THE LIFE HISTORY, HABITS, AND SOME ASPECTS OF THE NATURAL CONTROL OF *Choristoneura Fumiferana* (CLEMENS) (LEPIDOPTERA: TORTRICIDAE) IN NEWFOUNDLAND

HUBERT RALPH CRUMMEY

Copy 1

THE LIFE HISTORY, HABITS, AND SOME ASPECTS OF THE NATURAL CONTROL OF *CHORISTONEURA FUMIFERANA* (CLEMENS) (LEPIDOPTERA: TORTRICIDAE) IN NEWFOUNDLAND

A Thesis

Presented to

The Department of Biology

Memorial University of Newfoundland

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

---

by

Hubert Ralph Crummey, B.Sc., B.Ed.

May 1976

ABSTRACT

The eastern spruce budworm, *Choristoneura fumiferana* (Clem.), is a univoltine species in Newfoundland and has six larval instars. Head capsule width differences occurred between the sexes only in instars V and VI.

Needle mining occurred on all three host tree species, and was of the longest duration on black spruce.

Adults were present from late July to mid-August. The first adults to emerge were invariably males; females emerged several days later. The sex ratio was 1:1.

Females preferred white spruce and balsam fir to black spruce in laboratory experiments when all three hosts were offered simultaneously to them for oviposition. There was an average of 16 eggs per egg mass (21 eggs per mass in the field); 54% of the masses had two rows of eggs, 20% had two rows plus a partial third, and 26% had three rows. Hatching success of the eggs was 99%.

Based on 18-inch branch samples, there were 3 times as many larvae on white spruce as on black spruce and 4 times as many on balsam fir as on black spruce. Larval development was the fastest on white spruce and the slowest on black spruce.

Weather seemed to have little direct effect on budworm survival. The major predators were birds; ants and other insects may also have destroyed some. Thirteen primary parasitoid species, including one pupal parasitoid, were reared during the study. Mortality due to

parasitoids was less than 19% on average for the two years, but was higher in 1974 than in 1973. The two most important species were *Glypta fumiferanae* (Vier.) and *Apanteles fumiferanae* Vier., which accounted for about 18% of the total parasitism during the study, *Glypta* being more numerous.

Two species of fungi, *Entomophthora sphaerosperma* Fres. and *E. egressa* MacLeod and Tyrrell, were observed to cause mortality. The combined mortality of larvae and pupae due to these fungi for both years, was 16%.

Defoliation of the new growth on the sample trees in both 1973 and 1974 was approximately 99%, 87% and 70% for balsam fir, white spruce and black spruce, respectively.

ACKNOWLEDGEMENTS

I wish to thank Dr. W. J. Carroll, Director, Newfoundland Forest Research Centre, Environment Canada, St. John's, for suggesting the topic, for the use of the facilities of the Research Centre in St. John's and the field station at Pasadena, and for the opportunity to be employed during the summers of 1973 and 1974, during which time the data were collected. I hereby acknowledge his permission to use the data so gathered.

The plan of study was drafted under the direction of Dr. Imre S. Otvos, Research Scientist, Newfoundland Forest Research Centre. He has kindly provided the data on stomach analyses of birds collected at Pasadena, and has given permission for the use of Plate VIII. I wish to express my appreciation to Dr. Otvos for his personal interest during the study and for his criticism of the manuscript. Appreciation is also expressed to Professor John Phipps, Head (pro tem), Department of Biology, Memorial University of Newfoundland, for his cooperation, interest and criticism of the manuscript, and to Dr. Roger Gordon, Department of Biology, M.U.N., for his criticism of the thesis.

Thanks are extended to the Biosystematics Research Institute, Department of Agriculture, Ottawa, Ontario, for identification of ant and parasitoid specimens.

The assistance of Drs. Otvos, N.F.R.C., and Donald M. MacLeod, Insect Pathology Research Institute, Environment Canada, Sault Ste. Marie, Ontario, in the identification of fungal infected specimens, is gratefully acknowledged.

I also acknowledge the help of other members of the staff of the Newfoundland Forest Research Centre, St. John's, especially Mr. David Durling, Research Technician, for his assistance during the course of the study.

TABLE OF CONTENTS

	Page
ABSTRACT	ii
ACKNOWLEDGEMENTS	iv
LIST OF TABLES	viii
LIST OF FIGURES	x
LIST OF PLATES	xi
INTRODUCTION	1
MATERIALS AND METHODS	7
Study Area	7
Sampling Methods	12
Determination of Larval Instars	16
Determination and Evaluation of the Role of Some Natural Control Factors	19
Predators	19
Parasitoids	19
Disease	20
Mating Experiments	21
RESULTS	24
Life History	24
Eggs	24
Larvae	33
Larval Habits	40
Prepupae	57
Pupae	57
Adults	66

Page

Life History on Host Trees 68

Natural Control 71

Weather 71

Predators 74

Parasitoids 74

Disease 75

DISCUSSION 87

SUMMARY 98

REFERENCES 101

APPENDICES 107

LIST OF FIGURES

FIGURE Page

1. Location of the study area (Pasadena) in relation to major population centers of insular Newfoundland 8

2. Seasonal occurrence of the spruce budworm on balsam fir, 1973 (the sum of the widths of the lines representing the different stages at each sample day equals 100% - the total sample size). 25

3. Seasonal occurrence of the spruce budworm on balsam fir, 1974 (the sum of the widths of the lines representing the different stages at each sample day equals 100% - the total sample size). 27

4. Seasonal occurrence of the spruce budworm on black spruce, 1974 (the sum of the widths of the lines representing the different stages at each sample day equals 100% - the total sample size). 29

5. Seasonal occurrence of the spruce budworm on white spruce, 1974 (the sum of the widths of the lines representing the different stages at each sample day equals 100% - the total sample size) 31

6. Histogram of head capsule width measurements of spruce budworm larvae collected from balsam fir, 1973 (N = 1,267). 34

7. Mean number of spruce budworm collected from drop trays in 1973 and 1974 (N=10) 58

8. Mean number of spruce budworm per collection date based on 18-inch branch samples from the three host tree species, 1974 72

LIST OF TABLES

TABLE		PAGE
1.	HEAD CAPSULE WIDTHS (MM) OF SPRUCE BUDWORM LARVAE COLLECTED FROM HOST TREES AT PASADENA, 1973 AND 1974	37
2.	COMPARISON OF MEAN HEAD CAPSULE WIDTHS (MM) OF SPRUCE BUDWORM LARVAE FROM THE THREE HOST TREE SPECIES IN NEWFOUNDLAND FOR 1973 AND 1974 (OBSERVED) WITH THOSE CALCULATED ACCORDING TO DYAR'S THEORY OF GEOMETRIC PROGRESSION (EXPECTED)	38
3.	COMPARISON OF MEAN HEAD CAPSULE WIDTHS (MM) BETWEEN NEWFOUNDLAND AND ONTARIO SPRUCE BUDWORM LARVAE	39
4.	DAILY MEAN TEMPERATURES AND TOTAL PRECIPITATION AT THE STUDY AREA (PASADENA) AND THE NEAREST WEATHER STATIONS, AND THE NORMALS FOR THESE STATIONS	41
5.	PHENOLOGY OF THE HOST TREES AT THE STUDY AREA, 1974	47
6.	AVERAGE NUMBER OF SPRUCE BUDWORM LARVAE AND PUPAE COLLECTED FROM DROP TRAYS PLACED BENEATH INFESTED BALSAM FIR TREES, 1973 (N = 10)	55
7.	AVERAGE NUMBER OF SPRUCE BUDWORM LARVAE AND PUPAE COLLECTED FROM DROP TRAYS PLACED BENEATH INFESTED BALSAM FIR TREES, 1974 (N=10)	56
8.	RESULTS OF SINGLE-PAIR MATINGS OF SPRUCE BUDWORM ADULTS COLLECTED AS PUPAE FROM THE THREE HOST SPECIES, 1974	67
9.	OVIPOSITION OF SPRUCE BUDWORM MOTHS ON SMALL CAGED BALSAM FIR TREES UNDER FIELD CONDITIONS . .	69
10.	HOST SELECTION BY FEMALE SPRUCE BUDWORM ADULTS UNDER LABORATORY CONDITIONS	70
11.	PARASITISM OF SPRUCE BUDWORM LARVAE COLLECTED AND REARED BY HOST SPECIES, PASADENA, 1973 AND 1974	76

TABLE PAGE

12. RESULTS OF LABORATORY REARINGS OF FIELD COLLECTED SPRUCE BUDWORM LARVAE 78

LIST OF PLATES

PLATE		PAGE
I.	Typical stand condition at the study site	10
II.	Male spruce budworm larva with the gonads visible as dark spots in the mid-dorsal abdominal segments	17
III.	Second-instar spruce budworm larva on a mined bud	44
IV.	Late instar spruce budworm larva in its feeding shelter	48
V.	a) Typical reddish-brown coloration of a balsam fir stand as a result of moderate spruce budworm feeding	51
	b) Balsam fir trees with severe defoliation in the upper crowns caused by spruce budworm larvae	51
	c) White spruce showing the results of severe defoliation by the budworm for several years	51
VI.	Silken threads, spun by disturbed spruce budworm larvae, hanging from a severely infested tree	53
VII.	Prepupa of the spruce budworm in its natural habitat	60
VIII.	Spruce budworm pupa on balsam fir, with the larval skin visible beside it	62
IX.	Empty male and female spruce budworm pupal cases showing the relative size of the sexes	64
X.	*Glypta* larva emerging from its spruce budworm host	80
XI.	Cadaver of a spruce budworm larva infected with *Entomophthora* sp.	82

PLATE			PAGE
XII.	a) and b)	Spruce budworm larvae showing different stages of sporulation of *Entomophthora* sp. (note the halo-like effect around the larvae made by ejected conidia).	84
	c)	Conidia of *E. egressa* in various stages of germination (note the pear shape conidia, characteristic of this species) (x 400)	84

INTRODUCTION

The eastern spruce budworm, *Choristoneura fumiferana* (Clemens), is the most widely distributed, destructive, native forest insect in North America (Prebble and Carolin, 1967). It occurs from Virginia north to Labrador, and extends throughout the Boreal Forest Region of the northeastern United States and Canada to the prairies, and northwest to the MacKenzie River in the Yukon (Freeman, 1967; Prebble and Carolin, 1967).

