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MORTALITY FACTORS OF SATIN MOTH, *LEUCOMA SALICIS* [*LEP.* : *LYMANTRIIDAE*], IN ASPEN FORESTS IN MAINE (1)

T. L. WAGNER (2) & D. E. LEONARD

Department of Entomology, University of Maine, Orono 04469, U.S.A.

Natural control agents of the satin moth, *Leucoma salicis* (L.) were examined in 2 *Populus grandidentata* MICHAUX stands. Highest mortality occurred in overwintering larvae, with the causal agents 2 fungi, *Paecilomyces* sp. and *Hirsutella gigantea* PETCH, a factor causing death symptomatic of a pathogen, the parasite *Eupteromalis hemipterus* (WALKER) and death from unknown causes. Mortality from *Paecilomyces* sp. and *E. hemipterus* was reduced where overwintering sites were covered with burlap cloth. Parasites recovered from larvae and pupae included the braconids *Apanteles melanoscelus* (RATZEBURG) and *Meteorus versicolor* (WESMEAL), the ichneumonid *Coccygomimus pedalis* (CRESSON), the tachinids *Compsilura concinnata* (MEIGEN), *Carcelia laxifrons* VILLENEUVE, *Tachinomyia variata* CURRAN, and the sarcophagids *Sarcophaga aldrichi* PARKER and *Agria housei* SHEWELL. Larval and pupal predators included the carabid *Calosoma frigidum* KIRBY, pentatomids, and birds, particularly black-billed cuckoos, *Coccyzus erythrophthaimus* (WILSON). Eggs were parasitized by the scelionid *Telenomus* prob. *californicus* ASHMEAD and the trichogrammid *Trichogramma minutum* (RILEY). Predators of adult satin moths included the hermit thrush, *Hylocichla guttata* (PALLAS), and pentatomid bugs.

The satin moth, *Leucoma salicis* (L.), has been a periodic pest of ornamental poplar and willow species in eastern North America since its discovery in Massachusetts in 1920. Unlike Europe and Asia, where satin moth outbreaks have long occurred in forested areas, outbreaks in eastern North American forests appear to be a recent occurrence. Between 1966 and 1976, periodic outbreaks of satin moth were observed in stands of bigtooth aspen, *Populus grandidentata* MICHAUX, in north central Maine U.S.A. CLARKE & PARDY (1971) reported that many outbreaks of satin moth have occurred since 1953 in stands of trembling aspen, *Populus tremuloides* MICHAUX, in Newfoundland, Canada.

Because satin moth defoliation of Maine aspen forests was unique, we undertook studies of this insect to examine aspects of mating, oviposition and flight (WAGNER & LEONARD, 1979a), host preference (WAGNER & LEONARD, 1979b), and mortality factors. We report here the results of sampling satin moth populations in 2 aspen stands between fall

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(2) Present address: Department of Entomology, Texas A & M University, College Station 77843.

1974 and summer 1976. Our objectives were to record the mortality factors, determine the amount of mortality caused by each, and to evaluate the effectiveness of native and introduced parasites.

MATERIALS AND METHODS

STUDY SITES. Two 1 ha study sites separated by about 5 km were selected in bigtooth aspen stands in Piscataquis County, Maine. Stand 1 (S-1) was light to moderately stocked with aspen and contained many dead trees. Aspen trees had an average diameter at breast height (dbh) of 15.7 cm and an average height of 15.5 m. Light regeneration of *Abies balsamea* (L.), *Betula papyrifera* MARSHALL, and *Prunus pensylvanica* L. formed an open condition beneath the aspen canopy. Satin moth defoliation was 80 to 100 % in 1975 and 30 to 60 % in 1976.

Stand 2 (S-2) was moderately stocked with aspen which averaged 15.6 cm dbh and 17.0 m height. Regeneration of *Fagus grandifolia* EHRHART and *Acer pensylvanicum* L. formed a closed understory canopy at 9.5 m. S-2 was situated on a north-facing slope, and was cooler than S-1. Satin moth population densities were low during 1975 and 1976, with no noticeable defoliation in either year.

