This dissertation has been
microfilmed exactly as received

69-2278

ALLEN, Douglas Charles, 1940-

THE INFLUENCE OF INSECT PARASITES, INVERTEBRATE PREDATORS, AND OVER-WINTERING MORTALITY ON THE BIOLOGY OF THE JACK-PINE BUDWORM, CHORISTONEURA PINUS, IN MICHIGAN.

The University of Michigan, Ph.D., 1968
Agriculture, forestry and wildlife

University Microfilms, Inc., Ann Arbor, Michigan

THE INFLUENCE OF INSECT PARASITES, INVERTEBRATE PREDATORS, AND OVER-WINTERING MORTALITY ON THE BIOLOGY OF THE JACK-PINE BUDWORM, *CHORISTONEURA PINUS*, IN MICHIGAN

by
Douglas Charles Allen

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in
The University of Michigan
1968

Doctoral Committee:

Professor Fred B. Knight, Chairman
Associate Professor Burton V. Barnes
Associate Professor Irving J. Cantrall
Associate Professor George S. Hunt
Professor Henry K. Townes

ABSTRACT

THE INFLUENCE OF INSECT PARASITES, INVERTEBRATE PREDATORS, AND OVER-WINTERING MORTALITY ON THE BIOLOGY OF THE JACK-PINE BUDWORM, *CHORISTONEURA PINUS*, IN MICHIGAN

By Douglas C. Allen

Chairman: Professor Fred B. Knight

The objectives of this study were to: (1) identify and evaluate important insect parasites of the jack-pine budworm, (2) assess the potential of insect and spider predators as mortality factors in populations of the budworm, (3) observe the biology and behavior of important predators, and (4) lay the ground work for more detailed studies of natural mortality and ecological relationships in budworm epidemiology.

Parasites were reared from the early larval, late larval, and pupal stages of the budworm that were collected from the mid- and lower crown of jack pine in Baraga and Oscoda Counties, Michigan. Host material was collected at random from a cluster of 10 trees in each area for 2 generations. Apparent parasitism by species, crown level, area, and stage of the host were determined. The proportion of real mortality contributed by larval and pupal parasites was determined from partial life tables constructed from population sampling data.

Twenty-six species of primary parasites and 4 species of hyperparasites were reared from the budworm. Nine species are new records for this host. The largest amount of parasitism occurred in the early larval stages and was attributed predominantly to 2 species, *Apanteles fumiferanae* and *Glypta fumiferanae*. Mortality caused by them varied from 1.3% to 51.3%, and it was greatest at mid-crown.

Late stage parasitism of budworm larvae was variable. Five species of tachinid flies accounted for most of this mortality. The maximum

parasitism obtained by this group was 17.9%.

Itoplectis conquisitor was the most important parasite of the pupal stage; it killed 24.5% of the pupae in one sample.

The proportion of real mortality attributable to parasites of budworm larvae and pupae was low and variable, ranging from 0.4% to 8.5%.

Several species of insect and spider predators were studied in the laboratory and observed under field conditions to investigate their feeding responses and behavior. Observations were made on the biology of important predators in Baraga and Oscoda Counties, Michigan. The distribution, number, and kinds of spiders associated with 6 jack pines were investigated in Baraga County.

Eight species of insect predators were recorded preying on various stages of the budworm. *Anatis ocellata*, *Podisus serieventris*, and *Camponotus noveboracensis* were the most abundant of this group. Field observations indicated that only *P. serieventris* showed a substantial numerical response to increases in budworm numbers.

Fifty-one species of spiders were collected from jack pine. Three-quarters of them were hunting spiders belonging to the families Thomisidae, Salticidae, and Oxyopidae. A single species, *Metaphidippus flavipedes*, accounted for 48.0% of this group.

Theridion murarium, *Dictyna phylax*, and *Grammonota pictilis* were the most common web-spinners encountered.

Observations indicated that defoliation and natural stand closure adversely modify the habitat, and are important factors in limiting populations of spiders. No crown level or stand could be characterized by specific groups or species of spiders.

M. flavipedes, *Xysticus punctatus*, and *Philodromus pernix* were considered to be the most promising spider predators.

The location of overwintering sites of the budworm, and the occurrence of mortality within the hibernacula were investigated in Baraga County.

The majority of the hibernacula of *C. pinus* were spun under flakes of bark on the boles and main branches of jack pine. Mortality within the hibernacula may be high (e.g., 68.0%) and variable, and it is not influenced by position within the crown or location on the branch.

ACKNOWLEDGMENTS

I sincerely appreciate the time and guidance unselfishly contributed to this study by my advisor Professor Fred B. Knight. I am also indebted to the other members of my committee, Associate Professor Burton V. Barnes, Associate Professor Irving J. Cantrall, Associate Professor George S. Hunt, and Professor Henry K. Townes, for reviewing the manuscript and making many helpful suggestions.

Thanks are due Mr. John L. Foltz and Mr. William J. Mattson, Jr. for their assistance in the field and participation in helpful discussions during the course of the budworm project.

Appreciation is extended to the Forest Service, United States Department of Agriculture for providing financial support and materials.

To my wife Barbara, without whose support, sacrifice, and encouragement, this degree would never have been attained, I am deeply indebted.

TABLE OF CONTENTS

	PAGE
INTRODUCTION	1
THE JACK-PINE BUDWORM (*CHORISTONEURA PINUS* FREEMAN)	3
Review of the Literature	3
Life History and Biology	4
THE STUDY AREAS	8
Baraga County	8
Oscoda County	12
PARASITES OF *CHORISTONEURA PINUS*	15
Methods	15
Results and Discussion	17
Parasitism of early instars	24
Parasitism of late instars	28
Parasitism of the pupae	30
Parasitism of the eggs	32
Dissection of larvae	33
Conclusions	42
INVERTEBRATE PREDATORS OF *CHORISTONEURA PINUS*	45
Insect and Mite Predators	45
Methods	45
Results and Discussion	45
Podisus serieventris Uhler	47
Camponotus noveboracensis Fitch	50
Anatis ocellata (L.)	53
Deraeocoris albigulus Knight	57
Zelus socius Uhler	58
Formica exsectoides Forel	58

PAGE

F. pallidefulva nitidiventris Emery 59

Cecidomyiidae, Cecidomyiini 60

Conclusions 62

Spiders 63

Review of the Literature 63

Methods 64

Results and Discussion 65

Conclusions 80

OVERWINTERING MORTALITY 82

Methods 82

Results and Discussion 83

Conclusions 88

SUMMARY AND CONCLUSIONS 89

APPENDICES 93

LITERATURE CITED 110

LIST OF TABLES

TABLE		PAGE
1	Characteristics of trees sampled for parasites and predators	11
2	Population estimates of *C. pinus*	13
3	Parasites recovered from *C. pinus*	19
4	Apparent parasitism by crown level	22
5	Total apparent parasitism	23
6	Egg mass data for *C. pinus*	34
7	Comparison of larval parasitism determined by dissection and rearing	35
8	Partial life table for *C. pinus*, Oscoda County 1966	37
9	Partial life table for *C. pinus*, Oscoda County 1967	38
10	Partial life table for *C. pinus*, Baraga County 1966	39
11	Partial life table for *C. pinus*, Baraga County 1967	40
12	Predators of *C. pinus* on jack pine	46
13	Characteristics of jack pine trees stripped for spiders	66
14	Spiders collected on jack pine trees	68
15	Results of spider feeding experiment	71
16	Relative abundance of spiders on 6 jack pine trees	73
17	Summary of population structure of spiders on jack pine	76
18	Spider data from population samples of *C. pinus*	78

TABLE		PAGE
19	Analysis of variance of inter- and intra-tree distribution of hibernacula	84
20	Analysis of variance of inter- and intra-tree overwintering mortality	86
21	Analysis of variance of inter- and intra-tree larval emergence from hibernacula	86
22	Density of hibernacula from tree bole samples	87
23	Apparent parasitism of *C. pinus*, Oscoda County mid-crown, 1966	94
24	Apparent parasitism of *C. pinus*, Oscoda County lower crown, 1966	95
25	Apparent parasitism of *C. pinus*, Oscoda County mid-crown, 1967	96
26	Apparent parasitism of *C. pinus*, Oscoda County lower crown, 1967	97
27	Apparent parasitism of *C. pinus*, Baraga County mid-crown, 1966	98
28	Apparent parasitism of *C. pinus*, Baraga County lower crown, 1966	99
29	Apparent parasitism of *C. pinus*, Baraga County mid-crown, 1967	100
30	Apparent parasitism of *C. pinus*, Baraga County lower crown, 1967	101
31	Analysis of variance testing regression of mass length vs. eggs per mass	105
32	Distribution and condition of hibernacula from branch samples, 1966	106

TABLE PAGE

33 Distribution and condition of hibernacula from branch samples, 1967 107

34 Density of hibernacula from branch samples, 1966 108

35 Density of hibernacula from branch samples, 1967 109

LIST OF FIGURES

FIGURE		PAGE
1	Michigan counties included in the population dynamics study of *C. pinus*	10
2	Laboratory setup for rearing larvae of *C. pinus* . . .	18
3	Cocoons of overwintering parasites	25
4	Life stages of *Podisus serieventris*	48
5	Nests of *Camponotus noveboracensis*	52
6	Life stages of *Anatis ocellata*	54
7	Relationship between egg mass length and number of eggs per mass for *C. pinus*, masses 3 eggs wide	103
8	Relationship between egg mass length and number of eggs per mass for *C. pinus*, masses 2 eggs wide	104

INTRODUCTION

The jack-pine budworm, *Choristoneura pinus* Freeman (Lepidoptera: Tortricidae), has been a prominent defoliator of jack pine, *Pinus banksiana* Lambert, [1/] in the Lake States since the early 1920's. Outbreaks have occurred sporadically at 6 to 10 year intervals, persisting for 2 to 4 years (Benjamin 1956). Current infestations are centered in northern Wisconsin, northwestern Minnesota, and the Upper and northern Lower Peninsula's of Michigan (Bean and McCowan 1967).

Jack pine is an important tree because it will grow to merchantable size on dry, sandy sites where other species will not thrive (Fowells 1965), and it is second only to aspen as a major source of wood pulp in the Lake States (Blyth 1967). Thus, any insect that causes growth loss or mortality in stands of jack pine, or is potentially capable of doing so, is important to managers of those forests.

This study was an ecological investigation of the budworm and multifarious natural mortality factors. It was part of a project initiated at the University of Michigan in 1965 concerning a study of the population dynamics of this insect. My objectives were to: (1) identify and evaluate important insect parasites, (2) assess the potential of sundry insect and spider predators, (3) observe the biology and behavior of the more important predators, and (4) lay the ground work for more detailed studies of important mortality factors and ecological relationships in budworm epidemiology.

[1/] Names of plants according to Fernald, M. L. 1950. Gray's Manual of Botany, 8th ed.

The first section of this paper reviews the literature and life history of *C. pinus*, and presents new information on the bionomics of the insect. The second section deals with the effect of insect parasites on 2 populations of the budworm. In the third section the importance, distribution, and relative abundance of various invertebrate predators, are discussed. The final part is concerned with overwintering mortality and the location of wintering sites on jack pine.

THE JACK-PINE BUDWORM

Review of the Literature

Prior to 1953 *C. pinus* was considered a racial form of the spruce budworm, *Choristoneura fumiferana* Clemens, in spite of significant information obtained by Graham (1935) and Brown and MacKay (1943) regarding its biological and morphological distinctness. In a revision of the tortricid subfamily Archipinae, Freeman (1953) described *pinus* as a new species. The same writer in 1967 redescribed the jack-pine budworm, giving it a new status (*pinus pinus*) to separate it from a closely related form, *C. p. maritima* Freeman, which defoliates Virginia pine (*Pinus virginiana* Miller) and pitch pine (*P. rigida* Miller) in the east-central United States.

Early confusion between the jack-pine and spruce forms of *Choristoneura* impeded parasite work on the former insect for many years. Rearing and biological investigations by Barker (1947) in Manitoba, Walley (1953) in Manitoba and Ontario, Benjamin and Drooze (1954) and Drooze and Benjamin (1956) in Michigan, and Kulman and Hodson (1961) in Minnesota have added to the knowledge of natural mortality factors operating in various populations. Recent papers by Dixon and Benjamin (1963) and Benjamin (1964) summarized the above material and reported on parasite investigations in northern Wisconsin.

To date, 54 species of insect parasites and hyperparasites have been recovered from the jack-pine budworm (Dixon 1961). Only 1 invertebrate predator has been recorded (Hussey 1954).

Previous work on the bionomics of *C. pinus* was adequately reviewed by Bradshaw (1965).

More recently, Mattson *et al.* (1966) investigated the role of

vertebrate predation in populations of the budworm in northern Michigan. Their work indicated that birds show a functional response to changes in populations of the budworm up to a density of 4 late stage larvae per 100 jack pine tips. Censuses in semi-open jack pine forests revealed a paucity of birds and small mammals. Birds were most effective on the fifth and sixth larval instars. Flocking, non-resident birds accounted for twice as much larval and pupal mortality as the resident species.

Various sampling techniques previously used in *C. pinus* population studies were reviewed by Foltz (1967). The sampling procedure utilized throughout the University of Michigan budworm project was developed by Foltz and is described in his paper. The method involves collecting the apical 36 in. of 4 branches, 2 from both the mid- and lower crown, from 10 trees in each sample. The total number of tips and budworms are counted in the laboratory, and relative population density is expressed as the number of insects per 100 new growth tips.

Foltz indicated that larvae and pupae of *C. pinus* are more prevalent on the distal portions of branches and may be significantly, but unpredictably, concentrated into one crown level of the tree.

Life History and Biology

The budworm overwinters as a second instar larva in a silk hibernaculum [2/] spun beneath the bark scales, in old staminate flower heads, or in any other protected location on the bole or in the crown of the host tree. Activity is resumed in late May the following spring, when larvae migrate to the expanding staminate flowers and vegetative buds

[2/] A white, thin oval structure spun by the second stage larva.

to feed. This activity distributes the insect throughout the tree, the largest percentage residing at mid-crown where the heaviest concentration of tips is found (Foltz 1967).

During the fourth instar, larvae begin feeding on the expanding needles. New foliage is preferred by the late larval stages, noticeable feeding on old foliage occurring only when population numbers are high and new needles unavailable (MacAloney and Drooze 1965). The last 3 larval stages are partially protected by silk feeding tunnels. Needles are clipped off at the base and webbed together with adjacent branches as feeding progresses.

Laboratory rearing on an artificial diet and head capsule measurements of field collected larvae indicated that both sexes have 6 instars (Allen *et al.* 1968).

The larval feeding period lasts for 40 to 50 days, depending on weather conditions and quality of the food.

In northern Michigan the pupal period averages about 10 days, with the pupation period extending throughout most of July. Pupae reach a peak in numbers near the middle of that month. Pupation occurs amoung the webbed needles, the cases remaining in place long after adults have emerged. Moths are prevalent from late July to early August.

Field observations indicated that adult activity is restricted to a brief period in early evening, from 6:30 to 8:30 o'clock (Eastern Standard Time). The majority of the individuals flying are males, and flight is limited to the upper one-third of the tree crown. A pilot study with caged, virgin females suggested the presence of a pheromone emitted by this sex to attract males. Copulating

individuals were commonly seen throughout the crown of the host tree during daylight hours. In view of the fact that very little flight activity was observed at this time, pairing probably takes place only at dusk, pairs remaining *in copulo* for an extended period.

Egg laying occurs from late July to early August. Masses of eggs are laid on the flat surface of the old growth needles in 2 or 3 overlapping rows. Of 127 egg masses examined in 1965, 21.2% were 2 rows wide. The average number of eggs per mass varied according to needle length and width. Masses 3 eggs wide in the above sample averaged 57.2±16.5 eggs (n=100, p=.05), while the 2 rowed clusters averaged 34.2±7.6 (n=27, p=.05).

Thirteen pairs of pupae were collected from Baraga County in 1967 and reared in the laboratory in glass jars lined with waxed paper. Fecundity was variable, averaging 137.0±29.9 (p=.05) eggs per female. This is considerably less than the 264.0±21.9 (p=.05) reported by Allen *et al.* (1968) for females reared on artificial diet.

Eggs hatch in 7 to 10 days, and the first instar larvae search out an overwintering site shortly after eclosion. The first molt occurs within the hibernaculum. Feeding does not begin until the second instar.

Jack pine and red pine (*Pinus resinosa* Aiton) are the favored hosts of *C. pinus* (Freeman 1967). Eastern white pine (*P. strobus* L.) and lodgepole pine (*P. contorta* Douglas) are occasionally attacked (Dixon 1961). Severe defoliation of scots pine (*P. sylvestris* L.) has occurred in Michigan (Michigan Forest Detection Program Report 1950).

Life stages of the budworm were described in detail by Freeman

(1967), MacKay (1953, 1962), and Campbell (1953).

THE STUDY AREAS

Five Michigan counties were included in the budworm project (Fig. 1). Only 2, Baraga and Oscoda, were chosen for detailed parasite and predator studies. The former area, because of its accessibility to the field station, Camp Filibert Roth (Iron County), received substantially more attention than the latter. Enough information was obtained from each, however, to permit comparison of parasite material.

Baraga County

The stands studied are located near the eastern edge of a 1600-acre infestation in the west-central part of the county (T49N-R34W-S19) where jack pine is the dominant tree species, covering about 6000 acres in near continuous, pure stands. Red pine plantings and small openings diversify this continuity in some sections. Small clones of aspen (*Populus tremuloides* Michaux and *P. grandidentata* Michaux) have replaced the pine on better sites. The ground vegetation consists predominantly of bracken fern (*Pteridium aquilinum* (L.) Kuhn, sweetfern (*Comptonia peregrina* (L.) Coulter, reindeer lichen (*Cladonia* spp.), sand cherry (*Prunus pumila* L.), and several species of Gramineae.

Geologically, the region is considered a glacial outwash plain. The soil, a Rubicon-Omega-Onamia Association (Veatch 1953), is low in humus, dry, sandy, and acid. The terrain is very flat and well drained.

The open-grown, even-aged pine stands contain little regeneration. Stand characteristics of the study plot are shown in Table 1.

Budworm infestations were first reported in Baraga County in 1957.

Figure 1. - Michigan counties included in the study of *C. pinus*, 1965-1967. Parasite and predator study plots are indicated by black squares.