In eastern North America, the important host species of *C. fumiferana* are balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss.), black spruce (*Picea mariana* (Mill.) BSP.), and red spruce (*Picea rubens* Sarg.), balsam fir being economically the most important species (Greenbank, 1963a; Prebble and Carolin, 1967). Damage caused varies from partial loss of the new foliage in light and moderate infestations, to complete defoliation of the new growth in heavy infestations. Mortality of the host trees may occur after five years of continuous defoliation of the new growth (Prebble and Carolin, 1967).

Outbreaks of the spruce budworm in northeastern North America have occurred on at least five separate occasions, at irregular intervals, since about 1770 (Greenbank, 1963c; Coughlin, 1968), and have lasted for many years. The outbreaks in Newfoundland, reviewed by Clark (1972), are like those occurring elsewhere, being periodic rather than cyclic. The earliest recorded outbreak was on Bell Island, Conception Bay in 1942 and persisted until 1953. Three others have occurred since then. These

latter outbreaks were rather small and scattered throughout the west and southwest part of insular Newfoundland, and collapsed without causing extensive tree mortality. The present outbreak started in 1971 and has become the largest and most severe ever recorded in Newfoundland. By 1972, the outbreak had extended over 1 million acres and in 1973 it covered about 3.5 million acres (Clarke *et al.*, 1974).

Generalized accounts of the life history, habits and biology of the spruce budworm have been presented by numerous workers including McGugan (1954), Bean and Waters (1961), Miller (1963d) and Bakuzis and Hansen (1965). Morris (1963) gave a detailed analysis of the biology and population dynamics of *C. fumiferana* in New Brunswick, under epidemic conditions.

The eggs are laid as pale green clusters (masses) on the needles of the host trees in mid-summer (Bakuzis and Hansen, 1965; McKnight, 1968). Egg masses are of three types based on the number of rows of eggs present, i.e. 2 rows, 2 rows plus a partial third, or 3 rows. The arrangement of the eggs in the cluster is scale-like (McGugan, 1954; McKnight, 1968). The oval eggs are about 750μ long, 500μ wide and 200μ high (Stairs, 1960). Clusters can occur on either side of the needles of balsam fir and the first eggs are laid nearest the apex of the needles (McGugan, 1954). Incubation time under field conditions is variable, ranging from about 8 to 12 days (McGugan, 1954), with an average of 10 days.

The spruce budworm has six larval instars (McGugan, 1954). First-instar larvae are pale, yellowish-green with brown heads, and are approximately 2 mm long. These larvae do not feed, but form hibernacula

in which they molt and overwinter as second-instar larvae (Atwood, 1944; McGugan, 1954). The second-instar larvae emerge from the hibernacula and commence mining needles, feed on staminate flowers, or enter the unopened vegetative buds (McGugan, 1954). The two major dispersal periods for the budworm are during these stages: the first in the fall by first-instar larvae, and the other in the spring by second-instar larvae (Shaw and Little, 1973). The larvae later change to yellowish-orange with a blackish-brown head and a pale-brown prothoracic shield. Mature larvae are olive-brown with a black head and a brownish shield, and have conspicuous whitish-yellow tubercules (Jaynes and Carolin, 1952; McGugan, 1954; Bakuzis and Hansen, 1965). The dispersal during the later instars is less important and usually the result of food shortage (Morris and Mott, 1963).

Pupae are found at the larval feeding sites, or else occur towards the centre of the branch wherever sixth-instar larvae find a suitable place to pupate (Miller, 1963c). Newly formed budworm pupae are green or yellow, mature pupae are dark gray or dark brown, with no color differences between the sexes (Campbell, 1953). The duration of the pupal stage varies from 8 to 12 days (Miller, 1963c).

The sex ratio of the budworm is usually 1:1 (Miller, 1963c). Adult males emerge a few days earlier than females (McKnight, 1968). The flight activity of the moths spans about 3 weeks, but individual adults live for approximately 2 weeks. Miller (1963c) found that females laid approximately 200 eggs each, with 20 eggs per egg mass. Fecundity of the females seems to be affected by food quality (Blais, 1952, 1953; Miller, 1957, 1963b), and by high temperature (Sanders, 1967).

Balsam fir and white spruce are the preferred hosts for oviposition (Swaine *et al.*, 1924; Jaynes and Carolin, 1952). Jaynes and Speers (1949) and Wilson (1963) found that white spruce was preferred to balsam fir for oviposition by the budworm. Female moths prefer tall open-grown trees for egg-laying (Blais, 1952; Greenbank, 1963b), and defoliated branches are avoided as oviposition sites (Wilson, 1959, 1963; Greenbank, 1963a). Females oviposit near the branch tips of non-defoliated branches (Wilson, 1959).

The influence of natural control agents on budworm population changes has been investigated by numerous authors. Miller (1958) reported 15% mortality during the overwintering period. Miller (1958) and Mott (1963) found that dispersal of small larvae by the wind led to high mortality (up to 71%) through losses. Miller (1963c) also found that cool, wet weather prolonged development and, therefore, enhanced vulnerability to attack from control agents.

The effectiveness of birds as predators of the spruce budworm has been investigated by Tothill (1923), Kendeigh (1947), Mitchell (1952), Mook (1963), Gage (1968) and others. Spruce budworm mortality attributed to avian predators by these authors varied from 3 to 40% depending on the budworm population level. The general conclusion was that birds are important at endemic budworm population levels, but their role is negligible during epidemic levels.

Thomson (1957) considered ants to be important in controlling the budworm under some conditions. Warren (1954) and Thomson (1957) also suggested that *Dioryctria reniculella* Grt., the spruce coneworm, may be important as a predator of budworm pupae at endemic population

levels.

Loughton *et al.*, (1963) and Renault and Miller (1972) found that spiders were also important as predators of budworm larvae, but had only a limited effect at epidemic population levels.

Considerable work has been done on the parasitoids of the spruce budworm in eastern North America (Baird, 1947; Reeks and Forbes, 1950; Jaynes and Drooz, 1952; Blais, 1960, 1965; and Miller, 1963a). Reeks and Forbes (1950) listed 21 known species of parasitoids from the Maritimes, the more common ones being the same 12 to 15 species. The most important parasitoids of spruce budworm larvae are Hymenoptera: *Apanteles fumiferanae* Vier. and *Glypta fumiferanae* (Vier.), and in some locations, *Meteorus trachynotus* Vier. The most important pupal parasitoid is *Apechthis ontario* (Cress.). The only recorded parasitoid of budworm eggs is *Trichogramma minutum* Riley (Miller, 1953; Thomas, 1966), which caused only low mortality. Lewis (1960) determined that only one parasite of any species could survive in a single larva. Miller (1963a) suggested that only after the budworm population had been reduced by other factors, could parasitoids effectively control the budworm larval population.

Neilson (1963) found that disease organisms (microsporidia, fungi, viruses and bacteria) accounted for from 10 to 35% of the budworm larval mortality under epidemic population levels, but were of low virulence. Two species of fungi, *Entomophthora sphaerosperma* Fresenius and the recently described *E. egressa* MacLeod and Tyrrell were found to infect the spruce budworm in Newfoundland (Otvos, pers. comm.). Thomson (1958) observed that when budworm larvae were infected with the microsporidian,

Perezia fumiferanae Thom., the infection resulted in retardation of development, reduced pupal size, lowered fecundity and increased mortality.

Throughout this thesis the following terms, 'endemic' and 'epidemic', are used in reference to population levels. This terminology is commonly used in forest entomology. Endemic refers to the normal population level of a potentially destructive species; epidemic refers to a widespread high insect population level beyond normal proportions, and is usually accompanied by increased damage (Meyer and Eyre, 1958). The term 'outbreak' refers to epidemic population levels.

Although a great deal has been written about the spruce budworm from continental North America (Morris, 1963; McKnight, 1968), little is known about the biology and the population dynamics of this insect in Newfoundland. The 'fear' that the present outbreak might cause extensive tree mortality without chemical control, led to the present study.

The objectives of this study were to determine the life history and habits of the spruce budworm, to examine the effects of weather (temperature and precipitation) on the various life stages, and indirectly on the course of the outbreak, to assess the importance of parasitoids, and to a limited extent predators and disease, as control agents, and to compare the results obtained during this study with those published from other parts of eastern North America.

MATERIALS AND METHODS

Study Area

The study area was located approximately 16 km west of the town of Deer Lake near the Canadian Forestry Service Field Station at Pasadena, and some 30 km east of the city of Corner Brook (Fig. 1). The sample site was in a partially cut-over, mixed, conifer stand consisting mainly of balsam fir, some black spruce, and a small number of white spruce (Plate I). The trees were semi-open grown, approximately 7 m to 8 m in height with an age range of 30 to 40 years. A small part of the study area, cut over about 10 years ago, supported some balsam fir regeneration which varied in height from one to several meters. The stand in the study area supported a moderately-high spruce budworm population. Data were collected from late May to the end of August in both 1973 and 1974.

In 1973, only balsam fir was sampled. This species was chosen because of its primary importance to the forest industry in Newfoundland. In 1974, sampling was extended to include all three host tree species: balsam fir, black spruce and white spruce.

A weather station, consisting of a hygrothermograph and a rain gauge, was set up in the middle of the study area, and was maintained throughout the study period in both years. The hygrothermograph recorded temperature and relative humidity on a 7-day chart, which was changed weekly. The rain gauge was checked every sample day, or more frequently.

FIGURE 1.

Location of the study area (Pasadena) in relation to major population centers of insular Newfoundland.