DIAPAUSING LARVAL SAMPLES. Diapausing larvae were counted and collected from north- and south-facing areas of the bole of bigtooth aspens. Causes of mortality were identified and recorded in the field when possible, or larvae were taken to the laboratory for diagnosis. Sampling was as follows:

Thirty trees were selected in S-2 in fall 1974 with diapausing larvae sampled at 30 to 60 and 120 to 150 cm bole heights.

Thirty trees were sampled in each stand in spring 1975 with sample areas restricted to patches of bark 150 cm^2 at heights of 40 to 55 and 150 to 165 cm. Sixty trees were sampled in fall 1975 and spring 1976, with sample areas on 30 trees covered with 150 cm^2 burlap cloth in July prior to the onset of larval diapause. Trees covered with burlap were first cleaned with a wire brush at heights of 40 to 55 and 150 to 165 cm, and at 285 to 300 cm on 15 trees.

Student's t-tests were performed ($P = 0.05$) to determine overwintering site preference on the bole. Where variances differed, Cochran's approximation tests were performed (SNEDECOR & COCHRAN, 1967).

LARVAL AND PUPAL SAMPLES. Beginning with feeding in May, satin moth larvae, and subsequently, prepupae and pupae were collected at 5 day intervals from the bole and branches of 10 to 15 aspen trees in each stand. The number of satin moths in each stadium was recorded. In 1975, groups of satin moth larvae were reared on fresh aspen foliage in 10 × 2 cm plastic Petri dishes until parasites or adult satin moths emerged. In 1976, larvae were dissected and the parasites were identified using descriptions of CROSSMAN (1922) and MUESEBECK (1918). Prepupae and pupae were held individually in 30 ml plastic cups until parasites or moths emerged.

Adult parasites emerging from satin moths were preserved in ethanol for identification. Puparia of dipteran species undergoing diapause were held at $1°$ to $3°C$ for 6 months in a desiccator containing saturated NaCl solution. After cold storage, puparia were held at room temperature for adult emergence.

EGG SAMPLES. Satin moth egg clusters were counted at 0 to 1, 3 to 4, 6 to 7, and 9 to 10 m heights on 25 aspens in S-1 and 20 aspens in S-2 prior to egg hatch. A portion of the egg clusters were collected in 1975; however, due to the low number of clusters in 1976, additional clusters were collected from outside the sampling area. All clusters were placed in capped 30 ml plastic cups and held for 8 weeks when the number of hatched, unhatched, and parasitized eggs was recorded.

PREDATOR SAMPLES. Observations of predation were recorded while sampling all life stages of the satin moth. Whenever possible, predators were collected and preserved for identification.

RESULTS AND DISCUSSION

OVERWINTERING LARVAL MORTALITY. The satin moth is univoltine with a split-season life cycle (fig. 1). Eggs were laid in late June and early July, and hatched in about 2 weeks. Mean egg hatch was delayed about 1 week in 1976, until July 21. First and 2nd stage larvae skeletonized leaves during July and August, after which the newly molted 3rd stage larvae formed hibernacula and entered diapause. Diapause lasted about 9 months, during which time a high degree of mortality occurred (table 1).

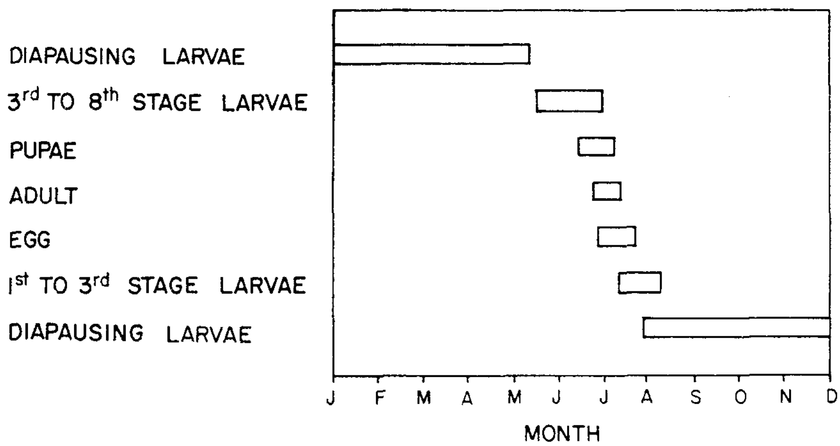

FIG. 1. Generalized life cycle of satin moth in north central Maine.