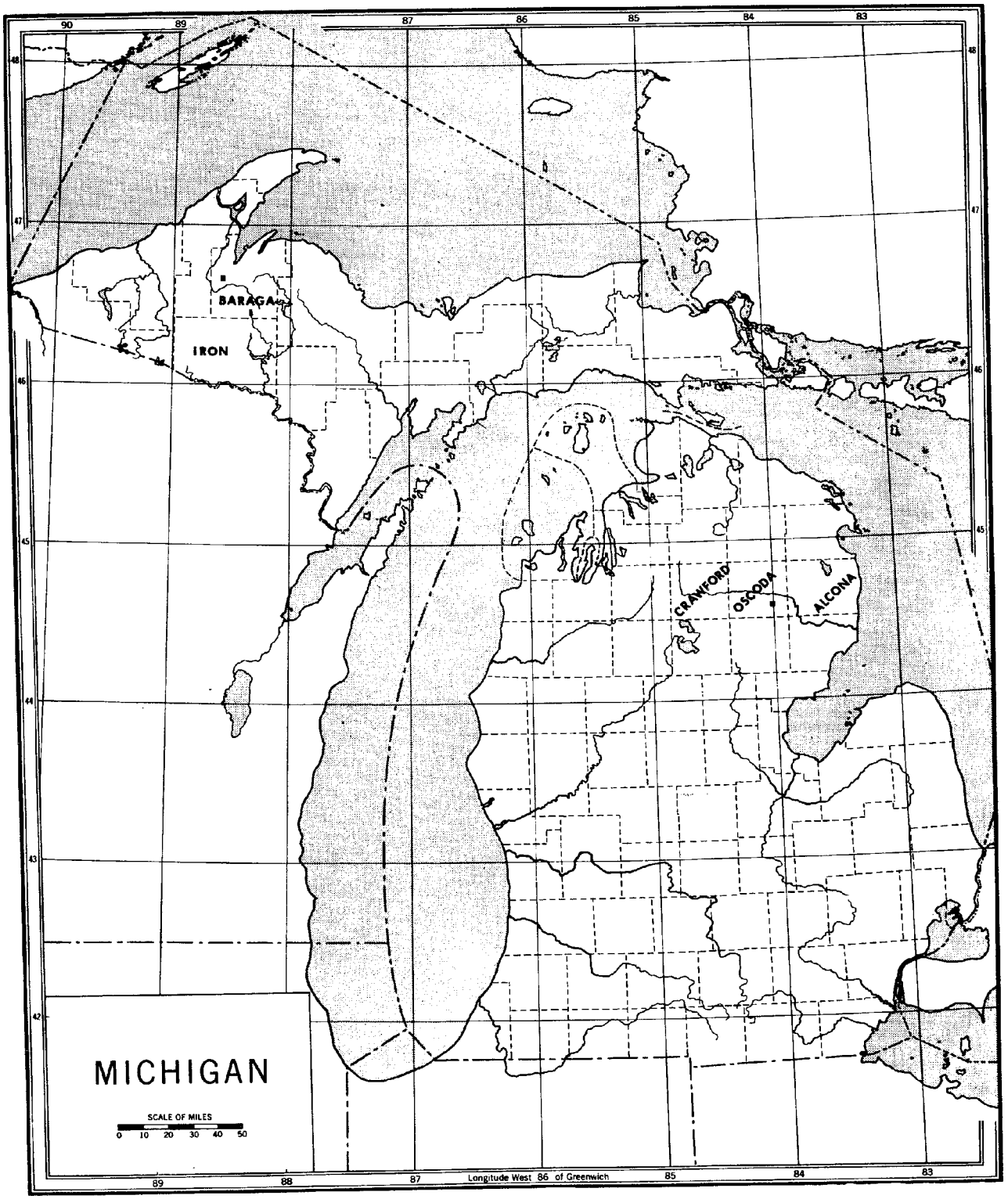

BARAGA
IRON
CRAWFORD
OSCODA
ALCONA
MICHIGAN
SCALE OF MILES
0 10 20 30 40 50
Longitude West 86 of Greenwich
90
89
87
86
85
84
83
48
47
46
45
44
43
42

Table 1. - Characteristics of jack pine stands sampled for insect parasites and invertebrate predators of *C. pinus*, Michigan 1965-1967. [a/]

County	Av. d.b.h.	Av. tree ht. (ft.)	Av. crown length (ft.)	Basal area/ acre (sq. ft.)	Trees/acre	
					<5.0 in. d.b.h.	>5.0 in. d.b.h
Oscoda	7.6	34.0	24.6	106	316	216
Baraga	8.7	41.8	37.2	20	265	48

[a] Data compiled by Mr. John L. Foltz, Department of Forestry, University of Michigan, Ann Arbor.

Light populations prevailed through 1958, increased in 1959, and severe defoliation and top killing occurred from 1960 to 1962. Insect numbers subsided in 1963 and 1964, resulting in only light damage (Michigan Forest Detection Program Report 1950-1964). Populations increased markedly in 1967, but egg counts indicated that a substantial reduction should occur in 1968 (Table 2).

Field surveys suggest that infestations characteristically begin in small pockets and spread locally from these areas. Defoliation is first noticeable in the upper one-third of the tree crowns, continuing downward as the season progresses. Mortality of trees is common in some areas, though most trees successfully flush again late in the season or the following spring. Trees in the understory are the most severely damaged and are the individuals most likely to be killed.

Oscoda County

This plot, located southeast of Mio, Michigan (T25N-R3E-S12), is situated in a large tract of jack pine covering several counties. Red pine appears as scattered, naturally seeded individuals throughout the stands, and northern pin oak (*Quercus ellipsoidalis* E. J. Hill) is a common associate. Sweetfern, blueberry, and various grasses make up the major part of the ground vegetation.

The soil, a Grayling-Rubicon (Veatch 1953), is similar to that at Baraga, but differs in having a clay floor at varying depths. The soil is very acid to a depth of 4 ft (Veatch *et al.* 1931).

The stand is comparatively young and closed, and the trees have short crowns (Table 1). Regeneration is sparse.

The budworm ravaged this region for years. Outbreaks were

Table 2. - *C. pinus* population estimates. Figures represent the number of insects/100 new tips, crown levels combined.

Stage sampled	1965	1966	1967	1968
		Oscoda County		
egg	-	265.0	175.0	53.0
early larval	-	52.6	6.3	-
late larval	25.1	14.3	4.6	-
pupal	16.8	12.9	1.3	-
		Baraga County		
egg	-	369.0	1083.0	232.0
early larval	-	69.7	15.5	-
late larval	-	54.0	19.0	-
pupal	-	46.2	10.7	-

recorded as early as the 1920's, and reoccurred in the mid-thirties (Graham 1935). Populations increased again from 1946 to 1950, and losses to understory trees and reproduction were substantial in 1951 and 1952. Damage declined in 1953 and remained stable from 1954 to 1955. Defoliation was heavy in 1956 and 1957. From 1958 to 1962 populations declined greatly, and no severe defoliation occurred. Heavy damage appeared again in 1963 and 1964, probably being intensified by drought conditions prevailing in Michigan at that time (Michigan Forest Detection Program 1950-1964). Budworm numbers remained high through 1966. The outbreak declined again during the past 2 seasons as indicated by the population estimates in Table 2.

Outbreak and defoliation characteristics were similar to those at Baraga. In spite of frequent heavy budworm populations in the past the stand in the study plot appears healthy, presently showing no visible signs of defoliation or permanent damage.

PARASITES OF *CHORISTONEURA PINUS*

An investigation of the parasite complex associated with *C. pinus* outbreaks in Baraga and Oscoda Counties, Michigan is discussed and compared to earlier work done in other regions. Data were collected on the parasite fauna present in these areas during 3 seasons and on the occurrence and distribution of parasites at 2 crown levels for 2 seasons. The mortality data are expressed as apparent parasitism so that comparisons can be made between interspecific and temporal variations in parasite numbers. Real mortalities and total parasitism are computed to assess the impact of groups of parasites at different points in the life cycle. [3/] The data were collected following the general suggestions outlined by Miller (1955) for the spruce budworm.

Methods

In 1965 host material was obtained from branches collected in the population sampling program, supplemented by additional pupal collections in Baraga and Iron County. Three crown levels and 4 stages of the budworm (instars 3-4, instars 5-6, pupal, and egg) were sampled.

Previous work (Dixon 1961) demonstrated the need for efficient rearing techniques when working with early stage larvae of the budworm. This stage is very small, making dissection a difficult process at best, and larval stages of the parasites involved are often impossible to identify. Descriptions of the immature forms of the 2 most common parasites of this stage, *Glypta fumiferanae* (Viereck) and

---

[3/] The terms apparent and real mortality are used in the sense discussed by Miller (1963).

Apanteles fumiferanae Viereck, were well documented by Brown (1946a,b). Investigations in 1965, however, indicated the presence of several species of *Apanteles* in some infestations and information on the relative importance of each was desired. Adult specimens are required for specific identifications.

In 1966 and 1967 Baraga and Oscoda Counties were selected for detailed parasite and predator studies because of their population histories and geographic locations. I collected material of all except the egg stage. This was obtained from foliage collected during population studies as in 1965. The mid- and lower crown of 10 trees in each area were randomly sampled when the host stage desired was at a peak. Collection dates corresponded (within a day or 2) to population sampling periods. This facilitated the computation of real mortalities based on an estimate of host population densities at the time of collection.

A pole pruner with a basket attached to the cutting head was used to collect branches. An equal number of the host was collected from each crown level, and individuals were picked from throughout the foliated region of each branch selected. In 1966 staminate flowers were very abundant in both study areas so flower heads were taken in place of individual larvae. This resulted in a much larger sample than that obtained in 1967, because several larvae feed in each head. Flowers were sparse the second year and larvae comparatively easy to locate individually.

The top third of the tree crowns was not sampled because this region was not included in the population sampling program, and the computation of real mortalities for this level would not have been possible. I believed that data on apparent parasitism alone would be

of limited value and not worth the extra effort.

Both larval stages were reared in 1-gallon, wide-mouthed glass jars covered with several layers of cheese cloth at the open end (Fig. 2). Ten staminate flower heads (collected when heads were plentiful and early stage larvae were difficult to count) or 10 to 15 larvae were placed in each jar with enough foliage to cover the bottom of the container while resting on its side. These rearing chambers kept the foliage in satisfactory condition (i.e., palatable) long enough for the small larvae to reach the sixth instar and the large larvae to pupate. Parasites were collected as they emerged and were pinned or stored in alcohol. The dried foliage and flower heads were carefully searched for additional parasites and larvae at the termination of the rearing period. Pupae were reared in large petri dishes in lots of 10.

Larvae to be dissected were starved for 12 hours, killed in X.A.A.D. solution (Peterson 1962), and stored in 70% alcohol.

Results and Discussion

A total of 26 species of primary parasites and 4 species of hyperparasites were recovered from *C. pinus* (Table 3). Nine of these had not been recorded previously for the jack-pine budworm.

The apparent parasitisms caused by the more common species are shown by crown level, area, host stage, and season collected in Appendix I (Tables 23 to 30), The data are combined in Table 4 to give total percent parasitism for each stage sampled by crown level. Crown levels are combined in Table 5, the percentage figures indicating total parasitism for each stage sampled. Host numbers for the late larval and pupal samples have been reduced by the number of late emerging parasites recovered that are known to attack earlier stages.

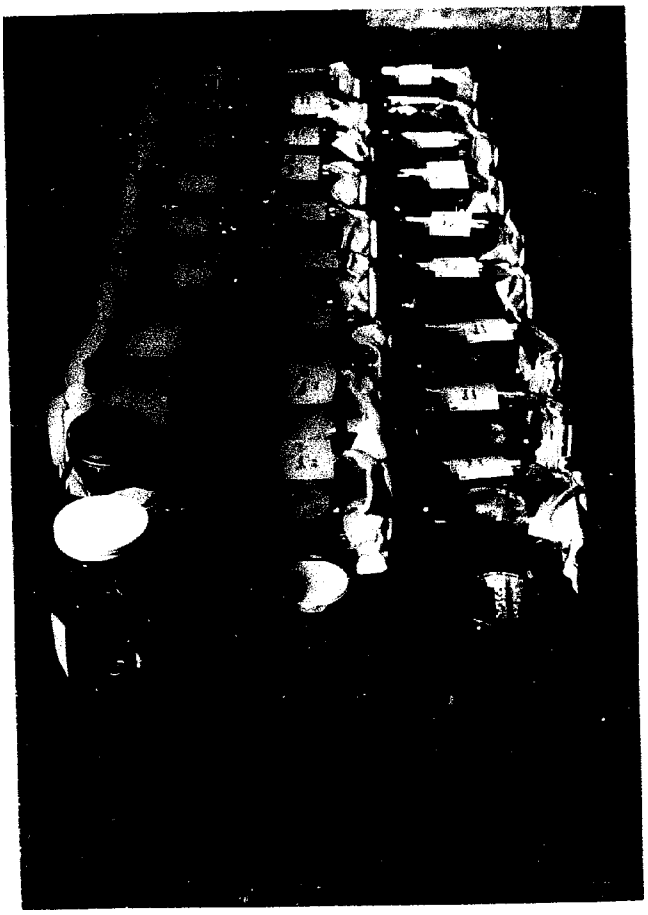


Figure 2. - Laboratory setup for rearing *C. pinus* larvae.

Table 3. - Parasites recovered from *C. pinus* in Michigan, 1965-1967, complete list.

Classification [a]	Attacks [b]	Emerges
Chalcididae		
Brachymeria compsilurae (Crawford)	P (H)	P
Eulophidae		
Tetrastichus coerulescens Ashmead	P (H)	P
Pteromalidae		
Amblymerus verditer (Norton)	P (H)	P
Encyrtidae		
**Copidosoma deceptor* Miller	P (H)	P
Braconidae		
Apanteles fumiferanae Viereck	PL	LL
A. polychrosidis Viereck	PL	LL
A. petrovae Walley	PL	LL
**Apanteles* sp.	PL	LL
**Meteorus tetralophae* Muesebeck	LL	LL
**Meteorus* sp.	LL	LL
Ichneumonidae		
**Acropimpla pronexus* Townes	P	P
Ephialtes ontario (Cresson)	P	P
**Exochus albifrons* Cresson	P	P
Gelis tenellus (Say)	LL,P	P
Glypta fumiferanae (Viereck)	PL	LL
**G. inversa* Cresson	?	LL
Itoplectis conquisitor (Say)	P	P

Table 3. - (cont.)

Classification	Attacks	Emerges
Mesochorus sp.	?	LL
Phaeogenes hariolus (Cresson)	P	P
**Phaeogenes* sp.	?	P
Scambus hispae (Harris)	LL,P	P
**Temelucha rhyacioniae* (Cushman)	LL	LL
Trichogrammatidae		
Trichogramma minutum Riley	E	E
Tachinidae		
Actia interrupta Curren	LL	LL,P
Aplomya caesar Aldrich	LL	LL,P
Lypha setifacies (West)	LL	LL,P
Madremyia saundersii (Williston)	LL	LL,P
Phryxe pecosensis (Townsend)	LL	P
Sarcophagidae		
Pseudosarcophaga affinis auct.	LL	LL,P
Sarcophaga aldrichi Parker	LL,P	P

[a] Identifications were made by the U. S. Dept. Agr., Insect Identification and Introduction Division, Beltsville, Maryland: Braconidae - C. W. Muesebeck, P. M. Marsh; Chalcidoidea - B. D. Burks; Tachinidae - C. W. Sabrosky. The Ichneumonidae were identified by H. K. Townes, Ann Arbor, Michigan. *T. minutum*, *P. affinis*, *S. aldrichi*, and *L. setifacies* were identified by the author using keys prepared by Ross (1952) and Wilson and Bean (1964).

Table 3. - (cont.)

[b] Symbols P, H, PL, LL, and E refer to pupal, hyperparasite, prewinter larval, late larval, and egg respectively.

? - status unknown

* - Species not previously recovered from *C. pinus*.

Table 4. - Parasitism of *C. pinus* by crown level, determined by rearing. Michigan, 1966-1967.

		1966				1967			
		Total no. host		Apparent parasitism (%)		Total no. host		Apparent parasitism (%)	
County	Stage sampled	mid	low	mid	low	mid	low	mid	low
Oscoda	egg [a]	98		1.0		76	32	3.9	9.3
	early larval	389	284	60.9	38.0	100	100	39.0	14.0
	late larval	126	64	20.6	12.5	115	115	7.0	5.2
	pupal	418	146	7.9	7.1	95	90	2.1	14.4
Baraga	egg	140		14.3		362	31	4.1	3.2
	early larval	339	192	42.5	25.0	150	150	1.3	1.3
	late larval	97	114	1.0	0.9	94	98	4.3	2.0
	pupal	1141	512	11.8	12.1	84	94	17.9	31.9

[a] Figures represent number of masses and % masses parasitized.

Table 5. - Parasitism of *C. pinus*, crown levels combined, determined by rearing. Michigan, 1966-1968.

County	Stage sampled	1966 Total no. host	1966 Parasitism No.	1966 Parasitism %	1967 Total no. host	1967 Parasitism No.	1967 Parasitism %	1968 Total no. host	1968 Parasitism No.	1968 Parasitism %
Oscoda	egg [a/]	98	1	1.0	108	6	5.6	2728	256	9.4
	early larval	673	345	51.3	200	53	26.5	-	-	-
	late larval	190	34	17.9	230	16	7.0	-	-	-
	pupal	564	42	7.4	185	16	8.6	-	-	-
Baraga	egg	140	20	14.3	393	16	4.1	13,260	358	2.7
	early larval	531	192	36.2	300	4	1.3	-	-	-
	late larval	211	2	0.9	192	6	3.1	-	-	-
	pupal	1653	228	13.8	178	45	25.3	-	-	-

[a] Figures for 1966 and 1967 represent number of masses and % masses parasitized; the 1968 data are based on actual egg counts.

Hyperparasitism is included in all mortality tables under pupal parasites.

Parasitism of Early Instars. - *G. fumiferanae* and *A. fumiferanae* were the 2 major parasites overwintering in second stage budworm larvae. Three additional species of *Apanteles* were recovered, and these individuals probably overwinter in the host also because of their emergence early in the life cycle. This group includes *A. petrovae* Walley, *A. polychrosidis* Viereck, and *Apanteles* sp. The genus as a whole is a difficult one taxonomically, and I believe that present identifications do not indicate accurately the incidence of the species involved. Therefore, individual species will not be considered.

Both *Glypta* and *Apanteles* spp. are univoltine, the former emerging from fifth or sixth instar larvae, the latter from the fourth or fifth instar. Lewis (1960) indicated that *Apanteles* is more successful than *Glypta* in parasitizing newly-hatched, freely moving spruce budworm larvae, whereas the reverse is true when the host is immobile within the hibernaculum. This is, in part, a function of ovipositer length, the structure being much longer in *Glypta*.

The insects pupate in the tree crown. Both cocoons are easy to identify, that of *Glypta* is a thin, white, transparent one 8.0 to 10.0 mm in length and that of *Apanteles* a bright white, densely spun structure 3.0 to 4.0 mm long (Fig. 3).

Apparent parasitism by *Glypta* was very low in the years, crown levels, and areas studied. Host mortality ranged from 0.0% to 3.5% and was relatively constant in each area. Dixon and Benjamin (1963) and Benjamin and Drooze (1954) reported similar findings in Wisconsin and Michigan. Working in Minnesota, Kulman and Hodson (1961) showed



Figure 3. - Overwintering parasite cocoons; A, *G. fumiferanae;* B, *A. fumiferanae.*

that parasitism by this species was heaviest on trees inside jack pine stands and in the upper crowns of trees on the edges of stands. I found parasitism to be more prevalent in the older infestation at Oscoda, and no apparent relationship between incidence of attack and crown level.

The abundance of this species was apparently not affected by changes in density of budworms. Host populations fluctuated considerably over the 3 year period studied, but the incidence of *Glypta* deviated little. The lower mortality figures, however, did correspond to periods of population decline. Such a relationship does exist between this parasite and *C. fumiferana* (Miller 1963).

The life history of this parasite was more fully described by Miller (1960), and its life stages were illustrated by Brown (1946b).