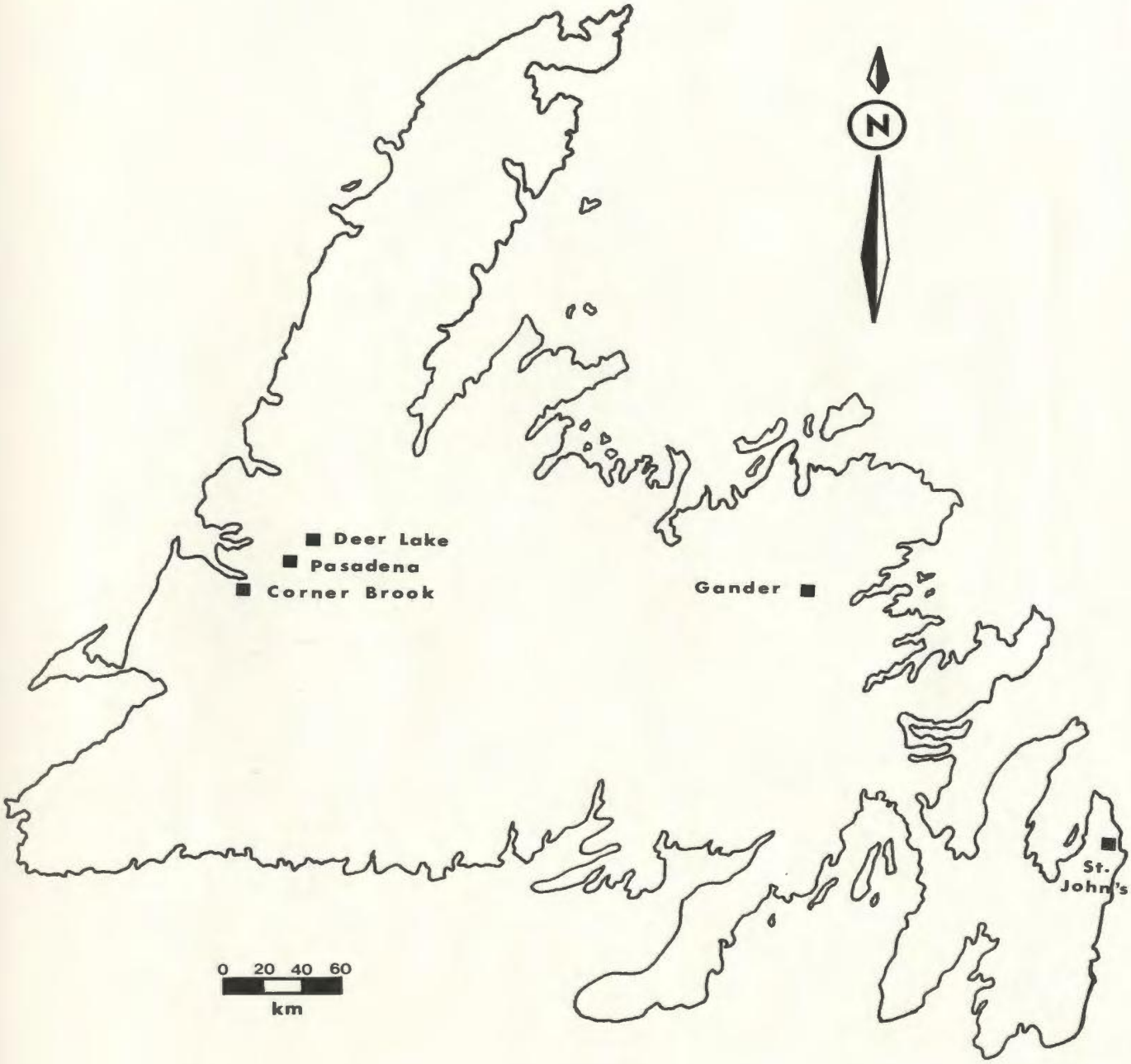

N
Deer Lake
Pasadena
Corner Brook
Gander
St. John's
0 20 40 60
km

PLATE I.

Typical stand condition at the study site.

Sampling Methods

Two sampling methods were used during this study. The first was the 'branch sample' method in which a pole pruner was used to cut a branch from the mid-crown level of the foliated portion of the tree, and the sample was then lowered to a canvas sheet. An 18-inch (45.7 cm) 'tip' was cut from the clipped branch by hand-held pruning shears, and each branch tip was placed separately into a plastic bag along with the appropriate information. At the time of collection, both the sample and the tree from which it was taken were marked so that information obtained could subsequently be related to the host tree. The samples were taken to the field station for examination, at which time the following data were recorded for each of the branch tips: (1) foliated area of branch (foliated length x foliated width of the branch at mid-point); (2) the number of buds or new shoots; (3) the number of needles mined; (4) the number of buds mined or shoots attacked; (5) the number of staminate flowers; (6) the number of larvae (live and dead) present in the buds, shoots, needles or staminate flowers; (7) the number of pre-pupae and pupae; (8) the number of old, empty pupal cases and new, empty pupal cases; (9) old egg masses; (10) the presence of other lepidopterous larvae; (11) the amount of defoliation, and any other information deemed of interest.

The second method of sampling involved foliage beating with two variations. The first variation consisted of using a 3 foot square (0.91 m x 0.91 m) beating sheet supported by wooden slats to collect specimens dislodged from the foliage with a 3 foot (0.91 m) beating stick,

a sampling technique commonly used for monitoring spruce budworm population levels (Sippell, 1969). This sampling technique will be referred to as the 'cubic yard' method, and the sample volume is assumed to be one cubic yard even though this volume is not entirely composed of foliage because of space between the branches. Samples were taken at random from the two opposite sides of each of 10 trees, for a total of 20 'cubic yards' per sample day. These trees were, of necessity, shorter (2 m to 3 m high) than those sampled with the pole pruner. The second variation consisted of beating the foliage on one side of a tree with a 10 foot (3 m) pole over a 7 foot by 9 foot (2.1 m x 2.7 m) canvas sheet spread beneath the crown of the tree. This method is also frequently used in spruce budworm surveys by the Forest Insect and Disease Survey of the Canadian Forestry Service. Approximately 3 vertical meters of foliage were beaten on each tree and three trees were sampled per collection day. Only the number of living and dead insects on the canvas sheet, dislodged from the crown, were counted with each of these beating methods.

In 1973, all three collection methods were used. The branch method was necessary early in the spring until mid-June when the new buds had fully opened and the larvae had become active feeders outside on the new shoots and were, therefore, more easily dislodged by beating. Sample trees were chosen at random throughout the stand. Trees were sampled twice a week, approximately every 3 days, unless inclement weather caused postponement. After 50 trees had been sampled using the branch method, these were then re-sampled by this branch method at intervals throughout the sample period to provide an indication of insect

development (the trees were selected by use of random numbers tables). The branch method was also used to sample for eggs; the trees were selected from both the previously sampled and unsampled trees. The beating methods were used from mid-June on, when the larvae became open feeders and were easily collected by this technique. The beating methods were used in order to compare data obtained in this study with those already published from the Maritimes. The beating methods provided more larvae per man-hour than did the branch method. Initially, the cubic yard method was used, but proved to be time consuming and was replaced by the 7 foot x 9 foot beating method (Appendix A).

In 1974, because of the data obtained in 1973, a different sampling plan was devised and used on the three host tree species. The branch method was used exclusively for this year, although some beating was carried out in addition to permit comparisons between the two methods. Samples were taken once a week, compared with twice a week during 1973, because of the increase in the number of samples (10 trees from each of the three host tree species). Initially, the 30 trees were selected at random from the stand, and these were re-sampled each week. To prevent the loss of later-instar larvae from the branch during sampling, a circular, canvas basket, 46 cm in diameter, was affixed just below the cutting unit of the pole pruner to retain the branch and budworm larvae while the pruner was disassembled and lowered vertically. As in 1973, the samples were numbered, labelled appropriately and taken to the field station for examination.

To determine the number of larvae lost from the trees at any one time, drop trays, made from unbleached cotton (91 cm x 91 cm), were

placed beneath the crowns of each of 10 randomly selected trees. The trays were approximately 60 cm above the ground. A 5 cm wide band of Tanglefoot[1] was applied around the edges of the drop trays to prevent the escape of crawling larvae which fell from the trees between observations. In 1973, the trays were set up in mid-June, and in 1974, new trays were set up under the same 10 trees during the first days of June. These trees, with the drop trays placed beneath them, were never sampled for larvae.

The heights and diameters of all trees sampled in 1973 were measured. In addition, crown heights, crown widths, and ages (as determined by increment borer samples taken at breast height) were also measured for approximately 50% of the sample trees. Balsam fir trees used in 1974 were similar to, and in most cases the same as, those branch sampled in 1973, so that additional measurements were not required. Some of the black spruce and white spruce sample trees were also measured in 1973. Defoliation of the new growth on the sample trees was estimated for three years, 1972, 1973 and 1974. The 1972 estimate was made in early June, 1973, before the new growth could obscure the damage caused in the previous year. Defoliation in both 1973 and 1974 was estimated in August of these years, after larval feeding had been completed. Defoliation was estimated visually following a technique used by the Forest Insect and Disease Survey of the Canadian Forestry Service. This technique involves the visual estimation of the

---

[1]Manufactured by the Tanglefoot Co., Grand Rapids, Michigan, U.S.A.

amount of new foliage which has been destroyed by the budworm larvae and expressing this as a percentage of the total amount of foliage produced in that year.

Determination of Larval Instars

In both 1973 and 1974, a sample of larvae from each collection date was separated by tree species and preserved in 70% ethyl alcohol. The head capsule of each larva was measured at its maximum width using an ocular micrometer attached to a dissecting microscope. These measurements were converted from ocular units into millimeters and plotted as a frequency histogram to determine the number of larval instars as represented by distinct peaks. With the aid of Dyar's rule (Dyar, 1890), these data (instar number related to head capsule width) were used to determine the age structure of larval populations collected on each sample date, thereby indicating developmental progress. The lengths of the larvae were also measured, and the color patterns of the larvae noted. The sex of each larva was determined whenever possible. Male larvae could be recognized by the presence of the two gonads appearing as dark spots in the mid-dorsal abdominal segments (Plate II). Absence of these did not necessarily indicate females, because parasitoids are known to delay development of the host and of its gonads.

PLATE II.

Male spruce budworm larva with the gonads visible as dark spots in the mid-dorsal abdominal segments.

Determination and Evaluation of the Role of Some Natural Control Factors

This following section applied for both 1973 and 1974.

Predators

The presence of predators was noted in the study area to a limited extent. All collected larvae and pupae were examined for signs of injury resulting from predator attack. Observations were also made on the presence of other insects, their relative abundance in the samples, and their predatory feeding habits. Avian predators were present at the study area and their feeding activity noted, but they were not collected by the author. Results of stomach analysis of birds collected from the study area and its vicinity in 1974, obtained by another worker (see Acknowledgements), were made available to this author. A list of these birds appears in Appendix D.