Two species of fungi [*Fungi Imperfecti* : Moniliales] were recovered from overwintering larvae, *Paecilomyces* sp. and *Hirsutella gigantea* PETCH. Mortality from *M. gigantea* never exceeded 2 %. Mortality from *Paecilomyces* sp. was generally highest in fall samples (table 1). Where overwintering sites were covered with burlap, larval mortality from *Paecilomyces* sp. was reduced about 3 to 6 fold. This reduction in mortality may be due to limiting larval exposure to this pathogen by scraping and covering overwintering sites.

A major contributor to overwinter mortality in S-1 in both sample years and in S-2 in 1976 was a factor symptomatic of disease. Cadavers retained their shape, but were soft and flexible. When mechanically distended, cadavers did not return to their original shape. Electronmicrographs of dead larvae taken by Dr. JEAN ADAMS (U.S. Department of Agriculture, Beltsville, Maryland) revealed small, unidentified bodies, primarily in the hypodermis, which were absent in healthy larvae. Dead larvae displaying these symptoms were most prevalent in spring samples and in S-1 where the population density of larvae was higher (table 1).

Larvae dead from unknown causes contributed substantially to the total mortality of overwintering larvae, with the percent mortality in each site higher in samples taken in the spring (table 1).

TABLE 1

Percent mortality of diapausing satin moth larvae from disease and Eupteromalis hemipterus *in samples with and without burlap coverings*

		% mortality due to:					
Stand and sample date	Sample size ([a])	*Pacilomyces* sp.	*H. gigantea*	"Disease"	Unknown	*E. hemipterus*	Total
S-1 —	—	—	—	—	—	—	—
Sites with no burlap:							
May 11, 1975	824	8.0	—	53.2	18.6	2.2	81.9
Nov. 21, 23, 1975	469	30.3	1.0	1.1	17.3	10.0	59.7
May 9, 1976	606	23.8	0.9	12.5	50.3	5.8	93.4
Sites with burlap:							
Oct. 24, 25, 1975	1427	7.3	—	0.6	5.7	0.3	13.9
May 6, 1976	1138	3.5	0.9	59.9	8.3	0.1	72.7
S-2							
Sites with no burlap:							
Nov. 10, 1974	750	39.6	—	0.0	24.3	5.5	69.3
May 9, 10, 1975	733	51.6	—	0.2	30.7	3.1	85.7
Nov. 1, 2, 1975	232	38.8	1.3	0.0	22.4	10.8	73.3
May 11, 1976	251	24.3	2.0	2.0	53.0	10.4	91.6
Sites with burlap:							
Oct. 31, 1975	928	11.7	0.9	0.0	5.9	0.0	18.5
May 1, 4, 1976	1247	7.3	2.1	30.7	10.4	0.1	50.6

(a) Based on all satin moth larvae sampled at overwintering sites except those parasitized by *Apanteles melanoscelus*.

The introduced external parasite, *Eupteromalis hemipterus* (WALKER) (= *nidulans* (THOMPSON)) *(Hym.: Pteromalidae)*, attacked overwintering larvae in both stands. Generally 1 parasite/host was found, but occasionally 2, and rarely 3 parasites were found on a host. Mortality from *E. hemipterus* ranged from about 5 to 11 % in fall samples, and 2 to 10 % in spring samples (table 1). Greater percent mortality was observed during the 2nd winter. Parasitism of larvae in sites covered with burlap never exceeded 0.3 %, possibly for the same reason pathogen mortality was reduced at these sites.

Observations from New England (PROPER, 1931) and Europe (BROWN, 1931) showed 2 generations of *E. hemipterus* in the fall. Whether *E. hemipterus* overwintered as pupae was not clearly documented. PROPER (1931) placed pupae of *E. hemipterus* in the field in December, and recorded adult emergence in the spring. Our data show *E. hemipterus* overwintered as both larvae and pupae. Of 47 *E. hemipterus* collected in S-1 in fall 1975, 40 % were pupae. The following spring, 49 % of 35 *E. hemipterus* were pupae. In S-2, one of 25 (4 %) *E. hemipterus* was a pupa in fall 1975, whereas 18 of 26 (69 %) were pupae in spring 1976.

