molecular species, important changes in the "quality" of the phenolics may have been overlooked. The importance of molecular structure on protein binding and other biological functions of tannins has been discussed extensively (Zucker, 1983; Hagerman & Butler, 1981; Beart et al., 1985; Wisdom et al., 1987). It would seem that a prerequisite to the establishment of meaningful ecological relationships between dietary phenolics and the gypsy moth would be identification of the active chemicals and their mode of action.

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DEVELOPMENT AND PHENOLOGY OF EGGS OF GYPSY MOTH, *LYMANTRIA DISPAR* (LEPIDOPTERA: LYMANTRIIDAE), IN ONTARIO

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INTRODUCTION

Gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), was first observed in Ontario in 1969 (Sippell *et al.* 1970). During the 1980s, the species underwent dramatic increases in distribution and population levels, which peaked in 1985 at about 246 X 10^3 ha of moderate-to-severe defoliation (Howse 1987). The insect is now distributed throughout the southeastern part of the province.

Several forms of biological control have been attempted against this insect. In the year following the peak of the infestation, approximately 103 X 10^3 ha were treated with multiple aerial applications of the biological insecticide, *Bacillus thuringiensis* (Howse 1987). During the early 1980s, several releases of biological control agents, especially egg parasitoids, were made (Wallace 1987). As an aid to timing spray operations, to releasing biological control agents and to understanding gypsy moth population dynamics, we began to develop a process-oriented phenology model to describe development of gypsy moth near the northern distribution of its range.

Oviposition by gypsy moth occurs in summer on a variety of substrates on and around the host plants (Johnson *et al.* 1983). Larval development within the egg is completed shortly after egg deposition (Masaki 1956). Embryonated eggs are the overwintering stage. Diapause in the egg stage is obligatory (Leonard 1968a) and is terminated after a prolonged chill period (Masaki 1956). There are sexual differences in egg hatching times; the first larvae to eclose are predominately females (Leonard 1968b).

Egg developmental times at constant temperatures have been determined from European populations of gypsy moth (Rubtsov 1938, Pantyukhov 1962). The threshold for egg development has been estimated to be from 3 to 6°C and apparently varies with the length of the cold storage period (Rubtsov 1938). Relative humidity has little effect on development times (ibid.). The effect of temperature and exposure time on diapause termination was investigated by Masaki (1956). Johnson *et al.* (1983) presented a degree-day (DD) accumulation model for initial and mean egg eclosion. A mathematical

model of egg eclosion was presented by Waggoner (1984) wherein hatching was described as a Poisson process. Giese and Casagrande (1981) reviewed the literature on egg development.

The most difficult and critical stage for which to predict phenological events, for most insects, is the overwintering stage. This results in part from our inability to differentiate between diapause termination and morphogenesis (Rubtsov 1938), and the extreme variability of spring temperatures, especially in northern climates. Estimated threshold temperatures for development are also difficult to estimate (Rubtsov 1938, Campbell et al. 1974), as are development times for insects reared at low temperatures.

The purposes of this paper are to: (1) determine the effects of temperature on post-diapause development of an Ontario strain of gypsy moth eggs in the laboratory; (2) investigate variability in egg hatch at constant temperatures; (3) examine the effects of spatial distribution on development variability and survival; (4) compare egg microclimatic temperatures with the standards of conventional meteorology; (5) compare DD egg hatch predictions with actual hatch in the field and (6) develop and validate a simulation model for phenology of gypsy moth eggs under variable temperatures in the field.

MATERIALS AND METHODS

Laboratory Rearing

Gypsy moth egg masses were collected from six sites in southern Ontario (Perth, Queensborough, Kaladar, Rock Lake, Depot Lake and McLean) in September of 1986. The egg masses were initially stored in a chamber at 15°C for 4 d and then moved to a chamber at 6°C. The temperature was then reduced to 2°C, and the egg masses remained at that temperature throughout the winter. In mid-March the egg masses were removed from cold storage and surface sterilized by submersion in a 10% solution of formalin for 1 h followed by rinsing in tap water for 1 h. The egg masses were placed individually in 7-dram plastic snap-cap vials. Ten egg masses were placed in each of 11 constant temperature chambers (5.5, 8.0, 11.0, 13.6, 15.0, 18.5, 20.4, 24.1, 27.5, 31.4 and 32.7°C).

Two additional sets of 10 egg masses were placed in each of the three chambers with the lowest temperatures. One of the two sets was alternated daily between the three low temperatures and 18.5°C. The other sets were left at the three low temperatures for 22 d and then were moved to the chamber set at 18.5°C.

Additional egg masses were collected in April 1987 simultaneously from two locations (Castleton and Gordon Rapids, Ont.) and at two vertical strata (above or below 1 m) at each location. These egg masses were transported to the laboratory in cold storage where they were surface-sterilized and placed in individual vials. Ten egg masses from each condition were reared at 27.5°C until the completion of hatch.

All egg masses were examined twice daily at about 0800 and 2000 hours until the completion of eclosion. Newly eclosed larvae were removed and counted.

Temperature-dependent Development

Development times and rates (1/time) were calculated for eggs hatching at each constant temperature. Estimated times (t_L) for development of individuals at low temperatures were determined from the following:

$$t_L = t_L / [1 - (t_H / \bar{t}_H)] \quad [1]$$

where t_L = actual time spent at the low temperature (i.e., 22 d), t_H = the time individuals spent at 18.5°C prior to eclosion and $\bar{t}_H$ = the average time required to complete development at 18.5°C.

A quadratic equation of the form $r(T) = A + BT + CT^2$ and a linear function of the form $r(T) = a + bT$ were used to describe development rates ($r(T)$) of eggs as a function of temperature T (°C).

Individual development times at each temperature were normalized by division by the mean time for the respective temperatures. Variation in hatch around the mean development times was described by means of a cumulative Weibull function (Eq. [2]) (Wagner et al. 1984):

$$F(x) = 1 - \exp(- ((x - \gamma)/\eta)^{\beta} \quad [2]$$

where $F(x)$ = the proportion of the population that had completed development by normalized time x, and γ, η and β are parameters estimated by nonlinear regression.

Field Development

In the fall of 1987, a Stevenson screen meteorological shelter (Atmospheric Environment Service, Environment Canada) was set up on a mown lawn in Tweed, Ontario. A data logger (Campbell Scientific Inc., Ogden Utah, Model CR-7) was connected to three copper-constantan thermocouples in the screen. Twenty egg masses were collected on 17 November 1987 from Frankford, Ontario and were placed in individual snap cap vials. One set of 10 vials was placed in an 18 by 13 by 11-cm plastic box in the Stevenson screen and another set was placed in a plastic box on the ground under the Stevenson screen. One thermocouple junction was placed in each of the plastic boxes while the third was suspended inside the Stevenson screen. The data logger was programmed to sample the thermocouples every 5 s and to output the average temperatures for every hour. On 7 April 1988 the box under the Stevenson screen was moved into the screen.

Twenty egg masses were marked in a hardwood stand 2.0 km ESE of the weather station and an additional 10 egg masses were marked in another stand 8.7 km ENE of the weather station prior to eclosion. A barrier of Tangletrap was placed around each egg mass to prevent the dispersal of newly eclosed larvae. These egg masses and the egg masses at the Stevenson screen were examined daily throughout the emergence period and newly eclosed larvae were counted and removed.

Bark Microclimate

Copper-constantan thermocouples (36-AWG) were taped to bark surfaces of trees within hardwood stands in which the egg masses were marked for examination of eclosion. The thermocouples were wired to a

data logger programmed as described previously. Bark temperatures were regressed as a linear function, after natural logarithmic transformation, of air temperature recorded at the remote weather station.

Degree-day Accumulations

To compare the prediction of Johnson et al. (1983) with observed field eclosion, DD above a threshold of 3.0°C were accumulated from 1 January until the end of egg eclosion from the hourly average temperatures recorded by thermocouples in the Stevenson screen and in the plastic boxes containing eggs. To determine the effect of threshold temperature (T_h) on DD accumulations, T_h was varied between 3.0 and 5.0°C in 0.5°C increments for air temperatures recorded in the Stevenson screen.

Formulation of Model

The development model used by Lysyk and Axtell (1987) for development of house fly immatures was adapted to simulate gypsy moth egg hatch. Development rates, for each hour of the day, were determined from the temperature-dependent solution to the linear or quadratic rate equations. Average hourly temperatures recorded in the Stevenson screen were used as model inputs. Mean rates were accumulated and used to solve Eq. [2] to determine the proportion of the population that had completed development. Simulations for each model were run with 1 January, 1 February, 1 March and 1 April starting dates.

RESULTS

Temperature-dependent Development

No eggs hatched at 5.5°C and a laboratory mishap prevented observation of hatch at 8.0°C. Development times and rates (1/days) for the other constant temperatures are listed in Table 1. For both development rates and times, coefficients of variation (CV) increased with increasing temperature (Table 1). Parameter estimates (SE) for the quadratic function (Fig. 1) relating development rate to temperature were A = -0.1079 (0.0187), B = 0.0145 (0.0019) and C = -0.0002 (R^2 = 0.977). This gives a development threshold of 8.4°C. For the linear relationship (Fig. 1) between development rate and temperature, parameters were a = -0.0143 (0.0002) and b = 0.0044 (0.00001) (r^2 = 0.855), the two highest temperatures with apparent high temperature inhibition being omitted. A linear development rate function was constructed from the average median hatch data (i.e., 317.2 DD) and the 3.0°C development threshold provided by Johnson et al. (1987). This function, r(T) = -0.0096 + 0.0032 T, is also illustrated in Figure 1 for comparison.

Estimated development times and rates for eggs either alternated daily or moved after 22 d from low to high temperatures are listed in Table 2. Estimated times and rates for both treatments are similar for 5.5 and 8.0°C. However, the CVs for the treatments are

considerably different. Among samples for which mean times and rates were estimated at 11.0°C, the sample moved after 22 d came closest to the observed time and rate. Analysis of Eq. [1] yielded an interesting property of the relationship. As the individual times at the high temperature (t_H) approach the mean time ($\bar{t}_H$) at the high temperature (i.e., ratio $t_H / \bar{t}_H \rightarrow 1$) the estimated time at low temperature (t_L) becomes very unstable (Fig. 2). As a result of this instability, estimated rates were not used in the construction of temperature-dependent rate functions.

Eggs collected from heights less than 1 m on the boles of host trees survived considerably better than did eggs collected above 1 m on the boles (Table 3). There were small significant differences (t-test, $\alpha = 0.05$) in development times for these eggs when they were reared in the laboratory at constant temperatures. Survival of the eggs did not affect variability of the eggs, as indicated by the values of the CVs (Table 3).

Variability in Development

Since the coefficients of variation for hatch times were temperature dependent, variability was described from the development times at the constant temperatures the insects were most likely to experience in the field. Consequently, a cumulative Weibull function (Eq. [2]) was fitted to normalized times for 11.0, 13.6, 15.0 and 18.5°C (Fig. 3). Parameter estimates (SE) for the cumulative function were $\gamma = 0.7519$ (0.0125), $\eta = 0.2704$ (0.0132) and $\beta = 2.9442$ (0.1389) ($R^2 = 0.961$).

A variance component procedure (SAS Institute 1985) was used to compare variability within and between egg masses. Normalized times were used so that egg masses exposed to each temperature could be pooled. The ratio of the between-egg mass variance component to the within-egg mass variance component was less than 1, an indication that most variation occurred within egg masses. The coefficients of variation for normalized hatch times for individual egg masses, when compared with pooled egg masses, increased only from 10.4 to 11.7%. Hence, if the effects of individual egg masses are ignored, only a small amount of variation remains unexplained.

Bark Microclimate

At higher temperatures, average bark temperatures were significantly higher than corresponding air temperatures recorded in the Stevenson screen. Bark temperature as a function of air temperature (Fig. 4) was:

$$y = 0.061\ (SE = 0.030) + 1.004\ (SE = 0.011)\ x\ (r^2 = 0.935) \quad [3]$$

where y = natural log of bark temperature and x = natural log of air temperature.

Degree-day Accumulations

DD accumulated above a 3.0°C threshold were compared with egg hatch of natural populations and eggs housed in the Stevenson screen (Fig. 5). For natural eggs, 2.0 and 8.7 km from the Stevenson screen, air temperatures resulted in an accumulation of about 352 DD to the

Table 1. Mean development times (SE) and rates (SE) for gypsy moth eggs reared at constant temperatures.

Temp (°C)	n	Mean time (d)	CV (%)	Mean rate (1/d)	CV (%)
32.7	1283	10.0 (0.04)	13.83	0.1022 (0.0004)	13.21
31.4	1297	9.7 (0.04)	15.25	0.1056 (0.0004)	14.04
27.5	2124	9.0 (0.03)	16.47	0.1142 (0.0004)	14.84
24.1	2551	9.6 (0.02)	12.71	0.1052 (0.0002)	11.32
20.4	2837	12.7 (0.03)	12.68	0.0801 (0.0002)	10.98
18.5	2286	13.3 (0.04)	12.97	0.0763 (0.0002)	11.79
15.0	2259	17.5 (0.03)	9.17	0.0577 (0.0001)	8.34
13.6	2284	25.3 (0.05)	9.04	0.0398 (0.0001)	8.64
11.0	2732	41.4 (0.04)	7.72	0.0243 (0.0000)	7.13

Table 2. Mean observed development times (SE) and estimated development rates (Eq. [1]) for gypsy moth eggs moved between low temperatures and 18.5°C.

Temp (°C)	n	Mean time (d)	CV (%)	Estimated time (d)	Estimated rate (1/d)
11.0[a]	2517	18.2 (0.03)	7.77	28.8	0.0347
8.0[a]	2717	21.8 (0.05)	11.52	60.4	0.0166
5.5[a]	2568	23.2 (0.05)	11.60	90.8	0.0110
11.0[b]	2982	27.5 (0.02)	4.01	37.5	0.0267
8.0[b]	2528	30.3 (0.02)	3.21	58.5	0.0171
5.5[b]	3147	31.9 (0.02)	3.03	86.1	0.0116

[a] alternated daily between indicated temperature and 18.5°C

[b] moved to 18.5°C after 22 d at indicated temperature

Table 3. Proportion surviving and development times (SE) at 26.0°C for eggs collected at two heights on the boles.

Location	Height	n[a]	Survival (%)	Time (d)	CV (%)
Castleton	> 1 m	3643	6.2	8.2 (0.06)	10.70
	< 1 m	3933	79.1	7.5 (0.01)	10.33
Gordon Rapids	> 1 m	2577	15.0	7.0 (0.04)	10.07
	< 1 m	3055	61.9	6.7 (0.02)	10.70

[a] initial number of eggs

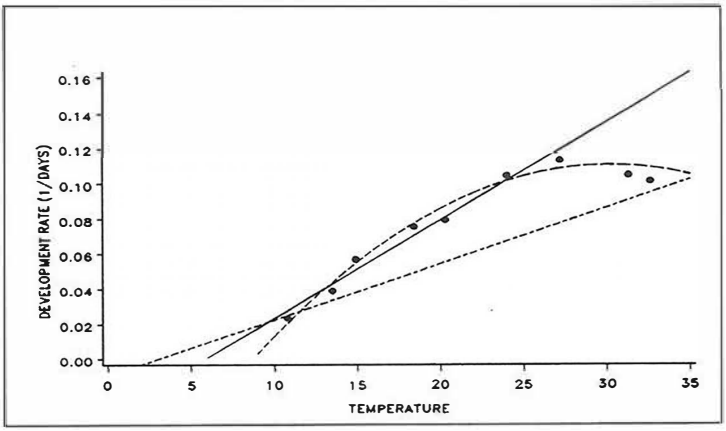

Fig. 1. Temperature-dependent development rates for eggs of the gypsy moth. Circles are observed mean rates, solid line is linear regression line, curve is quadratic regression line and dashed straight line is regression constructed from Johnson et al. (1983) data.

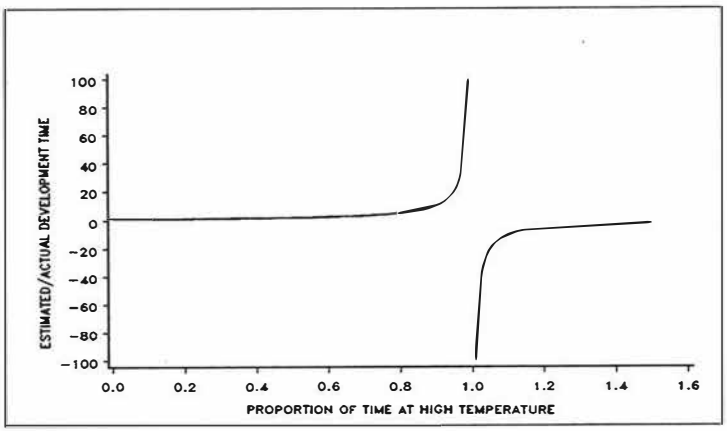

Fig. 2. Generalized proportion of estimated to actual development times from interpolation equation for varying values of the ratio t_H / $\tilde{t}_H$.

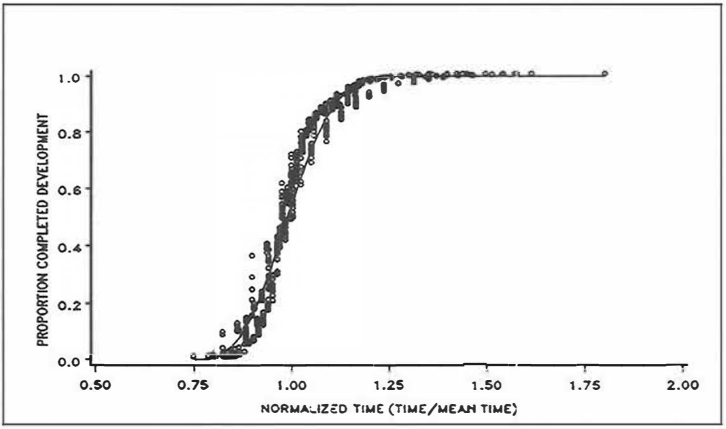

Fig. 3. Cumulative frequency distribution of egg hatch as a function of normalized time. Circles are observed values and line is cumulative Weibull function fitted by nonlinear regression.