Parasitoids

Uninjured larvae and pupae, collected from balsam fir in 1973 and from the three host tree species in 1974, were reared. The insects were separated by collection dates and tree species, placed in plastic vegetable crispers (27 x 31 x 11 cm approximately) and/or 4.5 ℓ cardboard containers with about 50 insects each, and provided with adequate ventilation and appropriate host tree foliage. All rearing containers were kept in an unheated room where the temperature ranged from 13°C to 16°C and the relative humidity varied between 50% and 70%. Rearings were checked every 3 to 6 days and fresh foliage was provided as required. The old foliage was checked for the presence of parasitoids, and live,

dead and diseased budworm larvae and pupae, before being discarded. Rearings were continued until the emergence of budworm adults.

Parasitoids emerging from the insect hosts as adults were killed and pinned, and those forming cocoons or puparia were removed from the rearing containers and put into labelled containers for the emergence of the adults. All adult parasitoids were pinned, labelled and sorted. A representative sample of each apparent species was determined at the Biosystematics Research Institute, Department of Agriculture, Ottawa. The remainder were identified by comparison with these known specimens. This information was obtained for each rearing lot and collection date to determine if variation occurred with respect to time or larval stage of the budworm.

Disease

Among the disease-causing pathogens, only fungi were investigated during this study. Dead larvae and pupae were either examined under a dissecting microscope for the presence of fungi or, when possible, were placed on microscope slides in petri dishes, along with wet filter paper to provide moisture for fungal development. The dishes were examined daily for the presence of mycelia and conidia. Diseased spruce budworm larvae and pupae from both collected and reared material were identified by comparing these, and microscope slides of these, with reference samples of fungal infected cadavers and typical slides of the fungi. The slide preparations were examined and compared under a Leitz microscope at up to 400 X.

Mating Experiments

Three types of experiments were conducted under this part of the study in both 1973 and 1974. These were individual matings in the laboratory, group matings under field conditions, and host preference of the ovipositing females in the laboratory. The adults used in these studies came from pupae collected in the field during sampling. They were sorted by sex and weighed individually to the nearest 0.01 gm. In the two laboratory experiments, fresh foliage was provided for the adults, and was placed in glass containers with water to keep it fresh. These mating experiments continued until all the adults had died, and the foliage was then examined for egg masses.

For the individual mating experiments, single pairs of emerging adults were placed in individual containers and the resulting number of egg masses and eggs, laid by each female, was recorded. In 1973, only pupae collected from balsam fir were used, 30 adult pairs being mated. One pair of adults was placed in each of 20 mason jars (455 ml size), which were lined with wax paper, and one pair was placed in each of ten wooden boxes (26 x 26 x 38 cm) with Saran insect screening[2] on two opposite sides for ventilation and a door fitted on a third side. Balsam fir was provided in all containers.

In 1974, pupae collected from the three host tree species were used, 18 pairs from balsam fir and 16 pairs from each of black spruce and white spruce. These were placed in single pairs in the wooden boxes used in 1973, as well as in new, 4.5 l cardboard containers provided with

---

[2]Manufactured by Barrday Ltd., 75 Moose St., Galt, Ontario.

adequate ventilation.

In the group mating experiments, 10 balsam fir trees were transplanted from the field, from an uninfested area, into the nursery at the field station in the spring of 1973. These trees were approximately one meter in height, and were covered with Saran insect screening prior to the emergence of spruce budworm adults in the field. The pupae used in these experiments were collected from balsam fir, and upon emergence, 10 pairs of adults were placed on each of three trees in 1973, and 5 pairs of moths on each of two trees in 1974 (the number of adults used was determined by the survival of those pupae set aside for the experiment and the number of trees used was determined by tree survival after transplanting).

The oviposition preference experiment was designed to show if female spruce budworm moths preferred certain host species for egg laying. Newly emerged adults, 20 pairs in 1973 and 30 pairs in 1974, were placed in a transparent plastic container (1 m x 0.5 m x 0.6 m) along with six, 30 cm-long branch tips, two each of balsam fir, black spruce and white spruce. Only one such experiment was attempted each year, and the pupae used in both cases were from balsam fir.

In 1974, one male and one female pupa were put in each of 10 petri dishes to determine the time interval from emergence to mating, oviposition, and death of the adults. Balsam fir foliage was provided, but without water because of space limitations.

The counting of eggs within an egg mass was tedious especially when the larvae had already hatched, and the separation between egg shells became indistinct. To facilitate this work and to reduce counting

time, the staining method used by Leonard *et al.*, (1973) was adopted with some modification. The egg masses were placed in a 1% aqueous solution of methyl blue for 10 seconds, removed, and then agitated in water for 10 seconds until the chorions became visible. The eggs were then counted under a dissecting microscope.

RESULTS

Life History

The life history and seasonal occurrence of the different life stages of the budworm in Newfoundland, as determined in the study, are shown in Figs. 2, 3, 4 and 5. The widths of the shapes represent the proportion of the sample in a certain stage of development at each collection date. The sum of the widths for a particular sample day represents 100% (the total sample size).

Eggs

The eggs are pale green and are laid in masses on the needles of all three host trees in an overlapping, shingle-like arrangement, the last eggs being laid towards the base of the needle. The masses are usually located on the underside of the needles of balsam fir, and on the upper or lower sides of the needles of black and white spruce. The location of the masses on the needles was more variable on the spruce trees than on balsam fir. Balsam fir needles are flat and somewhat oval in cross section having definitely two sides, while spruce needles are more rectangular and have a diamond shape, two of the sides forming the upper side and the other two sides forming the lower side of the needle.

Egg masses were found containing from 4 eggs to 40. A mass was arbitrarily defined as the arrangement of eggs in rows, and the smallest number of eggs satisfying this criterion was four (2 eggs in 2 rows).

FIGURE 2.

Seasonal occurrence of the spruce budworm on balsam fir, 1973 (the sum of the widths of the lines representing the different stages at each sample day equals 100% - the total sample size).

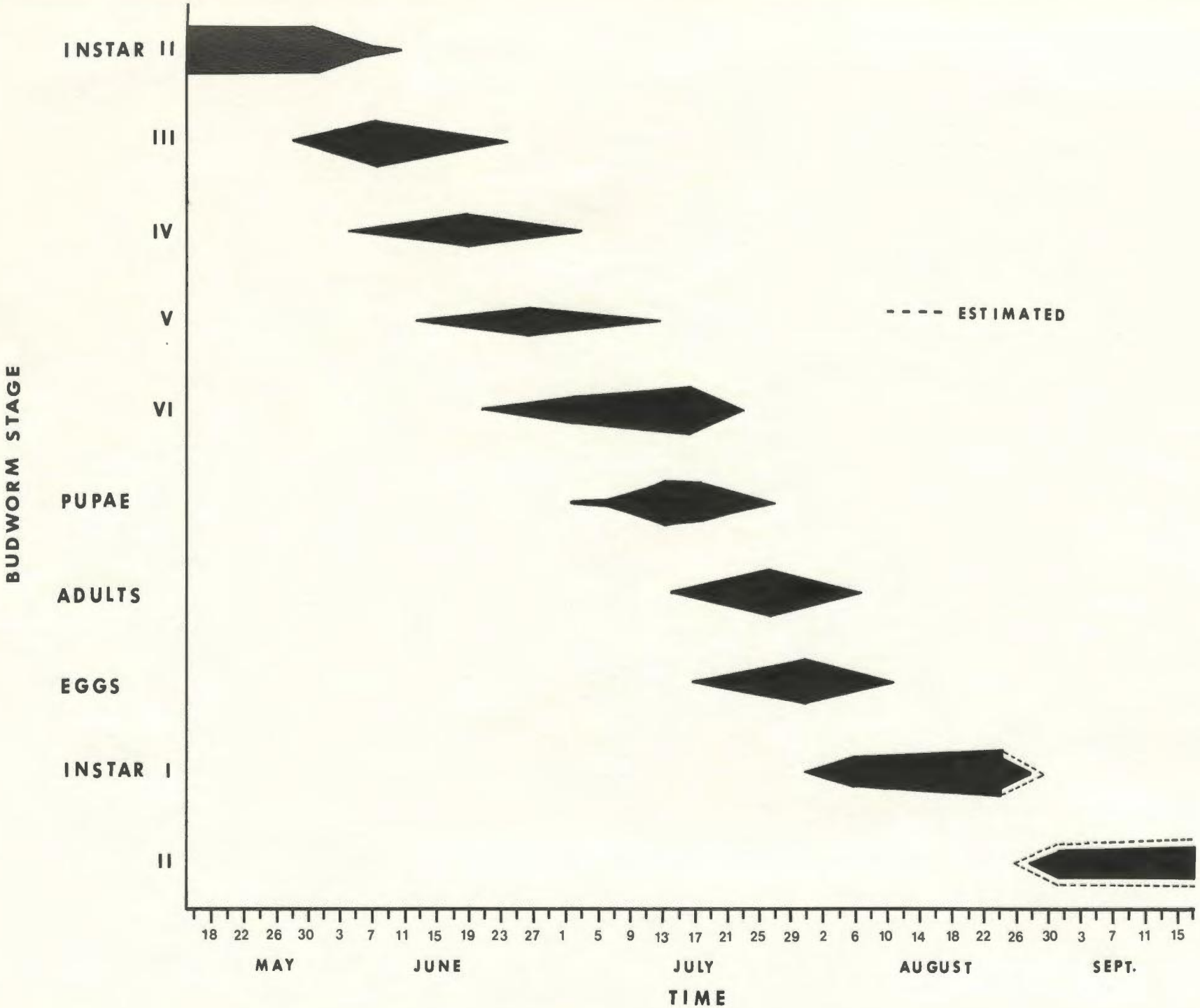

BUDWORM STAGE
INSTAR II
III
IV
V
VI
PUPAE
ADULTS
EGGS
INSTAR I
II
---- ESTIMATED
18 22 26 30 3 7 11 15 19 23 27 1 5 9 13 17 21 25 29 2 6 10 14 18 22 26 30 3 7 11 15
MAY
JUNE
JULY
AUGUST
SEPT.
TIME

FIGURE 3.

Seasonal occurrence of the spruce budworm on balsam fir, 1974 (the sum of the widths of the lines representing the different stages at each sample day equals 100% - the total sample size).