Two unidentified species of hymenopteran hyperparasites and *Paecilomyces* sp. were recovered from *E. hemipterus*.

Winter mortality, excluding that caused by parasites, was not influenced by the location of hibernacula on the tree bole (table 2). The mean number of diapausing larvae

TABLE 2

Mean number of diapausing satin moth larvae and percent mortality ([a]) *found in 150* cm^2 *at different tree bole locations in spring and fall*

Stand and sample location on tree bole	Non-burlap-covered sites						Burlap-covered sites		
	Spring 1975			Fall 1975 & spring 1976			Fall 1975 & spring 1976		
	No. of sites	$\bar{X}$ larvae/ site ± S.E.	% Mortality	No. of sites	$\bar{X}$ larvae/ site ± S.E.	% Mortality	No. of sites	$\bar{X}$ larvae/ site ± S.E.	% Mortality
S-1									
40- 55 cm ht	60	1.0 ± 0.25 (b)	62.7	122	1.0 ± 0.15 (b)	80.0	118	15.7 ± 2.15 (b); (b)	64.0
150-165 cm ht	60	13.3 ± 1.71 (b)	78.0	122	8.7 ± 0.89 (b)	78.0	124	4.7 ± 0.69 (b); NS	81.8
285-300 cm ht	—	—	—	—	—	—	60	4.7 ± 0.89 NS; (b)	66.1
North	60	7.8 ± 1.65 NS	78.4	122	6.3 ± 0.89 (b)	80.1	151	12.8 ± 1.73 (b)	67.2
South	60	6.4 ± 1.23 NS	75.1	122	3.4 ± 0.48 (b)	73.8	151	5.3 ± 0.68 (b)	70.1
S-2									
40- 55 cm ht	60	5.7 ± 0.85 NS	79.4	120	3.0 ± 0.25 (b)	68.7	116	10.2 ± 1.10 (b); (b)	36.2
150-165 cm ht	60	6.7 ± 0.67 NS	83.6	120	1.5 ± 0.21 (b)	78.0	117	7.4 ± 0.80 (b); NS	50.4
285-300 cm ht	—	—	—	—	—	—	62	8.3 ± 1.23 NS; (b)	43.2
North	60	5.7 ± 0.86 NS	83.6	120	2.1 ± 0.23 NS	76.0	148	9.8 ± 0.95 (b)	40.9
South	60	6.6 ± 0.65 NS	80.1	120	2.4 ± 0.25 NS	68.9	147	7.6 ± 0.71 (b)	45.4

(a) Based on larval mortality observed during spring samples excluding parasitism.
(b) Means are different at the 5 % level.

per sample site, however, varied with location on the bole. Most larvae in S-1 were at 150 to 165 cm height where lichen occurred. Lichen was absent in S-2 and larvae were distributed more evenly. Larvae favored lower sites where burlap was used. The higher incidence of larvae in lichen and under burlap suggests that larvae select more sheltered sites for overwintering. REEKS & SMITH (1956) reported that the distance from the foliage to the overwintering site was largely a function of the roughness of the bark. Roughened bark is more prevalent on the lower portion of bigtooth aspen boles.

MORTALITY TO POST-DIAPAUSE LARVAE AND PUPAE. Third stage larvae began to emerge from hibernacula on May 10, 1975, a week before aspens foliated. In 1976, 3rd stage larvae were first observed on May 11, but aspen foliation was delayed, probably by cool temperatures, until May 25 in S-2 and May 30 in S-1. Larval feeding occurred at swollen buds prior to leaf expansion, but larval development was slowed particularly in S-1. Although we have no data to substantiate the effect of delayed bud break on satin moth populations, satin moth numbers may have been affected by lengthening exposure of larvae to mortality agents.