Apanteles fumiferanae was the most common parasite recovered in the study. Parasitism by the *Apanteles* complex was extremely variable and high at all times, except for the 1967 collection at Baraga, when only 4 specimens were obtained. Mortality ranged from 1.3% to 59.1% and was consistently higher at the mid-crown level. The highest incidence of parasitism occurred at Oscoda in 1966, a year when the budworm population dropped markedly. This infestation is probably in a state of collapse as indicated by population figures for the past 3 seasons and egg mass data for the 1968 generation (Table 2).

In Baraga County budworm populations were greatly reduced in 1967 even though egg counts the previous year had foreshadowed a tremendous increase in numbers (Table 2). Parasitism by *Apanteles* was high, 41.0% at mid-crown and 24.0% in the lower crown, in 1966, but the high egg count in late summer of that year indicated that the braconids

had little effect in checking the increase. The drop in the budworm populations and incidence of *Apanteles* in 1967 was probably an outgrowth of increased dispersal loss in the spring. The increased dispersal loss probably resulted from a reduction in staminate flower production which forced the larvae to search longer for suitable and unoccupied feeding sites. Parasitized early stage larvae emerge later and are slower moving than non-parasitized individuals and are generally less susceptible to dispersal loss (Lewis 1960). Thus, when there is high budworm density and a scarcity of staminate flowers, dispersal loss of parasitized larvae would probably be increased because of a paucity of unoccupied feeding sites. Field observations indicated that staminate flowers can initially harbour up to 40 individuals per head, but that an expanding bud or vegetative shoot is suitable for a much smaller number.

The data indicate that *Apanteles* spp. have little influence in checking populations of the budworm at high levels. Seemingly, their impact is not manifested until parasite numbers have built up during periods of high host density, followed by a rapid decline brought about by other factors. At this time the parasites may play a role in hastening the decline.

Benjamin and Drooze (1954) concluded from their work in Michigan, that *A. fumiferanae* was one of the few parasites important in reducing populations of *C. pinus*. Dissection of overwintering larvae in some infestations in Wisconsin also indicated a high rate of parasitism by this braconid (Benjamin 1964).

The life history of *A. fumiferanae* and its actions as a parasite of *C. fumiferana* were discussed by Miller (1959). Life stages were

described by Brown (1946a).

Parasitism of Late Instars. - Mortality in these stages and the insect parasites involved varied from generation to generation. The major parasites were tachinids and sarcophagids (Diptera). These insects attack the fifth or sixth larval instars and emerge from the sixth larval instar or the pupal stage of the host.

Of the tachinids, the highest mortality was caused by *Aplomya caesar* (Aldrich), at Oscoda in 1966. At that time parasitism in the mid-crown and lower crown was about equal, at 12.7% and 12.5% respectively. Only 1 specimen was recovered at Baraga. The female lays microtype eggs on the pine needles, and the parasites gain entrance to the host by being eaten along with the foliage. The maggot overwinters in an alternate host (Wishart 1945).

Lypha setifacies (West) accounted for 8.6% of the mortality of large larvae at Oscoda in 1967. This species was not recovered in other collections. The parasite is larviparous. Maggots are discharged onto the foliage where they seek out a suitable host. Pupae overwinter in the duff (Brooks 1945).

Two other tachinids, *Phyxe pecosensis* (Townsend) at Oscoda and *Madreymia saundersii* (Williston) at Baraga, were recovered in small numbers, accounting for only 1.6% and 1.0% of the mortality of large larvae respectively. Both species lay their eggs on the host larva, and the maggot gains entrance by boring through the egg chorion and the host's cuticle. Winter is spent as an immature maggot in an alternate host (Maw and Coppel 1953, Coppel and Maw 1954).

A sarcophagid, *Pseudosarcophaga affinis* auctorum, was recovered in both areas, accounting for 0.9% of the mortality at Oscoda in 1967

and 6.3% at Baraga in the same year. The insect larviposits on the foliage and winters as a pupa in duff (House and Traer 1949).

Two ichneumonids, *Temelucha rhyacioniae* (Cushman) and *Phaeogenes* sp., were occasionally reared from the late larval stage.

Total parasitism of the late instars varied from 0.9% to 17.9%. Oscoda had the highest amount of mortality during this stage for both generations studied. Parasitism was consistently higher in the mid-crown samples. The difference between crown levels was small except for the Oscoda collection in 1966.

The limited and conflicting data indicate no relationship between host population trend and parasite abundance.

Dixon and Benjamin (1963) concluded that late larval parasitism in Wisconsin from 1954 to 1957 was of little importance to the population dynamics of *C. pinus*. Parasitism of large larvae is the most important aspect of spruce budworm mortality, because survival of the large larvae determines to a great extent survival within a generation of that insect (Miller 1963).

In view of the fact that all members of this group of parasites have at least 2 generations a year, according to the literature cited above, their abundance is probably directly related to the availability of alternate hosts.

Multiple parasitism occurs among some of these Diptera under conditions of low host density and high parasitism (Miller 1963). I never observed this phenomenon in the rearing work, and believe that host populations were high enough and parasitism sufficiently low to preclude its occurrence in the populations studied.

The extreme variation in apparent parasitism during the late

larval stage undoubtedly has some effect on the survival of a generation. Morris (1957) indicated that when contemporaneous mortality factors remain relatively constant, variation in late larval parasitism greatly influences the survival of a generation in the spruce budworm. Before the possible effect of variations in late larval mortality of *C. pinus* can be evaluated it is necessary to learn more about the level of mortality caused by other factors (e.g., dispersal, starvation, predation, etc.) and the relationship between all factors and density of the host population.

Mattson *et al.* (1968) demonstrated that at very low population levels one factor, bird predation, may account for as much as 65% of the late larval mortality. Bird predation is variable at all levels, however, and birds probably do not discriminate between parasitized and nonparasitized budworms. Parasitized pupae hang from the pupation site by their cremasters and are not concealed in the feeding tunnel like healthy individuals. This behavior makes them more vulnerable to predation by birds because they are very conspicuous. Such interactions between contemporaneous mortality factors makes interpretation difficult.

Parasitism of the pupal stage. - *Itoplectis conquisitor* (Say), *Phaeogenes hariolus* (Cresson), *Ephialtes ontario* (Cresson), and *Sarcophaga aldrichi* Parker were the pupal parasites recovered from the rearing samples. Combined parasitism by them varied from 8.6% to 25.3%.

I. conquisitor was by far the most common member of the group in both areas. Apparent parasitism by this species ranged from 2.1%

to 24.5%. Incidence of parasitism was consistently higher in Baraga than in Oscoda, and at the lower crown level in both regions. Benjamin and Drooze (1954) stated that *I. conquisitor* was the most prevalent species reared from *C. pinus* pupae in Michigan from 1951 to 1953, and that it played an important role in reducing populations. Similar findings were reported from northwestern Wisconsin (Dixon and Benjamin 1963).

P. hariolus was absent from the population in the Lower Peninsula and was first recovered at Baraga in 1966. [4/] Parasitism never exceeded 2.1%. The low parasitism observed is in agreement with results from other parasite studies of *C. pinus*, except for a high incidence of 11% to 28% reported by Kulman and Hodson (1961) on the Huron National Forest in Michigan.

The remaining 2 parasites were recovered from a single collection each, *E. ontario* at Baraga in 1967 and *S. aldrichi* at Oscoda in 1966. Parasitism by them was 2.1% and 1.9% respectively. *E. ontario* has not been reported as a common parasite of *C. pinus* to date, but *S. aldrichi* was prevalent in some infestations in Minnesota (Kulman and Hodson 1961).

Pupal parasitism increased in both areas in 1967, suggesting that the effect of this group may be accentuated in aging and/or declining populations.

The 3 ichneumonids parasitize and emerge from the pupal stage of the host. *P. hariolus* overwinters as an adult, *I. conquisitor* and *E.*

[4/] This parasite was incorrectly described as a new species, *Dirophanes banksianae*, by Allen (1967). It is a synonym of *P. hariolus*.

ontario do so in another host (Miller 1963). The sarcophagid, *S. aldrichi*, is larviparous and pupates in the soil (Hodson 1941, Arthur and Coppel 1953).

Stehr (1954) suggested that excessive handling of the pupae of *C. fumiferana* probably results in a lower rate of adult emergence in laboratory rearings than actually occurs in the field. My pupal material was handled very little, and I do not believe that results were significantly influenced by this factor. It is essential that pupae are collected before adult emergence because many of the dipterous parasites emerge early. Pupae that did not yield adult moths or parasites were probably killed by predators prior to collection, as they closely resembled individuals preyed on in the predator rearing studies. Early collection of pupae may result in a more conservative estimate of overall pupal mortality than the examination of empty pupal cases, because other factors operating in the field (e.g., bird predation, insect predation, etc.) might further reduce the population before adult emergence. Such factors, however, would not substantially alter the apparent parasitism figures unless a preference for non-parasitized pupae occurred, or *vice versa*. There is no evidence to date that such preferences exist.

Four species of hyperparasites were collected from the pupal stage (Table 3). *Amblymerus verditer* (Norton) was the most common one encountered. The group was not represented in the 1967 rearing collection from Oscoda, but hyperparasitism averaged 3.6% in the other samples.

Parasitism of the Egg Stage. - *Trichogramma minutum* Riley was the only parasite reared from the egg stage of *C. pinus*. Data were not

obtained on mortality of eggs in 1966 and 1967, only on the number of masses parasitized (Table 6). The portion of masses attacked varied from 1.0% to 14.3%. As a rule individual masses were not completely parasitized. Incidence of parasitism increased each year at Oscoda and declined in the Baraga population.

Percent parasitism of eggs was calculated for the 1968 generations (Table 6). Mortality was about 3 times greater at Oscoda (9.4%) than at Baraga (2.7%).

The abundance of this parasite is undoubtedly restricted by a paucity of alternate hosts. The higher incidence at Oscoda suggests that numbers will increase slowly as the epiphytotic ages. Such a trend was observed in Wisconsin by Dixon and Benjamin (1963). They reported 62.6% parasitism by *T. minutum* in some regions. The relationship between aging infestation and increase in parasitism did not prevail at Baraga, where mortality by this factor declined steadily over the past 3 years.

To date in Michigan, few mortality factors have occurred contemporaneously with parasitism of eggs in the populations observed. Seemingly, parasite mortality would have to attain levels such as that reported by Dixon and Benjamin before survival of a generation would be substantially reduced.

Dissection of Larvae. - Time permitted a limited amount of dissection work, and only in 1967. For the most part these data (Table 7) show the efficiency of the rearing technique. The major discrepancies were a result of small samples. The material used was obtained from the population sample branches.

Previous work done with *C. pinus* has expressed mortality in terms

Table 6. - Egg mass data for *C. pinus*, Michigan, 1966-1968.

County	No. masses			Total	Mean no.	No. masses	% masses	% eggs
	mid	low	total	no. eggs	eggs/mass	parasitized	parasitized	parasitized
Oscoda								
1966	53	45	98	5625	57.4	1	1.0	-
1967	76	32	108	4720	43.7	6	5.6	-
1968	31	24	55	2728	44.6	5	9.1	9.4
Baraga								
1966	105	35	140	8036	57.4	20	14.3	-
1967	362	31	393	21,811	55.5	16	4.1	-
1968	138	83	221	13,260	60.0	4	1.8	2.7

Table 7. - Comparison of data on the parasitism of *C. pinus* larvae determined by dissection and rearing. Michigan, 1967.

		Early larval		Late larval		No. dissected	
	Crown	% parasitism		% parasitism		early	late
County	level	dissect.	reared	dissect.	reared	larval	larval
Oscoda	mid	30.6	39.0	10.6	7.0	75	37
	lower	11.1	14.0	20.0	5.3	18	5
Baraga	mid	1.7	1.3	5.1	4.3	56	97
	lower	3.7	1.3	3.1	2.0	27	98

of apparent parasitism. Only 1 paper (Dixon 1961) attempted to illustrate the trend in the total effectiveness of all parasites from generation to generation. Dixon calculated aggregate percentage mortalities following a method described by Thompson (1939). Morris (1957) discussed the weakness inherent in such data and emphasized the need for frequent sampling of populations and development of life tables if mortality is to be expressed meaningfully.

Partial life tables for both generations of the budworm in each study area (Tables 8 to 11) illustrate the proportion of the real mortality in each cycle contributed by insect larval and pupal parasites.

Budworm population densities per 100 branch tips (lx) were calculated from the population sampling data for all but the egg stage by Mr. John L. Foltz.

Egg masses were collected after eclosion, making counts of individual eggs impossible due to the transparent and distorted appearance of the vacated egg shells. Using regression analysis a significant relationship was established between mass length and number of eggs per mass (Appendix II). Masses were measured and the number of eggs estimated from the regression equations. From these data the average number of eggs per mass (Table 6) was calculated, taking into consideration differences in the width of the egg masses. This average was used to convert masses per 100 tips to egg numbers as they appear in the partial life tables. As previously indicated, parasitism of eggs was not measured and the effect of this mortality on the populations can not be determined.

The number of insects dying in each age interval (dx) as a result

Table 8. - Partial life table for *C. pinus* indicating mortality attributed to insect parasites of the larval and pupal stages. Oscoda County, Michigan, 1966.

Age interval (x)	No./100 tips alive at beginning of x (lx)	Major factors responsible for dx (dF)	No. dying during x (dx)	dx as a % of lx (apparent parasitism) (100qx)
Egg	358.8	*T. minutum*	-	-
L_{3-4}	51.3	*Apanteles* spp. *G. fumiferanae*	26.3	51.3
L_{5-6}	13.8	*A. caesar* *L. setifacies* *P. pecosensis* others	2.5	17.9
Pupal	12.2	*I. conquisitor* *S. aldrichi*	0.9	7.4
Adult	7.8	-	-	-

Total no. killed by parasites during x = 29.7

Total real mortality = 97.8%

Real mortality due to larval and pupal parasites = 8.5%

Table 9. - Partial life table for *C. pinus* indicating mortality attributed to insect parasites of the larval and pupal stages. Oscoda County, Michigan, 1967.

(x)	(lx)	(dF)	(dx)	(100qx)
Egg	139.0	*T. minutum*	-	-
L_{3-4}	6.3	*Apanteles* spp. *G. fumiferanae*	1.7	26.5
L_{5-6}	4.6	*L. setifacies* others	0.3	7.0
Pupal	1.3	*I. conquisitor*	0.1	8.6
Adult	1.1	-	-	-

Total no. killed by parasites during x = 2.1

Total real mortality = 99.4%

Real mortality due to larval and pupal parasites = 1.5%

Table 10. - Partial life table for *C. pinus* indicating mortality attributed to insect parasites of the larval and pupal stages. Baraga County, Michigan, 1966.

(x)	(lx)	(dF)	(dx)	(100qx)
Egg	421.9	*T. minutum*	-	-
L_{3-4}	73.4	*Apanteles* spp. *G. fumiferanae*	26.6	36.2
L_{5-6}	48.0	*M. saundersii* *A. caesar*	0.4	0.9
Pupal	44.8	*I. conquisitor*	4.6	10.3
Adult	35.0	-	-	-

Total no. killed by parasites during x = 31.6

Total real mortality = 91.8%

Real mortality due to larval and pupal parasites = 8.2%

Table 11. - Partial life table for *C. pinus* indicating mortality attributed to insect parasites of the larval and pupal stages. Baraga County, Michigan, 1967.

(x)	(lx)	(dF)	(dx)	(100qx)
Egg	1012.3	*T. minutum*	-	-
L_{3-4}	15.5	*Apanteles* spp. *G. fumiferanae*	0.2	1.3
L_{5-6}	19.0	*P. affinis*	0.6	3.1
Pupal	10.7	*I. conquisitor* *P. hariolus* *E. ontario*	3.4	31.9
Adult	5.5	-	-	-

Total no. killed by parasites during x = 4.2

Total real mortality = 99.5%

Real mortality due to larval and pupal parasites = 0.4%

of insect parasitism is obtained by multiplying the population estimates by the appropriate combined percentage of apparent parasitism for each stage (100qx). Total real mortality (line 2 below each partial life table) indicates what proportion of the original population died from all causes between the egg and adult stages. The proportion of this mortality caused by larval and pupal parasites (line 3 below each table) is obtained by dividing the total number of insects killed by parasites during each age interval by the total dying within the generation.

In the 4 generations observed, real mortality ranged from 91.8% to 99.5%. The major portion occurred between eclosion and establishment of the fourth instar larvae on new foliage in early summer. Mortality during the remaining intervals was comparatively low, and variable.

The increase in the density of large larvae recorded at Baraga in 1967 was probably a combined result of larval redistribution and sampling error.

The proportion of real mortality attributed to larval and pupal parasites ranged from 0.4% to 8.5%, decreasing each year in both areas. The major portion of this mortality was caused by the early instar parasites, *Apanteles* spp.. The effect of pupal parasitism increased in both populations each year and could become more pronounced if infestations continue to decline. The importance of this group under such conditions was evidenced in the 1967 generation at Baraga. Uncommonly low parasitism in earlier stages of the cycle would have resulted in a much smaller reduction in host numbers had it not been for the high incidence of pupal parasites. Though contemporaneous mortality was seemingly

small during the pupal stage, apparent parasitism tripled over that in the preceding generation. This fluctuation was enough to account, in part at least, for a reverse in the population trend.

Overwintering mortality and dispersal loss, though great, probably have little effect on regulating population density, but seem to determine the general level at which regulation occurs (Chant 1963). A possible exception to this hypothesis is discussed in a later section. The unique situation indicated in the generation at Baraga in 1967 suggests the effect this type of mortality has on the parasites that overwinter in the host.

The impact of egg parasitism on the survival of a generation should be studied further. The crepuscular flight activity observed in the upper crown of jack pine may result in a substantial amount of egg laying in this region if defoliation is not too severe. Populations of *Trichogramma* might be higher than the figures presented above indicate.

No diseased larvae or pupae were observed in the rearing or field collecting work. This factor did not play a significant role in budworm epidemiology in the populations studied.

More work is required, observing several generations of *C. pinus*, before conclusions can be reached concerning the influence of insect parasites on survival of the host.

Conclusions

The largest amount of insect parasitism occurred in the second instar when the host was attacked by *Apanteles* spp. and *G. fumiferanae*. Parasitism by this group was substantially greater at mid-crown than in the lower crown. Incidence of *Glypta* was not affected by changes in host density. The prevalence of *Apanteles* spp. was greatest in older

infestations. Observations indicated that increased dispersal loss in the spring had a pronounced effect on the abundance of parasites of early stage budworm larvae.

Late stage larval and pupal parasitism was variable, the latter increased as an epiphytotic aged. Five species, *M. saundersii*, *P. pecosensis*, *A. caesar*, *L. setifacies*, and *A. interrupta*, appeared sporadically as parasites of late stage larvae. The group as a whole rarely appeared in a population, 1 or 2 species being prevalent at a time. *I. conquisitor* was the principle pupal parasite. Parasitism by this insect was greatest in the lower crown. The maximum apparent parasitism attained by it was 24.5%.

Parasitism of eggs by *T. minutum* was very low in 1965, but increased each year in the population at Oscoda. Mortality of eggs decreased yearly at Baraga. A closer examination of this mortality factor is warranted.

The percentage of real mortality attributed to larval and pupal parasites was low and decreased each year in both populations. Overwintering and dispersal loss were the greatest sources of mortality.