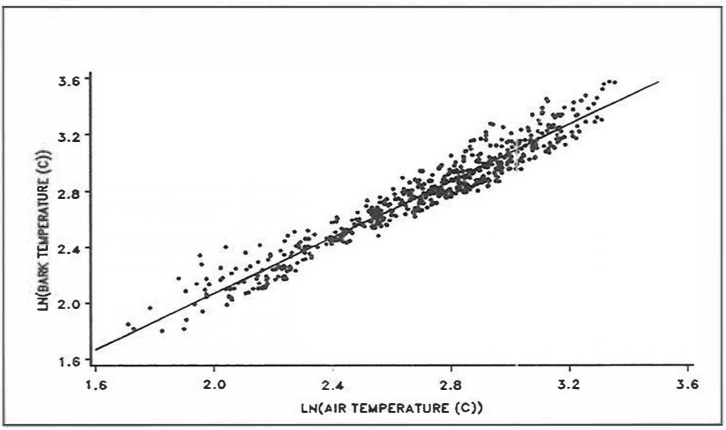

Fig. 4. Linear relationship between natural logarithm of bark temperature and natural logarithm of air temperature recorded in Stevenson screen.

onset of hatch and a median hatch at about 380 DD. Eggs housed in and under the Stevenson screen began to hatch at about 428 and 408 DD and median hatch occurred at about 445 and 500 DD, respectively. Correcting the air temperatures with the bark temperature function increased the number of DD to onset of hatch for field egg populations to about 385 and the median hatch to about 420. Some of the egg masses stored in and under the Stevenson screen got wet from snow melt in the spring, and low survival resulted. This may have accounted, in part, for the discrepancies in accumulated hatch as a function of DD between the natural and boxed egg masses.

Varying the development threshold from 3.0 to 5.0°C resulted in significant differences in accumulated DD by the time of larval eclosion from the eggs (Fig. 6).

Computer Simulations

Figure 7 shows the results of the computer simulations in which the three different rate equations were used. The four lines in each graph, from left to right, are the predicted eclosion for simulations beginning on 1 January, 1 February, 1 March and 1 April. For all three rate equations, the later the simulation starting date, the better the prediction. The linear model resulting from our constant-temperature rearing data deviated the most between predicted and observed for all starting dates. The linear model constructed from the temperature constant for median hatch and threshold provided by Johnson et al. (1983) was used in a successful prediction of egg hatch with a starting date of 1 April. When the model incorporating the quadratic function was used the onset of hatch was underestimated by only a couple of days for the same starting date. However, the model based on the quadratic function (Fig. 7C) was less sensitive to changes in the starting date than the models based on either linear rate. In all cases, our descriptions of variability seemed to reflect adequately the observed variability in egg hatch.

DISCUSSION

Development rate equations, derived from constant temperature rearings, coupled with a variability function, were used to construct rate-summation models of phenology for gypsy moth eggs. Techniques similar to those employed by Lysyk and Axtell (1987) for house fly immatures and Casagrande et al. (1987) for modeling the development of the larval and pupal stages of the gypsy moth were used to predict the spring eclosion of gypsy moth from the egg.

Estimation of development times, and consequently rates, at low temperatures has been considered essential for predicting the development of overwintering stages of an insect. Although insects may develop at these low temperatures, the protracted development time required generally results in poor survival. To overcome this problem, development times at low temperatures can be estimated from insects moved between low and high temperatures (Régnière 1987). Utilization of this technique for gypsy moth eggs resulted in some negative estimated development times. This prompted us to analyze the procedure through the use of simulation techniques. As the ratio of

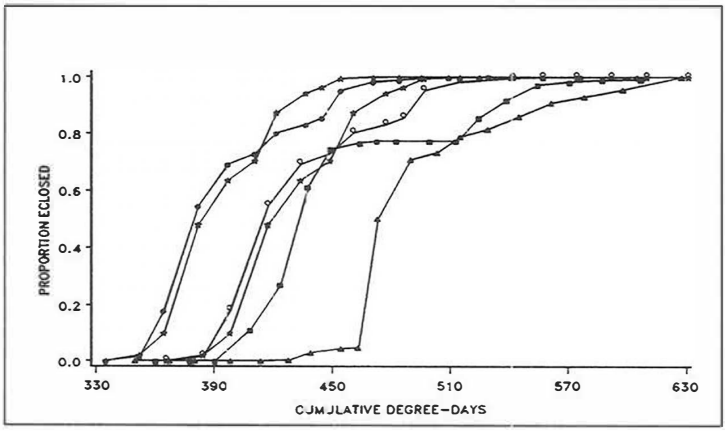

Fig. 5. Proportion of larvae that eclosed from gypsy moth egg masses in the field versus accumulated DD. Closed circles and stars are egg eclosion from sites 2.0 and 8.7 km from Stevenson screen, respectively. Open circles and stars are same data corrected with bark temperature correction function. Squares and triangles are egg masses kept in and below the Stevenson screen, respectively.

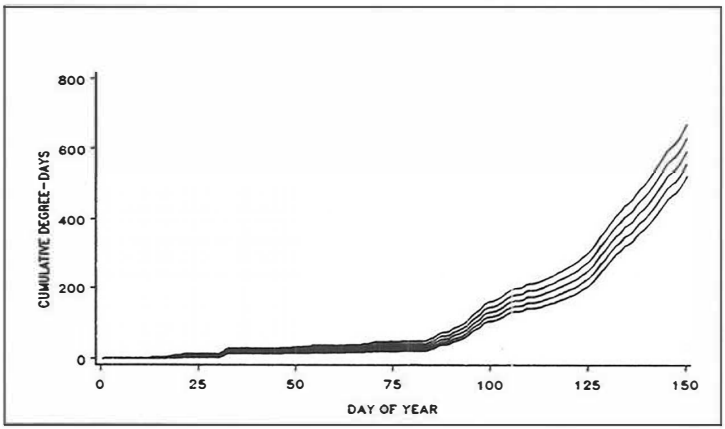

Fig. 6. DD accumulations from air temperature recorded in Stevenson screen. Lines from top to bottom represent 0.5°C changes in threshold between 3.0 and 5.0°C.

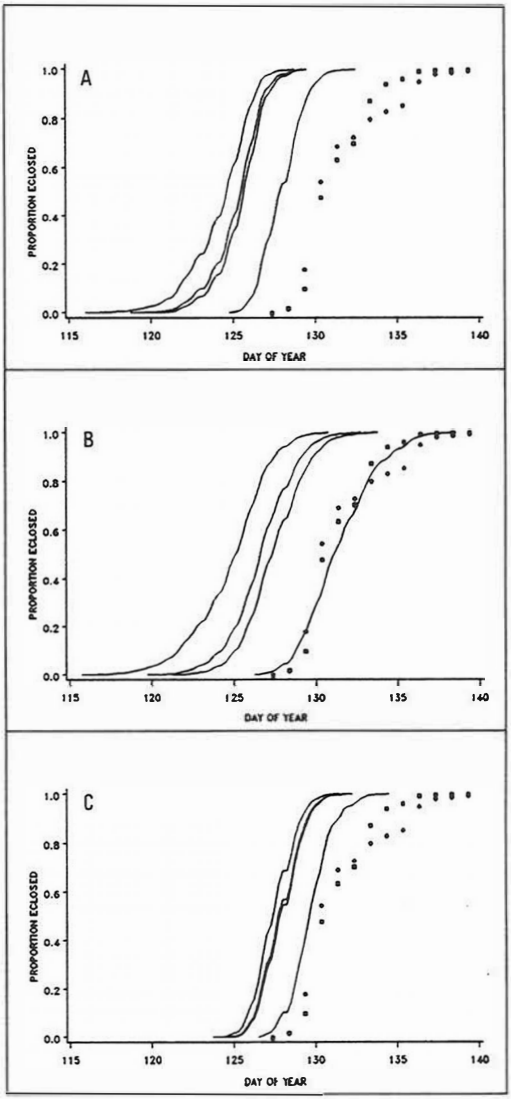

Fig. 7. Results of computer simulations with A) linear regression function, B) linear regression function from Johnson et al. (1983) and C) quadratic regression function. Solid lines, from left to right, in each graph represent 1 January, 1 February, 1 March and 1 April simulation starting dates.

time spent at the high temperature for completion of development, after movement from the low temperature, to the total development time required for complete development at the high temperature approached one, the relationship became very unstable. If individual development times were greater than the mean time required at the high temperature negative estimates resulted. Consequently, these estimated times were not employed in construction of temperature-dependent rate functions.

Most variability in egg eclosion times for gypsy moth eggs occurred within egg masses. Variability between egg masses only increased overall variability by a small amount. This suggests that small numbers of egg masses provide an adequate representation of variability and can be used in egg hatch investigations.

Low survival, in some years, of eggs well above the ground on the tree bole has been attributed to low winter temperatures (Leonard 1972). Eggs lower on the bole have a higher survival rate as a result of the insulating effects of snow cover. Campbell et al. (1974) suggested that low temperatures, resulting in mortality of insects, selectively kill individuals that cannot develop at low temperatures. Our observations indicate that when mortality caused by low temperatures occurs, the resulting variability of survivors is no different than that of egg masses that experience little or no mortality.

The use of normalized development times, pooled for all temperatures (Wagner 1984), is based on the assumption that variability is proportional to the mean development time for all temperatures. The observation made here that the coefficient of variation for development times of gypsy moth eggs varied with rearing temperature suggests that this assumption may not be valid for all insects and their stages. We conclude that normalized times derived from the constant temperatures within the range of average temperatures that the insects would experience in the field would be more appropriate.

Degree-day accumulations described by Johnson et al. (1983) were inadequate for predicting the onset or median of egg hatch observed in the present study. Degree-day accumulations were also extremely sensitive to small changes in threshold temperature and starting dates.

Considerable differences exist between the temperatures in the microenvironments in which insects dwell and the standards of conventional meteorology (Wellington 1950). Although these microclimatic differences have been investigated for the larval stages of gypsy moth (Anderson et al. 1987), such relationships have not been explored for the egg stage. Degree-day summations made by Johnson et al. (1983) for predicting egg hatch were based on daily maximum and minimum temperatures recorded at a weather station 2.0 km from the stand in which the eggs were collected. Empirical relationships presented here indicate that bark temperatures can be described as simple linear functions of meteorological standards. However, gypsy moth eggs are widely distributed throughout their habitat and occur in a variety of places; eggs are found at various heights on the tree, in different aspects with regard to solar radiation and on or under different substrates near the ground

(ibid.). These various microhabitats represent different microclimates in which the eggs undergo development. Nicolai (1986) has demonstrated that differences in temperature exist even between bark fissures and ridges in Quercus spp. A more thorough investigation of these relationships is required to predict gypsy moth egg hatch accurately.

The linear development rate equation, when incorporated into the rate summation model, was inadequate for predicting egg hatch regardless of the simulation starting date. The linear function constructed from Johnson et al. (1983) data permitted accurate prediction of the hatch date only for the simulation with a 1 April starting date. The quadratic function also enabled prediction of egg hatch within a couple of days of actual hatch and was less sensitive to starting date than the linear function-based models. That the quadratic function had a much higher threshold value (8.4°C) and was less sensitive to fluctuations of spring weather than were the linear models suggests that the threshold for development rate accumulation may not be as low as predicted with the aid of either linear function. For all models variability in egg hatch was well represented by the Weibull function.

Overwintering development of insects has been described as a biphasic process (Logan et al. 1979). The first phase consists of diapause development, while the second phase involves morphogenetic development. A portion of the population may complete diapause development and begin morphogenesis while the remainder of the population remains in diapause. This phenomenon may account for the discrepancies in reported development rates and thresholds, resulting from different storage treatments, that exist in the gypsy moth literature. Development rates for European eggs (Rubtsov 1938, Pantyukhov 1962) were much higher than the rates presented here. These higher rates probably reflect differences in storage temperatures and times rather than geographic differences. Eggs used in our development studies had probably completed diapause requirements and the 2°C storage temperature inhibited subsequent development. The late starting date of the accurate predictions suggests that a more complete knowledge of the temperature and time relationships for diapause termination in gypsy moth eggs may help us understand better the processes involved and may enhance our ability to predict this critical phenological event.

To predict gypsy moth phenology throughout the summer requires that spring development of the egg stage be accurately predicted. The model presented by Waggoner (1984) is inadequate for predicting variability in egg hatch and does not lend itself well to conventional modeling techniques used to model phenology of other stages of gypsy moth (Casagrande et al. 1987). The model described here employs similar techniques and would be a suitable starting point for such a comprehensive model.

SUMMARY

Rate-summation modeling techniques, incorporating development variability, were used to predict eclosion from the egg by gypsy moth. A quadratic temperature-dependent rate function was compared

with two linear functions and proved to be less sensitive to changes in the simulation starting dates. Variability increased with increased rearing temperature. Consequently, variability was mathematically described from temperatures that eggs would experience in the field. The greatest amount of variability in hatch times occurred from within egg masses; between egg masses added only a small amount of variability. Reductions in survival resulting from spatial distribution of egg masses had no effect on variability. Techniques used to estimate development times of eggs at low temperatures proved to be inappropriate. Published DD summations, to onset and median egg hatch, above a 3.0°C threshold, were inadequate for predicting egg hatch for field populations. Degree-day techniques are shown to be very sensitive to changes in threshold value. Differences between microclimatic temperatures and the standards of meteorology also influenced DD predictions.

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NUTRITIONAL ECOLOGY: *LYMANTRIA DISPAR* AS A MODEL SYSTEM FOR STUDY OF SERUM STORAGE PROTEINS

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The lepidopteran family Lymantriidae contains about 200 genera and about 2,500 described species, mostly from the Old World Tropics (DeWorms, 1983). Of the 46 recognized species and subspecies of Lymantriidae in North America, 30% are considered pests (Ferguson, 1978). The pest species include three introduced species which have become established in North America, the gypsy moth, *Lymantria dispar* (L.), the browntail moth, *Euproctis chrysorrhoea* L. and the satin moth, *Leucoma salicis* (L.). These exotic species are of particular interest to us because of their differing life history strategies and varying levels of success in North America. The satin moth is a minor pest of native and exotic species of poplar, but has on occasion defoliated aspen forests in North America. (Wagner & Leonard, 1979; 1980). The browntail moth is currently a refugial species in several maritime localities in eastern North America (Schaefer, 1974), but populations have recently rebounded (Leonard, 1988). The most successful of the invading Lymantriids is the gypsy moth, which continues to spread in North America.

With economically important species of Lymantriidae, a wide variation in the degree of polyphagy exists, from the rather narrow host ranges of the nun moth, *Lymantria monacha* L., the Douglas-fir tussock moth, *Orgyia pseudotsugata* (McD.), and the satin moth, to the more catholic appetites of the gypsy moth and browntail moth.

Within the wide range of hosts that gypsy moth will feed upon, performance and fitness can vary between species of hosts (Barbosa & Greenblatt, 1981; Barbosa *et al.*, 1981). The quality of a tree host species will differ according to foliage age, location of foliage on the tree, and site conditions. (Wallner, 1987 and references therein.). Leaf quality can decline in response to grazing by gypsy moth larvae (Lance *et al.*, 1986; Schultz & Baldwin, 1982; Valentine *et al.*, 1983; Wallner & Walton, 1979).

There is considerable current interest in insect-host interactions encompassing the emerging field of nutritional ecology. As noted by Slansky and Scriber (1985), the amount, rate, and quality of food consumed influences growth rate, developmental time, weight, dispersal ability, and probability of survival; thus, the processes of food

consumption and utilization underlie and link the physiological, behavioral, ecological, and evolutionary aspects of insect life. Nutrient requirements for insects, reviewed by Dadd (1975), include protein and amino acids, carbohydrates, minerals, water-soluble growth factors including B vitamins, lipogenic factors, ascorbic acids, nucleic acids, and lipid growth factors including essential fatty acids, sterols, and fat soluble vitamins. Host-plant selection by feeding insects involves attraction to a potential food plant, arrest or cessation of locomotion, and stimulation or deterrence of feeding (Hanson, 1983). Allelochemical composition of food can influence performance of an insect feeding on a particular food, and often act in a negative, anti-biotic manner (Slansky & Scriber, 1985).

The complexities of biotic and abiotic factors relating to the nutritional ecology of insects have produced a large and growing literature (e.g. Slansky & Rodriguez, 1987; Slansky & Scriber, 1985; and references therein). As noted by our esteemed colleague, Professor Vincent Dethier (1987), "Knowledge of all these newly revealed capacities of plants and insects forces us to reexamine our ideas of ecological relationships and evolutionary hypotheses. We cannot fully comprehend what populations are doing without understanding individuals nor what individuals are doing without some understanding of relevant features of their physiology and behavior."

Our group is utilizing a unique approach to nutritional ecology by examining the major nutrient storage systems in insects: the serum, cuticular, and yolk storage proteins. Insect storage proteins are synthesized predominantly (c.f. Palli & Locke, 1987) by the larval fat body, accumulate primarily in the hemolymph, and their concentration increases enormously in the later larval instars (Levenbook, 1985). The existence and persistence of distinct groups of storage proteins suggests that they have important functional roles in the physiology of insects, and the absolute or relative amounts of these proteins would be diagnostic of the insects nutritional, developmental, and behavioral state.

We have focused our attention on proteins, rather than on carbohydrates and lipids. Nitrogen-containing compounds play an essential role in growth processes of insects; cellular growth, differentiation, internal and external structural components, enzymes, carrier molecules, pigments, and chromosomal material require and involve a large investment of nitrogen (Mullins & Cochran, 1983.). The female gypsy moth is remarkably efficient in utilizing nitrogen for egg production, incorporating nearly half of that assimilated by last stage larvae into eggs (Montgomery, 1982). Serum storage proteins are not only essential for development of larvae, pupae, and adults, but also serve as a nutritional link between generations. Yolk proteins are the primary nutrient resources in eggs (Kunkel

& Nordin, 1985) and the nutritional quality of eggs is important to survival during embryogenesis, diapause, and survival of pre-feeding neonates. The Lepidoptera in particular have a complicated set of yolk proteins which include vitellogenin, microvitellogenin, and egg specific protein (Irie & Yamashita, 1983; Kawooya *et al.*, 1986; Zhu *et al.*, 1986). This complexity of stored nutrient allows for a complex message between the maternal and offspring generation.