The life cycle of *Apanteles melanoscelus* (= *solitarius*) (RATZEBURG) on satin moth in north central Maine is complex (fig. 2). Of 310 *A. melanoscelus* sampled as coccons from overwintering sites in both study areas during fall 1975, 61 % had emerged, 30 % were dead, and 9 % were alive. Similar results were obtained the following spring, with 57 % of 405 cocoons empty, 37 % dead, and 6 % alive. These and observational data suggest a partial summer generation of *A. melanoscelus* which emerged from 3rd and occasionally 4th stage hosts in late July and early August. Adults from this generation presumably oviposited in pre-diapausing satin moth larvae. These data also indicate that *A. melanoscelus* overwintered as prepupae in cocoons; however, dissection of diapausing satin moth larvae showed that *A. melanoscelus* commonly overwintered as larvae in hosts. *A. melanoscelus* rarely emerged from diapausing larvae in spring, but typically emerged from 5th stage hosts between May 31 and June 12, 1975. Emergence was delayed in 1976 when satin moth development was slowed, probably by cool temperatures and delayed leaf-bud break. Few *A. melanoscelus* emerged from 6th or 7th stage hosts. These were either 1st generation parasites produced by adults emerging from overwintering cocoons, or perhaps 2nd generation parasites from adults issuing from earlier stage larvae. *A. melanoscelus* emerging from 5th to 7th stage hosts attacked 1st and 2nd stage larvae in July.

The life cycle of *A. melanoscelus* on satin moth in Maine differs slightly from that found in other areas of North America. In the Canadian Maritimes, REEKS & SMITH (1956) found that 92 % of *A. melanoscelus* overwintered as prepupae in cocoons, with the remainder overwintering as larvae in hosts. Adult parasites emerging in spring attacked post-diapause satin moth larvae, with the 2nd generation adults attacking pre-diapause larvae in late July. In British Columbia, LEJEUNE & SILVER (1961) found *A. melanoscelus* overwintered as larvae in hosts, or rarely as prepupae in cocoons. Emergence and oviposition occasionally occurred before the onset of cold weather. Parasite development was rapid in spring after hosts became active, with adults emerging about mid-May. Some adults of the 2nd generation oviposited on late stage host larvae, but most attacked pre-diapause larvae of the next generation.

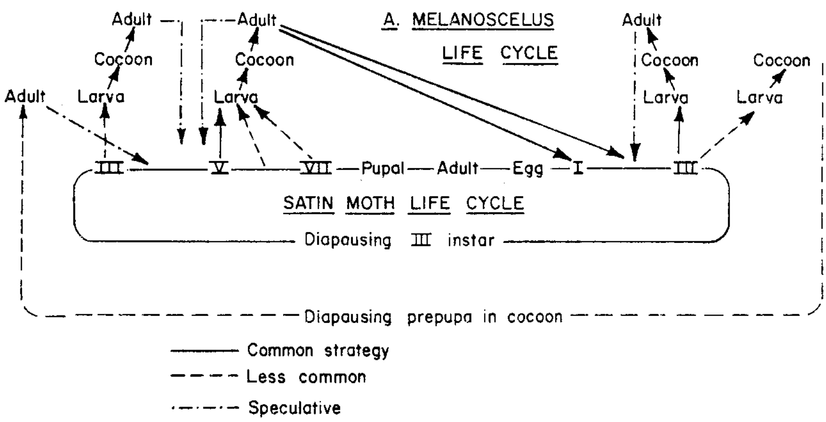

FIG. 2. Life cycle of *Apanteles melanoscelus* on the satin moth in north central Maine.

Percent parasitism by *A. melanoscelus* to 5th stage larvae was 12 % in S-1 and 14 % in S-2 during 1975, an increase from that observed in overwinter larval samples (table 3). The following summer, parasitism dropped to 3 % in S-1 and 4 % in S-2. Parasitism of late stage larvae was very low in both stands. The cause for the decline in percent parasitism by *A. melanoscelus* in S-1 from 5th to 3rd stage hosts in 1975 (table 3) is unknown. High satin moth population density prevailed into the 2nd generation in summer 1975 which may have reduced the percent parasitism. A similar decline in percent parasitism was not apparent in S-2 where populations remained low.