The incidence of late larval, pupal, and egg parasites was mainly restricted by the absence of alternate hosts. This restriction will probably continue because of the comparatively simple structure and harsh microclimatic conditions that limit faunal diversity in these jack pine communities. Parasite increases will continue to be slow, requiring increases in budworm numbers or aging of the infestations.

If the budworm population at Oscoda continues to decline, and egg samples for 1968 indicated that this trend will persist next year, the increased incidence of egg and pupal parasites should play a prominent

role in hastening the collapse of the infestation. The effect of total parasitism at Baraga will be reduced for the next few years until the decimated populations of *Apanteles* recover. This situation may be partly ameliorated by the increased parasitism of pupae and late stage larvae in 1967.

INVERTEBRATE PREDATORS OF *CHORISTONEURA PINUS*

Insect and Mite Predators

Methods. - Field observations were made on insects and mites associated with *C. pinus* in the crown and on the bole of jack pines. Species found feeding on various stages of the budworm or thought to be common associates were reared on the host in the laboratory.

To facilitate inspection of boles during the late larval stages, 10 trees were banded with a 4 in. strip of Tanglefoot at 2 to 5 ft above the ground. Banding accomplished 2 things: first, larvae attempting to move up the boles after spinning down on silk threads, tended to congregate around these barriers in prodigious numbers. Several predators were attracted to these areas, which facilitated observations. Second, I wanted to find out if any predators from the forest floor ascended the boles of jack pine in search of food. Those that did were either trapped when attempting to cross the Tanglefoot, or were found circling the strip or feeding below it.

Large plastic petri dishes (15 x 100 mm) and junior-sized, glass baby food jars (60 x 90 mm) were used as feeding chambers in the laboratory. A ball of cotton soaked in water provided moisture, and small quantities of foliage served as food for the budworm larvae and a substrate for the predators. A single predator (nymph, larva, or adult) was placed in each container with 3 live budworm larvae or pupae. The containers were checked daily and food was replaced when necessary.

Results and Discussion. - Eight species of insects were noted feeding on various stages of *C. pinus* in the field (Table 12). Three of them, *Podisus serieventris* Uhler, *Camponotus noveboracensis* Fitch, and *Anatis ocellata* (L.), were comparatively abundant and exerted a

Table 12. - Insect predators of *C. pinus* on jack pine in Michigan, 1965-1967.

Predator [a]	Host Stage attacked [b]	Predator stage
Coleoptera		
Coccinellidae		
Anatis ocellata (L.)	L	L,A
Hemiptera		
Pentatomidae		
Podisus serieventris Uhler	L,P	N,A
Miridae		
Deraeocoris albigulus Knight	P	A
Reduviidae		
Zelus socius Uhler	L,P	N,A
Hymenoptera		
Formicidae		
Camponotus noveboracensis Fitch	L	W
Formica exsectiodes Forel	L	W
F. pallidefulva nitidiventris Emery	L	W
Diptera		
Cecidomyiidae		
Cecidomyiini	L	L

[a] Identifications were made by the U. S. Dept. of Agr., Insect Identification and Introduction Division, Beltsville, Maryland: Coccinellidae - E. A. Chapin; Pentatomidae, Miridae, Reduviidae - R. C. Froeschner; Formicidae - D. R. Smith; Cecidomyiidae - R. J. Gagne.

[b] L=larval, P=pupal, A=adult, N=nymphal, W=worker

greater influence on the budworm populations than the remainder of the group. Predators, notes on their biology, and feeding results, where applicable, are discussed separately below.

Podisus serieventris Uhler

This pentatomid (Fig. 4), and several closely related species, prey on multifarious forest insects, mainly defoliators (Clausen 1940, Thompson and Simmonds 1965).

Recently, Ives (1967) reported *P. serieventris* as a predator of the larch sawfly, *Pristophora erichsonii* (Hartig), in Manitoba.

The life history of this predator and its habits in association with the black-headed budworm, *Acleris variana* Fernald, on Cape Breton Island, Nova Scotia, have been described by Prebble (1933). Observations on its life cycle in Michigan are in general agreement with Prebble's work.

The insect overwinters as an adult, probably on jack pine, and mates throughout late spring and early summer. Eggs are laid on old growth needles, dead twigs, or expanding shoots in clusters averaging 16.4±1.7 (n=21, p=.05) eggs. The nymphal stage lasts from 5 to 8 weeks and consists of 5 instars. Adults are present until early fall. Both the nymphal and adult stages are very active and continuously forage on bark surfaces and foliage.

The blackish-grey to greyish-brown adults have a distinct mottled appearance, are 6.0 to 7.0 mm wide between the lateral angles of the pronotum, and 12.0 to 13.0 mm in overall length. Lateral margins of pronotum are serrate; distal portion of corium with a reddish hue; each wing membrane with a characteristic brown band extending from the outer angle of the membrane to its center; connexivum banded alternately with

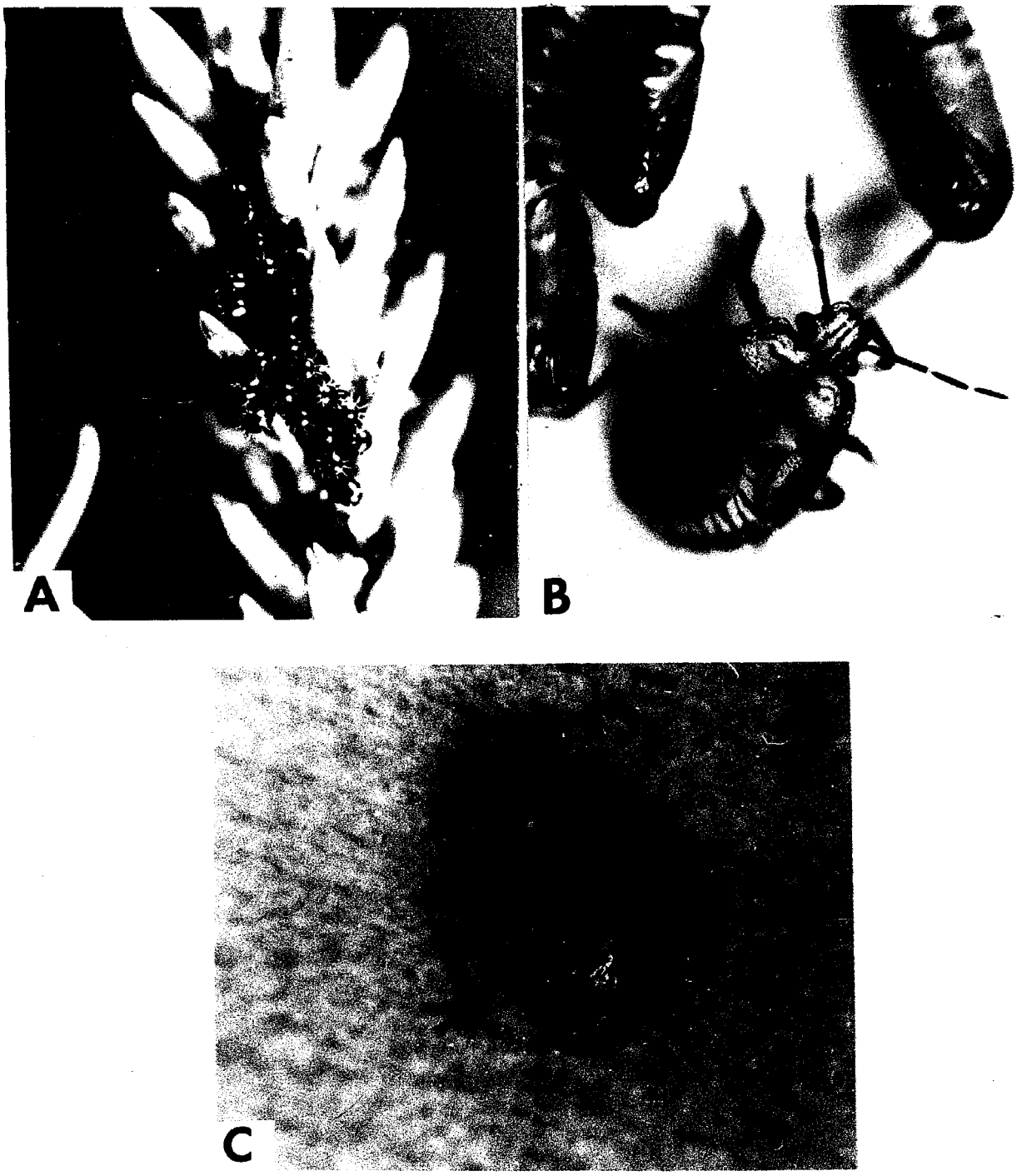


Figure 4. - *Podisus serieventris*. A, cluster of eggs; B, fifth instar nymph; C, adult.

yellow-brown and black; beak segments 1 to 3 light brown, segment 4 dark brown. Ventrally the ground color is mottled as above though much lighter with more light brown and yellow; abdominal segments 2 to 5 with a black spot in the medial ventral region, the marks increasing in size posteriorly.

Fifth instar nymphs 7.0 to 9.0 mm long and 4.0 to 5.0 mm wide at the widest point of the abdomen; possessing a black thorax with brown markings; abdomen cream colored with red transverse bands and dark brown lateral and medial areas. Nymphal instars were described in detail by Prebble.

The metallic bronze, caldron-shaped eggs possess a circular operculum with a dense armature of short, stiff, dark spines encircling the rim. Each egg is 1.2 to 1.3 mm high and 0.8 to 1.0 mm in diameter.

Prebble indicated that the first instar nymphs will not feed on small black-headed budworm larvae and require balsam fir, *Abies balsamea* (L.) Miller, foliage for food. I observed no predation on *C. pinus* larvae in the laboratory during the initial stage either, but noted that, if foliage was not available, the nymphs were cannibalistic on unhatched eggs or siblings. This behavior was enhanced by the fact that newly hatched nymphs remained clustered close to the eggs for 2 or 3 days following eclosion.

Fourth and fifth stage nymphs and adults were used in feeding experiments. The immature group consumed an average of 1 fourth or fifth stage budworm larva per day. Adults fed on a single sixth stage larva or pupa every 2 days. Feeding periods lasted from 7 to 10 days. Larvae that have been attacked look diseased; pupae, especially the wing pads, are hollow and take on a very light, amber color.

Budworm pupae, wrapped in a silk chamber and comparatively immobile on the foliage, are easy prey for *Podisus*. Late stage nymphs and adults were often seen feeding on larvae in the foliage or on the bole of jack pines. Predation by this pentatomid undoubtedly accounts for some of the unknown pupal mortality listed in the parasite collection data (Appendix I).

Early stage nymphs are inefficient predators because they have a difficult time negotiating the silk that surrounds the feeding larva.

Time did not permit sampling for population estimates of the predator. Field observations and inspection of foliage in the budworm population samples, however, indicated a substantial increase in bug numbers over the past 3 seasons where infestations had increased or remained at high levels (e.g., in Baraga and Iron Counties).

Prebble estimated that adults live an average of 63 days. The dependence of this stage on alternate hosts following emergence of the moths, probably limits the effectiveness of *P. serieventris* as a predator. Another factor to consider is the questionable ability of the bug to maintain high populations in the absence of or at low population levels of *C. pinus*.

A parasite, *Tissolcus podisi* Ashmead (Hymenoptera: Scelionidae) [5/] was reared from several eggs of *P. serieventris* collected in Oscoda County in 1967.

Camponotus noveboracensis Fitch

This carpenter ant was a common inhabitant in all stands of jack

---

[5/] Identified by P. M. Marsh, U. S. Dept. of Agr., Insect Identification and Introduction Division, Beltsville, Maryland.

pine studied. It has a 2 year life cycle (Sanders 1964), overwintering in nests in the soil beneath decaying logs or in the butts of dead standing trees (Fig. 5). The workers are active throughout the summer and are easily recognized by their red thorax, black head and gaster, and extremely large size (7.0 to 9.0 mm in length). A complete description was given by Wheeler (1910).

Workers forage throughout the foliage and surface of the bark of jack pine. When encountering a budworm, the ant quickly siezes the prey in its mandibles and drags it down the bole into an underground tunnel leading to the nest. *C. noveboracensis* has little success in attacking larvae on the foliage. The silk surrounding the feeding area and the feeding tunnel itself prevent a quick attack by the ant. At the slightest disturbance larvae spin down on silk threads and escape. Sometimes the ant will climb down the silk and trap the budworm in this manner. Workers scurry randomly about the trees, and do not perceive larvae until coming into physical contact with them.

A spider, *Coriarachne utahensis* Gertsch (Araneae: Thomisidae), was observed feeding on worker ants. This crab spider inhabits the boles and larger branches of jack pine, and its cryptic coloration is perfectly adapted for hunting on this substrate.

Sanders (1964) reported limited predation on the spruce budworm by *C. noveboracensis* in New Brunswick. Morris (1963) was of the opinion that ants as a group are scarce in the Green River watershed of New Brunswick. A closely related species present in small numbers, *C. herculeanus* (L.), was not collected from spruce or fir foliage. Some entomologists believe that the role of ants as important predators in the boreal forest is taken over by spiders (Steyn 1963). In

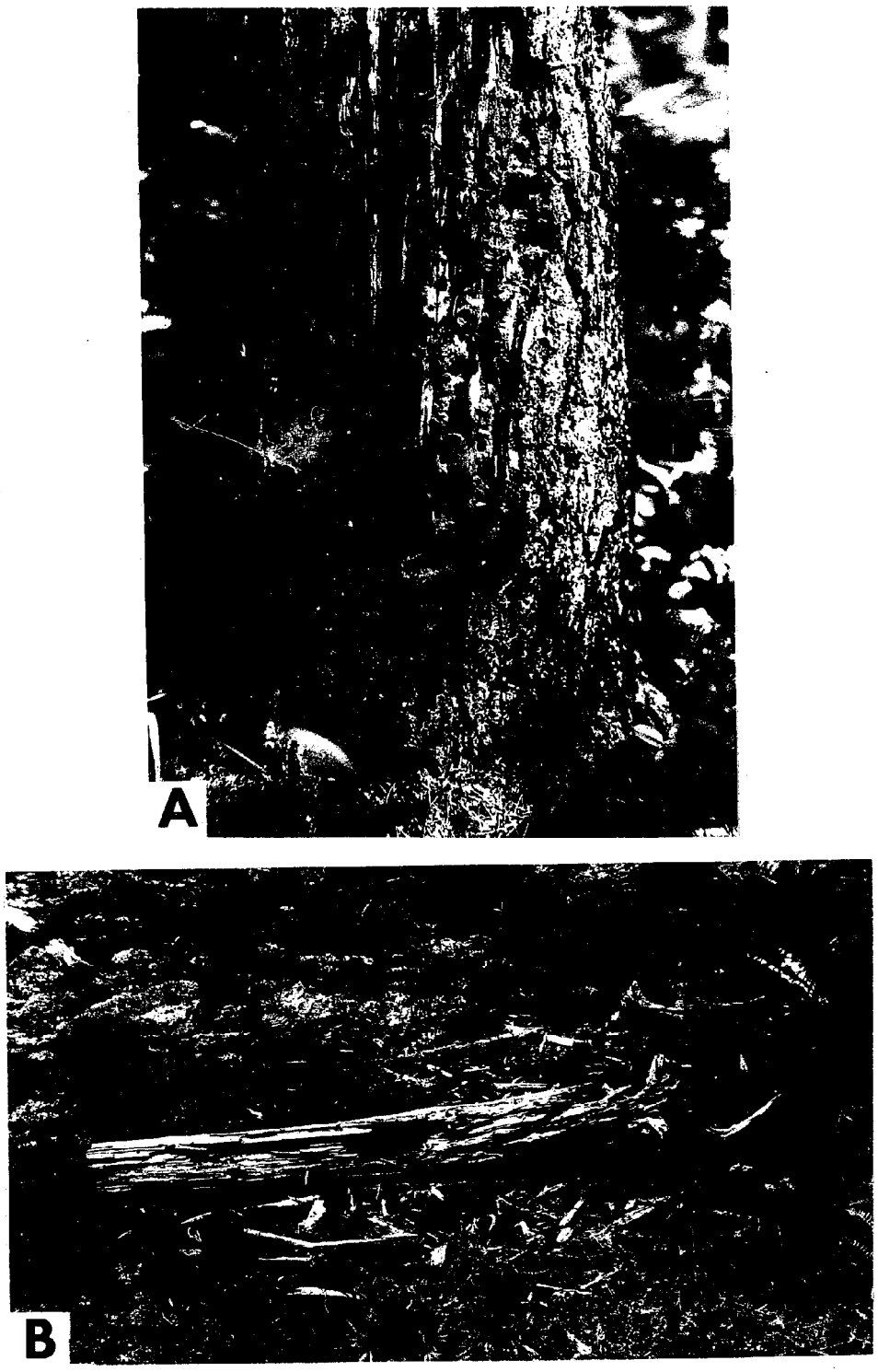


Figure 5. - Nests of *Camponotus noveboracensis* in a stand of jack pine. A, in the butt of a standing tree; B, beneath a rotting log.

British Columbia, Silver (1960) observed large numbers of *Camponotus vicinus* Mayr on spruce and fir foliage and surmised that many spruce budworm larvae were killed in the trees by this ant.

In stands where excessive ground vegetation and lack of insolation on the forest floor do not prohibit nest building, *C. noveboracensis* is a frequent predator of *C. pinus* larvae wandering on the boles and branches of jack pine. The ant is very catholic in its tastes, and does not depend solely on the budworm for food. Bradley and Hinks (1968) reported it commonly attending colonies of *Cinara banksiana* Pepper and Tissot and *C. gracilis* (Wilson) (Homoptera: Aphididae) on jack pine in Manitoba.

Anatis ocellata (L.)

This large coccinellid (Fig. 6) was encountered frequently on jack pine in both peninsulas of Michigan. Observations indicated that the insect is omnivorous, feeding on pollen in the staminate flower heads of jack pine as an adult and attacking larvae of *C. pinus* and other insects in both its adult and larval stages.

The beetle overwinters as an adult in the duff or in pine crowns. This stage emerges in mid-May and is present in the field throughout July. Egg laying begins in early June and continues as long as adults are present. Larvae pass through 4 instars and complete development in 5 to 6 weeks.