Animals are exposed to several thousand naturally occurring molecules in the food they ingest (Turunen, 1985). Our paradigm in studies of nutritional parameters is to examine how the nitrogenous compounds are utilized after being absorbed from the midgut of feeding larvae. From our prospective, the feeding gypsy moth larva is the ultimate biological filtering system, accomplishing the necessary steps in finding food, utilizing the appropriate behavioral and chemosensory repertoires required for ingestion, and in dealing with allelochemicals and other feeding-associated adaptations. Nitrogen-containing compounds absorbed through the midgut form the metabolic pool for biochemical and physiological processes necessary for development. From this pool the fat body will synthesize polypeptides and proteins and release them to the serum as storage proteins, the major internal pool of amino acid resource for development, growth and reproduction.

The gypsy moth is proving to be an excellent model system. The insect is readily cultured in the laboratory. Feeding and accumulation of nutrients occurs only in larvae, since adults are non-feeding. Reserves accumulated by the onset of the wandering stage in last instar larvae provide the store of amino acids and proteins for pupae, adults, and eggs. As perhaps the most studied of forest pests, field aspects of the biology and ecology of the gypsy moth are well documented, yet the underlying physiological and biochemical processes have received little attention.

PROTEINS ASSOCIATED WITH INSECT NUTRITION

Arylphorin (Ap).

The arylphorins are hexameric serum storage proteins which may also be stored in the fat body close to the time of metamorphosis (Tojo *et al.* 1978; 1980). Arylphorins have been described in several species of insects from several Orders, including an Ap isolated by our group from gypsy moth (Karpells, Leonard, & Kunkel, in ms). The Ap from gypsy moth is one of eight thus far described in lepidopteran species. The gypsy moth Ap is a native Mr

440,000 hexamer composed of nonidentical subunits of Mr 73,000 and 80,000. Ap has been suggested to supply the amino acids necessary for tissue remodeling during metamorphosis. Ap is high in aryl groups which may be related to the particular need by metamorphic stages for phenolic hard cuticle and tanning substrates (Munn & Greville, 1969; Levenbook, 1984). The greatest concentration of arylphorin occurs in hemolymph in the wandering stage, just prior to the prepupal stage. Ap may play a supportive role in supplying the conduit that amino acids must pass through in the hemolymph of the last stage larva in order to take part in the synthesis of vitellogenins in the fat body.

Female specific protein (FSP).

FSP is a hexameric storage protein described in five lepidopteran species. FSP, although structurally related to Ap, is compositionally distinct, lacking the high aryl content. FSP accumulates in the last larval instar and is cleared and stored prior to use in the fat body (Tojo *et al.*, 1981). FSP is more actively synthesized in females; in the best documented case, *Bombyx mori*, its disappearance from the hemolymph and fat body is correlated with the accumulation of vitellogenin (Tojo *et al.*, 1981). We are now reasonably certain that FSP is missing in *Lymantria dispar*. This absence is important, since lack of FSP puts more pressure on Ap as a storage vehicle for yolk protein synthesis.

Lipophorin (Lp).

Lipophorin is a major insect serum protein (Chino *et al.*, 1981) used to shuttle lipids and hydrophobic compounds between insect tissues. The level of Lp in insect serum is potentially important in the rate of supply of lipids to developing oocytes. Lp itself is taken up into oocytes in substantial enough amounts to be considered physiologically important within the oocyte (Kunkel & Nordin, 1985). Lp is also an important factor in transferring diglycerides to the developing oocytes, and substantial Lp is also itself incorporated into the oocytes of some species of insects (Kunkel & Nordin, 1985). It may be of nutritional and physiological value to the developing embryos as has been shown with *Bombyx mori* (Irie & Yamashita, 1980), and with *Musca domestica* (Agui *et al.*, 1985). Lp titer could also affect the physiology of male *L. dispar* moths as a transport of triglycerides required for flight.

Vitellogenin (Vg).

The vitellogenins are the maternal serum precursors of the major yolk proteins or vitellins (Vts), of the egg (Kunkel & Nordin, 1985). Vitellogenin is the generic name

for a unique group of proteins produced in the maternal fat body in most insects and transferred to the developing oocytes through the hemolymph (Hagedorn & Kunkel, 1979). Most often there are multiple immunologically distinct Vts in the egg (Storella *et al.*, 1985), and these may be used differentially during the embryonic development, such that one of them is being utilized by the embryo close to hatching (Kunkel & Nordin, 1985). Differential synthesis, or turnover, of one or multiple Vgs before storage in the egg could dramatically affect the nutritional supply by these proteins to the embryo or first instar larva. In lepidopterans which do not feed in the adult stage, such as the saturniid silk moths, Vgs are often synthesized starting in the late larval and the pupal stage (Pan *et al.*, 1969). With gypsy moth we have found that synthesis begins early in the ultimate stage of female larvae, with Vg appearing in the hemolymph in small amounts on day three. Vg accumulates most rapidly as Ap and FSP decline in the last instar or prepupae of *Bombyx mori*, suggesting that these proteins are the major potential sources or precursors for VG synthesis (Izumi *et al.*, 1989). In *Bombyx mori*, Vt is not essential for embryonic development (Yamashita & Irie, 1980); however, Vt may be an important nutritional reserve for the pharate first instar larva (Indrasmith *et al.*, 1987).

Egg-specific protein (ESP).

ESP is a yolk protein produced within the ovary of lepidopterans. Its use during embryonic development has been correlated with the early phase of embryogeny. ESP is synthesized in the ovary and may rely on other serum storage proteins, such as FSP or Ap in *L. dispar* to be transported into the ovary and serve as an amino acid source for egg proteins (Ono *et al.*, 1975). The quantity of ESP in the egg may determine the size, vigor, and subtle behavior of the resultant larva since early embryonic development consumes the stored ESP of an egg. Surveying ESP levels may allow one to assess the nutritional state of egg masses.

PROTEIN STUDIES OF GYPSY MOTH.

Production of antisera.

Antisera against purified proteins were obtained by immunizing male, white, New Zealand rabbits using a standard protocol (Kunkel, 1988). We have produced antisera for the storage proteins Ap, Lp, Vg, Vt, and for the ovarian protein, ESP.

Developmental profiles.

Profiles of Ap, Lp, and Vg have been developed for daily-staged larvae, and prepupae, using quantitative immunoelectrophoresis (QIEP) techniques outlined in Kunkel (1988). These profiles are based on individual animals reared at 24°C, 16:8 LD cycle, and fed *ad lib.* on the diet of Bell *et al.* (1982). Protein profiles of eggs have been determined by QIEP for Ap, Lp, and Vt and by gel electrophoresis for ESP using homogenates of individual eggs. For 1st and 2nd instar larvae we use whole tissue homogenates and for later stages we collect 1 ul of serum from a small puncture in a proleg. We sex larvae by dissecting and identifying testes or ovaries.

Maternal - egg profiles.

For correlations of maternal protein levels with those of their progeny, 1 ul of hemolymph from female prepupae is subjected to QIEP. The small puncture causes no apparent trauma, and we rear females to adulthood for mating and to obtain eggs to compare egg protein profiles with those of the maternal larva.

PROTEIN PROFILES OF GYPSY MOTH

Arylphorin.

During each larval stadium, the concentration of Ap (mg/ml) in the hemolymph shows a gradual increase, reaching the highest concentration at early apolysis. As apolysis progresses, Ap is rapidly cleared from the hemolymph, providing an amino acid source for the newly forming larval tissues. Newly molted larvae contain very low levels of Ap. The titers of Ap in male and female larvae of instars III and IV are similar until the metamorphic instar, V in males and VI in females. These stadia are longer in duration, and more Ap accumulates, reaching a level of 26.2 mg/ml in males and 44.8 mg/ml in females. The extra larval instar in females results in a substantially greater absolute amount of Ap accumulation than in males. The titer of Ap in eggs is low.

Lipophorin.

Lipophorin also displays some of the same cycling as seen with Ap, but the concentration of Lp is much lower, and remains at constitutive levels throughout development. Lp reaches it's highest concentration of about 5 mg/ml in female prepupae and 4 mg/ml in prepupal males (Karpells, Leonard & Kunkel, in prep.) with the higher concentrations

as a function of the longer duration of the ultimate instars. Concentration of Lp in eggs is highest in newly-laid eggs.

Vitellogenin.

Vitellogenin appears in the hemolymph in low levels at day three, and accumulates rapidly during the later third of the ultimate instar of females. In wandering stage larvae, Vg levels are ca. 25 mg/ml, and increase to ca. 30 mg/ml in prepupae. Vt levels in eggs are highest in newly oviposited eggs, and our preliminary studies show about 1/2 of the Vt is utilized during embryogenesis, and about 90% is utilized by the time of eclosion of neonates.

Egg Specific Protein.

Titers of ESP are highest after eggs are deposited. At completion of embryonation ESP is completely utilized.

IMPACT OF NUTRITIONAL STRESS ON PROTEIN LEVELS

The raising of antisera to Ap, Lp, Vg and ESP and determination of their titer on daily stage animals fed *ad lib.* provides us with the opportunity to compare the base line levels of serum proteins of healthy animals with levels in animals that have been stressed in the laboratory or in field populations. These studies are just beginning but our initial results show that various nutritional stress factors affect concentrations of proteins in serum and chorionated eggs.

Defoliation-induced changes in leaf quality have been shown to affect the population quality of the gypsy moth (e. g. Capinera & Barbosa 1976, 1977; Lance *et al.*, 1986; Rossiter *et al.*, 1988; Schultz, 1983; Schultz & Baldwin, 1982; Valentine *et al.*, 1983; Wallner & Walton, 1979). Lance *et al.* (1986) found that the addition of tannin at 2.5% of the total dry weight of the diet fed to third and fourth stage gypsy moth larvae could induce behavioral changes that approximated those observed during the shift in diel periodicity in dense field populations of the gypsy moth. In our studies (Leonard, Montgomery & Kunkel, unpubl.) larvae fed continuously on 0.5% (wt/wt) diet with tannin until apolysis of instar IV had 3 to 4% of the amount of Ap found in larvae fed normal diet, levels too low for molting to occur. Larvae switched from control to tannin diet at stage IV and bled at apolysis IV had reductions in Ap and Lp of ca. 30% and 20% respectively of that in control-fed larvae.

Mid- and late-stage larvae show a reduction in Ap and Lp levels in the serum after a two day period of food

deprivation. In ultimate stage female larvae, starvation after day four causes about a one-third reduction in the level of Vg in hemolymph of prepupae.

Leonard (summarized in 1974; 1981) described a series of qualitative changes in the gypsy moth, including variation in the rate of development, supernumerary molts, coloration (phase polymorphism), fecundity, and size and quality of eggs associated, in part, with nutrition. Nutritional stress will be manifested in the amount and quality of nutritional components (proteins) biosynthesized for the egg by late-stage female larvae of the previous generation. While the amount of storage proteins could clearly be a factor in determining the number of eggs produced by the female, it is our hypothesis that the absolute and/or relative amounts of the storage proteins may be causal or at least be correlated with the quality of the eggs of gypsy moth such that a different behavior is exhibited by the next larval generation.

We have initiated studies to determine protein profiles of metamorphic female larvae in the wandering or early prepupal stage after feeding has been completed, to correlate maternal reserves with fecundity and partitioning of Vt, ESP, and Lp in eggs. The role of vitellin reserves in newly hatched larvae relative to dispersal of neonates is of particular interest to us. Mason & McManus (1981) summarized their studies on dispersal, reviewed the research of others, and note that dispersal is an important process in the population dynamics of the gypsy moth and is still a subject of much controversy. The gate for dispersal is narrow. McManus (1973) considered dispersal as an innate tendency that larvae must satisfy before feeding. Collections of dispersing larvae show that they produce frass with little or no leaf constituents (Leonard, 1970a; 1971). Mason & McManus (1981) suggest that the "turnoff mechanism" for dispersal is likely associated with the expending of energy reserves, the inability to produce silk, and starvation. We believe that the tendency of a 1st instar larva to disperse greatly affects its reproductive fitness in a given population level, and that this propensity is reflected by both physiological and behavioral adaptations. These factors would logically be influenced by the amount, quality, and utilization of nutritive reserves in the egg and in newly hatched larvae to sustain it during dispersal. The parameters relating to the nutritive condition of eggs are: (1) a function of synthesis storage proteins during late instars of female larvae since adults do not feed; (2) the quality and quantity of proteins available to the developing oocyte, and (3) the utilization of proteins during the egg stage.

The role of yolk reserves and dispersal of neonates remains to be resolved. Large gypsy moth eggs contain about twice the yolk content of small eggs (Capinera *et al.*, 1977, Capinera & Barbosa (1967), Greenblatt & Barbosa (1979), Campbell (1981) and Lance & Barbosa (1981) consider

that larvae from larger eggs have a higher tendency to disperse, whereas Leonard (1970) suggested that larvae from smaller eggs or larvae that had depleted yolk reserves were more active and dispersed more readily. McManus & Mason (1983) suggest that physical factors probably exert greater control of the extent of dispersal than size and quality of individuals. Our technique of using QIEP to quantify protein levels in individual animals provides an opportunity to examine the nutritional status of dispersing larvae. Using the wind tunnel of Carde & Hageman (1979) to induce dispersal behavior of neonates, we have begun making direct measurements of Vt of larvae which disperse as well as those that remain on the platform in the airstream.

SUMMARY

We are utilizing a unique approach to examine the influence of nutritive parameters on the population biology of the gypsy moth by examining the major nutrient storage system in insects, the serum and yolk storage proteins. By development of specific antibodies for the major serum storage proteins, vitellogenin, lipophorin, and arylphorin, and the ovarian-produced egg-specific protein, we can examine changes in the titer and the profiles of these proteins during development, and determine the influence of stress factors such as the change in diel periodicity of larvae, and influence of leaf polyphenols such as tannin, on the quantity and quality of these proteins. One of the advantageous features of our study is the ability to obtain hemolymph samples for analyses of storage proteins without sacrificing the insect. This allows us to compare the profiles of prepupae of the previous generation which are diagnostic of the major pool of nutrient reserves available to the progeny via the egg. This approach will permit an examination of the influence of events occurring in the previous generation on fitness (nutritional) factors which are important in the survival, dispersal, and the dynamics of the succeeding generation. Interest in the identification of serum storage proteins is growing. Relatively few have been identified from a limited number of insect species, but our efforts will add at least five from the gypsy moth. We know of no other research group, however, that has begun an intensive study of the role of storage proteins in biological and behavioral parameters relating to population quality or population trends. The gypsy moth lends itself as an excellent model for such a study, because of the importance of nutritional status as it relates to behavior, dispersal, and host anti-herbivore responses. Equally exciting to us is the potential of using data generated from immunoelectrophoresis to develop discriminant functions to predict population trends.

Discriminant function analysis of biochemical parameters has not yet been applied to assess a physiological or behavioral class in insects.

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S P A T I A L R E L A T I O N S H I P S O F D O U G L A S-F I R T U S S O C K M O T H D E F O L I A T I O N W I T H I N H A B I T A T A N D C L I M A T I C Z O N E S

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INTRODUCTION

The distribution and abundance of organisms are two resultants of the same dispersal process; changes in density over time are related to changes in distribution over time (Andrewartha and Birch 1954) . Studies in population dynamics are often based on detailed changes in survival over time with a view to determining the regulatory factors of density. An alternate but just as valid approach may be to study the changes in spatial distribution over time. Comparing outbreak patterns with various environmental patterns could also provide information on regulatory factors. An important advantage of this approach is that regulatory factors detected through pattern comparisons can be tested experimentally through population introductions or changes in host species distributions within different habitat types. A second practical consideration is that modifications of the environment or host species may be indicated to reduce pest impact. The purpose of this study is to determine frequency of defoliation caused by Douglas-fir tussock moth, (Orgyia pseudotsugata (McDunnough), in British Columbia within Biogeoclimatic subzones, zones of climatic moisture deficit/surplus, and zones of growing degree days.

Differences between areas in soils, topography, climate, etc. result in new opportunities for organisms to become established and compete. Over time, a climax plant community develops which is characteristic for that area or site. In Europe, ecozones characterized by basic groups of coinhabitating plants are termed plant associations (Braun-Blanquet 1932), in western U.S.A. they are called habitat types (Daubenmire 1968), and in British Columbia they are called biogeoclimatic subzones (Krajina 1965, Pojar et al. 1987). Where topography is relatively smooth or gently rolling, environmental factors tend to change gradually. Habitat types and plant species form a gradient of change without distinct boundaries (Curtis and McIntosh 1951). In mountainous topography, environmental factors change rapidly and habitat types are distinct with narrow ecotones or boundaries. The forests of southern British Columbia fall into the latter situation and an ecosystem classification characterized by plant communities has proven quite useful in forest and land management.

The differences between habitat types also affect the next trophic level, i.e. the insect grazers, which are dependent for their

survival and well-being upon finding the correct species of host plants within a suitable climate. The fidelity of insects to specific habitat types varies considerably, just as the specificity of plants to certain habitat types varies from species to species. This habitat specificity which often applies to the distribution of species, also may apply to the distribution of outbreaks and result in a unique defoliation pattern (Shepherd 1977).

A complicating factor in determining the correspondence between defoliation and environmental patterns is the insect's ability to disperse. We assume that there is not a mass transport of insects which are capable, in themselves, of causing defoliation; i.e. there must be local build up in a favourable environment before defoliation can take place. This assumption is particularly valid for Douglas-fir tussock moth as the female moths are flightless and dispersal is restricted to short-distance travel by silk-drifting larvae (Mitchell 1979).

The best historical records of outbreak patterns of a forest insect in British Columbia are for Douglas-fir tussock moth. Outbreaks of this insect have, on the average, occurred somewhere in British Columbia at about nine-year intervals. High larval densities and the resultant defoliation usually lasts 1 to 4 years, then the population disappears until the next outbreak period. Defoliation, primarily on Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, in British Columbia, is at the northern limit of outbreaks for this insect which extends south through western United States into Arizona and New Mexico (Shepherd et al. in press). The spatial relationships between these outbreak and various environmental patterns can now be studied relatively easily because of recent developments in geographic information systems. Computer mapping analysis provides rapid quantification and integration of complex shapes from various map overlays.