A 2nd braconid parasite, *Meteorus versicolor* (WESMEAL), is bivoltine with larvae of the 1st generation emerging from 4th stage hosts in late May, 1975 and mid-June, 1976. Adults emerged from cocoons 7 to 8 days later. Second generation *M. versicolor* emerged from 7th and 8th stage hosts, with adults ovipositing on pre-diapause larvae. Over-

TABLE 3

Percent parasitism of satin moth larvae by Apanteles melanoscelus

	Stage of host					
	Diapausing III		V		VI-VII	
Collection site and year	No. of hosts	% parasitism	No. of hosts	% parasitism	No. of hosts	% parasitism
S-1						
1975	854	3.5 (a)	206	11.7	213	0.0
1975-1976	3901	6.7 (b)	993	2.6	580	0.5
S-2						
1974-1975	1491	0.5 (b)	173	14.5	166	0.6
1975-1976	3112	14.6 (b)	825	4.1	312	0.6

(a) Spring sample only. See table 1 for sample date.
(b) Fall and spring samples. See table 1 for sample dates.

wintering occurred in the host. This life cycle corresponds to that found in British Columbia (LEJEUNE & SILVER, 1961) and Europe (BROWN, 1931).

REEKS & SMITH (1956) and SAILER (1972) stated that attempts to establish *M. versicolor* in eastern North America on the satin moth had been relatively unsuccessful. This has not been the case in Maine. Percent parasitism by *M. versicolor* in S-2 increased from 1st to 2nd generation and from 1975 to 1976, but a similar pattern was not observed in S-1 (table 4).

TABLE 4

Percent parasitism of satin moth larvae and pupae by Meteorus versicolor *and dipteran spp.*

	M. versicolor				Dipteran parasites		
	IV		VII-VIII			VII-VIII	Pupae
Collection site and year	No. of hosts	% parasitism	No. of hosts	% parasitism	No. of hosts	% parasitism	% parasitism
S-1							
1975	98	3.1	213	0.5	602	0.0	3.2
1976	693	2.9	580	2.9	873	4.9	21.3
S-2							
1975	92	5.4	166	17.5	280	1.1	4.6
1976	647	6.6	312	21.2	308	1.3	9.4

A number of dipteran parasites, including *Compsilura concinnata* (MEIGEN), *Carcelia laxifrons* VILLENEUVE, *Tachinomyia variata* CURRAN *(Tachinidae)*, *Sarcophaga aldrichi* PARKER, and *Agria housei* SHEWELL *(Sarcophagidae)* emerged from late stage satin moth larvae, prepupae and pupae. Of these, *C. concinnata, S. aldrichi*, and *C. laxifrons* were most abundant. The percent of dipteran parasites emerging from prepupae and pupae increased from 3 to 21 % in S-1, and from 5 to 9 % in S-2 during the 2 years of the study (table 4). Parasitism to late stage larvae likewise increased but was < 5 % in both stands. The large increase in parasitism during 1976, especially in S-1, may be associated with the decrease in satin moth numbers, leaving a large reservoir of parasites to attack a smaller number of hosts. Of 65 *S. aldrichi* pupae, 49 % were attacked by the hyperparasite *Aphaereta ?* sp. *(Braconidae)*. Colonies of *Megaselia hesperia* BORGMEIER *(Phoridae)* were found on satin moth larvae and pupae, often in association with other parasites. Their trophic status is unclear, but ASKEW (1971) suggests that many phorid species are facultative, polyphagous parasites.

Coccygomimus pedalis (CRESSON) *(Hym. : Ichneumonidae)* was recovered from satin moth pupae in both study stands, but accounted for < 0.5 % parasitism.

Calosoma frigidum KIRBY *(Col. : Carabidae)* adults attacked 6th to 8th stage satin moth larvae and prepupae in S-1, and were most abundant in 1975. This predator was 1st observed on June 2, 1975 and June 6, 1976 attacking larvae by opening a wound on the dorsum and feeding, but rarely consuming all of the larval contents. Although killed larvae were not counted, it was apparent that large numbers of hosts were attacked in S-1. Only 1 *C. frigidum* was observed in S-2.

Black-billed cuckoos, *Coccyzus erythrophthaimus* (WILSON) (Cuculiformes: *Cucilidae*), were observed feeding on satin moth pupae in 1976. Pentatomid bugs were observed feeding on larvae and pupae.

EGG MORTALITY. The number of egg clusters deposited at 4 sample heights in S-1 averaged 15.4 (± 6.3 S.D.) per bole in 1975 and 1.0 (± 1.3 S.D.) in 1976. In S-2, egg clusters averaged 4.8 (± 2.9 S.D.) per bole in 1975 and 0.1 (± 0.3 S.D.) in 1976. Mortality from embryonated and infertile eggs in 1975 was 12 % in S-1 and 10 % in S-2, increasing in 1976 to 29 % in S-1 and 13 % in S-2 (table 5). The percent infertile eggs was not determined in 1975, but accounted for an average of 2 % for both stands in 1976.