Adults are 8.0 to 10.0 mm long and oval shaped. The elytra vary from light to dark chestnut-brown and possess 8 black spots, each one encircled by a very light brown to yellow colored ring. Two additional smaller black spots may be present in the light brown region surrounding the black scutellum. The prothorax is light brown to

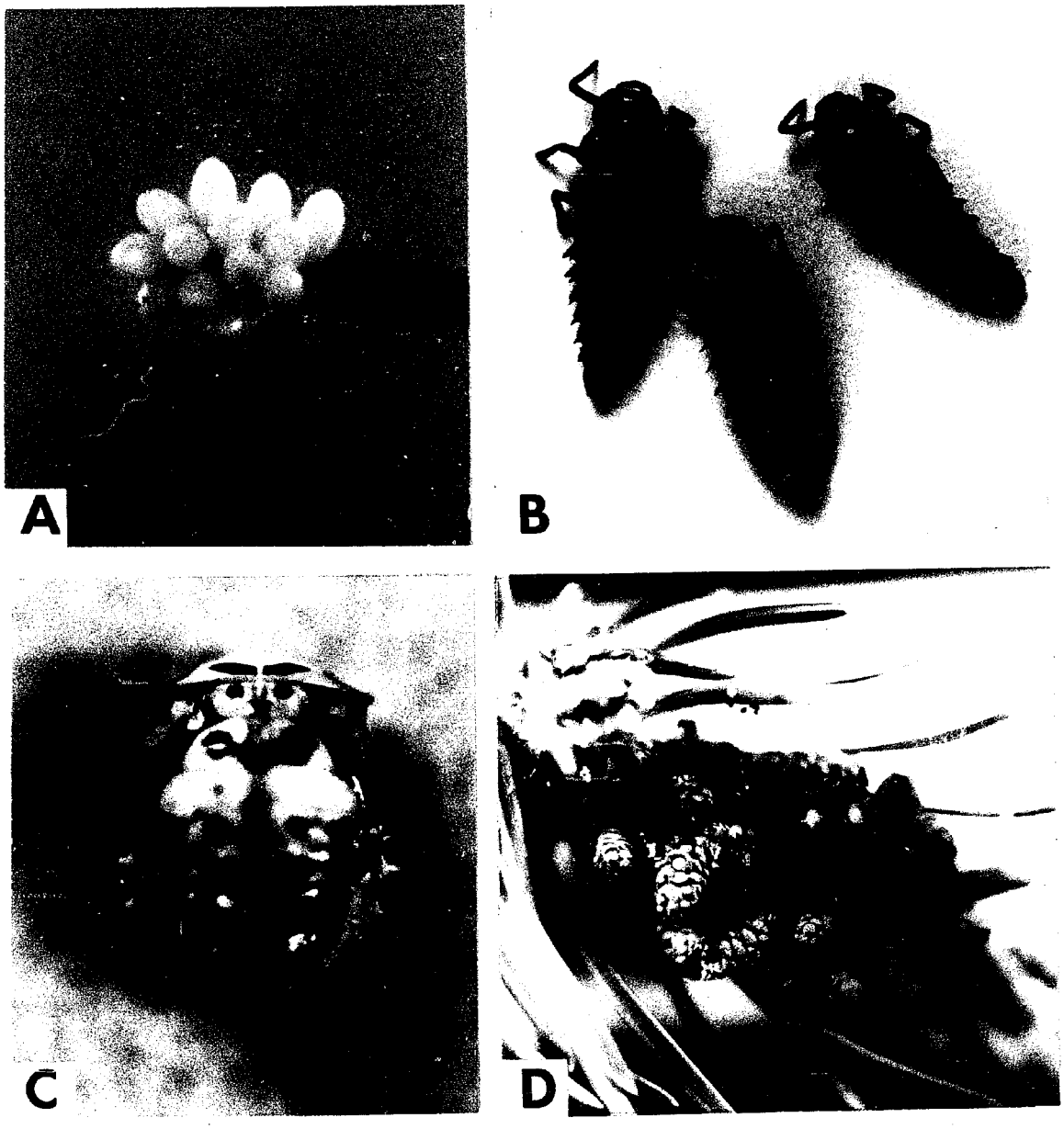


Figure 6. - *Anatis ocellata*. A, cluster of eggs; B, fourth stage larvae; C, pupa; D, adult.

yellow with a variable black pattern covering half or more of its surface. All legs are light to dark reddish-brown; and the ventral region of thorax and abdomen black except for the yellow mesepimera. The head is black with 2 large yellow spots on the face dorsad of the clypeus, 2 smaller yellow spots below each eye, and the apical margin of the clypeus and labrum yellow.

The fourth stage larva is 14.0 to 16.0 mm long; thoracic segments with a dorsal pair of parascoli, pleural regions of meso- and metathorax with a single parascolus; abdominal segments 1 to 8 with a dorsal, dorsolateral, and lateral pair of senti. Legs, dorsal region of head, prothorax, ninth abdominal segment, and all parascoli and senti except the lateral senti of abdominal segments 1 and 2 dark brown. Face, pronotal margin, lateral senti of abdominal segments 1 and 2, base of remaining lateral senti, and entire ventral region of larva pale yellow to yellow. Prothorax with a posterior median yellow spot dorsally; remaining thoracic segments with a dorsal pair of large dark brown spots. Metathorax and abdominal segments 1 to 7, each frequently with a dorsal pair of light yellow spots on the posterior margin.

Except for the size and yellow markings on the head and prothorax, the second (5.0 to 7.0 mm long) and third (8.0 to 10.0 mm long) instars are similar in appearance to the mature larva. The first instar is 3.0 to 4.0 mm long, light colored beneath and uniformily light brown dorsally.

The bright yellow, elongate-elliptical eggs are laid in clusters of varying size on needles or dead branch tips. Twenty-one clusters collected in 1967 averaged 12.7±1.6 ($p=.05$) eggs. Each egg is 1.7

to 2.1 mm long and 0.8 to 0.9 mm wide.

The first 2 larval instars are small (3.0 to 7.0 mm long), slow moving, and not able to negotiate silk spun by budworm larvae. These stages probably rely on aphids, mealybugs, and other comparatively immobile insects for food. The newly hatched larvae are cannibalistic. This behavior accounts for a large amount of larval mortality and is a source of quality food for the early stages (Banks 1956).

Later instars and adults are common predators of *C. pinus* on the boles and in the foliage. Adults have a characteristic pattern of attack when confronting a larva. Random searching is the paramount means of budworm discovery. Within a distance of one-half to three-quarters of an inch from the prey, however, visual stimuli play a role in illiciting the attack of a hungry beetle. Adults of *A. ocellata* observed under laboratory and field conditions stopped about this distance from the prey momentarily before moving forward and quickly snatching it in their mandibles. Physical contact was not required to arouse an attack. This apparent visual acuteness, though effective for only a short distance, increases the efficiency of the predator.

Five adults fed on an average of 0.4 fifth and sixth stage budworm larvae per day over a 30-day period under laboratory conditions. Third and fourth stage larvae fed on 2 fourth stage larvae of the budworm per day for 20 days. Consumption of a larva by the beetle required 3 to 5 minutes.

Little information is available on the biology and feeding habits of *A. ocellata* in North America. A taxonomic and anatomical review of the genus *Anatis* was presented by McKenzie (1936). Notes on the biology and a description of the immature stages were presented by Dinther

(1951). Several papers by Smith (1965, 1966a,b) described the feeding behavior of a closely related species (*A. mali* auctorum). In Europe, *A. ocellata* was reported as a predator of the spruce sawfly, *Lygaeonematus* (= *Pristophora*) sp., (Nolte 1938) and *Dreyfusia* (= *Adelges*) *picea* Ratzburg (Dinther 1951).

Deraeocoris albigulus Knight

The grey-black mottled coloration of the elyta, pronotum, and head of this mirid is very similar to that of *P. serieventris*. Some specimens are very dark fuscous to black in these regions, and paler beneath. The lighter colored individuals have dark antennae and calli, a pair of large black spots on the pronotal disk, and a dark spot at the tip of the corium and cuneus. The legs vary from amber to dark brown in color. Occasionally the tibiae possess light brown annulations. The membrane of the front wing is banded apically with brown. Adults are 7.0 to 8.0 mm long. A more detailed description was given by Knight (1917).

Adults of *D. albigulus* were collected from the foliage of jack pine; other stages were not recovered. The bug was observed feeding only on the pupal stage of *C. pinus*. Five adults averaged 0.4 pupae killed per day over a period of 17 days in the laboratory.

The nymph of an undetermined species of mirid was observed feeding on a third stage larva of the budworm at Baraga on June 21, 1967. The bug is 3.0 mm long, with light brown legs and antennae, a dark brown beak, and dark red body. The venter of its abdomen is light red. The family determination was made using a key to the immature stages of Hemiptera prepared by Lawson (1959).

Zelus socius Uhler

This large reduviid (14.0 to 15.0 mm long) is dark brown to black in color with white markings on the lateral areas of the prothorax, mesothorax, and apical region of the corium. Specimens were collected at Oscoda only and were reared on budworm larvae and pupae.

The shiny, brown, white-capped eggs of this bug are cemented together in tight masses on the pine needles. Each egg has a small hole in the center of its cap.

Socius nymphs and adults move very slowly on the foliage, stopping momentarily when approaching the prey, crouching, and then springing forward to grasp the prey with their front legs.

This species is closely related to Z. *exsanguis* (Stål), a predator of the forest tent caterpiller, *Malacosoma disstria* Hübner, and gypsy moth, *Porthetria dispar* (L.) (Readeo 1926, Downe and West 1954). The habits and biology of Z. *exsanguis* were discussed by West and Delong (1955), and my field observations suggest that Z. *socius* follows a similar pattern. There is 1 generation a year, the insect overwintering in the fifth and final instar. Eggs are laid in the spring. Members of this genus are general feeders.

Heinrichs and Thompson (1968) reported Z. *socius* as a predator of *Choristoneura houstana* (Grote) in Kansas.

Formica exsectoides Forel

The alleghaney mound builder is an associate of the budworm in jack pine types where the soil is suitable for nest building (i.e., sandy, well drained, etc.) and stands of trees are open enough to permit sunshine to reach the forest floor (Headly 1943, Haviland 1948). The nest characteristically takes the form of a mound 2 to 3 ft across

and up to 30 in. in height. Nest openings are located in the side walls, and the mound is covered with small sticks, needles, and grass. According to Andrews (1940), the ants winter deep within the mound in the subsoil until activated by warm temperatures in early spring.

Workers are 6.0 to 7.0 mm long with dark brown mandibles, reddish colored head, thorax, and petiole, and a black gaster. The legs are dark brown.

Though present in many of the infestations studied, this insect maintained its greatest numbers at a location (T25N-R7E-S15) in Alcona County. There were well over 100 nests to the acre throughout most of this area and up to as many as 400 per acre in some locations. Every tree in the stand was continually covered with the ants. Any budworm that fell to the ground was immediately attacked by a worker and dragged to a nest. When larvae are disturbed on the foliage and spin down from the feeding site the ants commonly scurry down the silk after them. The feeding tunnels protect the larvae, however, and this is probably the main reason why the ants have not been able to exert more of an influence on the budworm population. If this protection were lacking, chance encounter alone would eliminate a large proportion of the host.

Formica pallidefulva nitidiventris Emery

A few nests of this species were found in the Baraga study area, and the ants were taken from boles and lower limbs of jack pine.

Workers superficially resemble those of *F. exsectoides* except for their lighter, reddish-yellow colored legs and mandibles. Also, their gaster is never black, but varies from red to piceous. Many specimens look entirely reddish-brown. When color variations overlap,

the 2 species can be readily separated by the longer antennal scape and rounded propodeum characteristic of *F. p. nitidiventris* (Creighton 1950).

Nests are constructed in the soil, are very flat, and are located in stand openings where little debris has accumulated and no herbaceous vegetation is established. Workers when foraging will readily attack and carry off any budworm larvae encountered.

Cecidomyiidae, Cecidomyiini

While searching beneath bark scales for hibernacula in early spring, 3 cecidomyiid maggots were observed feeding on second stage larvae of the budworm. The maggots were 1.5 to 1.6 mm long and fulvous to rusty-yellow in color. One specimen was observed pulling a budworm larva out of its hibernaculum; this behavior may account for some of the empty hibernacula that were found.

A single adult female was successfully reared, but males are required for specific determinations. Mr. R. J. Gagné (personal communication) [6/] stated that the antennal structure of this specimen was unique in that it is the type usually found on males.

Dowden and Carolin (1950) reported that several specimens of a cecidomyiid maggot were observed feeding on larvae of the spruce budworm in New York. They attributed a small amount of overwintering mortality to this insect.

Several additional species of potential egg and larval predators were collected during the hibernacula and spider investigations, but those discussed above were the only ones actually observed feeding on

---

[6/] U. S. National Museum, Washington, D. C.

the budworm.

Checkered beetle larvae (Coleoptera: Cleridae) were commonly seen scurrying beneath bark scales in the vicinity of the hibernacula. Wilkes *et al.* (1948) recorded a clerid, *Hydnocera lecontei* Wolcott, preying on late stage spruce budworm larvae in British Columbia.

Two species of click beetles, *Ctenicera propola propola* (LeConte) and *C. mediana* (Germer) (Coleoptera: Elateridae) [7/] were prevalent on the foliage of jack pine. Adults coexisted with *C. pinus* throughout most of its larval and pupal stages. Thomson (1957) observed adult elaterids feeding on spruce budworm pupae in Ontario.

The most common arthropod collected on jack pine was a red mite, *Leptus* sp. (Acarina: Erythaeridae). [8/] These animals are parasitic on insects as larvae, but highly predaceous and free-living in the adult stage (Barker and Wharton 1952). This species was prevalent in jack pine stands throughout the growing season. Spruce budworm egg predation is attributed mainly to mites, which are about as common as spiders on the foliage of fir trees (Loughton *et al.* 1963). Precipitin tests with red mites by these workers indicated that this predator assumed considerable significance in some populations.

An unidentified species of mite (Acarina: Smarididae) was collected as an external parasite of adults of *C. pinus* in Baraga County.

[7/] Elateridae identified by T. J. Spilman, U. S. Dept. Agr., Insect Identification and Introduction Division, Beltsville, Maryland.

[8/] Acarina identified by E. W. Baker, U. S. National Museum, Washington, D. C.

Conclusions. - Insect and mite predators have little, if any, influence on outbreak populations of the jack-pine budworm. Those species that are able to maintain high numbers when host populations are low and are capable of responding numerically to initial budworm increases, may play a limited role in temporarily checking increases in populations. The ubiquitousness, mobility, and feeding habits of 3 species, *P. serieventris*, *C. noveboracensis*, and *A. ocellata* suggest that these insects belong in such a category.

In situations where it is extremely abundant (e.g., Alcona County) *F. exsectoides* undoubtedly exerts some influence on the maintenance of low populations until other factors (e.g., weather conditions, immigration, etc.) favor a population explosion.

P. serieventris offers the most promise as a predator of *C. pinus*. Based on field observations only, this insect has shown a substantial numerical response to increases of the host at Baraga County. Such a response may be of questionable importance, however, in that it may lag far behind the budworm's own response to favorable conditions.

Detailed studies concerning the biology and predatory responses of the insects discussed above are required before ecological relationships between these organisms and the budworm can be reasonably well understood.

Spider Predators

Of the many arthropods collected on jack pine, spiders made up the largest group numerically, excluding the budworm itself at epidemic levels. The habits of this group and their presence in stands from May to November place them high on the list of potential predators.

Review of the Literature. - A recent paper by Bradley and Hinks (1968) is the only comprehensive report on spiders associated with jack pine. They listed 42 species collected on jack pine reproduction in Manitoba. An average of 6 spiders were taken from each of 11, 6-foot trees in one sample. The families Thomisidae and Salticidae were best represented. Most species were important predators of aphids.

Turnbull (1956) considered the salticid family to be the most important spider predators of *C. fumiferana* on Douglas fir, *Pseudotsuga taxifolia* (Poiret) Britton, in British Columbia. Members of this group, especially *Metaphidippus flavipedes* Peckham, were aggressive hunters of larvae and adults of the budworm. Thomisids were abundant on fir, but did not capture many budworms.

Loughton *et al.* (1963) reviewed the few published accounts of predation by spiders on forest insect pests prior to 1963. Miller (1966) demonstrated that various species of *Philodromus*, *Grammonota*, and *Metaphidippus* readily attack freely moving black-headed budworm larvae. Radioisotope tracer techniques used by Pointing (1966) indicated that a sheet-web spider, *Frontinella communis* (Hentz) was an inefficient predator of adults of *Rhyacionа buoliana* (Schiffermüller).

More recently, Warren *et al.* (1967) reported 4 species of spiders collected from fall webworm, *Hyphantria cunea* (Drury), nests taken in

northwest Arkansas. A single species, *Aysha gracilis* (Hentz) (Araneae: Anyphaenidae), accounted for 41.4% of the total number of spiders collected. Several species of salticids were also observed preying on larvae of the webworm.

A thorough analysis of spider predation and its effects on epidemic populations of the spruce budworm was described by Loughton *et al.* (1963). Precipitin tests by these people gave a fairly accurate picture of spider predation at high levels of the host. Serological data indicated that predation was low until the fourth instar, when the larvae stop mining buds and needles and move out on the foliage. The family Micryphantidae, especially *Grammonota pictilis* (O. P. - Cambridge), was the most important group because of its large numbers on balsam fir foliage. The Theridiidae (*Theridion* spp.) proved to be the most effective predators, based on the percentage found to have fed on the budworm. Of the hunting spiders, the salticids were considered to be important predators. Thomisids, though present in large numbers were not efficient predators. Spiders showed a functional response to host populations and a pattern of predation throughout the season.

Watt (1963) indicated that spiders showed no numerical response to populations of the spruce budworm in New Brunswick.

Methods. - General spider collections were made in 1966 and 1967 during inspection of branches from the regular samples of the budworm population. This material was of limited value in that it only represented individuals present on the distal 36 in. of the branches, many specimens were lost while handling the foliage, and weather conditions

were not always conducive to spider activity on sampling days. This material did, however, add to the species list and gave a conservative indication of the number and variety of spiders present periodically throughout the summer in the crown regions of highest budworm density.

These data were supplemented by more detailed collections from 6 jack pine trees at Baraga County in 1967. Trees were stripped a limb at a time by crown level, and each branch was shaken vigorously over a 10 x 14 ft plastic drop cloth on the ground. Branches from the upper levels of the crown were handed to an assistant or dropped on the cloth. Spiders were collected with a pair of forceps or an artist's brush soaked in alcohol and the specimens were stored in 70% alcohol.

Tree, stand, and accompanying budworm population descriptions are shown in Table 13. Trees were selected on the basis of stand condition and degree of defoliation. All collections were made on clear, sunny days except for the lower crown of tree No. 1 which was stripped during overcast, rainy weather.

Several species were reared on larvae of *C. pinus* in the laboratory following the same procedures outlined under insect predators. This work gave some indication of the acceptability of larvae as food for the various groups, and it provided an estimate of specific rates of feeding.

Results and Discussion. - Fifty-one species of spiders representing 15 families were collected from the bark and foliage of jack pine (Table 14).

Of 1731 specimens obtained in 1966 and 1967, 72.0% were hunting spiders (Thomisidae, Salticidae, Oxyopidae, Lycosidae, and Clubionidae).

Table 13. - Characteristics of jack pines stripped for spiders in Baraga County, Michigan. July 1-14, 1967.

Tree no.	d.b.h. (in.)	Height (ft)	Live crown length (ft)	Notes [a]
1	5.4	24	20	open stand, light defoliation
2	7.9	32	32	open stand, light defoliation
3	7.0	47	27	closed stand, light defoliation
4	4.7	28	16	closed stand, moderate defoliation
5	5.4	28	20	intermediate stand, heavy defoliation
6	10.0	42	42	open stand, heavy defoliation

[a] Stand description:

Open - live crowns extending to ground.

Intermediate - trees partially exposed, crowns reaching ground on at least 2 sides.

Closed - crowns closed, branches on lower third or more of bole dead.

Defoliation description:

Light - feeding damage not conspicuous.

Moderate - feeding damage and webbing easily discernible.

Heavy - at least upper third of crown stripped of foliage.