LITERATURE REVIEW

Research on the relation between Lymantrid pests and climatic and habitat types has been carried out using many approaches, all different from those used in this paper for the tussock moth. In California, outbreaks of Douglas-fir tussock moth on white fir occurred more frequently in open stands on poor sites or ridge tops (Williams et al. 1979). Similar outbreak patterns of tussock moth occurred in the grand fir host type of Idaho (Stoszek et al. 1981) where, again, defoliation was greater on ridgetop sites with shallow soils. Stoszek theorized that high densities of biomass on poorer sites created a stress in the trees to which populations responded. Clendenen (1975) found some significant correlations between various climatic factors and population changes but did not establish any cause-effect relationships to explain the correlations.

The nun moth, Lymantria monacha L., is one of the worst defoliators of European forests. The longest period of time studied was that of Cramer (1962) for the Schwetzingen forest of West Germany beginning in 1844, comparing 3-year averages of temperature and

rainfall during critical insect activity periods. Outbreaks usually occurred when mean monthly temperatures during May and June for the preceding 3 years were above 32.6°C and total May precipitation during the same years averaged less than 8 mm. Only 22 years had these characteristics. Eight were build-up years and 11 were outbreak years leaving only three cases when an outbreak did not follow.

In a study of climate during a 20-year period of nun moth population build up within Moravia, Czechoslovakia, Svestka (1971, 1973, 1982) found that warm dry weather for 2 to 3 years during the insects active periods preceded outbreaks. Once underway, 1 year of cool wet weather was not enough to deter the outbreak. Populations were differentially affected because of differences in temperature and precipitation at different elevations. Many of the outbreaks were in Norway spruce, Picea abies (L.), stands of uniform age on dry southerly exposed soils. In Denmark, Bejer (1985) and Jensen (1985) also found outbreaks on spruce following a period of warm dry summers; the outbreaks only occurred in forests growing on dry sandy soils. Soil type was more important than the species of conifer present. Similar patterns occurred in the Netherlands with outbreaks starting on poor sandy soils after one or two hot summers (Grijpma et al. 1986). The collapse of the population in the Netherlands was attributed, in part, to asynchrony between nun moth larval emergence and bud burst of host trees (Steijlen et al. 1987). Svestka (1971) also stressed the importance of the bud burst/larval emergence synchrony.

Analysis of weather patterns in eight different areas of Russia (Benkevich 1964) and in Romania (Marcu 1970) led to the conclusion that gypsy moth, Lymantria dispar L., outbreaks occurred following cold winters and warm dry springs. A study of 35 years of records for New York city indicated a correlation between warm summer temperatures and upward population trends (Watt 1968). Heavy precipitation adversely affected infestations in Wisconsin (Braham and Witter 1978). In contrast, population fluctuations still occurred in Spain and Morocco even though the weather was favourable all the time (Romanyk 1973, Fraval 1986). Predictive equations from a climatic study of New England populations, when applied in Wisconsin, showed significant divergence between the projected and recorded patterns (Biging et al. 1980). A number of authors have emphasized that this insect is rather adaptable (Kyryeyeva 1973) and each population responds differently to a local climatic pattern (Kolybin et al. 1974) thus making correlation analysis among many populations difficult.

Site characteristics of outbreak and non-outbreak areas of gypsy moth were extensively studied in New England by Houston and Valentine and were previously reviewed (Houston 1981). In brief, susceptible sites are characterized by the following conditions: hot dry climates; excessively drained soils; open ridge tops or other exposed physiography; and open, scattered stands caused by logging, fires, storm drainage, etc., which allow for increased stand temperatures. In such conditions height growth is poor and crowns sparse and open. In contrast, resistant stands occur on good, moist sites with vigorous well-stocked stands of many species. The species of host trees in the stand are of less importance than the ecological conditions. Stand disturbances, which open up the crown, increase temperatures and

provide more protected resting niches thus providing a more favourable environment for the insect (Bess et al. 1947). A similar observation has been made in the Quercus cerris coppice stands of Czechoslovakia which have been thinned and damaged by grazing (Patocka and Capek 1971). Opening of the stands has also been found important at low population levels within the USSR; Golubev and Semevsky (1969) found 44 times as many egg masses along forest borders and in disturbed forests than in deep untouched forests.

A geographic information system was used for the analysis in this paper; similar systems have been widely used in urban planning, landscape ecology, resource inventories and forest management, but seldom in forest pest management. The impacts of control actions against mountain pine beetle infestations on forest resources were studied by Forrester and Vanderwall (1987) and risks of gypsy moth infestation were assessed by Parks et al. (1987) using a geographic information system. In neither case, however, were cause-effect relations established as we have attempted in this study.

METHODS

Douglas-fir tussock moth defoliation in British Columbia has been mapped by the Forest Insect and Disease Survey of the Canadian Forestry Service for eight outbreak periods beginning in 1916 (Shepherd in press, Harris et al. 1985) (Fig. 1). Data for six of these periods fell within our study area: 1924-32, 1932-41, 1942-50, 1960-68, 1969-77 and 1978-1986. Yearly defoliation patterns within each period were amalgamated into one pattern per period. Before 1950, mapping was carried out from the ground; after that date, it was done from aircraft and consisted of sketching defoliated areas on topographic maps usually at a scale of 1:100,000. The purpose was to give an estimate of size, location and annual changes of defoliated areas; forest stand cover maps were not used in the initial sketching.

Biogeoclimatic and climatic maps supplied by the British Columbia Ministries of Forests and Lands and Environment and Parks have been drawn on the same topographic base maps as those used for outbreak sketching. Environmental maps were available for only part of the total outbreak area but this covered 60 or 70% of the outbreaks and amounted to almost 1 million ha. Forest cover maps, used at a scale of 1:50,000, indicated the percentage of dominant species in 20 or 30% classes by stand volume. The climatic moisture deficit/surplus maps displayed the isolines of the average difference between the total precipitation and total potential evapotranspiration during the growing period of May 1 to September 30. The growing degree-day maps displayed isolines of the average accumulated difference between the mean daily temperature and 5°C (positive values only) over the same growing season.

Accuracy of mapping outbreaks from a fixed-wing aircraft depends on the experience of the mapper, defoliation intensity, visibility and flying conditions. Accuracy of biogeoclimatic and climatic maps depends on the intensity of the basic studies to establish the elevation-related relationships and the experience of the cartographer,

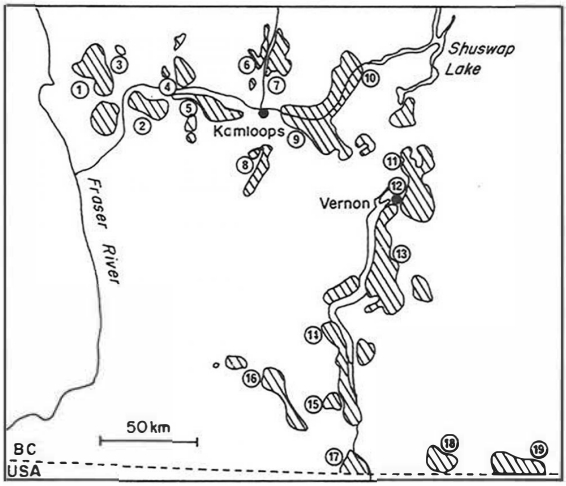

Figure 1. Amalgamation of Douglas-fir tussock moth outbreaks since 1916 in British Columbia. Numbers indicate pheromone trap monitoring locations as part of a pest management system for this pest.

as considerable interpretation and interpolation is required. Therefore, we took a conservative approach and estimated that any particular feature was mapped within an accuracy of 1 km^2 or 100 ha; when calculating statistical tests, sample size was based on the number of 100-ha units within a climatic zone or biogeoclimatic subzone.

Defoliation boundaries for each period, and isolines for biogeoclimatic subzones, climatic moisture deficit zones and growing degree zones were digitized and analyzed using a geographical information system employing overlay software developed by Northwest Digital Research of Vancouver, British Columbia. The system operates on a Hewlett-packard 237 workstation[1]. This allowed calculation

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[1] Mention of specific commercial products, services or formulations does not consitute endorsement or lack of such by the Canadian Forestry Service.

of areas within any designated zone and also areas of overlap and non-overlap between superimposed zones from 2 or more maps. The proportion of ecological or climatic zones which had sustained outbreaks were thus determined. During the analysis, more than 600 overlays, intersections, unions or subtractions of map polygons were made and areas of the unique polygons were determined to the nearest hectare. The percentage of the area defoliated was determined individually for each zone based on the total area available in that zone and histograms were prepared. No defoliation estimate was made unless there was at least 100 ha present per zone. A subsample of 586,913 ha was analyzed for cross comparisons and percentage defoliated was calculated based on the area falling within each cell. Circle diagrams of relative percentage were prepared by assigning a value of 100 to the cell with the highest percentage defoliated and values for other cells were calculated relative to the maximum.

RESULTS & DISCUSSION

A preliminary subsample of 23,466 ha was selected to test the usefulness of including forest composition information in the study. The area selected had the most detailed and recent defoliation information and was expected to result in the best correspondence between forest composition and percentage defoliated. A broad approach was initially taken (Table 1) but no consistent relationships could be determined from this analysis. A second, more detailed approach, was attempted in which the percentage of Douglas-fir present, in 20 or 30% classes, was compared to the percentage of area defoliated (Table 2). Again no differences were evident except where Douglas-fir was less than 20% or where lodgepole pine was dominant. The latter class only occurred at higher elevations above stands normally defoliated by tussock moth. The results of this initial analysis illustrated the problems which arose when two surveys were compared which had been mapped at different resolutions. The forest cover maps were made from aerial photographs and each small stand is detailed. In contrast, the defoliation maps only indicated blocks of forest within which there was some defoliation; defoliation history of each stand was not identified. As no consistent relationships could be found between defoliated area and forest composition, as depicted by the scale of maps available, this variable was deleted from further analysis.

Each outbreak period was initially recorded separately. It was thought that multiple outbreaks might be a better indicator of susceptibility than single outbreaks. When compared to a random distribution of expected frequency of outbreaks (Table 3), there was a significant difference. There were more stands with two outbreaks and fewer with only one outbreak than would be expected due to random chance; this indicated that some stands were more susceptible than others. However, the distribution between biogeoclimatic subzones and climatic zones were essentially the same for both one and two periods. As an example, the distribution between growing degree zones is given in Figure 2. Therefore, subsequent analysis was carried out

Table 1. Percentage of area defoliated and non-defoliated in stands in which the presence or absence of Douglas-fir was indicated on forest cover maps within Douglas-fir and Ponderosa pine Biogeoclimatic Zones

Biogeoclimatic zone	Douglas-fir >20%		Douglas-fir <20%	
	Defoliated	Non defoliated	Defoliated	Non defoliated
Interior Douglas-fir	16	44	8	32
Ponderosa Pine Bunch Grass	10	12	17	61

Table 2. Percentage of area defoliated within stands of different composition

Stand Composition	Area ha	Defoliated ha	Defoliated %
D.-fir[1] >80%	5099	1149	23
D.-fir 50-80%, P. pine 20-50%	1602	456	28
P. pine >50-80%, D. fir 20-50%	2034	484	24
L. pine 50-80%, D. fir 20-50%	670	1	0
D.-fir <20%	14227	1811	13
	23632		

[1] D.-fir = Douglas-fir, P. pine = Ponderosa pine, L. pine = lodgepole pine.

Table 3. Comparison of the frequency of outbreaks of the Douglas-fir tussock moth

Number of periods in which outbreaks occurred within each 100-ha unit	Expected frequency by random chance. # of 100-ha units	Observed number which occurred. # of 100-ha units
0	4332	4345
1	457	432
2	24	36
3	9	11

$X^2 = 7.81$, $p_2 = .027$

using one overlay amalgamated from all outbreaks as this provided a much bigger sample base. Any stand that had been defoliated in one or more periods was considered to have sustained an outbreak. Of the total defoliated area, 90% had been defoliated once, 8% defoliated twice, and 2% defoliated three times. Even though multiple outbreaks had been recorded in a region with the same place name, exact geographical overlaps were not common.

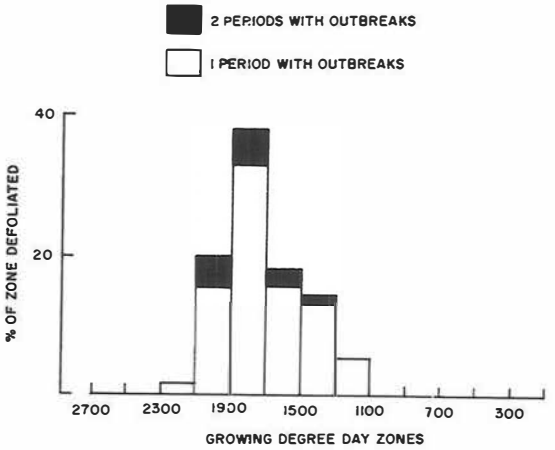

Figure 2. Percentage of stands defoliated within zones of accumulated degree-days above 5°C during the growing season. Stands defoliated in one and two separate outbreak periods are illustrated.

The biogeoclimatic subzones had been subdivided on the maps into variants and subvariants. These were initially kept separate, but the reduction in data for any one subdivision was too great to retain confidence in the sample. Therefore, the data was accumulated to the subzone level. An example of an overlay of outbreaks for one

biogeoclimatic map is presented in Figure 3.

The percent area of each biogeoclimatic subzone defoliated during at least 1 outbreak period is given in Table 4. The order of listing in this table follows a progression from the cool moist forests of the Engelmann Spruce Subalpine Fir subzone (ESSF) down to the hottest and driest Ponderosa Pine Bunch Grass subzone (PPBG) at valley bottom. The PPBGa subzone is essentially a grassland with small clumps of Ponderosa pine mixed with lesser amounts of Douglas-fir. Of the total area, 4.8% had been defoliated, but because Douglas-fir makes up so little of the area, a much larger proportion of the Douglas-fir present was probably defoliated (Table 4).

Table 4. Percentage of area defoliated within biogeoclimatic subzones

Biogeoclimatic subzone	% Defoliated	Number of 100 ha units
	Cool and Moist Subalpine	
$ESSF_{e \text{ to } p}$	0 d[1]	458
$ESSF_d$	.2 d	222
MS_b	0 d	450
MS_c	.2 d	1244
ICH	0 d	184
IDF_b	.9 d	2081
IDF_d	.5 d	432
IDF_j	1.6 d	325
IDF_a	8.6 b	1824
IDF_c	12.7 b	144
$PPBG_d$	20.3 a	974
$PPBG_a$	4.8 c	902
	Hot and Dry Valley Bottom	

[1]Values with the same letter are not significantly different, $p \leq .05$.

The largest percentage defoliated occurred in the next subzone, PPBGd. This subzone consists of more forest than grassland but, Douglas-fir is still not the dominant species. A defoliated area of 20.3% means that a high proportion of Douglas-fir had again suffered defoliation. The difference in percentage defoliated between PPBGa and PPBGd may reflect the amount of Douglas-fir present; the susceptibility to defoliation may be equally high in both subzones.

At elevations above the ponderosa pine forest are many Interior Douglas-fir subzones. They make up the largest block of forest within these valleys, but it is only the lowest stands which have had significant area defoliated (IDFa and IDFc). Above those stands, only an insignificant amount of defoliation has occurred and some of these records probably reflect earlier mapping inaccuracies. The standard

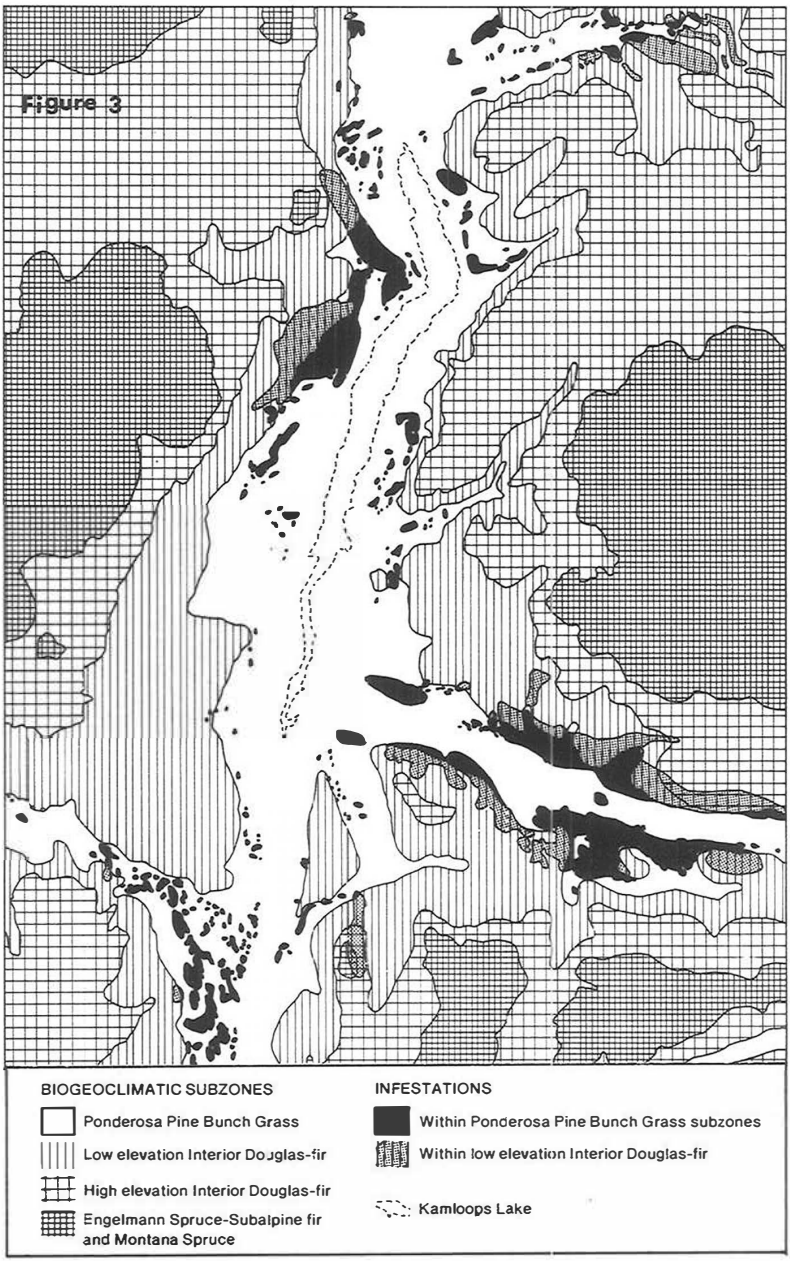
Figure 3
BIOGEOCLIMATIC SUBZONES
Ponderosa Pine Bunch Grass
Low elevation Interior Douglas-fir
High elevation Interior Douglas-fir
Engelmann Spruce-Subalpine fir and Montana Spruce
INFESTATIONS
Within Ponderosa Pine Bunch Grass subzones
Within low elevation Interior Douglas-fir
Kamloops Lake

error of proportion is indicated by a vertical bracket on the histogram of percentage of area defoliated within biogeoclimatic subzones (Fig. 4).