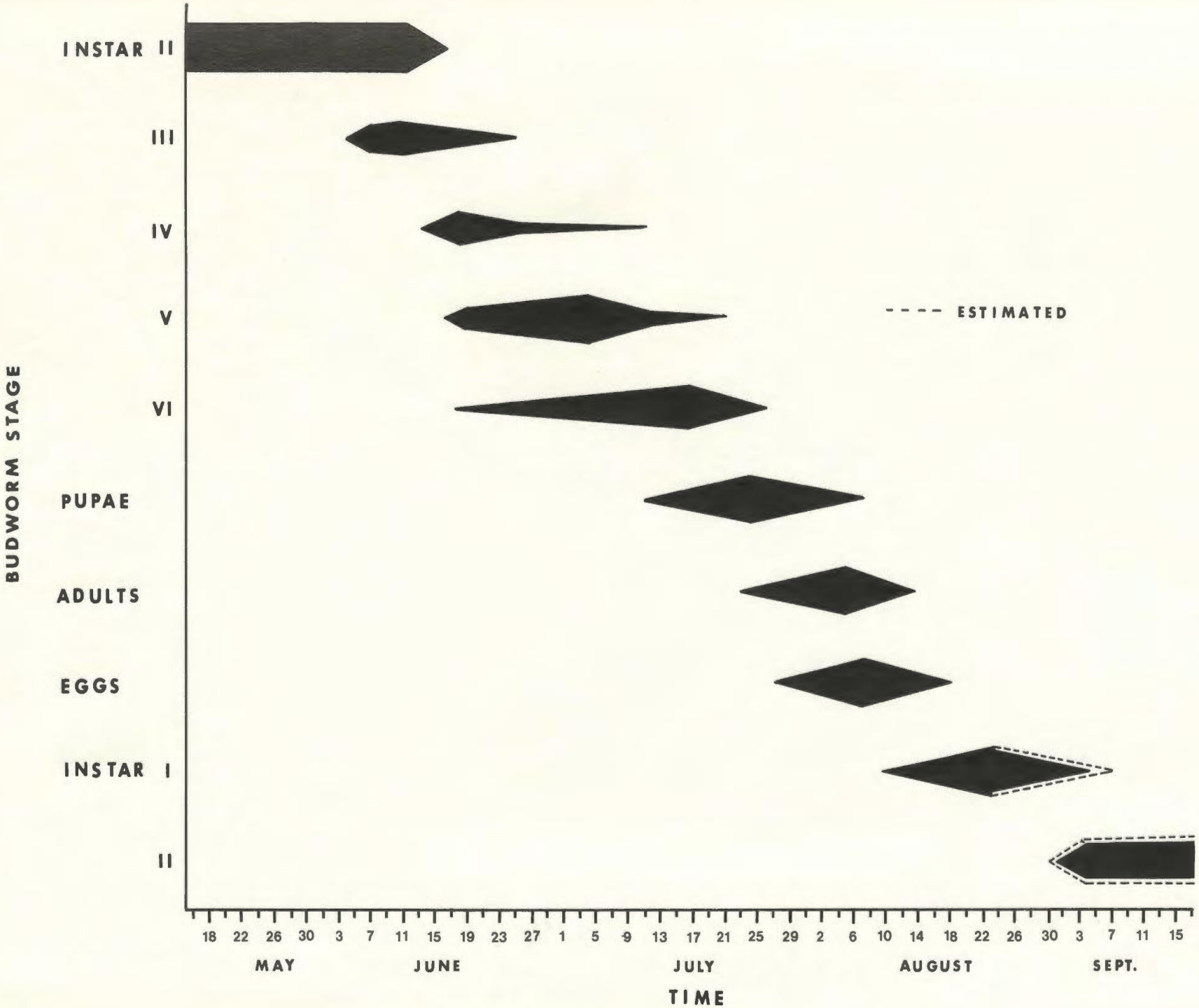

BUDWORM STAGE
INSTAR II
III
IV
V
VI
PUPAE
ADULTS
EGGS
INSTAR I
II
---- ESTIMATED
18 22 26 30 3 7 11 15 19 23 27 1 5 9 13 17 21 25 29 2 6 10 14 18 22 26 30 3 7 11 15
MAY
JUNE
JULY
AUGUST
SEPT.
TIME

FIGURE 4.

Seasonal occurrence of the spruce budworm on black spruce, 1974 (the sum of the widths of the lines representing the different stages at each sample day equals 100% - the total sample size).

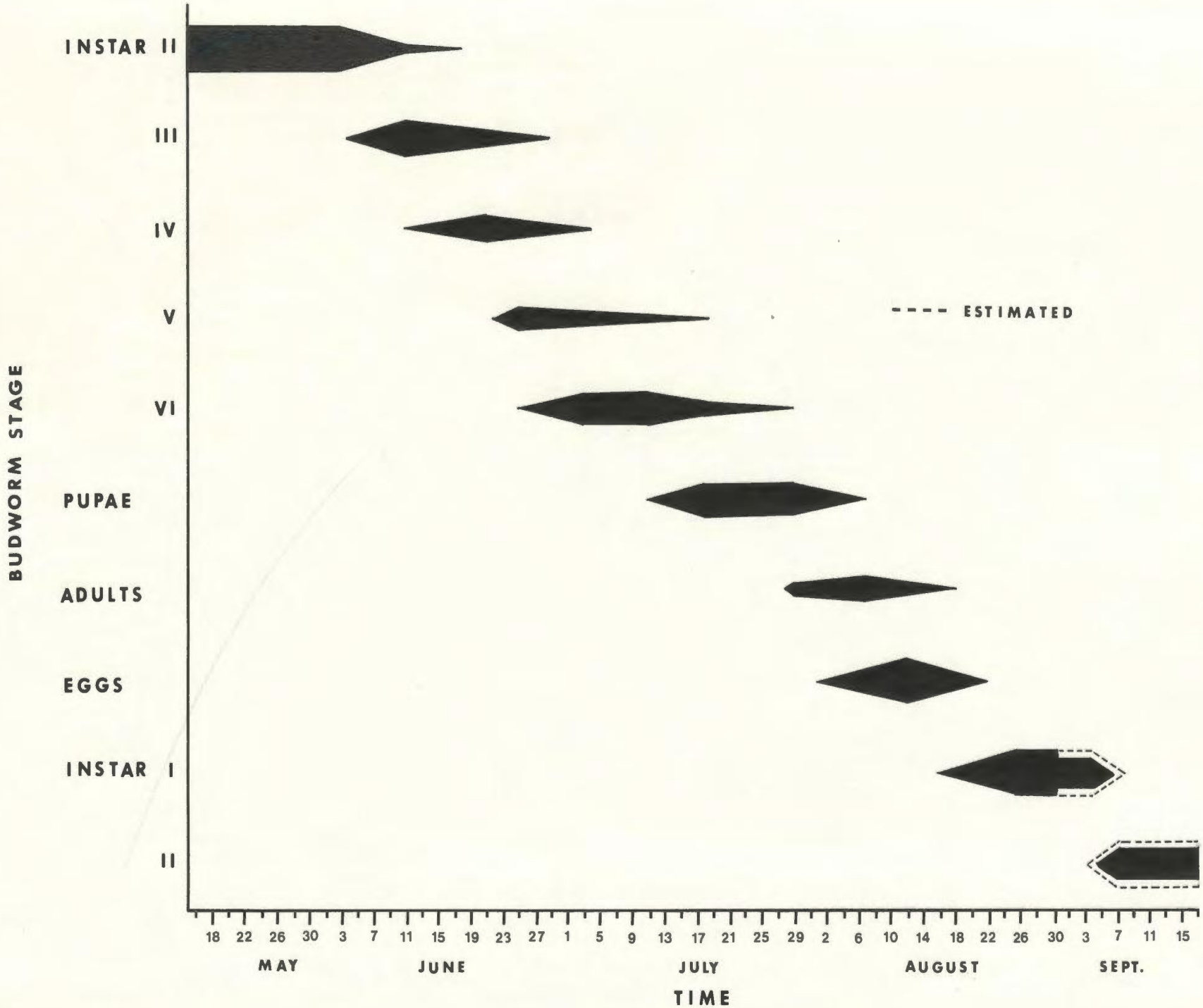
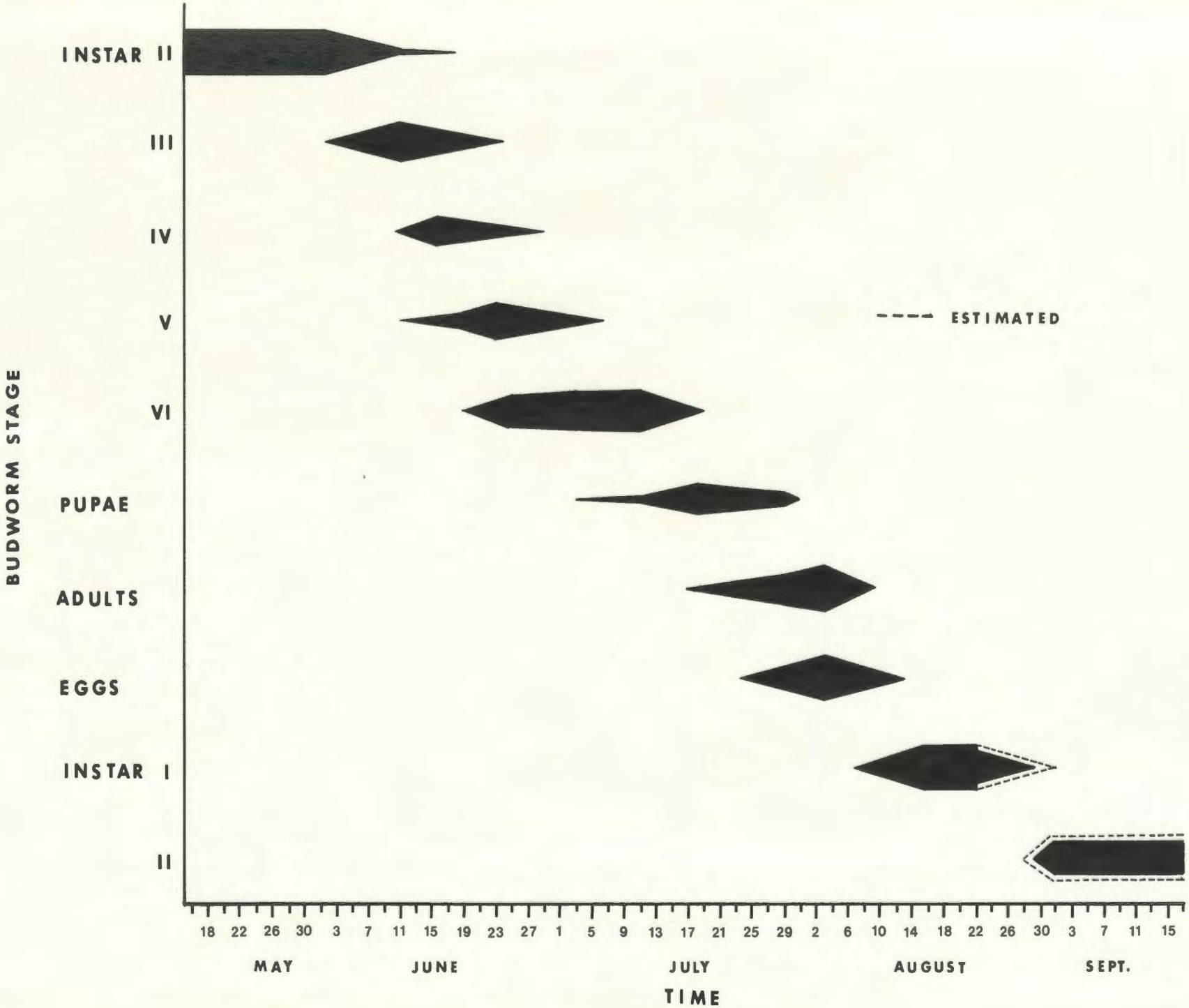