Nearly half (48.0%) of this group was accounted for by a single species, *Metaphidippus flavipedes*. Other hunters that were abundant include *Xysticus punctatus* Keyserling (14.5%), *Philodromus pernix* Blackwell (14.4%), *Oxyopes scalaris* (5.6%), and *Coriarachne utahensis* (4.1%). additional species in the last four genera mentioned were present only rarely. All juveniles, therefore, were included in the values given, and the figures may be slightly high for each species.

The most common web-spinner encountered was *Theridion murarium* Emerton which represented 32.6% of this group. *Grammonota pictilis* and *Dictyna phylax* Gertsch and Ivie accounted for 10.3% and 4.7% of the spinners respectively. The 3 families best represented in this group were the Theridiidae, Dictynidae, and Micryphantidae.

Feeding results (Table 15) indicated that adults of 5 of the more prevalent species (i.e., *T. murarium*, *M. flavipedes*, *P. pernix*, *C. utahensis*, and *X. punctatus*) closely approximated each other in their rate of feeding. All juveniles fed comparatively little; females had the highest rate of feeding. Larvae of *C. pinus* were acceptable to all species tested. The last 4 species mentioned above and a sheet-web spider, *Frontinella communis*, were the only spiders observed preying on the budworm in the field.

The collecting method, though time consuming (the larger, more heavily foliated trees required 1.5 to 2.0 working days to complete), was efficient and the data accurately indicate the spider fauna present. One weakness in the procedure was the failure to methodically collect specimens from the tree boles. Several spiders were obtained from this region, but many were overlooked or lost while climbing and

Table 14. - List of spider species by family collected on jack pine in Michigan, 1965-1967. a/

Web-spinners

Agelenidae

undetermined juvs.

Amaurobiidae

undetermined juv.

Araneidae

Araniella displicata (Hentz)

Aranea nordammi (Thorell)

Epeira sp.

Eustala anastera (Walckenaer)

Singa sp.

Dictynidae

Dictyna coloradensis Chamberlin

D. phylax Gertsch & Ivie

Dictyna sp.

Linyphiidae

Frontinella communis (Hentz)

Linyphia marginata C. L. Koch

Micryphantidae

Ceraticelus fissiceps (O. P. - Cambridge)

Grammonota pictilis (O. P. - Cambridge)

Oedothorax montiferus (Emerton)

Tetragnathidae

Tetragnatha sp.

Table 14. - (cont.)

Theridiidae

Enoplognatha intrepida Sorenson

Euryopis limbata (Walckenaer)

Steatoda borealis (Hentz)

Theridion differens Emerton

T. murarium Emerton

Theridion sp.

Hunting spiders

Clubionidae

Agroeca ornata Banks

Clubiona sp.

Gnaphosidae

Herpyllus vasifer (Walckenaer)

Zelotes sp.

Lycosidae

Lycosa sp.

Pardosa distincta (Blackwell)

Pardosa sp.

Schizocosa avida Walckenaer

Tarentula aculeata (Clerck)

Tarentula sp.

Mimetidae

Mimetus notius Chamberlin

Oxyopidae

Oxyopes scalaris Hentz

Oxyopes sp.

Table 14. - (cont.)

Salticidae
Admestina tibialis (C. L. Koch)
Euophrys monadnock Emerton
Evarcha hoyi (Peckham)
Metaphidippus flavipedes Peckham
Phidippus mystaceus Hentz
Phidippus sp.
Thomisidae
Coriarachne utahensis Gertsch
C. versicolor Keyserling
Philodromus pernix Blackwell
P. placidus Banks
Thanatus coloradensis Keyserling
Tibellus oblongus Walckenaer
Xysticus punctatus Keyserling
X. elegans Keyserling
X. ferox (Hentz)
X. triguttatus Keyserling

[a] Family Lycosidae indentified by Mr. Wilton Ivie, American Museum of Natural History, New York; *M. flavipedes* females and juvs. by Mr. Larry Pinter, Harvard Museum, Cambridge; all other determinations by Mr. Daniel T. Jennings, North Central Forest Exp. Sta., St. Paul, Minnesota.

Table 15. - Results of spider feeding experiments with fifth and sixth stage larvae of *C. pinus*.

Species	Sex or stage	No. days fed	No. larvae eaten	No. eaten per day
T. murarium	female	49	17	.45
	male	11	3	.37
M. flavipedes	female	25	11	.44
	female	25	14	.56
	male	11	4	.36
	male	10	2	.20
	male	15	4	.27
G. pictilis	female	49	6	.12
	female	10	1	.10
O. scalaris	female	10	0	.00
	juv.	10	1	.10
P. pernix	female	10	3	.30
	juv.	10	2	.20
D. phylax	female	10	1	.10
C. utahensis	female	10	3	.30
	female	10	4	.40
X. prob. *punctatus*	juv.	19	4	.19
	juv.	24	3	.10
	juv.	10	1	.10
	juv.	10	1	.10
X. punctatus	female	28	13	.48
X. ferox	female	10	3	.30

working at high levels. The 2 most prevalent genera that inhabited boles, *Philodromus* and *Coriarachne*, are hunters.

The relative abundance of spiders collected from the 6 jack pines at Baraga is presented in Table 16. The thomisids, salticids, and theridiids made up the largest proportion of the population, and *M. flavipedes*, *P. pernix*, and *T. murarium* were the most common species.

The highest populations occurred on open-grown trees with little defoliation. With the exception of tree No. 4, closed stands and/or heavy defoliation appeared to have a negative effect on spider abundance. This was probably a result of a reduction in foliage area which reduced the abundance of alternative prey and adversely altered the microclimate. The effect of defoliation on a population was demonstrated by the low number of specimens recovered from tree No.6. This pine was one of the largest trees in the group and open-grown. The upper half, however, was heavily attacked by the budworm. The low population on tree No. 3 was a result of a reduction in crown area and alterations of the habitat brought about by closing of the stand.

The abundance of spiders in the open-grown, lightly defoliated trees (Nos. 1 and 2) decreased with tree height. This was to be expected as the available habitat decreased similarly. In the denser stands with light to moderate defoliation (Nos. 3 and 4), however, this pattern was partially or wholly reversed. Such a trend could have been a result, in part, of too much shade in the lower crown or the physical disturbance resulting from the branches of neighboring trees that were whipped by the wind.

The distribution of spiders on tree No. 5 also can be explained

Table 16. - Relative abundance of families and species of spiders occurring on 6 jack pine trees in Baraga County, Michigan, 1967.

Family and species	Number of specimens	% of family	% of total [a/]
Thomisidae			
P. permix	87	53.4	15.9
X. prob. *punctatus*	51	31.3	9.3
C. utahensis	23	14.1	4.2
P. placidis	1	0.6	0.2
Xysticus sp.	1	0.6	0.2
Total	163	100.0	29.8
Salticidae			
M. flavipedes	127	100.0	23.8
Oxyopidae			
O. scalaris	48	100.0	8.8
Clubionidae			
Clubiona	16	83.3	2.9
A. ornata	2	16.7	0.4
Total	18	100.0	3.3
Lycosidae			
Tarentula sp.	1	50.0	0.2
Pardosa sp.	1	50.0	0.2
Total	2	100.0	0.4
Linyphiidae			
F. communis	3	100.0	0.5

Table 16. - (cont.)

Family and species	Number of specimens	% of family	% of total [a/]
Theridiidae			
T. murarium	63	78.8	11.5
T. differens	12	15.0	2.2
E. limbata	3	3.6	0.5
Theridion sp.	1	1.3	0.2
E. intrepida	1	1.3	0.2
Total	80	100.0	14.6
Micryphantidae			
G. pictilis	6	27.3	1.1
C. fissiceps	1	4.5	0.2
unknown juvs.	15	68.2	2.7
Total	22	100.0	4.0
Araneidae			
Singa sp.	2	4.3	0.4
E. anastera	1	2.2	0.2
A. displicata	1	2.2	0.2
unknown juvs.	42	91.3	7.7
Total	46	100.0	8.5
Dictynidae			
Dictyna sp.	26	70.3	4.8
D. phylax	9	24.3	1.6
D. coloradensis	2	5.4	0.4
Total	37	100.0	6.8

[a] Based on a total of 546 specimens, Grand Total Table 17.

according to these hypotheses. Shading and disturbance modified the environment enough to limit the population in the lower crown, and heavy defoliation restricted numbers in the upper level.

The number of species collected in each crown level varied considerably, though the majority of them were hunters (Table 17). The data indicate that heavily defoliated trees or trees in closed stands have a smaller variety of spiders than open-grown, uninfested individuals. This may be a result of a physical reduction in foliage area when stands close, or the lack of suitable habitat as a result of defoliation by the budworm. Also, the forest floor beneath closed stands probably is not suitable for ground dwellers which contributed to the faunal variety of open-grown trees.

The data on spiders obtained from the population samples of *C. pinus* deserves some mention, bearing in mind the inadequacies in the collecting procedure enumerated under Methods.

All species collected in the study of 6 trees were encountered in the 36 in. branch samples, and no species or group of species characterized any crown level, branch position, or region of a branch in either collection. The density of spiders per 100 pine tips is summarized in Table 18. This method of expressing density was used for convenience and is of limited value also, because no relationship was established between the number of tips and number of spiders. The data as expressed, however, suggest that spider numbers fluctuate substantially from year to year and throughout the growing season in some stands. Sampling collections were several days apart and provide little information on population peaks and periods of adult dominance. This material combined with other collections suggests that populations

Table 17. - Summary of the population structure of the spider fauna associated with 6 jack pines in Baraga County, Michigan, 1967.

Tree no.	Crown level	No. specimens	No. species	% adults	Dominant group (% of total for each level)
1	lower	60	15	49.0	hunters (53.3)
	mid	21	8	57.1	hunters (52.3)
	top	15	6	45.5	hunters (66.7)
	Total	96			
2	lower	102	15	20.6	hunters (73.5)
	mid	64	18	25.0	hunters (75.0)
	top	58	11	24.5	hunters (86.8)
	Total	219			
3	lower	2	1	0.0	hunters (100.0)
	mid	14	4	9.1	hunters (71.4)
	top	19	6	8.3	hunters (73.6)
	Total	35			
4	lower	3	1	0.0	hunters (100.0)
	mid	57	9	9.5	web-spinners (59.6)
	top	26	4	6.3	hunters (50.1)
	Total	86			
5	lower	15	6	33.3	hunters (66.7)
	mid	27	9	33.3	hunters (55.6)
	top	5	3	50.0	hunters (80.0)
	Total	47			

Table 17. - (cont.)

Tree no.	Crown level	No. specimens	No. species	% adults	Dominant group (% of total for each level)
6	lower	32	8	37.5	hunters (71.9)
	mid	28	9	27.8	hunters (67.9)
	top	3	1	100.0	hunters (66.7)
	Total	63			

Table 18. - Density of spiders per 100 jack pine tips from populations samples of *C. pinus* collected in 5 counties in Michigan, 1966-1967.

	1966			1967		
		Spiders/100 tips			Spiders/100 tips	
County [a/]	Date	Mid crown	Lower crown	Date	Mid crown	Lower crown
Iron	6/15	0.3	0.3	6/12	0.6	0.6
	7/7	0.2	0.1	6/27	0.5	0.5
	7/19	0.2	0.1	6/24	0.2	0.4
	-	-	-	8/4	0.4	0.5
Baraga	6/17	0.3	0.2	6/20	0.4	0.7
	7/8	0.1	0.1	7/7	0.7	0.6
	7/22	0.2	0.2	7/31	0.4	0.6
	-	-	-	8/14	0.5	0.7
Crawford	6/9	1.4	1.1	6/12	0.1	0.2
	6/27	0.4	0.4	6/26	0.4	0.5
	7/13	0.1	0.1	7/16	0.6	0.7
	-	-	-	8/8	0.7	1.2
Oscoda	6/10	1.4	1.4	6/13	0.7	0.8
	6/28	0.2	0.1	6/27	0.4	0.2
	7/14	0.1	0.3	7/17	0.6	0.7
	-	-	-	8/9	0.3	0.4
Alcona	6/10	0.2	0.5	6/13	0.5	0.1
	6/28	0.0	0.1	6/27	0.2	0.6
	7/14	0.2	0.1	7/17	0.3	0.7
	-	-	-	8/9	0.6	0.7

[a] Iron and Baraga County data represent 3, 10-tree clusters in 1966 and 4 in 1967. The remaining counties represent 1, 10-tree cluster each.

reach peak numbers in the spring and early summer and again in late summer and early fall. Adults make up the largest proportion of the populations from mid- to late summer.

Several species (e.g., *X. punctatus*, *O. scalaris*, *M. flavipedes*, and *T. murarium*) inhabited the terminal shoots of jack pine and constructed their egg sacs in this region. Webs of *D. phylax* and *F. communis* were observed on the branch tips also. The web-spinners probably feed only on dispersing larvae blown to their snares by the wind and are of little importance. The hunters, however, feed actively in the region of the crown of high budworm density and offer some potential as predators. Dispersing larvae that end up on tree boles and migrating second stage larvae, are susceptible to predation by several spiders that inhabit the tree bole. The important spiders on this substrate included *Coriarachne* spp., *Philodromus* spp., and *M. flavipedes*. Several species such as *Tarentula aculeata* (Clerck), *Lycosa* spp., *Pardosa* spp., and *Schizocosa avida* Walckenaer are ground dwellers that forage on the boles of pine and certainly exert some predatory influence. Members of this group were commonly observed below the Tanglefoot barriers or scurrying around the base of a tree in the duff.

Conclusions. - Almost three-quarters of the spiders found on jack pine in northern Michigan were hunting spiders. Five species, *M. flavipedes*, *X. punctatus*, *C. utahensis*, *P. pernix*, and *O. scalaris* accounted for 86.0% of this group.

Two species, *T. murarium* and *G. pictilis* comprised 43.0% of the web-spinning group.

Heavy defoliation of jack pine by *C. pinus* adversely altered the

trees as a habitat suitable for the maintenance of high populations of spiders. Shading of the lower crowns of trees in dense stands also restricted the number and variety of spiders. These interactions probably limit the ability of many species of spiders to respond numerically to increases in populations of the budworm.

Because of their abundance and feeding habits, 3 species, *M. flavipedes*, *X. punctatus*, and *P. pernix*, should be studied more closely because they may be influential predators in populations of *C. pinus* under suitable stand conditions and low levels of budworm populations.

All species collected in the study were well distributed throughout the trees sampled, except the ground dwellers, and no crown level or branch region was characterized by certain species or group of species.

OVERWINTERING MORTALITY

Population samples indicated that the greatest amount of budworm mortality occurred between egg hatching in late summer and establishment of the third stage larvae on foliage the following spring. A large percentage of this mortality was the result of dispersal loss prior to hibernacula spinning in the fall and during the migration period in late May and early June (J. L. Foltz, personal communication). Dessication, enhanced by a paucity of suitable overwintering sites when high populations exist, may have claimed its share of budworms also.

Spruce budworm mortality during the overwintering stage varied between 9% and 22% in the Green River area of New Brunswick (Miller 1958). Earlier investigations by Jaynes and Drooze (1952) in the northeastern United States indicated that mortality may be as high as 41% in the hibernacula of *C. fumiferana*.

Methods

Two branches, 1 each on the north and south sides, from the mid- and lower crown of 5 trees were collected in late May, 1966, and from 3 trees during the same period in 1967 at Baraga County.

All bark flakes were removed separately from each main branch with a pair of forceps. Lateral branches were discarded. The position of each hibernaculum was marked with a thumb tack and paper tag indicating whether the structure was empty or contained a live or dead larva. Hibernaculum density was expressed as the number per foot of branch length.

A few lateral branches on several limbs were examined in 1967, as were 50 old staminate flower heads.

Beginning at ground level, a 12 in. band was examined at 5 foot intervals on the bole of 2 trees in 1966. Wintering sites were marked in the manner described above. Density was expressed as the number per inch of section diameter. Diameter measurements were made at the center of each section.

A hand lens facilitated close examination of all larvae. Many individuals had emerged by late May, and those remaining should have been far enough out of diapause to react to prodding with an insect pin. Those larvae that did not were considered to be dead. Most of the larvae in this category were shriveled, further indicating that they had succumbed. Conclusions drawn from the data were based on this assumption.

Both year's data were considered, but only the information collected in 1966 was subjected to an analysis of variance to determine if significant differences in survival existed between crown levels and quadrants, or if a certain position within the tree or on a branch was preferred as a spinning site. The 1967 sample was too small for such an analysis.

Results and Discussion

The basic data are presented in Appendices III and IV. An analysis of the 1966 material indicated that there were a significantly larger number of hibernacula spun in the mid- than in the lower crown (Table 19). This was to be expected as a higher proportion of the egg masses are laid in this region of the trees.

Cardinal direction was not a significant factor in determining the density of hibernacula, although in 94% of the samples, branches with a southern exposure exceeded their northern counterpart in the

Table 19. - Analysis of variance of inter- and intra-tree distribution of hibernacula of *C. pinus*. Baraga County, Michigan, 1966.

Source of variance	Degrees of freedom	Sum of squares	Mean square	F-ratio
Trees	4	472.76	118.19	0.706
Levels	1	2066.55	2066.55	12.339 *
Error (T x L)	4	669.55	167.48	
Quadrants	1	175.84	175.84	3.710
L x Q	1	249.91	249.91	5.273
T x L	4	529.45	132.36	2.793
Error (T x L x Q)	4	189.56	47.39	
Total	19	4354.01		

* Significant at the .05 level, using first error term.

number per foot of branch length. Hibernacula were randomly distributed throughout each branch. The data from 1967 exhibited similar relationships.

Mortality within the overwintering structure on each branch ranged from 24.0% to 68.0% the first year of the study, and from 0.0% to 25.0% the second (Appendix III). In 1966 there was no significant difference between crown levels in mortality (Table 20), or the number of larvae that had emerged at the time of branch inspection (Table 21). Larval emergence figures include a certain amount of predation. Due to the small size and inaccessible location of the hibernacula, predators probably remove the host from the structure to feed on it. This occurred in the 1 case of predation observed. The hypothesis is further substantiated by the fact that larval remains, other then shed head capsules, were never found within the hibernacula.

Hibernacula density on the boles of jack pines was greatest in the upper half of the tree crown (Table 22). The highest concentration per inch of diameter occurred at mid-crown. Mortality on the boles varied, ranging from 0.0% to 53.2%.

Several workers (Bess 1946, Blais 1952, Jaynes and Speers 1949) indicated that *C. fumiferana* prefers staminate flower bracts and bud scales as overwintering sites. Miller (1958) detected no preference for either branch sections or branches. MacAloney and Drooze (1956) considered old flower bracts, needle fascicles, and under bark scales on the trunk and larger limbs as favored sites for *C. pinus*.

The flower bracts and lateral branches examined in this study produced very few hibernacula. The lateral branches of jack pine have very tight bark and offer few suitable locations for spinning.

Table 20. - Analysis of variance of inter- and intra-tree overwintering mortality of *C. pinus*. Baraga County, Michigan, 1966.

Source of variance	Degrees of freedom	Sums of squares	Mean square	F-ratio
Trees	4	454.14	113.53	3.455 NS
Level	1	7.05	7.05	0.215 NS
Error	4	131.45	32.86	
Total	9	592.64		

Table 21. - Analysis of variance of inter- and intra-tree emergence of *C. pinus* larvae from the hibernacula. Baraga County, Michigan, 1966.