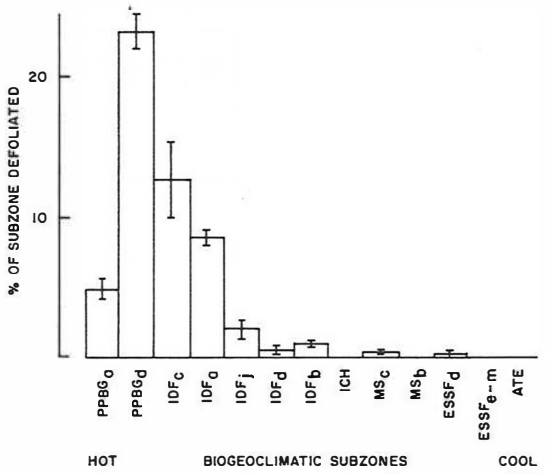

Figure 4. Histogram of percent area defoliated within biogeoclimatic subzones. Brackets indicate standard errors of proportion.

The percentage defoliated for each climatic moisture deficit zone is illustrated in Figure 5. About 1% of the area in the driest zone (-500 to -400 mm) was defoliated. This zone covers about the same area as PPBGa and probably also had a low percentage defoliated because of the lack of Douglas-fir. The highest amount defoliated occurred in the next zone (-400 to -300 mm); the percentage gradually decreased with succeeding zones. There was almost no defoliation in zones with a positive water balance.

The percentage defoliated for each zone of growing degree days is illustrated in Figure 6. The distribution of percentage defoliated among zones was nearly symmetrical with the peak being in the 1700 to 1900 D° zone. The histograms of Figures 5 to 7 were based on an identical land base and therefore covered the same range of

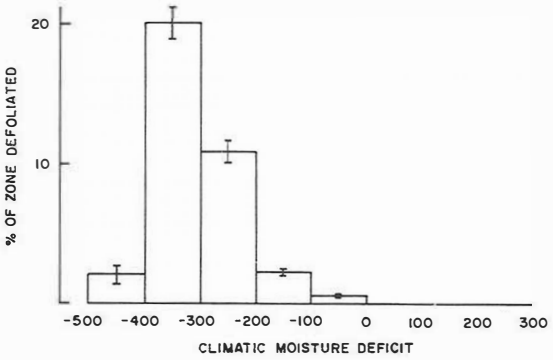

Figure 5. Histogram of percent area defoliated within climatic moisture deficit zones. Brackets indicate standard errors of proportion.

environmental conditions. Choices of class sizes by the different cartographers made direct comparison of these histograms difficult and statistical tests invalid.

Cross comparisons of the relative percentage defoliated by two ecological or climatic classifications are illustrated by circle diagrams in Figures 7 to 9. These showed that the PPBGd and IDFa zones had the greatest amount defoliated and, within those zones, the percentage increased with increasing climatic moisture deficits to -300 to -400 mm. In contrast, when the PPBGa zone was divided into growing degree-day zones, the maximum defoliated was not in the hottest zone but in the moderate 1500 to 1700 and 1700 to 1900 D° zones. Above 2300 or below 1100 D° outbreaks rarely occurred. Distribution of outbreak incidence was significantly different from the average for central cells (Figs. 8 and 9) of both the climatic moisture deficit and growing degree-day cross classifications within biogeoclimatic subzones (x^2 test, $p<.001$). This indicates that the Douglas-fir tussock moth usually rises to outbreak levels within moderate temperature zones, but within a moisture gradient, outbreaks occur most frequently in the driest zone available which contains Douglas-fir.

This study provides information of the environmental requirements and limitations for outbreaks of this pest species in British Columbia. It would be useful to compare these results with similar studies carried out where this insect defoliates different host species and

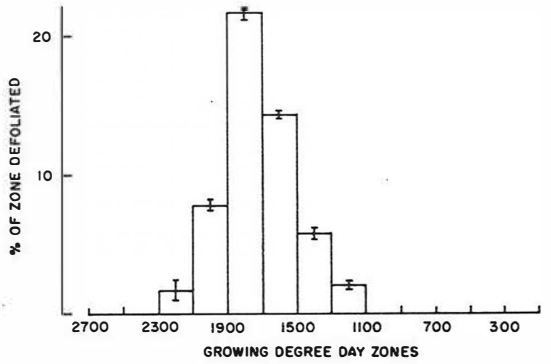

Figure 6. Histogram of percent area defoliated within zones of accumulated degree-days during the growing season. Brackets indicate standard errors of proportion.

where the frequency and synchrony of outbreak cycles is different (Shepherd, in press). It also provides a hypothesis for experimental testing of survival rates of seeded populations.

An understanding of the role of temperature and moisture in the regulation of population trends and in the location of outbreaks provides the basis for predictions of population changes and damage which can be expected following climatic shifts because of atmospheric pollution or possible greenhouse effects. Such an understanding is also useful when making forest management decisions regarding which tree species to plant, which spacing densities to use, the expected need for pest control applications, and other silvicultural treatments (Shepherd and Otvos 1986).

A practical outcome of this study is that a relatively small climatic zone within the range of Douglas-fir has been identified as being susceptible to outbreaks; this zone can be defined on maps and recognized in the field through the plant communities present. This is an important step in a pest management system now operating in British Columbia (Shepherd and Otvos 1986) which provides for the early detection of rising populations by monitoring with pheromone traps within the susceptible zone. An early treatment of threatening populations with an effective specific virus can then be applied to prevent outbreaks from reaching damaging levels.

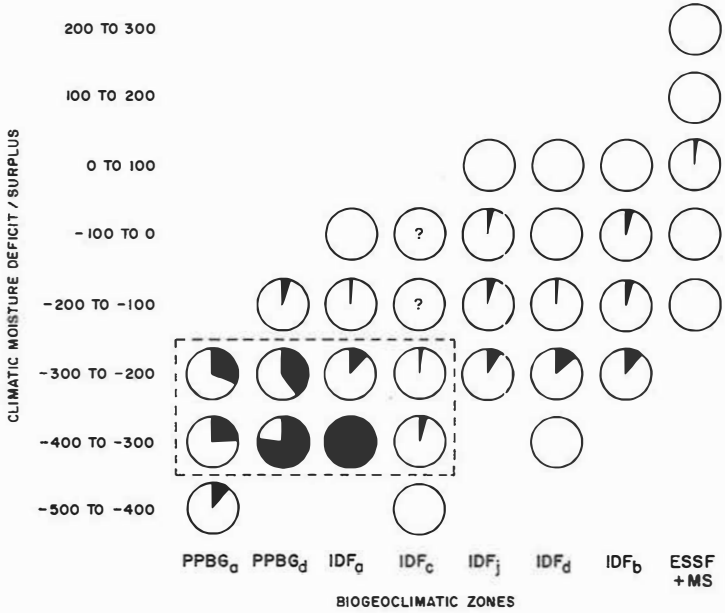

Figure 7. Cross comparison of the incidence of defoliation between biogeoclimatic zones and climatic moisture deficits. Maximum area defoliated was assigned a value of 100 and those for other cells were calculated relative to the maximum. Sample base: 586,913 ha. Box indicates cells used in x^2 test. "?" indicates data not usable.

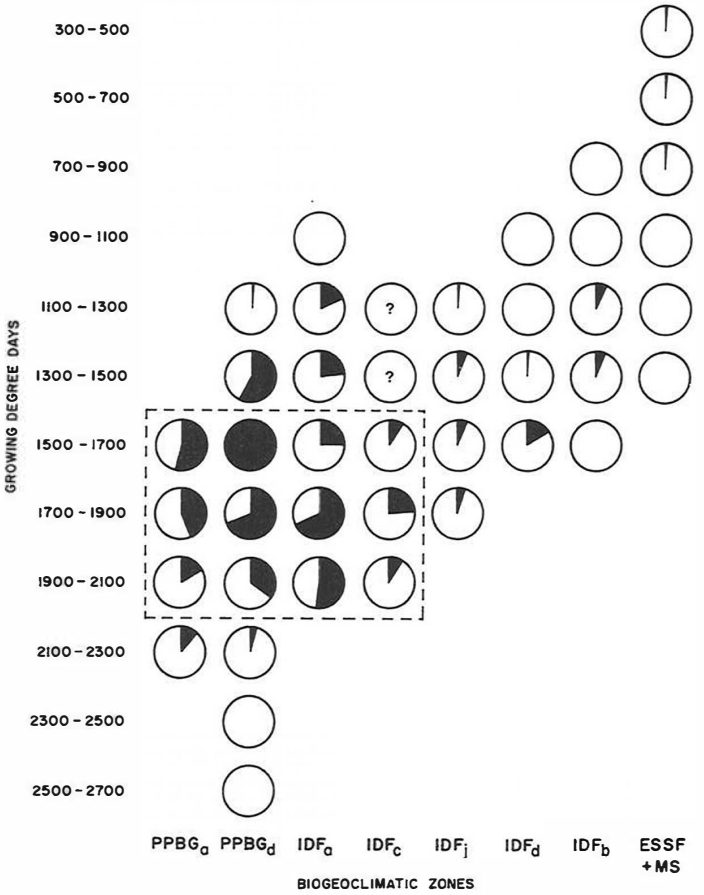

Figure 8. Cross comparison of the incidence of defoliation between biogeoclimatic zones and accumulated growing degree-days. Maximum area defoliated was assigned a value of 100 and those for other cells were calculated relative to the maximum. Sample base: 586,913 ha. Box indicates cells used in x^2 test. "?" indicates data not usable.

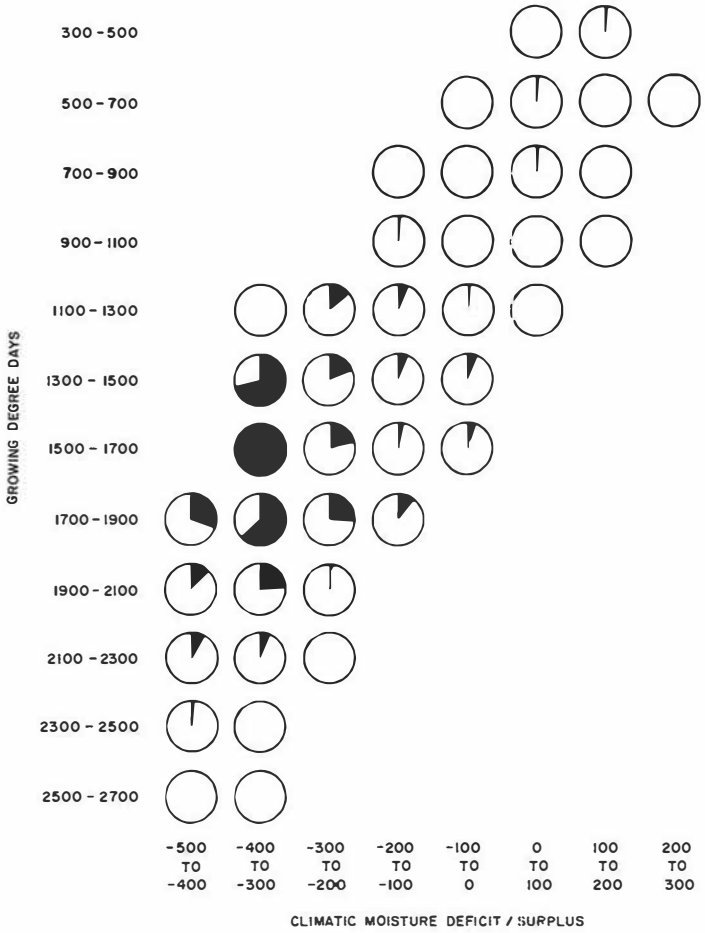

Figure 9. Cross comparison of the incidence of defoliation between zones of climatic moisture deficit and accumulated growing degree-days. Maximum area defoliated was assigned a value of 100 and those for other cells were calculated relative to the maximum. Sample base: 586,913 ha.

SUMMARY

Six outbreaks of Douglas-fir tussock moth mapped in British Columbia were overlayed on forest habitat and climatic maps to determine correspondence between defoliated areas and different ecozones. Analysis using a geographic information system indicated that outbreaks occurred most frequently in the Ponderosa-Pine Bunch grass a and d Subzones and the Interior Douglas-fir a and c Subzones. Within these stands, defoliation most often occurred where temperatures were moderate (1500 to 1900 accumulated degree-days per growing season) and where climatic moisture deficits were extreme (-300 to -500 mm per growing season). Identification of susceptible forest communities is useful for pheromone trap monitoring to detect rising populations. Knowledge of climatic conditions most prone to outbreaks is useful to understand the dynamics of the pest and to predict where and when defoliation may occur under current or future modified stand and climatic conditions.

Acknowledgements

Mr. Stuart Taylor, British Columbia Ministry of Forests, contributed considerable time on an earlier attempt of this analysis.

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

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INTRODUCTION

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

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

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

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

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

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

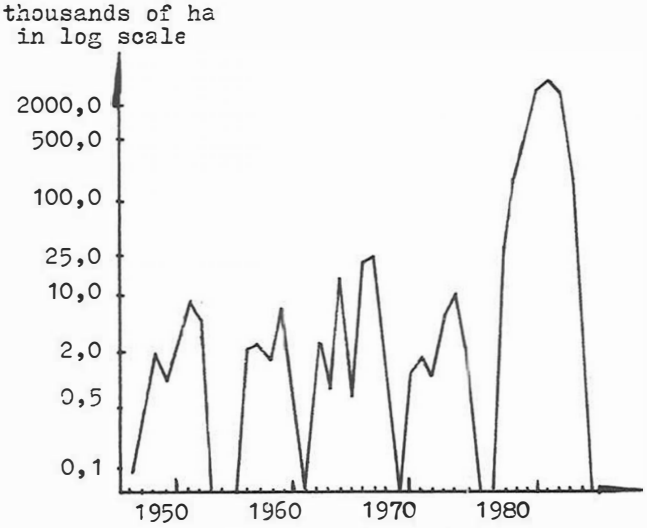


Fig.1 Area of the nun moth control in the years 1946 - 1984

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

METHODS

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

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

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

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

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

Viral Diseases

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

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

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

Bacterial Diseases

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

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

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

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

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

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

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

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

Control with the Use of B. efficiens

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

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

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

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

The first and second trials were performed in the years 1979-1980 in the Szczytno forest district. Five and 8 ha of 40-50 year-old pine stands were sprayed at 5×10^7 and 3×10^7 PIB/ml. The product was obtained from larvae bred on pine twigs sprayed with suspension of polyhedra (5×10^9 PIB/ml), kindly delivered by Dr. Edwin Donaubauer from the Federal Forest Research Institute in Vienna.

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

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

Control with the use of B. thuringiensis

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

RESULTS AND DISCUSSION

Viral Diseases

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

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

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

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

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

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

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

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

Bacterial Diseases

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

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

the reduction of resistance of caterpillars to intestinal microflora.

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

Diseases of Unexplained Etiology

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

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

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

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

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

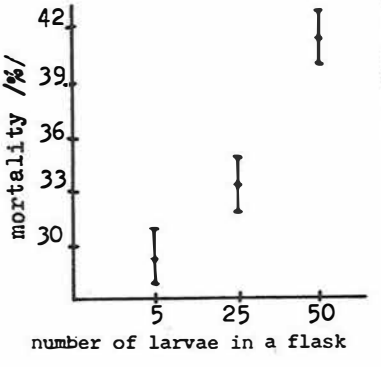
Table 1. Mortality of the nun moth and frequency of B. efficiens in the years 1982-84 (put together according to years of the outbreak)

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

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

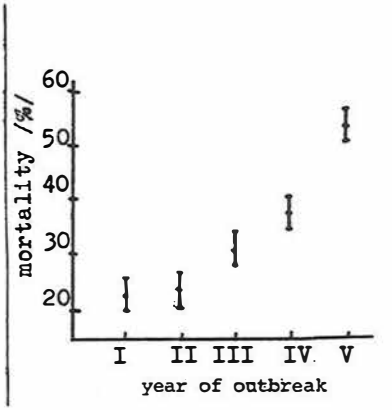
Source of variation	Degrees of freedom	Mean square	F theor. significance
a - density	2	574.9998	21.325xx
b - number of eggs	2	17.2377	0.639
c - year of mass appearance	4	1400.3549	51.935xx
Error	36	26.9638	-
Total	44	176.2857	-

xx = significance level $\alpha = 0.01$



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

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



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

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

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

Induction of Latent B. efficiens in the Laboratory

In 1982, we bred in flasks with diet 15,000 larvae originating from 152 samples of eggs collected in 50 forest districts. During 3 weeks of breeding, 4,753 (31.47%) of the larvae died. B. efficiens was observed in 260 cases; i.e., in 1.72%. In 1983, 13,625 larvae from 136 samples of eggs sent from 49 forest districts were bred. During 3 weeks, 5.944 (43.62%) larvae died; B. efficiens was observed in 103 (0.75%) cases. In 1984, the mass appearance of larvae was ending and from seven forest districts only small numbers of eggs were obtained. We bred 1,100 larvae, from which 500 (45.45%) died during 3 weeks, and viruses were found in 8 (0.72%) cases. Totally, from among 30,000 larvae bred on diet, the polyhedrosis developed in 371 larvae, amounting to 1.24%. Taking into account that the eggs for breeding were collected in pine stands, where the viruses did not occur in the previous generation of the insects and that the eggs were superficially sterilized, we can consider that the viral diseases in the first 3 weeks of breeding were caused by the induction of the latent form of B. efficiens.