BUDWORM STAGE
INSTAR II
III
IV
V
VI
PUPAE
ADULTS
EGGS
INSTAR I
II
---- ESTIMATED
18 22 26 30 3 7 11 15 19 23 27 1 5 9 13 17 21 25 29 2 6 10 14 18 22 26 30 3 7 11 15
MAY
JUNE
JULY
AUGUST
SEPT.
TIME

FIGURE 5.

Seasonal occurrence of the spruce budworm on white spruce, 1974 (the sum of the widths of the lines representing the different stages at each sample day equals 100% - the total sample size).


BUDWORM STAGE
INSTAR II
III
IV
V
VI
PUPAE
ADULTS
EGGS
INSTAR I
II
ESTIMATED
18 22 26 30 3 7 11 15 19 23 27 1 5 9 13 17 21 25 29 2 6 10 14 18 22 26 30 3 7 11 15
MAY
JUNE
JULY
AUGUST
SEPT.
TIME

Single eggs and two or three eggs have been observed on the needles, but this was not common. The average number of eggs per egg mass for both years together was 21.1 ± 8.4 ($\bar{X}$ ± S.D., N = 34) at the study site.

Egg masses have been found with two rows, three complete rows, and two rows plus a partial third row of eggs. In 1973 and 1974, a combined total of 162 egg masses were examined with the following results: 54% had two rows of eggs, 20% had two rows plus a partial third, and 26% had three rows of eggs.

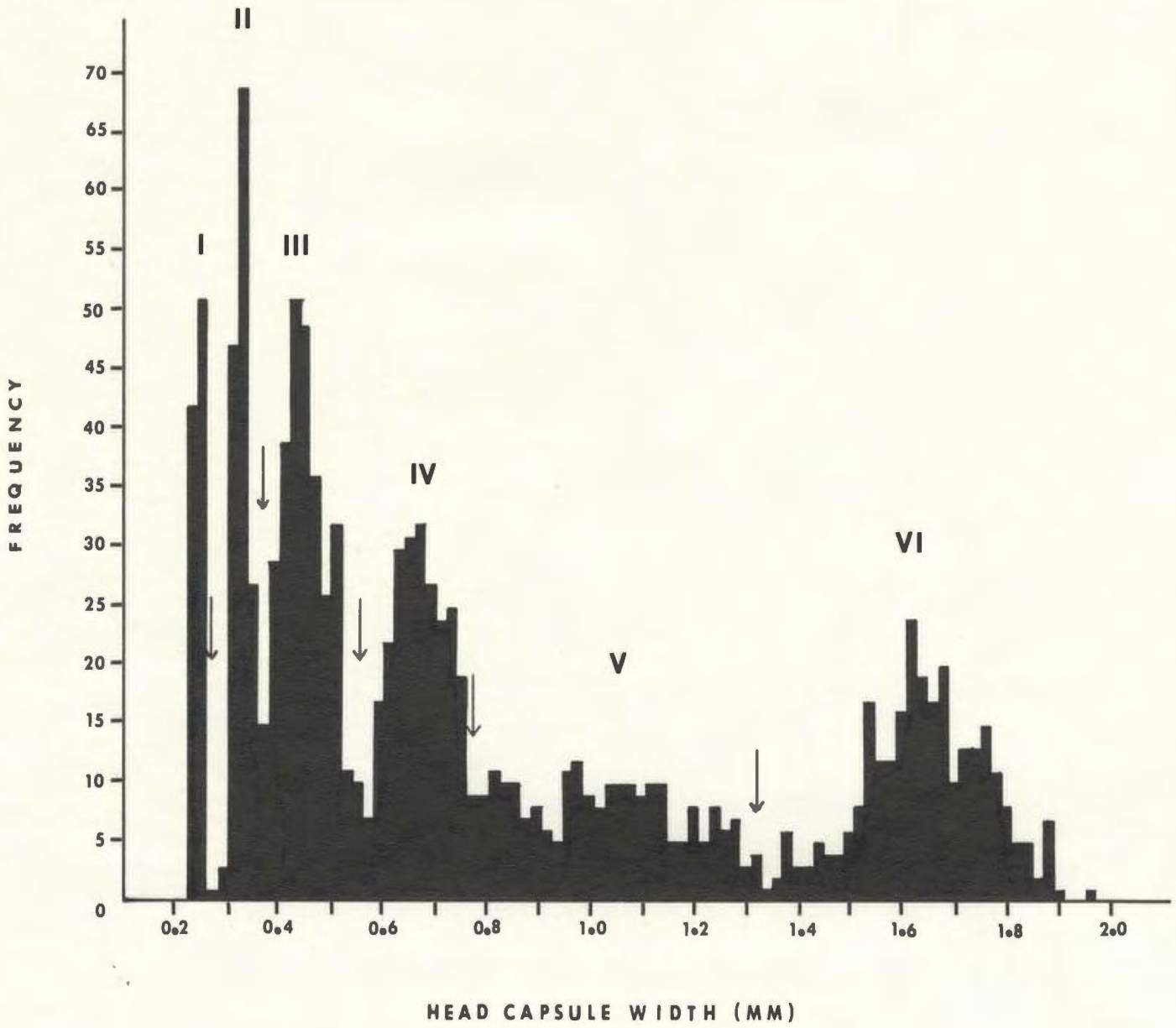
The eggs hatched in approximately two weeks under field conditions, depending upon the weather. The time interval between observing the first eggs and the first larvae was this two week period (Figs. 2, 3, 4 and 5).

Larvae

A total of 1,267 and 841 spruce budworm larvae were collected from the study site for head capsule width measurements in 1973 and 1974, respectively. The frequency distribution of the measurements revealed six major peaks (Fig. 6), indicating six larval instars. There was considerable overlap between the instars especially between the last three. The limit of the ranges of adjacent instars were arbitrarily decided on the basis of a greater separation between them in a larger histogram using width measurements expressed to three decimal places. This provided little or minimal overlap of the ranges, the extent of which, particularly for the last two instars and the less obvious peak of the fifth-instar, can be attributed to sex differences and the influence of parasitoids which will be discussed. The mean head capsule width and the standard deviation for each instar is

FIGURE 6.

Histogram of head capsule width measurements of spruce budworm larvae collected from balsam fir, 1973. (N = 1,267)(arrows indicate the separation between instars).


I
II
III
IV
V
VI
FREQUENCY
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
HEAD CAPSULE WIDTH (MM)

presented in Table 1. Table 2 shows a comparison of the observed head capsule widths for larvae collected from the three host tree species in 1973 and 1974 with widths calculated using the average observed growth ratio according to the theory of geometric progression proposed by Dyar (1890). He determined that the increase in head capsule size from one instar to the next was a geometric progression obtained by dividing the measurement of one instar by that of the previous instar. The resulting ratios could then be averaged which in turn could then be used to find the expected measurement of any instar. The measured values did not differ greatly from those expected (Table 2), and, therefore, it is concluded that the spruce budworm has six larval instars in Newfoundland. Table 3 shows the differences between the head capsule widths of both sexes in the last three instars. These differences are statistically highly significant between the sexes in the fifth- and sixth-instars ($t = 4.08$ and $t = 4.86$, respectively, $p < 0.01$).

The proportion of the different instars per collection date during larval development is illustrated in Figs. 2, 3, 4 and 5 (pp. 25-31). The approximate duration of the instars, excluding the first, was calculated from these figures using the median value or peak of each instar as a reference point, and determining the interval between these median values on the time axis. The duration of the larval stages based on the above criterion as well as laboratory and field observations, was estimated as follows: Instar I, 14 days; Instar II, 280 days (over-wintering stage); Instar III, 8 days; Instar IV, 9 days; Instar V, 7 days; Instar VI, 16 days. Specific values are dependent upon climatic

TABLE 1

HEAD CAPSULE WIDTHS (MM) OF SPRUCE BUDWORM LARVAE COLLECTED FROM HOST TREES AT PASADENA, 1973 AND 1974**

Year	Host tree	Statistics	Larval instar					
			I	II	III	IV	V	VI
1973	Balsam fir	N	94	150	289	245	219	270
		$\bar{X}$	0.246	0.332	0.455	0.672	1.028	1.637
		S.D.	0.0071	0.0148	0.0424	0.0540	0.1490	0.1208
1974	Balsam fir	N	15	81	124	54	78	73
		$\bar{X}$	0.247	0.321	0.435	0.648	1.050	1.646
		S.D.	0.0064	0.0190	0.0430	0.0534	0.1729	0.1288
	Black spruce	N		33	27	8	43	70
		$\bar{X}$	*	0.317	0.455	0.612	1.097	1.676
		S.D.		0.0169	0.0518	0.0714	0.1548	0.1707
	White spruce	N		44	42	22	43	84
		$\bar{X}$	*	0.317	0.435	0.685	1.017	1.732
		S.D.		0.0179	0.0451	0.0467	0.1806	0.1331

*Not sampled.

**The standard deviation was calculated to four decimals to facilitate the comparison with the data given in McGugan (1954).