Source of variance	Degrees of freedom	Sum of squares	Mean square	F-ratio
Trees	4	421.36	105.34	1.600 NS
Levels	1	156.02	156.02	2.371 NS
Error	4	329.00	65.80	
Total	9	906.38		

Table 22. - Density of the hibernacula of *C. pinus* on jack pine boles, Baraga County, Michigan. May 30 - June 4, 1966.

	Tree no. 1		Tree no. 2	
Height of section off ground (ft)	No. hibernacula/ inch section diameter	% larvae dead	No. hibernacula/ inch section diameter	% larvae dead
0-1	0.2	0.0	0.8	0.0
6-7	0.9	0.0	3.0	27.8
12-13	7.8	4.0	91.5	23.5
18-19	28.6	53.2	89.0	24.7
24-25	16.3	32.3	-	-

Reliable counts from flower heads were hindered by deposits of pitch and silk spun by feeding larvae of the preceding year. Wintering sites seem to be concentrated on the bole and scaly branches of jack pine. The large number found on the boles suggests that larvae are capable of traveling several feet before spinning.

The data indicate that this mortality within the hibernacula was highest during periods of low populations of the budworm (1966), and declined substantially with an increase in the population (1967).

Conclusions

The majority of the hibernacula of *C. pinus* were spun under flakes of bark on the boles and main branches of jack pine. The paucity of loose bark on small branches precluded this region as an overwintering site. A significantly larger number were spun in the mid- than in the lower crown.

Mortality within the hibernacula was high, variable, and not influenced by position within the crown or location on the branch.

Mortality during this stage, because of its magnitude and variability, could be an important factor in determining survival of a generation of the budworm. Considerably more data are needed before this hypothesis can be substantiated.

Predators removed larvae from the hibernacula. Therefore, their influence was confounded with larval emergence data and could not be determined.

SUMMARY AND CONCLUSIONS

Apparent parasitism of the early larval, late larval, and pupal stages of the jack-pine budworm in a heavily defoliated stand of jack pine in Baraga County, and a lightly defoliated stand in Oscoda County, Michigan, was determined in 1966 and 1967. Observations in the field and laboratory were made from 1965 to 1967 on multifarious invertebrate predators collected in 5 counties in Michigan. An investigation of the abundance and distribution of spiders on jack pine trees was accomplished in Baraga County in 1967. The location of the overwintering sites of the budworm, and the occurrence of overwintering mortality within the hibernacula were investigated in Baraga County in 1966 and 1967.

Twenty-six species of primary parasites and 4 species of hyperparasites were reared from the budworm. Nine species are new records for this host.

The largest amount of parasitism occurred in the early larval stages and was attributed predominantly to 2 species that overwinter in the host, *Apanteles fumiferanae* and *Glypta fumiferanae*. Mortality during this stage varied from 1.3% to 51.3% and was greater than 25.0% in all populations except 1. Of the 2 crown levels sampled, parasitism was greatest at mid-crown in all areas. Abundance of *Glypta* was not affected by the density of the host. *Apanteles* was more prevalent in the older infestation. Low populations of early instar parasites in 1967 were attributed to increased dispersal loss of the host in early summer of that year.

Late stage parasitism of budworm larvae was variable. Five species of tachinid flies accounted for most of the mortality during these

stages, and all of them appeared sporadically in the infestations. The maximum parasitism obtained by this group was 17.9%.

Itoplectis conquisitor was the most important parasite of the pupal stage; it accounted for as much as 24.5% of the pupal mortality in one sample. Parasitism of pupae was greatest in the lower crown, and increased with the aging of populations of the host.

A single species of egg parasite, *Trichogramma minutum*, was recovered. Parasitism of eggs was low in all populations.

The proportion of real mortality attributable to parasites of larvae and pupae was low and variable, ranging from 0.4% to 8.5%. The incidence of parasites of late larvae, pupae, and eggs was restricted by the paucity of alternate hosts in the jack pine communities. The greatest influence by parasites was manifested in aging and/or declining populations of the host.

Information on insect parasites is essential for the construction of comprehensive life tables at a later date. It is imperative that this type of mortality be evaluated continuously concomitant with other age-specific mortality factors and budworm population sampling, if the true perspective of parasitism is to be ascertained when evaluating survival of generations of *C. pinus* in the future.

Eight species of insect predators were recorded preying on various stages of the budworm. *Anatis ocellata*, *Podisus serieventris*, and *Camponotus noveboracensis* were the most abundant of this group. Field observations indicated that only 1 species, *P. serieventris*, showed a substantial numerical response to increases in budworm numbers, and it was considered the most important insect predator. Detailed descriptions of various stages of the more common predators were

presented where such material was found to be inaccessible or unavailable in the literature.

Fifty-one species of spiders were collected from jack pine. Three-quarters of them were hunting spiders belonging to 3 families, Thomisidae, Salticidae, and Oxyopidae. A single species, *Metaphidippus flavipedes*, accounted for 48.0% of this group.

Theridion murarium, *Dictyna phylax*, and *Grammonota pictilis* were the most common web-spinners encountered. This group was considered unimportant as predators of the budworm.

Defoliation and natural stand closure adversely modify the habitat, and were considered to be important factors in limiting populations of spiders. No crown level or stand could be characterized by specific groups of spiders. Most species were ubiquitous.

Field observations and the data collected indicated that populations of spiders reached a peak in early summer and early fall. Adults were most prevalent in late summer.

M. flavipedes, *Xysticus punctatus*, and *Philodromus pernix* were considered to be the most promising spider predators of the budworm, because of their abundance on the tips of branches and feeding behavior.

The invertebrate predation work was necessarily general in nature. It is important to have a broad knowledge of the potential predators associated with *C. pinus* before more detailed studies are undertaken. These initial data indicated the relative abundance of the various groups (*viz.*, insects, spiders, and mites) present on jack pine.

The 3 most significant insect predators, i.e., *P. serieventris*, *A. ocellata*, and *C. noveboracensis*, should be considered for future

study to determine the relative importance of predation, as opposed to parasitism, on the survival of generations of *C. pinus*. Information on relative abundance, the nature of the predation (i.e., functional and numerical responses), predator-prey interactions, predator and prey characteristics (e.g., defense mechanisms and attack techniques), etc., will help elucidate the role of these organisms in the dynamics of budworm populations.

The abundance and feeding behavior of several hunting spiders on jack pine, especially *Metaphidippus flavipedes*, suggests that similar work with these predators is warranted.

Research in these areas will contribute substantially to a comprehensive understanding of the life system of *C. pinus* in northern Michigan, and, ultimately, in determining the efficient use of artificial control techniques.

APPENDICES

APPENDIX I

Table 23. - Apparent parasitism of *C. pinus* by species, Oscoda County, Michigan, 1966. Mid-crown, determined by rearing.

Stage of the host	No. of hosts	No. of host parasitized	% parasitism	Parasite(s)
early larval	389	230	59.1	*Apanteles* spp.
		7	1.8	*G. fumiferanae*
late larval	126	16	12.7	*A. caesar*
		2	1.6	*P. pecosensis*
		1	0.1	*T. rhyacioniae*
		7	5.6	Misc. Diptera
pupal	418	9	2.2	*I. conquisitor*
		8	1.9	*S. aldrichi*
		16	3.8	Hyperparasites
		21	5.0	Moths failed to emerge, cause unknown

Table 24. - Apparent parasitism of *C. pinus* by species, Oscoda County, Michigan, 1966. Lower crown, determined by rearing.

Stage of the host	No. of hosts	No. of host parasitized	% parasitism	Parasite(s)
early larval	284	98	34.5	*Apanteles* spp.
		10	3.5	*G. fumiferanae*
late larval	64	8	12.5	*A. caesar*
pupal	146	4	2.7	*I. conquisitor*
		5	3.4	Hyperparasites
		8	5.5	Moths failed to emerge, cause unknown

Table 25. - Apparent parasitism of *C. pinus* by species, Oscoda County, Michigan, 1967. Mid-crown, determined by rearing.

Stage of the host	No. of hosts	No. of host parasitized	% parasitism	Parasite(s)
early larval	100	37	37.0	*Apanteles* spp.
		2	2.0	*G. fumiferanae*
late larval	115	7	6.1	*L. setifacies*
		1	0.9	*T. rhyacioniae*
		2	1.7	Cause of mortality unknown
pupal	95	2	2.1	*I. conquisitor*
		1	1.1	Moths failed to emerge, cause unknown

Table 26. - Apparent parasitism of *C. pinus* by species, Oscoda County, Michigan, 1967. Lower crown, determined by rearing.

Stage of the host	No. of hosts	No. of host parasitized	% parasitism	Parasite(s)
early larval	100	14	14.0	*Apanteles* spp.
late larval	115	4	3.5	*L. setifacies*
		1	0.9	*T. rhyacioniae*
		1	0.9	*P. affinis*
pupal	90	13	14.4	*I. conquisitor*

Table 27. - Apparent parasitism of *C. pinus* by species, Baraga County, Michigan, 1966. Mid-crown, determined by rearing.

Stage of the host	No. of hosts	No. of host parasitized	% parasitism	Parasite(s)
early larval	339	139	41.0	*Apanteles* spp.
		1	0.3	*Meteorus* sp.
		4	1.2	*G. fumiferanae*
late larval	97	1	1.0	*M. saundersii*
pupal	1141	93	8.2	*I. conquisitor*
		1	0.1	*P. hariolus*
		40	3.5	Hyperparasites
		56	4.9	Moths failed to emerge, cause unknown

Table 28. - Apparent parasitism of *C. pinus* by species, Baraga County, Michigan, 1966. Lower crown, determined by rearing.

Stage of the host	No. of hosts	No. of host parasitized	% parasitism	Parasite(s)
early larval	192	46	24.0	*Apanteles* spp.
		1	0.5	*G. fumiferanae*
		1	0.5	*Phaeogenes* sp.
late larval	114	1	0.9	*A. caesar*
pupal	512	44	8.6	*I. conquisitor*
		18	3.5	Hyperparasites
		32	6.3	Moths failed to emerge, cause unknown

Table 29. - Apparent parasitism of *C. pinus* by species, Baraga County, Michigan, 1967. Mid-crown, determined by rearing.

Stage of the host	No. of hosts	No. of host parasitized	% parasitism	Parasite(s)
early larval	150	2	1.3	*Apanteles* spp.
late larval	94	4	4.3	*P. affinis*
		2	2.1	Cause of mortality unknown
pupal	84	11	13.1	*I. conquisitor*
		1	1.2	*P. hariolus*
		3	3.6	Hyperparasites
		11	13.1	Moths failed to emerge, cause unknown

Table 30. - Apparent parasitism of *C. pinus* by species, Baraga County, Michigan, 1967. Lower crown, determined by rearing.

Stage of the host	No. of hosts	No. of host parasitized	% parasitism	Parasite(s)
early larval	150	2	1.3	*Apanteles* spp.
late larval	98	2	2.0	*P. affinis*
pupal	94	23	24.5	*I. conquisitor*
		2	2.1	*P. hariolus*
		2	2.1	*E. ontario*
		3	3.2	Hyperparasites
		13	13.8	Moths failed to emerge, cause unknown

APPENDIX II

RELATIONSHIP BETWEEN THE LENGTH OF EGG MASSES OF *C. PINUS* AND THE NUMBER OF EGGS PER MASS

Egg masses of *C. pinus* were collected before hatching from all of the study areas in 1965, so that direct egg counts could be made. The relationship between mass length (mm) and number of eggs per mass was investigated in hopes that length could be utilized to estimate the number of eggs in a mass that had hatched, and, concomitantly, per 100 branch tips. Population sample collections were made after eclosion when accurate direct counts of eggs were impossible.

Masses varied from 2 to 3 rows in width, therefore, separate regression equations were computed for each size (Figs. 7 and 8). The relationship in both instances was significant at the 1% level (Table 31).

To determine if this relationship varied significantly from year to year, 49 masses (3 eggs wide) were collected in 1966, and the number of eggs per mass was counted both directly and estimated from the prediction equation based on the previous year's data. A "t"-test at the 1% level ($t = 2.629$) indicated that there was no significant difference between actual count and estimate (computed $t = 0.619$). Therefore, use of the regression equations to estimate the number of eggs per mass was valid for the 3 year period studied.

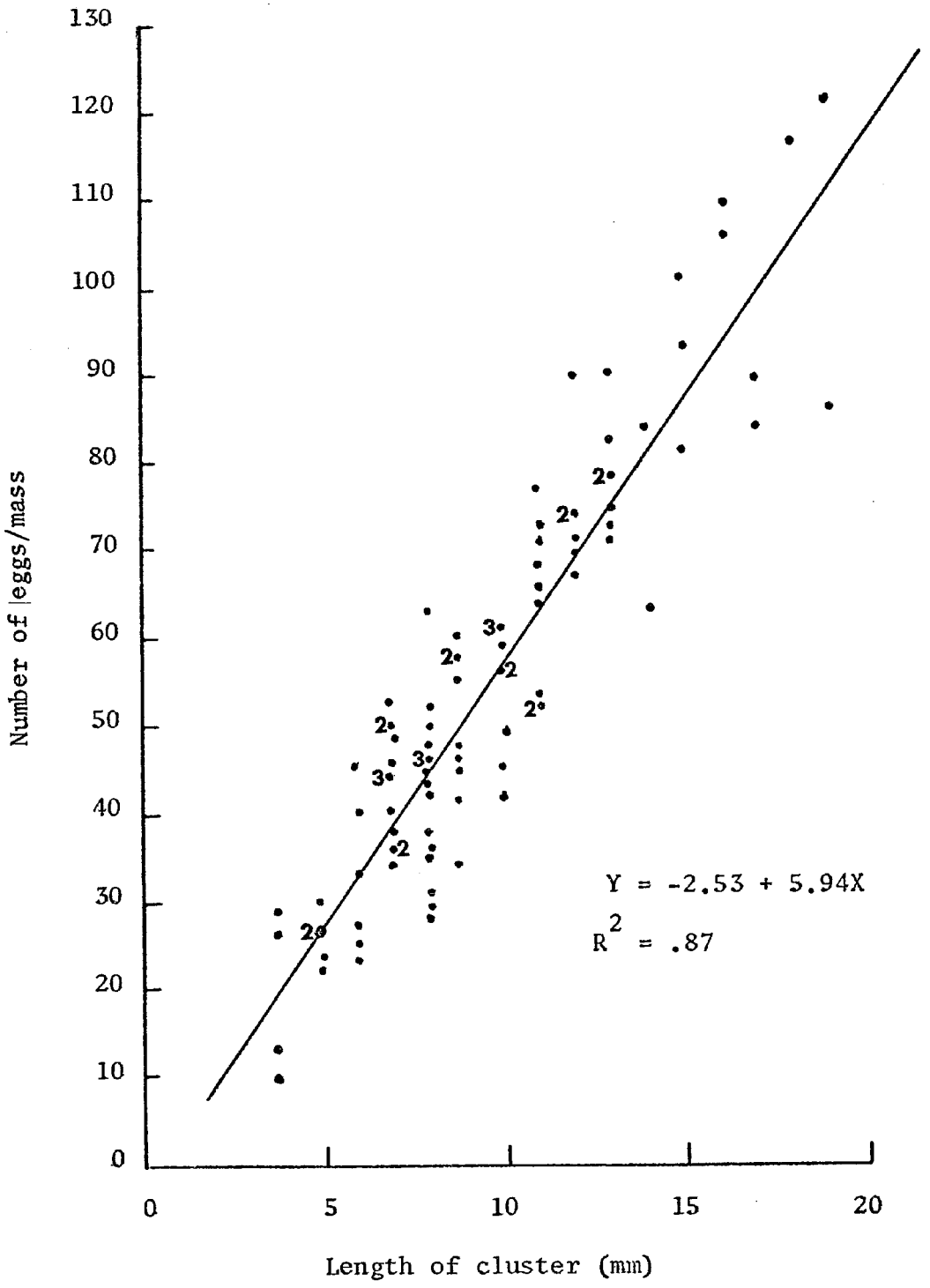


Figure 7. - Relationship between the number of eggs per mass (y) and mass length (x) for *C. pinus*; egg masses 3 rows wide.

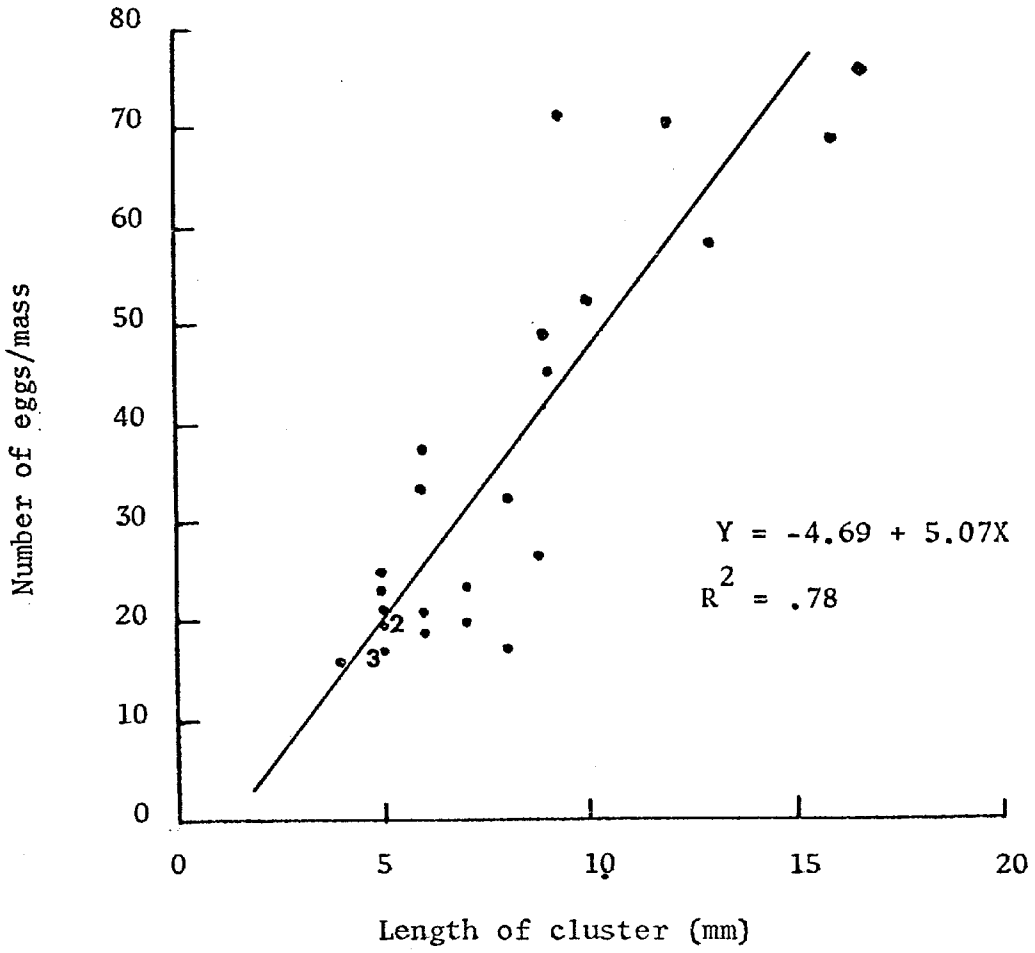


Figure 8. - Relationship between the number of eggs per mass (y) and mass length (x) for *C. pinus*; egg masses 2 rows wide.

Table 31. - Analysis of variance testing for significant regression of mass length vs. number of eggs per mass, Michigan, 1965.