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

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

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

Control with the use of B. efficiens

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

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

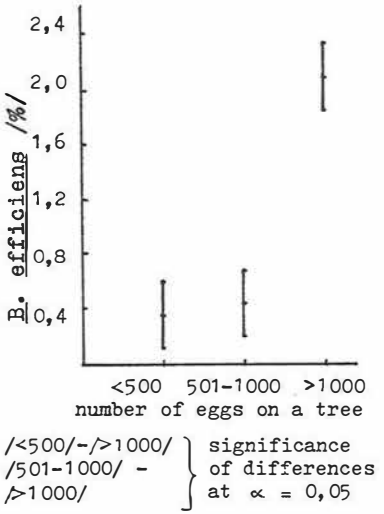


Fig. 4. Induction of B. efficiens in the nun moth depending on the number of eggs on a tree.

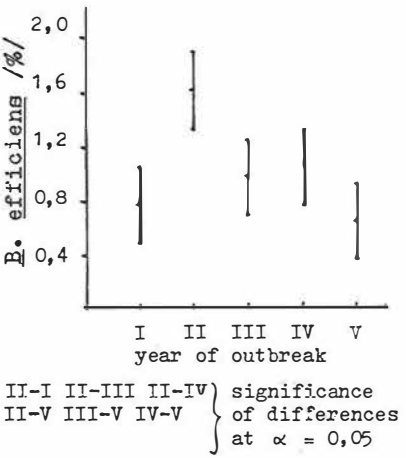


Fig. 5. Induction of B. efficiens in the nun moth depending on the year of outbeak.

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

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

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

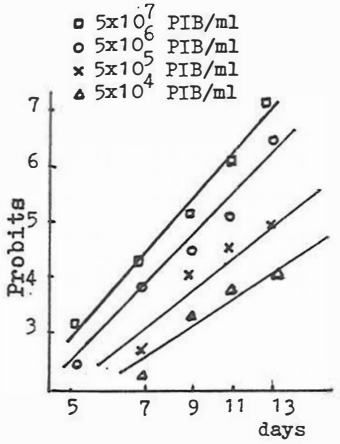


Fig. 6. Regressions of mortality of the nun moth at 4 concentrations of B. efficiens on diet.

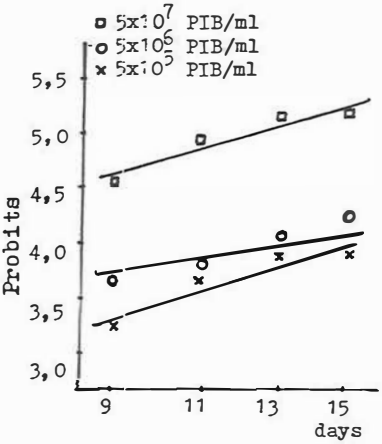


Fig. 7. Regressions of mortality of the nun moth at 3 concentrations of B. efficiens on pine trees.

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

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

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

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

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

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

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

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

Control with the use of B. thuringiensis

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

Different efficacy of control on pine and spruce resulted from varying crown coverage by the product. In the case of spruce trees with conical, long and dense crowns, even an increased dose of liquid up to 100 1/ha did not ensure sufficient coverage,and the efficacy of treatments often appeared to be unsatisfactory. In pine stands with umbrella-shaped tree crowns, good coverage was obtained at expenditure of 50 1 liquid per ha.

SUMMARY

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

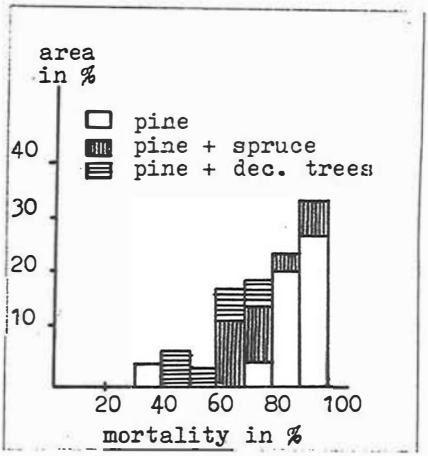


Fig. 8. Mortality of the nun moth after treatment with Bactospeine (1.2 kg/ha).

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BACILLUS THURINGIENSIS IN THE MANAGEMENT OF GYPSY MOTH POPULATION ERUPTIONS

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INTRODUCTION

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

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

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

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

DEVELOPMENT OF BT FOR USE AGAINST THE GYPSY MOTH

It was not until the early 1960's that efforts began in earnest to develop Bt for use against this major forest defoliator, even though it had been known since 1929 that this pesticide kills the gypsy moth (Dubois, 1931). But field trials were characterized by erratic, inconsistent, and sometimes unpredictable results. Timing seemed to be critical, both as it related to the development of the larvae and to weather following application; if most larvae were beyond the second larval stadium, or if rainfall occurred within a day or two after application, results of spray programs were generally judged to be unsatisfactory. Early formulations were not as potent as those currently available, and in most cases two applications were needed if there was to be any hope at all of success. Needless to say, the logistics of repeated treatments, compounded by economic considerations, mitigated against enthusiastic acceptance of Bt as the pesticide of choice. Too often treatments 'failed'--they neither reduced the numbers of larvae adequately nor did they do it quickly enough; they did not protect foliage from further consumption; they did not reduce subsequent egg mass numbers to the (rather arbitrary) goal of 125 per hectare or fewer.

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

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

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

CHOICE OF BT FOR USE AGAINST THE GYPSY MOTH

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

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

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

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

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

Environmental concerns

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

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

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

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

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

Protection goals

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

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

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

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

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

Host reservoir for natural enemies

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

Timing

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

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

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

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

Gypsy moth population density

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

Costs of application

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

Eradication of isolated infestations

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

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

CONCLUSIONS

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

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

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

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

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

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INTRODUCTION

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

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

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

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

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

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

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

METHODS

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

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

Infectivity testing. LD_{50} tests on large larvae (3rd instar and older) were conducted by feeding measured volumes of PIB suspensions dried on *C. monogyna* leaf fragments of a size which is rapidly and totally consumed by an individual larva. For smaller larvae

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

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

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

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

Spray trials: (i) post-hibernation trial. This was conducted on third instar larvae emerging from overwintering nests previously stored at 4°C. Potted *C. monogyna* plants (two/pot), *circa* 1m tall, were infested with 250 larvae per pot. A sample of these larvae was individually weighed and allocated to instar. Five trees were apportioned to each treatment and the spraying conducted inside a large draught free building, the Turbair Fox being held 2m from the line of trees and moved along the line at approximately 1.3m/sec. Five dosages were used ranging from $2x10^7$ to $2x10^9$PIB/m of spray lane. After spraying the trees were placed in a greenhouse; due to high levels of defoliation by 6 days post spray the larvae were then transferred to large plastic boxes, kept at room temperature and fed fresh foliage *ad libitum*. Ten days post spraying samples of 50 larvae were taken and and placed in smaller boxes. These were checked daily until 27 days post spraying and any dead larvae removed and diagnosed for NPV infection. Further details of this experiment can be found in Kelly *et al.* (1988).

Spray trials: (ii) pre-hibernation trial. A field trial of the virus was conducted in an area of infested *R. fruticosa* at Portsmouth. Twenty four 3m sections, each separated by a buffer zone of at least 3.5m, were marked out in a hedgerow 200m long. Existing nests were redistributed to produce 12 nests per plot. Because of variation in bush size, a stratified random allocation of treatments was employed in which each treatment group of three had one 'small', one 'medium' and one 'large' bush replicate. A series of five doses from $2x10^7$ to $1x10^9$PIB/m, was applied plus a further treatment of $1x10^8$PIB/m applied with the others on 18:9:87 and again one week later. Two control treatments were included, one unsprayed and one sprayed with the 20% Actipron carrier fluid. No dead

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

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

RESULTS

Quantitative host-EcNPV relationships. The LD_{50} was measured in four larval instars (Table 1). These values were plotted logarithmically against larval weight (Figure 1) where it can be seen that for Lepidoptera the apparently linear relationship is

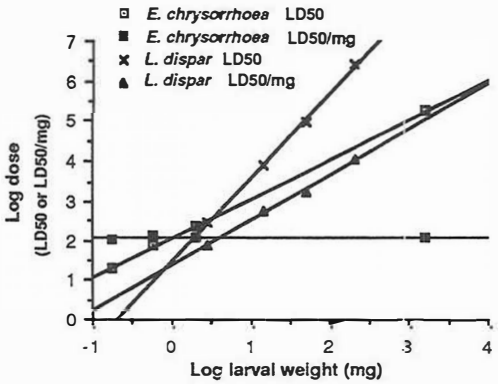

Figure 1. Relationships of log LD50 and LD50/mg with log initial body weight for *Euproctis chrysorrhoea* and *Lymantria dispar* (data for *L.dispar* from Burgerjon *et al.*, 1981).

not abnormally steep. Dividing the LD_{50} by larvae weight produced a linear relationship of zero slope against larvae weight.

EcNPV and heterologous 'hosts'. Using challenging doses of $1x10^3$ and $1x10^6$PIB to individual second instar larvae, no EcNPV replication was detected in any of 66 other species of Lepidoptera (in 11 families, including Lymantriidae) tested. Cross-infection was also absent in the honey bee, *Apis mellifera* L., and two species of sawfly.

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

Spray trials: (i) post-hibernation trial. The larvae in this trial were third instars with a mean weight of 3.2mg at the time of spraying. The development of virus-related mortality over time is shown in Figure 2 (the top dose shown is $1x10^9$PIB/m; the highest dose of $2x10^9$PIB/m gave similar results to this dose). The two top doses delivered distinct sigmoid responses of mortality against time, starting 11 days post spraying and reaching *circa* 90% by 17 days. Deaths in other doses began later and largely levelled off by 20 days. Application of probit analysis to the final virus mortality:dose relationship (up to $1x10^9$PIB/m) gave a spray LD_{50} of $1.3x10^8$PIB/m and an LD_{90} of $8.5x10^8$PIB/m.

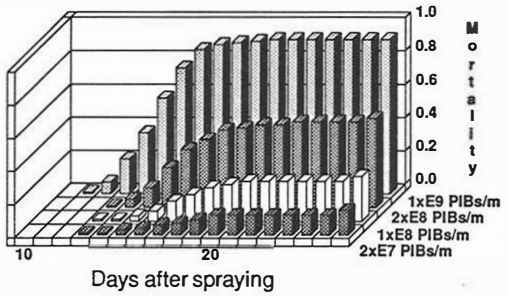

Figure 2. Virus mortality in *E. chrysorrhoea* populations on potted *C. monogyna* bushes sprayed with a series of doses in the post-hibernation trial.

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

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

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

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

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

EcNPV infection cycling and disease dispersal. Rapid defoliation of bushes in the spring led to large scale emigration of larvae. Initial densities had ranged from 332-6500 larvae/m^2, but, at ten days post introduction of infected larvae density had fallen to about 50 larvae/m^2. No relationship was found between initial density and subsequent levels of infection. Whilst larval infection, almost certainly laboratory derived, was found at ten days none was detectable after this date until 52 days after introduction when a significant second peak of infection began. However, not all bushes developed this second peak, and Figure 3 illustrates infection levels in two plots in which the peak was present. No relationship was found between the size of this second peak and the proportion of infected larvae introduced.

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

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

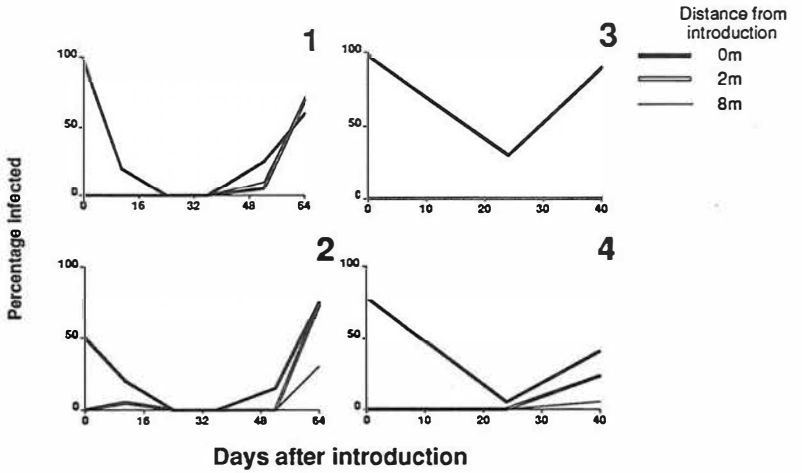

Figure 3. Examples of bushes which showed secondary infection cycles following primary introduction of laboratory infected larvae in the spring (1 &2) and in the autumn (3 & 4).

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

DISCUSSION

A highly infectious NPV isolate (i.e. low LD_{50}) is essential for good insecticidal effect, since as susceptibility decreases the quantities of virus required to establish control rapidly become uneconomic. To fully assess the infectivity of an NPV, and contrast it with others, it is necessary to study its impact throughout the host larval period. The susceptibility of lepidopterous larae to infection is known to decline strongly with increasing weight (e.g. Entwistle & Evans, 1985). However, the degree to which this occurs appears to vary greatly with different NPV-host species systems. There seems to be a generally good linear relationship between log larval weight at inoculation and log LD_{50}/unit weight (mg). The gradient of this regression and the LD_{50} *per se* of very early instar larvae (i.e. during the ideal period when NPV spraying would be conducted) provide two valuable parameters for contrast. In estimating the

effect of the virus it is, however, important to take larval feeding rate, and hence the rate at which larvae acquire virus from plant tissue, into account; larger species may well feed faster and thus compensate for an inately higher LD_{50}.

In Figure 1 the responses of EcNPV and *Lymantria dispar* (L.) NPV (LdNPV; the use of this virus is very well documented) are contrasted in terms of the mutual relationships of log LD_{50} and log LD_{50}/mg to log body weight. It is evident that, although the LD_{50} values for the various instars of *L. dispar* are much higher than for *E. chrysorrhoea*, the values of LD_{50}/mg are most favourable for the former species (data from Burgerjon *et al.*, 1981, and interpreted by Briese, 1986).

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

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

The application of EcNPV as an insecticidal spray using the Turbair Fox machine was an efficient method of control for the spring emergent larvae under the specific conditions of the trial described here (notably the lack of wind). It appears unlikely that 100% primary mortality can be achieved since a dose increase from $1x10^9$ to $2x10^9$ PIB/m resulted in no increase in mortality. Spray coverage is never likely to be totally uniform, and a proportion of larvae must escape ingestion of a lethal dose.

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

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

Post-hibernation, for reasons explained above, it was not possible to continue quantitative assessments. However, the data indicated strongly that in at least on of the replicat plots of each treatment a high level of infection had been achieved. This was particularly apparent in the next to lowest dose, $1x10^8$PIB/m, suggesting that control in the autumn could be achieved using lower doses than in the spring. It seems likely that the wide variation in the results achieved in this trial was due largely to poor spray coverage achieved on the leaves in some replicates, due to prevalent wind conditions and the orientation of the leaves. Good coverage is of particular importance in the autumn given the limited feeding area of the larvae.

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

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

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

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

SUMMARY

Larvae of the univoltine lymantriid *Euproctis chrysorrhoea* (L.), which overwinters gregariously in tents in the second or third instar, have intensely urticating hairs. They feed preferentially on woody roasaceous plants and, because of the damage inflicted and public health problem presented, are a notable pest in urban areas. In such a situation, and in nature reserves, chemical insecticidal control is unacceptable and a more specific biological approach seems appropriate. A nuclear polyhedrosis virus of *E. chrysorrhoea* (EcNPV), isolated in Britain, has an exceptional degree of host specificity and, by LD_{50} tests, seems highly infective to host larvae. Therefore, post- and pre-hibernation EcNPV spray application trials were conducted. The results demonstrated a strong primary mortality response to the virus. The nature of these trials precluded demonstration of the possibility of secondary infection cycles developing in surviving larvae of the sprayed generation. This question was separately investigated. Introduction of pre-infected larvae into the autumn and spring stages of a single generation resulted in secondary infection cycles. Collectively the data acquired will be employed to conduct control trials designed to assess the comprehensive effect of virus sprays in controlling *E. chrysorrhoea* larval infestations. EcNPV is potentially the most acceptable and practicable means of controlling this pest, especially in environmentally sensitive areas.

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EPIZOOTIOLOGY OF GYPSY MOTH NUCLEOPOLYHEDROSIS VIRUS

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INTRODUCTION

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

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

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

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

FACTORS AFFECTING PATHOGENICITY AND PERSISTENCE OF NPV

Genetic Variability

Different strains of NPV differ in their pathogenicity. When isolates from Europe, North America, and Asia were tested against a laboratory strain of gypsy moth, the LD_{50}s ranged from 1.7×10^3 to 5×10^6 OB/ml (Shapiro et al., 1984). The results of several studies in which potencies of viruses from various sources were compared were reviewed by Lewis et al. (1981).

Persistence and Plant/Pathogen Interactions

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

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

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

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

FACTORS INFLUENCING HOST SUSCEPTIBLITY TO NPV

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

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

Developmental factors can also influence host susceptibility to viral pathogens. In general, resistance increases with the age of the host (Briese, 1987). The LC_{50} for second-instar gypsy moths tested with the Hamden Standard NPV was about 200 times lower than the LC_{50} for fourth instars (Lewis et al., 1981). This age-related increase in resistance is largely accounted for by the increase in body weight in gypsy moth, however, an additional age-related factor also appears to be involved (Briese, 1987). Briese (1987) suggests that the development of specific defense mechanisms against viral infection in older insects could be involved. Other developmental factors such as growth rate, hormonal levels, metamorphosis, diapause, and stage of development may also affect host susceptibility (Briese and Podgwaite, 1985; Watanabe, 1987). Shapiro and Robertson (1987) reported that the number of OBs in infected gypsy moths was reduced 12-fold during the transformation from larva to pupa and 115-fold during the metamorphosis from pupa to adult. This suggests that metamorphosis is deleterious to virus or that adult and pupal tissues are less favorable for viral growth than are larval tissues.

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

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

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

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

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

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

FACTORS AFFECTING TRANSMISSION AND DISSEMINATION OF NPV

Transmission in Space

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

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

Woods and Elkinton, 1987). Epizootics of the disease result from increasing rates of transmission within and between generations of the gypsy moth as the host density increases. Neonates which become infected upon emergence from contaminated egg masses, die and serve as primary inoculum for uninfected second and third instars (Doane, 1969, 1976; Woods and Elkinton, 1987). A second wave of mortality occurs among older larvae as the environment becomes increasingly contaminated (Doane, 1969, 1976; Woods and Elkinton, 1987). In outbreak populations, trees may become covered with debris mats, formed by the build-up of larval silk, which accumulate larval and pupal cadavers and exuviae and also serve as oviposition sites. These debris mats and other environmental surfaces become heavily contaminated with NPV (Doane, 1976; Weseloh and Andreadis, 1986) and may serve as a source of inoculum for larvae that encounter them or for eggs deposited in them, thus altering the density-dependent pattern of transmission. After a number of years, environmental degradation of the virus reduces the inoculum to low levels until the next population cycle.