TABLE 2

COMPARISON OF MEAN HEAD CAPSULE WIDTHS (MM) OF SPRUCE BUDWORM LARVAE FROM THE THREE HOST TREE SPECIES IN NEWFOUNDLAND FOR 1973 AND 1974 (OBSERVED) WITH THOSE CALCULATED ACCORDING TO DYAR'S THEORY OF GEOMETRIC PROGRESSION (EXPECTED)

	1973		1974					
	Balsam fir		Balsam fir		Black spruce		White spruce	
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
Instar I	0.246	0.246	0.247	0.247	*		*	
Instar II	0.332	0.359	0.321	0.363	0.317	0.317	0.317	0.317
Instar III	0.455	0.524	0.435	0.534	0.455	0.485	0.435	0.485
Instar IV	0.672	0.766	0.648	0.785	0.612	0.742	0.685	0.742
Instar V	1.028	1.118	1.050	1.153	1.097	1.135	1.017	1.135
Instar VI	1.637	1.632	1.646	1.695	1.676	1.737	1.732	1.737

*These larvae were not measured.

TABLE 3

COMPARISON OF MEAN HEAD CAPSULE WIDTHS (MM) BETWEEN NEWFOUNDLAND AND ONTARIO SPRUCE BUDWORM LARVAE

Instar	Newfoundland[1]			Ontario[2]	
	Sex	N	$\overline{X}$ ± S.D.[4]	N	$\overline{X}$ ± S.D.[4]
I		94	0.246 ± 0.0071	110	0.252 ± 0.0125
II		150	0.332 ± 0.0148	117	0.314 ± 0.0140
III		289	0.455 ± 0.0424	318	0.445 ± 0.0303
IV	M	110	0.674 ± 0.0504	348	0.682 ± 0.0652
	F	135	0.670 ± 0.0569		
		(245	0.672 ± 0.0540)		
		"t" value 0.58 N.S.		"t" value not given	
V	M	90	0.979 ± 0.1554	150	1.06[3] ± 0.0794
	F	129	1.062 ± 0.1351	154	1.15[3] ± 0.0940
		"t" value 4.08*		"t" value 18.0*	
VI	M	104	1.595 ± 0.1071	348	1.63[3] ± 0.0820
	F	166	1.664 0.1223	232	1.79[3] ± 0.0897
		"t" value 4.86*		"t" value 50.2*	
Total		1,267		1,777	

*99% level. [1]Larvae collected from balsam fir, 1973.
[2]From McGugan (1954); material for measurements was also collected from balsam fir ($S_{\overline{X}}$ converted into S.D.). [3]Third decimals not given.
[4]The standard deviation from Newfoundland was calculated to four decimal places to facilitate the comparison with the data given in McGugan (1954).

conditions and host tree.

Larval Habits

First-instar larvae, with their dark head capsules, are clearly visible inside the transparent egg shells just before hatching. During hatching, the larva gnaws a hole in the egg shell and crawls through it. The egg mass remains attached to the needle for some time. The newly hatched larvae are usually positively phototropic and crawl towards the tip of the branches. The first-instar larvae have not been observed to feed. The young larvae are easily blown off the branches and have often been observed to hang on silken threads just after hatching, providing an excellent opportunity for easy passive dispersal. The larvae actively search for hibernacula sites shortly after hatching.

The second-instar larvae become active in the spring from mid- to late May, the emergence from the hibernacula being temperature dependent. In 1973, the larvae had already emerged from the hibernacula prior to the commencement of sampling on May 31. In 1974, spring came later than in 1973, and so the activities of the second-instar larvae, from emergence from the hibernacula to bud mining, could be observed. The temperatures for May 1973 were above normal, while those for May 1974 were below normal (Table 4). There was a late fall of snow at the end of May 1974 which lay several days before it melted. After this, there were several days of very high temperatures (over 14°C), which led to the emergence of the overwintering larvae. This started at Pasadena on May 31, when the first larvae were seen hanging by spun threads from the branches of a semi-open grown white spruce tree. The maximum temperature for this day was 12°C. It was not until June 3 that larvae were

TABLE 4

DAILY MEAN TEMPERATURES AND TOTAL PRECIPITATION AT THE STUDY AREA (PASADENA) AND THE NEAREST WEATHER STATIONS,[1] AND THE NORMALS FOR THESE STATIONS.[2]

Year	Month	Temperature (Daily mean) (°C)			Total precipitation (mm)		
		Pasadena	Stations	Normal	Pasadena	Stations	Normal
1973	May	*	7.1	6.6	*	66.3	72.1
	June	12.9	12.4	11.8	194.3	158.0	74.9
	July	19.9	19.3	16.4	55.9	83.3	77.5
	Aug.	16.1	14.9	15.8	154.2	136.7	99.6
1974	May	*	4.4	6.6	*	39.1	72.1
	June	11.9	12.8	11.8	13.0	17.0	74.9
	July	13.4	14.7	16.4	72.1	82.8	77.5
	Aug.	14.6	15.8	15.8	61.7	59.4	99.6

[1]The nearest weather stations were located at Corner Brook, Deer Lake Airport and Deer Lake, 30, 16 and 18 km, respectively, from the study area. Data were obtained from these stations from the Monthly Records compiled by the Atmospheric Environment Service, Environment Canada. An average of the daily mean temperatures, monthly precipitation and their respective normals were calculated for the three stations. These values are entered under the appropriate "Station" and "Normal" headings.

[2]Both temperature and precipitation have originally been measured in °F and inches, respectively. These values, however, were converted and are presented in SI units.

*No measurements were obtained in the study area until the end of the month.

observed in large numbers hanging by silk threads from all three host tree species. The day was clear and sunny with a maximum temperature of 22°C and some light wind (15-25 km/hr). The emergence of larvae continued for several days and the temperatures remainded at about the same level. The temperatures before May 31 were below 7°C. The number of degree-hours above the threshold temperature of 2.5°C (Bean,1961) was not determined at the study site.

Upon emerging from the hibernacula, the larvae react photopositively and move towards the branch tips where they search for food. Having reached the tips, the larvae may be blown off by the wind, and have been observed hanging on silk threads up to several meters in length. Strong wind can carry these larvae varying distances, depending upon the height of the larvae above the ground and the velocity of the wind. The second major dispersal of the larvae happens during this spring larval activity between emergence of the larvae from the hibernacula and the establishment of the larvae in the feeding sites.

The first sign of feeding activity of second-instar larvae in the spring is usually the presence of mined needles. Needle mining was observed on all three host species. The entrance hole on balsam fir was located on the underside of the needle, either near the base or near the middle of the needle. The larva first spun a small shelter of silk on the needle and then entered the needle from this shelter. It then mined out most of the needle leaving only the epidermis, almost always working towards the apex from the entrance point. On spruce trees, possibly because of the smaller needle size, two or three needles were usually webbed together prior to mining, and these were often all fed upon to

some extent. The hole in a spruce needle was on the upper side towards the apex of the twig on which the needle grew. Mined spruce needles were more easily dislodged from the branches than mined fir needles. The mined needles were mostly in the foliage of the previous year's growth on all host species. On branches with total defoliation of the growth of the previous year(s), mined needles occurred on the first section of the branch with foliage back from the new buds. It was not determined whether or not all larvae engage in needle mining. Larvae which emerged early from the hibernacula invariably mined needles, the only source of food at the time.

Branches with staminate flowers, particularly from balsam fir, had more larvae than those without flowers, suggesting that staminate flowers are an excellent source of food for the young larvae. Of 20 branch samples in 1973, 7 contained staminate flowers with an average of 40 larvae compared with an average of 26 larvae on branches without staminate flowers. Larvae on branches with staminate flowers were usually on the flowers and these flower feeders were larger and in a later instar than larvae occurring elsewhere on the same branch or on non-flowering branches. Of 90 larvae collected on June 4, 1973, 30 were found in the flower cups and 60 elsewhere on the branch or on non-staminated branches. Of the 30 larvae, 17% were second-instar, 73% were third-instar and 10% were fourth-instar. Of the 60 larvae collected, 78% were second-instar and 22% third-instar.

When staminate flowers are no longer available, the larvae move to the vegetative buds and/or shoots (Plate III). In the process of bud mining, the larva spins a silken shelter on the outside of a bud, usually

PLATE III.

Second-instar spruce budworm larva on a mined bud.

near its base. In many cases, the shelter was between two buds or between a bud and a needle rather than on the exposed surface of the bud. The larva entered the bud and fed on the developing new growth. Damage caused to the new growth may be minimal if the bud and shoot develops rapidly and there is only one larva per feeding site, or if the larva enters the bud after shoot elongation has started. Damage can be extensive if the larva feeds faster than the new growth can elongate, or if several larvae are present, or if the larva enters the bud prior to shoot elongation.

Field observations indicated that on balsam fir, particularly, complete destruction of the bud often occurred prior to the bud caps coming off. The phenological development of the three host species is given in Table 5. The new growth on white spruce developed more rapidly than on fir, and in most cases the shoot elongated before the larva(e) could completely consume it. On white spruce, the larvae often webbed the bud caps to the terminal needles of the new growth, which provided a ready-made shelter for the earlier instars in the spring. The development of the new growth was slowest on black spruce and consequently black spruce provided less food for the early instar larvae than the other two host species.

As the bud cap comes off and the shoot elongates, the larva frequently 'ties' two or three of the shoots together with silk thread, thus forming a feeding shelter in which development can be completed (Plate IV). Larvae usually remain with this new growth unless it is consumed or they are disturbed. When the new growth is consumed in and around the feeding shelters, the larvae must move either to other

TABLE 5

PHENOLOGY OF THE HOST TREES AT THE STUDY AREA, 1974[1]

Date		Host					
		Balsam Fir		Black Spruce		White Spruce	
		Cardinal direction of the branches					
		North	South	North	South	North	South
June 4	$\bar{X}$	5.90	5.70	4.25	4.35	5.70	5.70
	S.D.	1.45	1.09	0.92	0.85	1.09	1.27
June 10	$\bar{X}$	6.95	7.10[2]	4.67	4.89	7.45	7.45
	S.D.	1.54	1.56	0.71	0.96	1.66	1.48
June 14	$\bar{X}$	10.30[3]	10.30[3]	6.55	6.85	11.90[3]	12.65[3]
	S.D.	3.16	2.84	1.69	1.55	4.37	4.53
June 17	$\bar{X}$	16.15[4]	15.85[4]	8.55[2]	9.00[2]	20.20[4]	20.90[4]
	S.D.	3.93	4.37	2.44	2.22	6.32	7.61
June 24	$\bar{X}$	31.44[5]	30.11[5]	15.30[4]	16.05[4]	41.50[5]	48.80[5]
	S.D.	5.41[6]	5.95[6]	4.90	5.16	11.84	15.48

[1]Mean bud and/or shoot length in mm; N = 10 for each host tree, except when noted. [2]First observed caps off buds. [3]50% of buds opened (approximately). [4]Most of buds opened. [5]All of buds opened. [6]Based on 9 trees--the new growth of the branch was stripped on the 10th tree before the bud had a chance to open.