TABLE 5

Satin moth egg mortality, including combined infertile and unhatched eggs, and parasitism

Collection site and year	No. egg masses	Eggs/mass $\bar{X} \pm$ S.E.	% mortality due to: Infertile and unhatched eggs	*T.* prob. *californicus*	*T. minutum*	Total
S-1						
July 1975	94	205 ± 9.8	1.6	2.9	0.3	14.8
July 1976	48	258 ± 16.7	29.3	17.9	0.2	47.4
S-2						
July 1975	48	151 ± 16.8	9.8	16.4	0.2	26.4
July 1976	5	274 ± 35.3	12.7	26.4	0.0	39.1

Two parasitic Hymenoptera species were reared from satin moth eggs; *Telenomus* prob. *californicus* ASHM. *(Scelionidae)*, and *Trichogramma minutum* (RILEY) *(Trichogrammatidae)*. *T. californicus* parasitized 3 % of the eggs in S-1 during 1975, and 18 % during 1976 (table 5). Percent mortality by this parasite also increased in S-2 from 16 % in 1975 to 26 % in 1976. Parasitism by *T. minutum* did not exceed 0.3 %.

ADULT MORTALITY. Adult satin moths were preyed upon by the hermit thrush, *Hylocichla guttata* (PALLAS) (*Passeriformes : Turdidae*), and pentatomid bugs.

CONCLUSIONS

Satin moth population densities were greatly reduced in 1976, with a 15-fold reduction in egg masses in S-1, and a 48-fold reduction in S-2. Percent satin moth mortality was greater in 1976 relative to 1975.

Introduced parasite species found in Maine included *A. melanoscelus, M. versicolor, E. hemipterus (Hym.), C. concinnata* and *C. laxifrons (Dip.)*. Native parasite species, which had less combined impact on satin moth populations, included *C. pedalis, T.* prob. *californicus, T. minutum (Hym.), A. housei, S. aldrichi* and *T. variata (Dip.)*.

Although mortality factors do not prevent periodic, scattered satin moth outbreaks in Maine forests, the high incidence of mortality, particularly of overwintering larvae, probably plays an important role in reducing the duration of outbreaks and lengthening the period between outbreaks.

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RÉSUMÉ

Facteurs de mortalité du Bombyx du saule, *Leucoma salicis* [*Lep.* : *Lymantriidae*]
en forêts de tremble dans le Maine

Les agents de mortalité naturelle du Bombyx du saule, *Leucoma salicis* (L.) ont été étudiés dans deux peuplements de *Populus grandidentata* MICHAUX. La plus forte mortalité est intervenue chez les larves hivernantes. Elle a été provoquée par 2 champignons, *Paecilomyces* sp. et *Hirsutella gigantea* PETCH., un facteur paraissant être un agent pathogène d'après les symptômes, le parasite *Eupteromalis hemipterus* (WALKER) et des causes inconnues. La mortalité par *Paecilomyces* et *E. hemipterus* fut diminuée dans les sites d'hibernation recouvert d'une toile d'emballage. Les parasites issus des larves et des chrysalides furent : les braconides *Apanteles melanoscelus* (RATZEBURG) et *Meteorus versicolor* (WESMEAL), l'ichneumonide *Coccygomimus pedalis* (CRESSON), les tachinaires *Compsilura concinnata* (MEIGEN), *Carcelia laxifrons* VILLENEUVE, *Tachinomyia variata* CURRAN, et les sarcophagides *Sarcophaga aldrichi* PARKER et *Agria housei* SHEWELL. Les prédateurs des larves et des chrysalides comprenaient le carabique *Calosoma frigidum* KIRBY, des pentatomides et des oiseaux notamment le coucou, *Coccyzus erythrophthaimus* (WILSON). Les œufs furent parasités par le scelionide *Telenomus* probablement *californicus* ASHMEAD et le trichogranne *Trichogramma minutum* (RILEY). Parmi les prédateurs des papillons il y avait la grive, *Hylocichla guttata* (PALLAS) et des pentatomides.

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