Anderson and May (1980) developed mathematical models which predict that natural populations of invertebrate hosts are regulated by the density-dependent cycling of virulent pathogens. While there is abundant evidence that gypsy moth populations are regulated at high-densities by NPV it is apparent that other mortality agents are more important at lower densities (Campbell, 1967; Campbell and Podgwaite, 1971).

Larval behavior, which is affected by population density, environment, or infection, influences transmission and dissemination of NPV. Larvae in high-density populations remain in the canopy throughout the day and night and tend to feed more during the day, in contrast to the typical diel activity rhythm exhibited by low-density larvae which feed only at night and seek cryptic resting locations during daylight hours (Lance et al., 1987).

Neonates can acquire NPV from contaminated substrates (Weseloh and Andreadis, 1986; Woods et al., in press) presumably by transferring the inoculum to their food where it is is subsequently ingested. Doane (1970) suggested that the rapid spread of NPV is enhanced by the normal behavior of early instars which results in their aggregation in the canopy. Other factors which affect larval behavior, such as weather and stage of development, could have an indirect effect on transmission, acquisition, and dissemination of virus.

Movement of infected insects also serves to disseminate virus. First instars are the primary dispersing stage as adult females are flightless. Leonard (1970) suggested that dispersal from dense populations is greater than from low-density populations. However, findings of a more recent study (Capinera and

Barbosa, 1976) were contradictory. It is apparent that certain factors do influence dispersal rates but the importance of dispersal in dissemination of NPV has not been studied.

Infection can alter larval behavior (Watanabe, 1987). The NPV disease of the nun moth was originally termed 'Wipfelkrankheit' or 'tree-top disease' because infected larvae climb to the top of trees where they die (Benz, 1963). Our observations of NPV-infected and healthy larvae on oak trees demonstrate that infected gypsy moth larvae also exhibit this altered behavior just prior to death (unpublished data).

Parasites and predators are also involved in transmission and dissemination of NPV. The parasitoid, Cotesia melanoscelus, was shown to be capable of vectoring NPV to gypsy moth larvae (Raimo et al., 1977). Infective NPV has been found in feces of avian and mammalian predators (Lautenschlager and Podgwaite, 1977, 1979), therefore, these animals may carry virus from one area to another after feeding on infected gypsy moths.

Abiotic factors, such as rain and wind, have been implicated in the dissemination of insect viruses. Rain can spread virus on plants and wash inoculum into the soil and litter. In one study the number of shoots contaminated with Douglas-fir tussock moth NPV rose from 18% before rain to 100% two days following rains (Thompson, 1978). Rain was also shown to be important in dissemination of a sawfly NPV within the tree canopy (Bird, 1961). Virus may also be carried from one area to another by wind. Thompson (1978) examined the infectivity of dust-borne Douglas-fir tussock moth virus applied to foliage. He found that dust from forested sites remained infective 10 years following an epizootic, but suggested that, except for unusual disruption of the soil such as during logging or cattle drives, wind-borne dust probably is not an important route for movement of virus back onto the foliage. The importance of wind in movement of gypsy moth NPV has not been examined. The role of precipitation in the gypsy moth system is discussed below.

Transmission in Time

Primary inoculum associated with gypsy moth egg masses is an important component in the development of epizootics (Doane, 1976; Woods and Elkinton, 1987). Much of the early literature suggested that NPV is readily transmitted from infected adults to progeny within the egg (ie. transovarial transmission) (Longworth and Cunningham, 1968; Swaine, 1966). However, conclusive evidence for this mode of transmission among the Lepidoptera are lacking (Evans, 1986). Doane (1969) showed that chemical disinfection of the surface of gypsy moth eggs reduced the incidence of NPV-caused mortality

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

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

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

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

SUMMARY

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

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

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

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IMPORTANCE OF MICROSPORIDIA IN INSECT POPULATIONS

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

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

MICROSPORIDIA OF GYPSY MOTHS

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

likely that microsporidia are widespread in European gypsy moth populations.

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

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

* Species description.

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

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

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

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

IMPORTATION OF PATHOGENS AS A BIOCONTROL STRATEGY

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

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

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

FOREIGN EXPLORATION

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

Portugal: Dr. Maria Teresa Cabral, Mr. Fernando Barbosa, and Mr. Antonio Completo
Yugoslavia: Dr. Radovan Marovic and Mr. Aleksandar Mancic
Czechoslovakia: Dr. Jiri Vavra and Dr. Jaroslav Weiser

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

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

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

CHARACTERISTICS OF MICROSPORIDIA OBTAINED FROM EUROPE

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

Table 2. Characteristics of five species of microsporidia obtained from Europe.

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

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

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

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

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

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

Regulatory Issues

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

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

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

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

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

OBJECTIVES

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

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

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

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

METHODS

Introduction Methods

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

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

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

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

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

and the intensity of infections in larvae released into the woodlot relative to the density of the feral larval population.

(5) The newly emerged larvae become infected as they exit the egg mass and exhibit their normal dispersal behavior; thus, the microsporidian infections are distributed naturally among the feral population.

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

Larval Sampling Methods

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

Method 1

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

Method 2

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

Method 3

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

Diagnosis of Infections

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

RESULTS

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

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

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

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

FUTURE STUDIES AND OBJECTIVES

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

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

Acquisition of additional microsporidian isolates.

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

Taxonomy

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

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

Laboratory evaluations

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

Field studies

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

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

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

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

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

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INTRODUCTION

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

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

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

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

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

PREDATORS AS AN AGENT IN NATURAL SELECTION

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

PREDATION AND POPULATION DYNAMICS

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

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

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

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

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

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

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

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

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

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

No./ha	Location	Percentage eaten by vertebrates	Percentage eaten by invertebrates	Percentage dead of other causes	Percentage survival
2,491	Flap	13	19	15	52
	Bole	14	17	17	52
	Litter	45	22	8	25
712	Flap	7	15	11	68
	Bole	22	19	11	49
	Litter	42	25	7	26
237	Flap	2	13	6	78
	Bole	3	14	8	76
	Litter	9	37	3	52

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

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

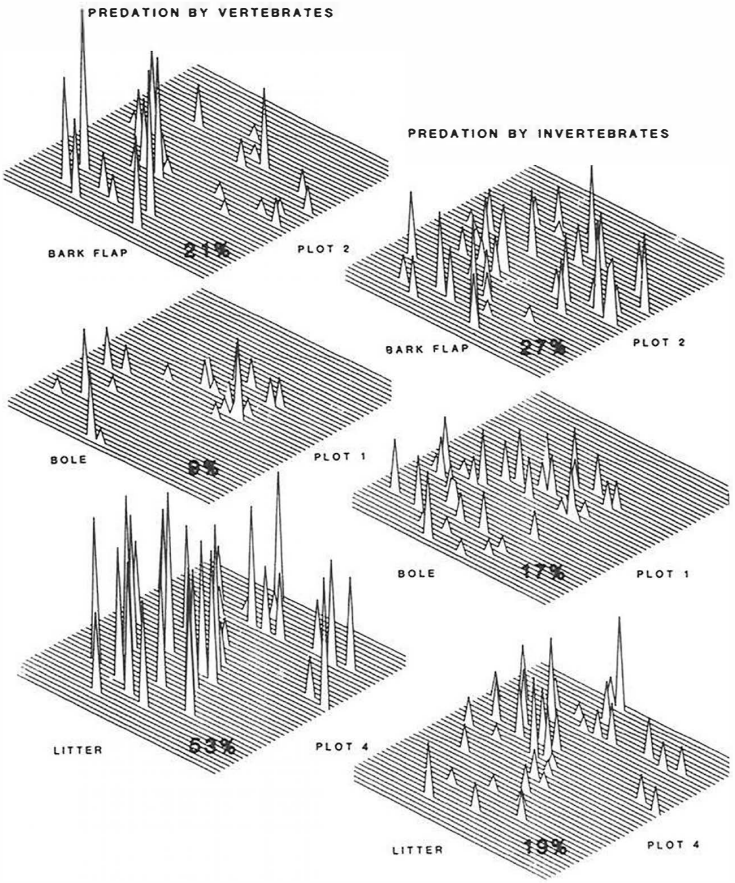

Fig. 1. Pattern and percentage of predation of gypsy moth pupae by vertebrates and invertebrates within selected microhabitats. (Peak indicates range of mortality from 1 to 12.)

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

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

Douglas-fir tussock moth
Orgyia pseudotsugata

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

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

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

PREDATION BY OTHER LYMANTRIIDAE

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

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

UNDERSTANDING MECHANISMS OF PREDATION

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

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

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

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

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

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

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

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

(n) Bryant Mountain, 1983.

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

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

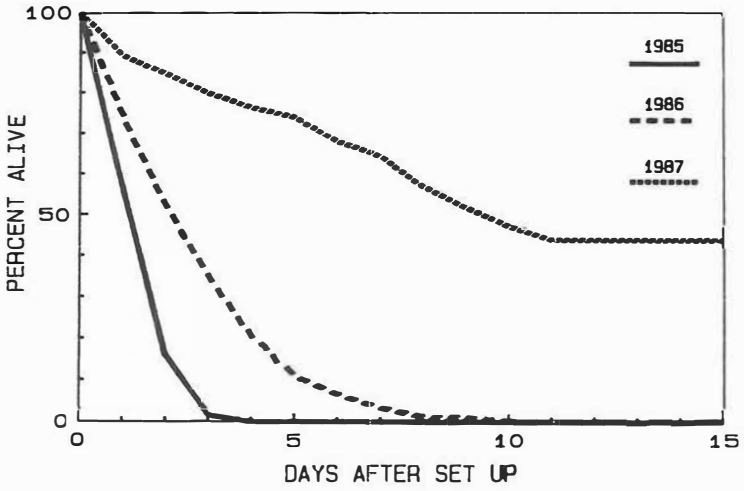

Figure 2. Survivorship curves of gypsy moth pupae in a resistant forest.

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

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

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

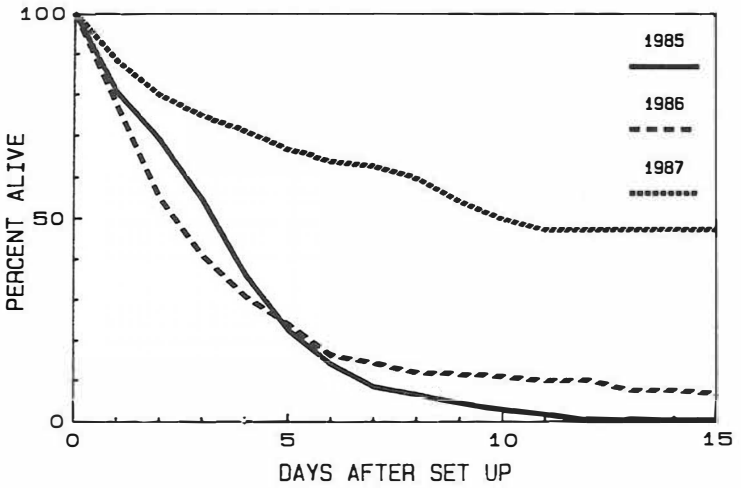

Figure 3. Survivorship curves of gypsy moth pupae in a susceptible forest.

SUMMARY

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

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

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

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

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PREDATION OF LYMANTRIIDS BY ARTHROPODS

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INTRODUCTION

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

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

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

GENERAL PREDATORS

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

CALOSOMA SYCOPHANTA, A SPECIFIC PREDATOR

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

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

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

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

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

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

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

DISCUSSION

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

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

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

SUMMARY

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

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A COMPARISON OF THE PARASITE COMPLEXES ATTACKING TWO CLOSELY RELATED LYMANTRIIDS

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INTRODUCTION

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

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

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

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

METHODS

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

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

RESULTS

Brief Description of Host Life Cycles

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

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

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

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

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

Inventory of Parasite Species

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

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

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

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

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

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

Ecological Homologues

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

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

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

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

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

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

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

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

Structure of Parasite Complexes

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Table 7. Dominant parasites of the Indian Gypsy Moth

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

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

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

Role of Parasites in Host Population Dynamics

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

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

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

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

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

DISCUSSION

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

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

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

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

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

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

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SUMMARY

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

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

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A REVIEW OF TECHNIQUES FOR MEASURING THE IMPACT OF PARASITOIDS OF LYMANTRIIDS

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INTRODUCTION

Accurately measurlng the lmpact of parasltolds on pest lnsects ls an lmportant component of entomological research. Values of percentage parasltlsm, calculated ln varlous ways, are used for purposes such as estlmatlng the effectlveness of lnundatlve parasltold releases, determlnlng the effect of management treatments on parasltlsm levels, and constructlng llfe-tables. In many studles, howèver, lnsufflclent thought ls glven to the methods used to derlve values of percentage parasltlsm and the blases that affect them (Van Drlesche 1983). For thls reason, the results of many prlor attempts to estlmate parasltold lmpact on lymantrlld populatlons are dlfflcult to lnterpret and have been generally unsatlsfactory. In addltlon, researchers have often not been sufflclently specllc when describlng methods used to obtaln values of percentage parasltlsm.

The lmpact of a parasltold on lts host populatlon can be measured ln two ways. One can measure the proportlon of lndlvlduals that enter the host stage(s) susceptlble to parasltlsm that are ultlmately attacked by parasltolds (stage-specllc parasltlsm) or the proportlon of lndlvlduals present at the beglnnlng of a tlme lnterval that are attacked durlng the lnterval (tlme-specllc parasltlsm). Most of the values of percentage parasltlsm reported ln the llterature purport to estlmate the stage-specllc lmpact of parasltolds but these values are often severely blased. These blases can be the result of elther host and parasltold populatlon phenologles and mortalltles or blases lnherent ln the method of calculatlng percentage parasltlsm. In thls paper we wlll revlew the advantages and dlsadvantages of each of four methods for estlmatlng stage-specllc percentage parasltlsm that have been used ln the past (peak sample percentage parasltlsm, "pooled"

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

Method 1: Peak Sample Percentage Parasitism

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

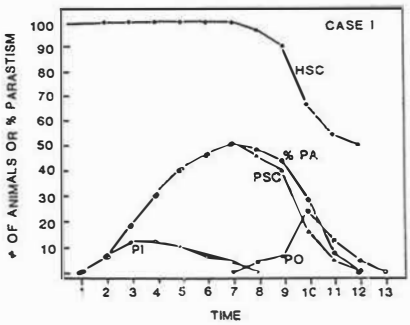

Fig. 1. Trends in sample percent parasitism values, under Case I. HSC = Host Standing Crop, PSC = Parasitoid Standing Crop, %PA = Percent parasitism, PI = Parasitoid oviposition, and PO = Parasitoid emergence. Reprinted with permission from Environmental Entomology. Copyright 1983, Entomological Society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

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

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

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

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

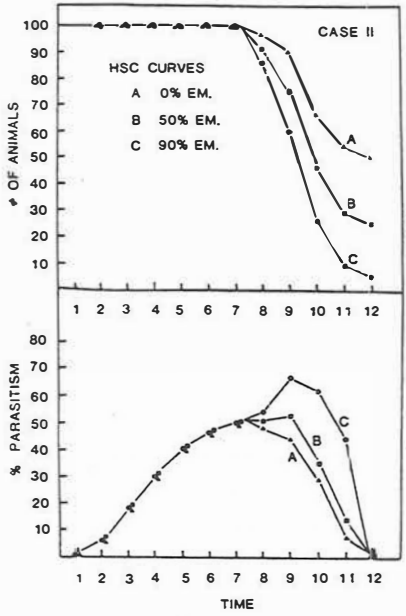

Fig. 2. Effect of early emergence (EM) of non-parasitized hosts.

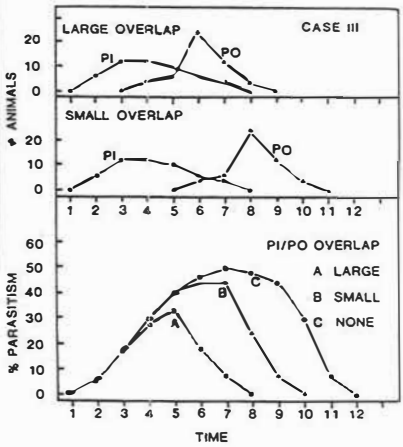

Fig. 3. Effect of overlapping parasitoid oviposition and emergence.

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

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

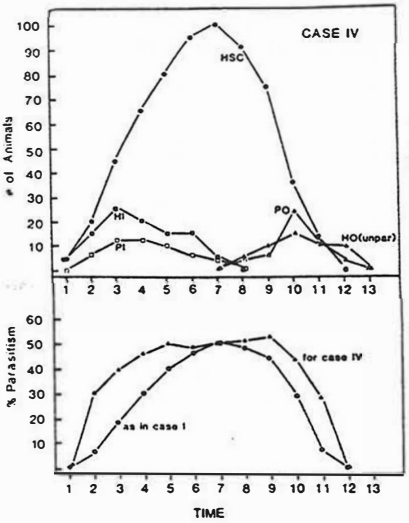

Fig. 4. Effect of gradual entry and exit of hosts.

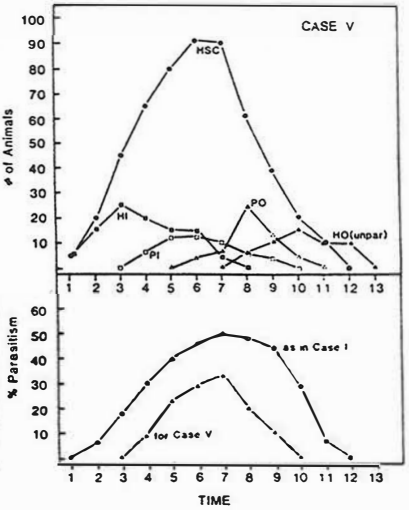

Fig. 5. Effect of competing entry and leaving rates between parasitoids and hosts.

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

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

Method 2: "Pooled" Percentage Parasitism

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

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

of estimating stage-specific parasitism levels for dynamic systems.