Source of variance	Degrees of freedom	Sum of squares	Mean square	F-ratio
Masses 3 eggs wide				
regression	1	59,842.74	59,842.74	668.11**
error	98	8777.86	89.57	
Total	99	68,620.60		
Masses 2 eggs wide				
regression	1	7868.21	7868.21	89.24**
error	25	2207.89	88.17	
Total	26	10,076.10		

** Significant at the 0.01 level.

Table 32. - Distribution and condition of the hibernacula of *C. pinus* from branch samples of jack pine, Baraga County, Michigan. May 23-28, 1966.

Tree no.	Branch [a]	Distribution of hib. on branches (%)			Condition of hib. (%) [b]		
		Basal ⅓	Mid ⅓	Distal ⅓	Empty	Live larvae	Dead larvae
1	MN	26	26	48	25	35	40
	MS	22	64	14			
	LN	45	55	0	40	34	26
	LS	27	32	41			
2	MN	36	21	43	58	18	24
	MS	40	45	15			
	LN	21	36	43	58	18	24
	LS	33	0	67			
3	MN	66	7	27	13	32	55
	MS	24	54	22			
	LN	32	36	32	16	16	68
	LS	24	21	55			
4	MN	19	58	26	14	46	40
	MS	45	47	8			
	LN	31	40	29	54	16	30
	LS	41	41	18			
5	MN	51	36	13	38	31	31
	MS	33	13	38			
	LN	83	6	11	24	30	46
	LS	0	67	33			

[a] M=mid-crown; L=lower crown; N=North; S=South

[b] Cardinal directions combined in each crown level.

Table 33. - Distribution and condition of the hibernacula of *C. pinus* from branch samples of jack pine, Baraga County, Michigan, May 22 - June 10, 1967.

Tree no.	Branch [a]	Distribution of hib. on branches (%)			Condition of hib. (%)		
		Basal ⅓	Mid-⅓	Distal ⅓	Empty	Live larvae	Dead larvae
1	MN	23	41	36	76	1	21
	MS	39	41	20	76	4	25
	LN	42	32	26	79	10	11
	LS	24	41	35	77	1	22
2	MN	40	39	21	21	79	0
	MS	39	27	34	36	57	7
	LN	48	19	33	9	82	9
	LS	48	37	15	19	70	11
3	MN	44	40	16	81	12	7
	MS	26	12	62	18	68	14
	LN	16	33	51	4	87	9
	LS	35	63	2	12	83	5

[a] M=mid-crown; L=lower crown; N=North; S=South

APPENDIX IV

Table 34. - Density of the hibernacula of *C. pinus* from branch samples, Baraga County, Michigan. May 23-28, 1966.

Tree no.	Branch position & cardinal direction [a]	Number hib./ foot of branch length
1	MN	4.4
	MS	15.9
	LN	3.2
	LS	6.7
2	MN	16.9
	MS	32.7
	LN	2.3
	LS	0.5
3	MN	2.6
	MS	33.7
	LN	3.1
	LS	10.9
4	MN	47.0
	MS	31.6
	LN	7.0
	LS	3.1
5	MN	23.0
	MS	45.0
	LN	12.0
	LS	0.7

[a] M=mid-crown; L=lower crown; N=North; S=South

Table 35. - Density of the hibernacula of *C. pinus* from branch samples, Baraga County, Michigan. May 22 - June 10, 1967.

Tree no.	Branch position & cardinal direction [a]	Number hib./ foot of branch length
1	MN	30.3
	MS	83.8
	LN	4.3
	LS	27.8
2	MN	29.6
	MS	34.1
	LN	6.0
	LS	4.5
3	MN	55.7
	MS	18.4
	LN	7.2
	LS	15.1

[a] M=mid-crown; L=lower crown; N=North; S=South

LITERATURE CITED

Allen, D. C. 1967. A new species of *Dirophanes* (Hymenoptera: Ichneumonidae) parasitic on *Choristoneura pinus* in northern Michigan. Can. Entomol. 99: 893-5.

_____, F. B. Knight, and J. L. Foltz. 1968. A technique for rearing *Choristoneura pinus* (Lepidoptera: Tortricidae) on artificial diet. Ann. Entomol. Soc. Amer. 61: 362-4.

Andrews, E. A. 1940. Ant mounds in winter woods. Sci. Monthly 51: 419.

Arthur, A. P., and H. C. Coppel. 1953. Studies on dipterous parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). I. *Sarcophaga aldrichi* Park. (Diptera: Sarcophagidae). Can. J. Zool. 31: 374-91.

Banks, R. B. 1956. Observations on the behavior and mortality in Coccinellidae before dispersal from the egg shells. Proc. Royal Entomol. Soc. London (A)31: 56-60.

Barker, R. B. 1947. Budworm pupal parasite survey. Can. Dept. Agr., Forest Biol. Div. Bi-monthly Progr. Rep. 3(1): 2.

Barker, E. W., and G. W. Wharton. 1952. An introduction to Acarology. MacMillan Co., New York. 465 p.

Bean, J. L., and V. F. McCowan. 1967. Forest pest conditions in the northeastern states, 1966. p. 37. *In*: Forest Pest Conditions in the United States, 1966. U. S. Dept. Agr., Forest Service. 42 p.

Benjamin, D. M. 1956. Jack-pine budworm surveys. Coop. Econ. Insect Rep., Plant Pest Control Branch, U. S. Dept. Agr. 6: 705-9.

_____. 1964. Evaluations of outbreak populations of the jack-pine budworm, *Choristoneura pinus* Freeman (Lepidoptera). Proc. XII Int. Congr. Entomol. London, 1964(1965).

_____, and A. T. Drooze. 1954. Parasites affecting the jack-pine budworm in Michigan. J. Econ. Entomol. 47: 588-91.

Bess, H. A. 1946. Staminate flowers and spruce budworm abundance. Can. Dept. Agr., Forest Biol. Div. Bi-monthly Progr. Rep. 2(2): 3-4.

Blais, J. R. 1952. The relationship of the spruce budworm (*Choristoneura fumiferana* (Clem.)) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). Can. J. Zool. 30: 1-29.

Blyth, J. E. 1967. Pulpwood production and consumption in the north central region by county, 1966. U. S. Forest Service, North Central For. Exp. Sta. Resource Bull. NC-3, 27 p.

Bradley, G. A., and J. D. Hinks. 1968. Ants, aphids, and jack pine in Manitoba. Can. Entomol. 100: 40-50.

Bradshaw, W. G. 1965. Population dynamics of the jack-pine budworm. Masters' Thesis, Sch. Nat. Res., Univ. of Mich., Ann Arbor. 61 p.

Brooks, A. R. 1945. New Canadian Diptera (Tachinidae). Can. Entomol. 77: 78-96.

Brown, N. R. 1946a. Studies on parasites of the spruce budworm, *Archips fumiferana* (Clem.). I. Life history of *Apanteles fumiferanae* Vier. (Hymenoptera: Braconidae). Can. Entomol. 78: 121-9.

_____. 1946b. Studies of parasites of the spruce budworm, *Archips fumiferana* (Clem.). II. Life history of *Glypta fumiferanae*

(Vier.) (Hymenoptera: Ichneumonidae). Can. Entomol. 78: 138-47.

Brown, A. W. A., and M. R. MacKay. 1943. The jack-pine budworm and the spruce budworm, *Cacoecia* (i.e., *Archips*) *fumiferana* (Clem.) (Tortricidae). Can. Entomol. 75: 207-11.

Campbell, I. M. 1953. Morphological differences between the pupae and the egg clusters of *Choristoneura fumiferana* (Clem.) and *C. pinus* Free. (Lepidoptera: Tortricidae). Can. Entomol. 85: 134-5.

Chant, D. A. 1963. Some mortality factors and the dynamics of orchard mites. Mem. Entomol. Soc. Can. 32: 33-40.

Clausen, C. P. 1940. Entomophagous insects. McGraw-Hill Co., New York. 688 p.

Coppel, H. C., and M. G. Maw. 1954. Studies of the dipterous parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). IV. *Madremyia saundersii* (Will.) (Diptera: Tachinidae). Can. J. Zool. 32: 314-23.

Creighton, W. S. 1950. The ants of North America. Harvard Mus. Comp. Zool. Bull. 104. 585 p.

Dinther, J. B. M. 1951. Two coccinellidae as predators of *Dreyfusia picea* Ratz. Tijdschr. Entomol. 94: 168-88.

Dixon, J. C. 1961. The biology and ecology of the jack-pine budworm in Wisconsin with special reference to insect parasites. Ph.D. Thesis, Univ. of Wisc., Madison. 164 p.

_____, and D. M. Benjamin. 1963. Natural control factors associated with the jack-pine budworm, *Choristoneura pinus*. J. Econ. Entomol. 56: 266-70.

Dowden, P. B., and V. M. Carolin. 1950. Natural control factors affecting the spruce budworm in the Adirondacks during 1946-1948. J. Econ. Entomol. 43: 774-83.

Downe, A. E. R., and A. S. West. 1954. Progress in the use of the precipitin test in entomological studies. Can. Entomol. 86: 181-4.

Drooze, A. T., and D. M. Benjamin. 1956. Parasites from two jack-pine budworm outbreaks in the Upper Peninsula of Michigan. J. Econ. Entomol. 49: 412-3.

Foltz, J. L. 1967. A technique for sampling populations of the jack-pine budworm. Masters' Thesis, Sch. Nat. Res., Univ. of Mich., Ann Arbor. 64 p.

Fowells, H. A. 1965. Silvics of forest trees of the United States. U. S. Dept. Agr., Forest Service, Agr. Hand. No. 271. 762 p.

Freeman, T. N. 1953. The spruce budworm, *Choristoneura fumiferana* (Clem.) and an allied new species on pine (Lepidoptera: Tortricidae). Can. Entomol. 85: 121-7.

_____. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. Can. Entomol. 99: 449-55.

Graham, S. A. 1935. The spruce budworm on Michigan pine. Univ. of Mich., Sch. of For. and Cons. Bull. No. 6. 56 p.

Haviland, E. E. 1948. Mound changes after 10 years in colonies of *Formica exsectoides* Forel. Ann. Entomol. Soc. Amer. 41: 438.

Headly, A. E. 1943. The ants of Ashtabula County, Ohio (Hymenoptera: Formicidae). Ohio J. Sci. 43: 30.

Heinrichs, E. A., and H. E. Thompson. 1968. Parasites, predators, and other arthropods associated with *Choristoneura houstanana* (Lepidoptera: Tortricidae) on *Juniperus* species in Kansas.

Can. Entomol. 100: 33-39.

Hodson, A. C. 1941. An ecological study of the forest tent caterpillar, *Malacosoma disstria* Hbn., in northern Minnesota. Univ. Minn. Agr. Exp. Sta. Tech. Bull. 148. 55 p.

House, H. L., and M. G. Traer. 1949. An artificial diet for rearing *Pseudosarcophaga affinis* Fall., a parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.). Ann. Rep. Entomol. Soc. Ontario 79(1948): 50-55.

Hussey, R. F. 1954. Some new or little-known Miridae from the northeastern United States (Hemiptera). Proc. Entomol. Soc. Wash. 56: 192-202.

Ives, W. H. G. 1967. Relations between invertebrate predators and prey associated with larch sawfly eggs and larvae on tamarack. Can. Entomol. 99: 607-22.

Jaynes, H. A., and C. G. Speers. 1949. Biological and ecological studies of the spruce budworm. J. Econ. Entomol. 42: 221-5.

_____, and A. T. Drooze. 1952. The importance of parasites in the spruce budworm infestations in New York and Maine. J. Econ. Entomol. 45: 1057-61.

Knight, H. H. 1917. Monograph of the North American species of *Deraeocoris* (Heteroptera: Miridae). Univ. of Minn. Agr. Exp. Sta. Tech. Bull. 1: 77-210.

Kulman, H. M., and A. C. Hodson. 1961. The parasites of the jack-pine budworm, *Choristoneura pinus*, with special reference to parasitism at particular stand locations. J. Econ. Entomol. 54: 221-4.

Lawson, F. A. 1959. Identification of the nymphs of common families of Hemiptera. J. Kansas Entomol. Soc. 32: 88-92.

Lewis, F. B. 1960. Factors affecting the assessment of parasitism by *Apanteles fumiferanae* Vier. and *Glypta fumiferanae* (Vier.) on spruce budworm larvae. Can. Entomol. 92: 881-91.

Loughton, B. G., C. Berry, and A. S. West. 1963. Spiders and the spruce budworm. P. 249-68. *In*: R. F. Morris (ed.). The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. of Can. 31. 332 p.

MacAloney, H. J., and A. T. Drooze. 1956. The jack-pine budworm. U. S. Dept. Agr., Forest Service Leaflet No. 7. 4 p.

MacKay, M. R. 1953. The larvae of *Choristoneura fumiferana* (Clem.) & *C. pinus* Free. (Lepidoptera: Tortricidae). Can. Entomol. 85: 128-33.

_____. 1962. Larvae of the North American Tortricinae (Lepidoptera: Tortricidae). Can. Entomol. 93, Suppl. 28.

Mattson, W. J., F. B. Knight, D. C. Allen, and J. L. Foltz. 1968. Vertebrate predation on the jack-pine budworm in Michigan. J. Econ. Entomol. 61: 229-34.

Maw, M. G., and H. C. Coppel. 1953. Studies on dipterous parasites of the spruce budworm *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). II. *Phryxe pecosensis* (Tns.) (Diptera: Tachinidae). Can. J. Zool. 31: 392-403.

McKenzie, H. L. 1936. An anatomical and systematic study of the genus *Anatis* of America (Coleoptera: Coccinellidae). Calif. Univ. Pub. Entomol. 6: 264-72.

Michigan Forest Detection Program Report. Forestry Section, Mich. Dept. of Conservation, Lansing. 1950-1964.

Miller, C. A. 1955. A technique for assessing spruce budworm larval mortality caused by parasites. Can. J. Zool. 33: 5-17.

_____. 1958. The measurement of spruce budworm populations and mortality during the first and second larval instars. Can. J. Zool. 36: 409-22.

_____. 1959. The interaction of the spruce budworm, *Choristoneura fumiferana* (Clem.), and the parasite *Apanteles fumiferanae* Vier. Can. Entomol. 91: 457-77.

_____. 1960. The interaction of the spruce budworm, *Choristoneura fumiferanae* (Clem.), and the parasite *Glypta fumiferanae* (Vier.). Can. Entomol. 92: 839-50.

_____. 1963. Parasites and the spruce budworm. P. 228-244. *In*: R. F. Morris (ed.). The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. 332 p.

_____. 1966. The black-headed budworm in eastern Canada. Can. Entomol. 98: 592-612.

Morris, R. F. 1957. The interpretation of mortality data in studies on population dynamics. Can. Entomol. 89: 49-69.

_____. 1963. Predation and the spruce budworm. P. 244-248. *In*: R. F. Morris (ed.). The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. 332 p.

Nolte, H. W. 1938. Über einige Nematusfiende und ihre Bedeutung. Forstwiss. Centralbl. 60: 629-34.

Peterson, A. 1962. Larvae of insects. Part I. Lepidoptera and plant infesting Hymenoptera. Edward Bros., Ann Arbor, Michigan. 315 p.

Pointing, P. J. 1966. A quantitative field study of predation by the sheet-web spider, *Frontinella communis*, on European pine shoot moth adults. Can. J. Zool. 44: 265-73.

Prebble, M. L. 1933. The biology of *Podisus serieventris* Uhler, in Cape Breton, Nova Scotia. Can. J. Res. 9: 1-30.

Readeo, P. A. 1926. Studies on the eggs of some Reduviidae (Heteroptera). Univ. of Kansas Sci. Bull. 16: 5-291.

Ross, D. A. 1952. Key to the puparia of dipterous parasites of *Choristoneura fumiferana* (Clem.). Can. Entomol. 84: 108-12.

Sanders, C. J. 1964. The biology of carpenter ants in New Brunswick. Can. Entomol. 96: 894-909.

Silver, G. T. 1960. Notes on a spruce budworm infestation in British Columbia. For. Chron. 36: 362-74.

Smith, B. C. 1965. Growth and development of coccinellid larvae on dry foods (Coleoptera: Coccinellidae). Can. Entomol. 97: 761=8.

_____. 1966a. Effects of food quality and age on the larval activities of *Anatis mali* auct. (Coleoptera: Coccinellidae). Can. J. Zool. 44: 251-5.

_____. 1966b. Effects of food on the longevity, fecundity, and development of adult coccinellids (Coleoptera: Coccinellidae). Can. Entomol. 97: 910-9.

Stehr, G. 1954. A laboratory method for rearing the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Can. Entomol. 86: 423-8.

Steyn, J. J. 1963. P. 248. *In*: R. F. Morris (ed.). The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. 332 p.

Thompson, W. R. 1939. Biological control and the theories of the interaction of populations. Parasitology 31: 299-388.

_____, and F. J. Simmonds. 1965. A catalogue of the parasites and predators of insect pests. Sec. 4. Host predator catalogue. Commonwealth Institute of Biological Control, Ottawa. 198 p.

Thomson, H. M. 1957. A note on the predation of spruce budworm pupae. Can. Dept. Agr., Forest Biol. Div. Bi-monthly Progr. Rep. 13(4): 2.

Turnbull, A. L. 1956. Spider predators of the spruce budworm, *Choristoneura fumiferana* (Clem.) at Lilloot, B. C., Canada. Proc. 8th Pacif. Sci. Congress 3(4): 1579-94.

Veatch, J. O. 1953. Soils and lands of Michigan. R. R. Donnelley, Co., Chicago. 241 p., map.

_____, L. R. Schoenmann, C. E. Miller, and A. E. Shearin. 1931. Soil survey of Oscoda County. Bureau of Chemistry and Soils, U. S. Dept. Agr., No. 20. 42 p.

Walley, G. S. 1953. Hymenopterous parasites of *Choristoneura pinus* Free. (Lepidoptera: Tortricidae). Can. Entomol. 85: 152.

Warren, L. O., W. B. Peck, and M. Tadic. 1967. Spiders associated with the fall webworm, *Hyphantria cunea* (Lepidoptera: Arctiidae). J. Kansas Entomol. Soc. 40: 382-95.

Watt, K. E. F. 1963. The analysis of the survival of large larvae in the unsprayed area. P. 52-63. *In*: R. F. Morris (ed.). The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. 332 p.

West, A. S., and B. Delong. 1955. Notes on the biology and laboratory rearing of a predatory insect, *Zelus exangius* (Stål) (Hemiptera:

Reduviidae). Ann. Rep. Entomol. Soc. Ontario 86: 97-101.

Wheeler, W. M. 1910. The North American ants of the genus *Camponotus* Mayr. Ann. New York Acad. Sci. 20: 295-354.

Wilkes, A., H. C. Coppel, and W. G. Mather. 1948. Notes on the insect parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.) in British Columbia. Can. Entomol. 80: 138-55.

Wilson, L. F., and J. L. Bean. 1964. A field key to the adult hymenopterous parasites of the spruce budworm in Minnesota. U. S. Dept. Agr., Forest Service, Lake States For. Exp. Sta. Res. Note LS-53. 4 p.

Wishart, G. 1945. *Aplomya caesar* (Aldrich), a tachinid parasite of the European corn borer. Can. Entomol. 77: 157-67.