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

The "graphical" method of Southwood & Jepson (1962) can be used to estimate numbers of hosts, parasitoids or both that enter specified stages of a given generation (Bellows et al. 1988, 1989). To make such estimates, the number of insects per sample unit is plotted versus accumulated degree-days as measured in the field. The area under the resulting curve has units of individuals * degree-days and when divided by the number of degree-days required for complete development of an individual, estimates of the number of individuals that entered the stage are obtained. Stage-specific parasitism estimates can be constructed from this approach by dividing a graphical estimate of numbers of parasitized hosts by a graphical estimate of total hosts (in which counts of parasitized and healthy hosts are pooled). This approach assumes that being parasitized does not change the residence time of the host in the stage used to calculate total hosts, an assumption that may be true for some species and stages, but explicitly is not true for all cases. This method has been employed to date only in a few cases (Garglullo & Berisford 1983, Schneider et al. 1988, Van Driesche et al. 1989) and only once in studies of Lymantriidae (Kolodny-Hirsch et al. 1988, in a study of inundative releases of Cotesia melanoscela).

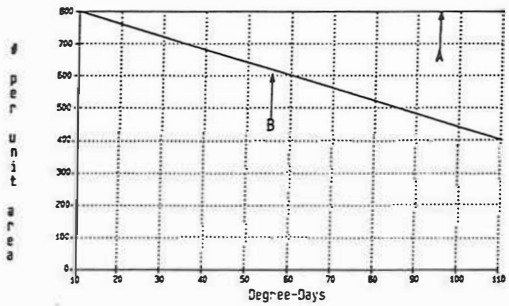

Fig. 6. The effect of mortality on estimates of the area under the curve and thus numbers entering a stage. A: No mortality B: With mortality

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

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

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

Method 4: Direct Assessment of Host and Parasitoid Recruitment

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

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

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

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

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

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

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

Method 5: Time Specific K-Value Analysis

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

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

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

DISCUSSION

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

SUMMARY

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

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MODELS FOR THE POPULATION DYNAMICS OF *LYMANTRIA DISPAR*

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INTRODUCTION

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

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

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

WITHIN-GENERATION MODELS

Phenology

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

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

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

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

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

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

Growth

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

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

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

Density, Location

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

Dispersal

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

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

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

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

Mortality Sources

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

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

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

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

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

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

Fecundity

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

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

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

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

Sex Ratio

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

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

MULTIPLE-GENERATION REGRESSION MODELS

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

Generation Trend

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

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

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

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

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

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

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

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

Egg Density

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

Egg-mass Density

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

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

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

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

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

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

MULTIPLE-GENERATION PROCESS MODELS

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

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

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

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

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

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

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

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

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

Two population models were briefly described by Etter (1981): a simplified NPV compartment model, and a more complex process model. The latter model simulated gypsy moth and host phenology, gypsy moth growth and foliage consumption, and mortality caused by NPV and by other factors. Etter (1981) reported that the process model was very sensitive to the degree of synchrony between budbreak and egg hatch, but details of this model have not been published.

To assess the influence of gypsy moths on existing oak forests, Valentine (1981) linked a forest growth model with a gypsy moth population model. Tree volume growth was modelled as a function of photosynthate production, which was assumed to decline when defoliation occurs, and respiration. Increased tree mortality was also simulated following defoliation. Valentine et al.'s (1976) model of gypsy moth growth and foliage consumption was the basis for the population model, to which mortality sources representing starvation, NPV, and other density-dependent factors were added. Application of either NPV or insecticides could be simulated. In 16-year projections with no defoliation, predicted basal area closely matched observations. The gypsy moth portion of this model was most sensitive to parameters affecting larval growth and consumption and foliage phenology.

Another forest-gypsy moth model was developed by Byrne et al. (1987) to explore potential long-term impacts of gypsy moth populations on succession in North Carolina forests. They used Johnson's (1977) forest succession model to simulate 12 forest types, each with 3 tree-size classes. Based on species composition, forest types were assigned to one of three preference groups, and gypsy moth populations were simulated using development times and mortality rates that varied with lifestage and preference group. Additional gypsy moth mortality due to first instar dispersal, starvation, and NPV was also included. For all but the least preferred hosts, this model predicted that gypsy moth populations would increase steadily until they reached densities that trigger a NPV epidemic and subsequent population crash. Forest mortality was simulated as a direct function of defoliation in the

current and previous years. Byrne et al.'s (1987) model predicted short-lived outbreaks at approximately 8 year intervals, with outbreak frequency and severity largely controlled by forest composition.

The most comprehensive forest-gypsy moth model developed to date is the Gypsy Moth Life System Model (GMLSM), which was initially developed through a series of workshops (McNamee and others, 1983) and later extensively revised and expanded (Sheehan, in press; Sheehan et al., in preparation). This degree-day model uses daily weather to drive the development of gypsy moth cohorts, foliage, and certain parasites. Within GMLSM, a stand submodel that was modified from previously existing stand models (JABOWA, from Botkin et al. [1972] and FORET, from Shugart and West [1922]) translates defoliation into effects on tree growth, mortality, and recruitment; a wide range of silvicultural treatments may be simulated. To predict defoliation, the gypsy moth submodel predicts gypsy moth growth and foliage consumption (based largely on Valentine and Talerico [1980]), foliage growth (taken from Valentine [1983a]), larval movement, and fecundity. Mortality sources that may be simulated by the GMLSM include: NPV (either naturally-occurring or applied), Bt, four predator groups, six parasite species, starvation, released pheromones, insecticides, or released sterile eggs or males. Aside from the gypsy moth and host phenology sections (Sheehan, in review), this recently-developed model has not been tested; testing will become a major emphasis in the ongoing work on this model.

SUMMARY

A wide range of mathematical models has been developed to simulate the population dynamics of gypsy moth. The primary goal of some of these models has been to forecast gypsy moth densities, while other models were developed to summarize existing knowledge, guide research, or predict what might occur in areas quite different from the current North American infestations. Two alternative approaches have generally been used: regression-based models, which use regression analyses to identify statistical relationships among observed variables, and process models, which quantify and incorporate the biological, chemical, and physical processes that affect population dynamics.

Potential users of these models often face a dilemma. Regression-based models that are available in the literature generally have been developed for only a limited number of locations and years, often include variables that can not be used in other areas (such as specific tree species with limited distributions), and cannot readily be modified to address new questions. On the other hand, process models that have been developed often include variables that are not easily measured, generally are either very complex (and difficult to interpret or evaluate) or very simple (with results obviously dictated by model structure and parameter values), and in many cases only cover a portion of the system under study. Only a small proportion of the models using either approach have been tested, especially for multiple-generation models.

Both approaches to modeling -- regression-based versus process -- have inherent strengths and weaknesses, and the best choice for a given situation depends on the objectives of the user, available data, and

current biological understanding of the system. The large number of untested models described in this review is a tribute to the need for model builders to place greater emphasis on model testing.

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NEW AND OLD WORLD LYMANTRIIDAE: DISCUSSION AND RESEARCH ISSUES

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Following each presentation, a 15-minute discussion period encouraged the expression of views and observations by participants. These discussions identified unresolved issues and indicated where additional research is necessary for their clarification. Statements made were not necessarily endorsed by all attendees and comments were recorded and later synthesized into general topics as follows.

OUTBREAK PERIODICITY

Is there outbreak periodicity for different species of Lymantriidae? In Europe, outbreaks of the nun moth are related to drought, particularly in forests that are not optimal for the insect. High summer temperatures preceded by low spring temperatures appear to be good predictors of outbreaks. There is a possible sunspot relationship for nun moth in Europe; defoliation often occurs 2 years following sunspots. In New England there appears to be local periodicity of 7-9 years between gypsy moth outbreaks. There is intensive defoliation by gypsy moth followed by years of decline. This pattern seems to occur from west to east in the state of Connecticut but has not been documented elsewhere.

The actual periodicity of gypsy moth outbreaks has not been proven. It has been suggested that periodicity shown on a spatial scale disappears when examined on a time scale. In Europe, where annual surveys of life stages of the gypsy moth are measured over the same area, periodicity of population peaks has been observed, but these peaks do not necessarily produce defoliating outbreaks. In the United States, where defoliation is used as the criterion for assessing outbreaks, population peaks are often missed and it has been difficult to demonstrate population periodicity. There is a need to look at the Eurasian and U.S. data on a similar scale (population peaks or defoliation, or both) to determine whether periodicity exists.

SYMPATRY OF LYMANTRIID SPECIES

Where there is sympatry of the brown-tail moth and the gypsy moth in Europe, the brown-tail moth tends to be displaced. The latter will relocate if gypsy moth already has stripped trees of foliage needed for egg deposition by the female brown-tail moth. This may have contributed to the decline of brown-tail moth populations in the United States. Mechanical destruction of nests has continued in the United States since the 1920's, but it is unlikely that this alone is responsible the population decline. There is no effective method for surveying areas where the brown-tail

moth once occurred and there still may be residual localized populations that have gone undetected. Pathogens introduced against the brown-tail moth may have been the primary reason for its reduction. However, habitat/host relationships appear to limit the distribution of brown-tail moth to coastal regions of Europe and the United States. Are these regions less favorable to other lymantriids so that sympatry is less intensive or is weather limiting survival to these discrete habitats? Is there evidence of other sympatric interactions, such as with Douglas-fir tussock moth and other Western United States lymantriids?

POPULATION DENSITY ESTIMATES

While protocols have been developed and others are being evaluated for low-density sampling of several lymantriid species, universal techniques are lacking. Factors that complicate this problem include differences in behavior and development of low- and high-density populations; effect of the spatial scale and forest physiography; and a poor understanding of the role of dispersal. All of these have a bearing on the size of research study areas. Dispersal also is important when assessing spray techniques. In the ridge and valley system of Pennsylvania the gypsy moth appears to have a greater range of dispersal than was previously reported. It has been difficult to evaluate spray efficacy in subsequent years because even in blocks of 1,000 hectares, reinvasion makes it difficult to distinguish the boundary of sample or treatment areas. This raises the question of the magnitude of the spatial scale of the sample area. What is the ideal sampling unit? The individual tree? A hectare plot? When sampling Lymantriidae, there always is the possibility of migration into or immigration from trees. Cooperation with other researchers to establish tests and evaluate standardized techniques internationally would be beneficial.

HOST AND STAND RELATIONSHIPS

It is generally agreed that host type, condition and stand structure influence various Lymantriidae. Yet we lack a complete understanding of these complex relationships. Host choices of the nun moth differ in various countries. In Japan, the nun moth develops fastest on larch; in Europe there are only small larch stands and nun moth outbreaks rarely begin there. Nun moth does not generally pose a problem in Western Europe, but in the French Alps, an outbreak of nun moth began on larch. Three outbreaks of nun moth are known in this century--usually triggered by a period of dry weather. However, where there are larch stands in an area of outbreak, the trees are defoliated but the larch produces new needles. When defoliation of spruce exceeds 80 percent, trees die; spruce stands are killed in the first year of the outbreak, pine trees survive one defoliation, and larch stands survive. Development of the caterpillars is faster on larch. A suggested reason for the decline in outbreaks of the nun moth on pine in the second year of defoliation is that the insect consumes the new flowering buds, which

depletes food in the following year. One generation consumes the food for the next generation causing the outbreak to die out.

The issue of the relationship of pollution and insect pests was addressed. In Oregon, there seemed to be no relationship between reduction in pollution and pest outbreaks. In fact, in recent years the worst tussock moth outbreaks have occurred despite improved air quality. The relationship between the Mount. St. Helen's eruption and a reduction in populations of Douglas-fir tussock moth and western spruce budworm is believed associated with ash deposits on the foliage.

There appears to be a similarity in host composition and stand structure in forests that are traditional epicenters for gypsy moth outbreaks. In fact, the physiography of susceptible stands in New York and Vermont are similar to outbreak sites in China and Crimea, U.S.S.R. Are there consistent habitat requirements for the Lymantriids per se? If so, how can factors associated with forest physiography be used by researchers and pest managers worldwide?

FECUNDITY

How important is the assessment of fecundity in Lymantriidae? In latent populations there is little difference in fecundity from one year to the next on a single host plant, but fecundity would vary significantly from host plant to host plant. Temperature also influences fecundity. It is not clear at what spatial scale fecundity should be calculated. Use of eggs per unit area will vary by forest type and condition. For example, species stands such as are found in Europe would probably require a different spatial scale than multispecies stands.

Do all Lymantriidae produce large numbers of eggs capable of outbreak proportions? Some species deposit their eggs intermittently (this is true of species that feed on grasses and sedges) while others deposit all of their eggs at one time. Some species are destined to outbreak; others seem to avoid it. Comparison of outbreak and nonoutbreak species on the basis of egg deposition characteristics and larval aggregations would be useful in understanding population dynamics and predicting outbreaks.

FEMALE FLIGHT

For gypsy moth, the difference between a descending flight, which more resembles a flutter of wings as the insect descends to a resting location (as found in the United States and Western Europe) and an ascending flight, where the insect can choose a variety of egg deposition sites, (as found in Eastern U.S.S.R. and Asia) is not clearly understood. There appears to be diminution in flight ability from Eastern to Western U.S.S.R. and only flightless females are found in the Federal Republic of Germany. One would expect that in those cases where the female has lost the ability to fly, dispersal is not lost but shifts to a different life stage, such as first-instar larvae. In Japan, deposition of egg masses by flying females is not affected by density. Nothing is known about the

genetics of flight in the overlap zone in the Soviet Union, where some females fly and others do not. Information is needed on the ecological correlates of wing reduction and dispersal and mate finding. Patterns of defoliation associated with difference in flying and nonflying female gypsy moth populations need to be assessed with respect to adult flight and vagility.

BIOLOGICAL CONTROL

Is biocontrol successful? Some parasites introduced into the United States are successful against several Lymantriids. However, there has been no documentation that parasites have been instrumental in reducing outbreaks or maintaining Lymantriid species at low levels. It is not clear whether the recent change in distribution and behavior of the brown-tail moth on Cape Cod, Massachusetts is due to the collapse of unknown control factors or whether a period of adjustment is required before an introduced pest increases dramatically.

What is considered "unknown" mortality by Tachinids might be overlocked. This would occur when a parasite attacks a larva that dies without producing a parasite. The difference between mortality in sites which favor Tachinids and those that do not might be correlated with this unassessed mortality.

There is considerable concern about the methods of determining percent parasitism. In the past, parasitism has been expressed as either the highest sample percent parasitism value or an average of all sample values. Since there are often large biases associated with these methods, a new method has been developed which uses "K values" which are calculated for short periods of time and added together to give the total impact of the parasitcid. It is apparent that there is a need for uniformity in reporting parasite assessments both in the field and the laboratory.

What is the proper spatial area to measure and what resolution is most appropriate for parasites? Should they be studied at a different resolution than that for predators? In fact, habitat has significant effects on the predator community in that extreme differences can be expected within short distances. Thus, the role of predators must be evaluated carefully with respect to habitat variation.

How should predation be assessed? For example, some small mammals are effective insect predators that in turn are preyed on by other animals. These relationships must be understood as insect management schemes are developed. This is true for the deployment and assessment of bird nest boxes as nest boxes may be used by animals other than those intended.

With the use of Bacillus thuringiensis (Bt) there is the problem of extended egg mass hatch period combined with a short effective period of Bt in the field. In the Western United States, 3-4 applications are used in field trials. The terrain in treated areas often encompasses a range of elevations. This makes it difficult to monitor individual sites where the geographic area is large and the hatch is sparse. An important question is why spray programs are not initiated before pest populations become too large. The answer seems

to be that it is difficult to obtain a financial commitment for such programs when populations are low. In the Northeastern United States much of the land is privately owned, making it difficult to obtain the necessary cooperation.

Should virus control be attempted for the brown-tail moth? In one report, the treatment area was 10-20 square meters. It is too early to determine whether virus control is economical. Reporting of results should be uniform as differences in formulation and application must be taken into account. Also, dosage (weight or international units) should be reported consistently.

The methodology of treating gypsy moth eggs with NPV varies. In the Federal Republic of Germany, there is no attempt to treat all of the egg masses--just enough to transport the virus into the population. This was recommended for isolated infestations. It is not recommended for large gypsy moth outbreak areas.

Infection of adults by gypsy moth NPV has not been determined completely. A sublethal dose of NPV fed to larvae with no evidence of NPV in the next generation does not necessarily mean the virus was not transmitted. Efforts should be made to determine the presence of the virus in the adult (female) stage of generation one.

Microsporidia evaluation is ongoing and needs input from studies of other populations in Europe. There is a need to clarify the taxonomy of the isolates on hand. The role of introduced microsporidia into North American gypsy moth populations requires careful assessment. Possible adverse effects from introduced microsporidia include: sublethal effects such as lower percent hatch, reduced fecundity, higher mortality of progeny in infected females, and poor mating of males. Spatial and temporal effects of microsporidia may have an impact on other factors such as parasitism and overwintering. Research on the spread of microsporidia from inoculated areas is being considered in the United States. Currently, only isolated infestations can be treated. In the laboratory, these microsporidia infect other Lepidoptera. But even though they could infect another host, microsporidia may not necessarily cause an epizootic. How microsporidia move between species would be an important line of international research.

GENETICS

Is the gypsy moth polymorphic since there are several known races? Controversy exists over the application of this term to certain insect species since polymorphism, when defined loosely as "distinct forms" conflicts with the classic genetic definition of "single gene difference." There is a need for a more accurate definition of terms.

There is a possibility (unconfirmed) that some gypsy moth escapees from Asia to the Western United States were not eradicated. However, they may not be identified easily if they occur in low numbers. The goal is to delineate the populations in Asia to see what differences can be identified. Genetic markers can answer some of the questions of origin if one is willing to devote the time and money involved. Through collaboration it is possible to look at populations from a genetic point of view for Oregon or other

subpopulations of gypsy moth in the United States. It has been suggested that no difference would be found without the use of high-resolution genetic analysis. The techniques for this analysis have been refined and now there is a need for samples from diverse areas. There are problems involved in crossing different populations of gypsy moth for control purposes. Genetic manipulation has inherent problems and it has been suggested that this is not a viable strategy. This is an area of research which would require a multinational cooperative effort.

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Thirty-four papers on biology and population dynamics of lymantriid moths presented at an international conference, plus a summary and discussion of research issues.