PLATE IV.

Late instar spruce budworm larva in its feeding shelter.

buds/shoots on the same branch, or to other branches on the same tree, or else move to other trees, usually to smaller trees in the understory which they frequently completely defoliate. Relocation can either take place by the active search of the larvae for new growth, or possibly with the help of the wind when the larvae lower themselves on silken threads. Back-feeding (the feeding on older foliage) occurs when insufficient new foliage is available, and usually involves late instar larvae. If larval density is very high, back-feeding may occur and foliage other than the current growth will also be fed upon and will be partially stripped from certain branches or trees. Back-feeding was not observed in 1973, but in 1974 it occurred on some of the sample trees when foliage produced in the previous year was consumed or if this was not present, foliage from the year before. Back-feeding was most severe on balsam fir at about 9%, approximately 2% on white spruce, and less than 1% on black spruce, based on visual estimations similar to those used to determine defoliation. The average defoliation of the current (new) growth of the sample trees in 1974 was 99% for balsam fir, 87% for white spruce and 70% for black spruce. The percent defoliation in 1973 was similar. Defoliation is illustrated in Plate V. Budworm larvae have also been observed to feed on larch trees located beneath or next to heavily infested primary host trees. The larvae quickly consume the succulent but sparse larch needles, leaving only the woody part of the branches. The mining of needles or buds on larch has not been observed.

Budworm larvae are continually dropping on silken threads from the branches during development (Plate VI). Tables 6 and 7 list the

PLATE V.

a) Typical reddish-brown coloration of a balsam fir stand as a result of moderate spruce budworm feeding.

b) Balsam fir trees with severe defoliation in the upper crowns caused by spruce budworm larvae.

c) White spruce showing the results of severe defoliation by the budworm for several years.

a

b

c

PLATE VI.

Silken threads, spun by disturbed spruce budworm larvae, hanging from a severely infested tree.

TABLE 6

AVERAGE NUMBER OF SPRUCE BUDWORM LARVAE AND PUPAE COLLECTED FROM DROP TRAYS PLACED BENEATH INFESTED BALSAM FIR TREES, 1973 (N = 10)

Collection date		Larvae		Pupae	
		Live	Dead	Live	Dead
June 14	$\bar{X}$	2.50			
	S.D.	2.37			
June 19	$\bar{X}$	4.30			
	S.D.	3.13			
June 21	$\bar{X}$	5.60			
	S.D.	3.34			
June 25	$\bar{X}$	7.75			
	S.D.	2.36			
July 2	$\bar{X}$	11.10			
	S.D.	6.03			
July 5	$\bar{X}$	5.60			
	S.D.	4.93			
July 9	$\bar{X}$	2.70	0.10	0.20	
	S.D.	2.36	0.32	0.42	
July 13	$\bar{X}$	1.10		0.40	
	S.D.	0.74		0.52	

TABLE 7

AVERAGE NUMBER OF SPRUCE BUDWORM LARVAE AND PUPAE COLLECTED FROM DROP TRAYS PLACED BENEATH INFESTED BALSAM FIR TREES, 1974 (N=10)

Collection date		Larvae		Pupae	
		Live	Dead	Live	Dead
June 3	$\bar{X}$	1.10			
	S.D.	1.29			
June 4	$\bar{X}$	11.80			
	S.D.	9.50			
June 10	$\bar{X}$	2.70			
	S.D.	4.81			
June 14	$\bar{X}$	3.50			
	S.D.	2.95			
June 17	$\bar{X}$	5.50			
	S.D.	2.64			
June 24	$\bar{X}$	12.20			
	S.D.	8.39			
July 3	$\bar{X}$	49.00			
	S.D.	29.50			
July 12	$\bar{X}$	17.60			
	S.D.	10.48			
July 22	$\bar{X}$	9.10		1.70	
	S.D.	7.17		1.49	
July 26	$\bar{X}$	0.90		0.10	
	S.D.	1.52		0.32	
Aug. 7	$\bar{X}$		0.10		0.10
	S.D.		0.32		0.32

collections from the drop trays for 1973 and 1974, respectively. In 1973, the trays were not set up until June 12. In 1974, the trays were set up before the completion of emergence of the second-instar larvae from the hibernacula. There was much variation in the numbers obtained as seen in the two preceding Tables. Figure 7 shows the changes in the numbers of specimens in the drop trays with time. This will be further discussed later.

Prepupae

The prepupal stage is the brief period during which larvae transform into pupae, and was the shortest stage in the life cycle. It was estimated to be 6 days under field conditions and as little as 3 days in the laboratory. The transformation of larva to pupa usually occurs within the larval feeding shelter (Plate VII), although occasionally the prepupa may be found elsewhere on the branch.

Pupae

The duration of the pupal stage under field conditions was estimated as approximately two weeks in Newfoundland. Pupae are usually found within the larval feeding shelters unless they have been dislodged, or the larvae were disturbed and left the shelter just prior to pupation (Plate VIII). Pupae have also been found attached to foliage other than that of the usual host trees. Female pupae are generally larger than male pupae, and the relative size of the sexes is illustrated in Plate IX.

FIGURE 7.

Mean number of spruce budworm collected from drop trays in 1973 and 1974 (N=10).

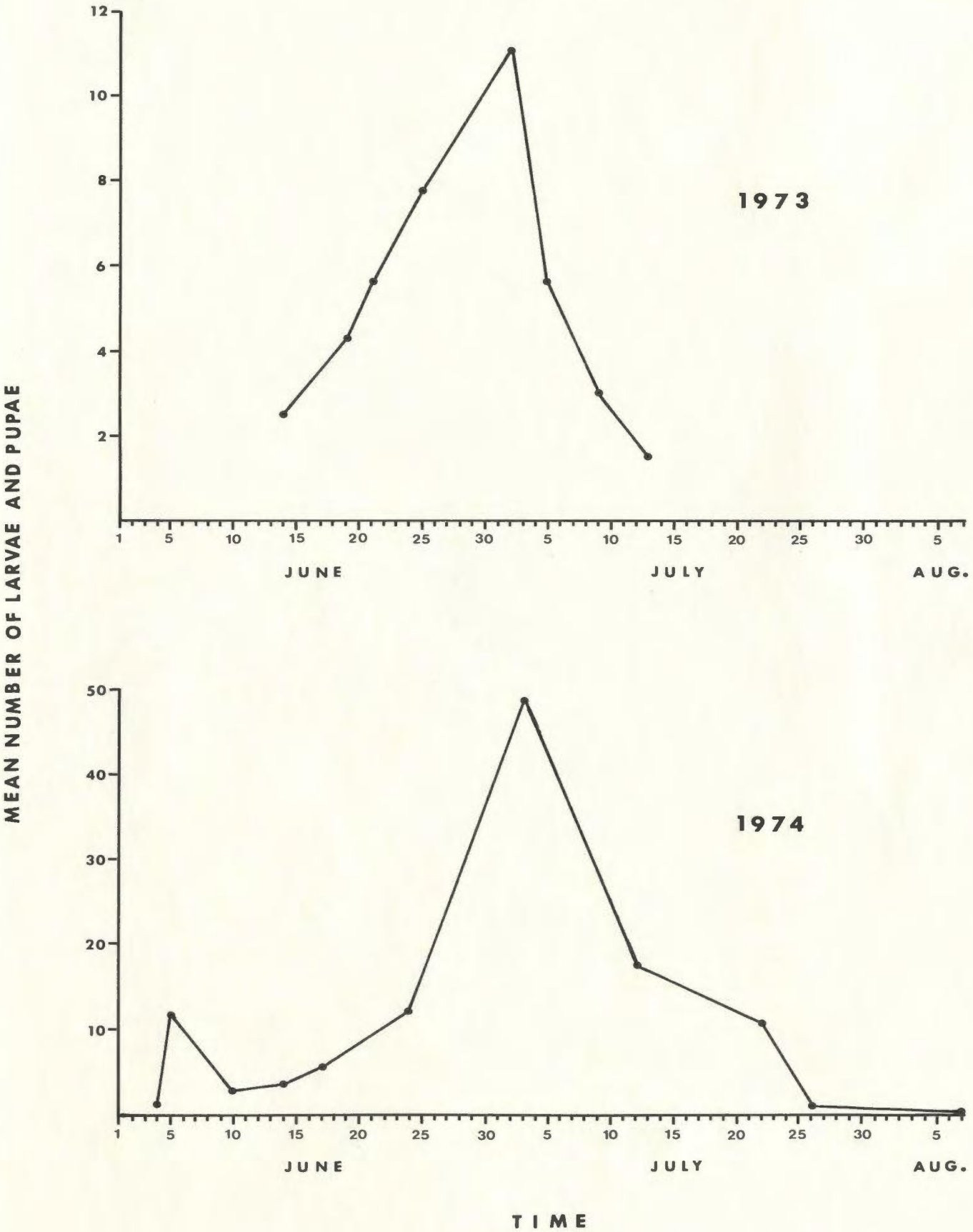

MEAN NUMBER OF LARVAE AND PUPAE
12
10
8
6
4
2
1973
1 5 10 15 20 25 30 5 10 15 20 25 30 5
JUNE
JULY
AUG.
50
40
30
20
10
1974
1 5 10 15 20 25 30 5 10 15 20 25 30 5
JUNE
JULY
AUG.
TIME

PLATE VII.

Prepupa of the spruce budworm in its natural habitat.

PLATE VIII.

Spruce budworm pupa on balsam fir, with the larval skin visible beside it.

PLATE IX.

Empty male and female spruce budworm pupal cases showing the relative size of the sexes.


M
F

Adults

Invariably, the first adults to emerge from the pupae were males, females emerging several days later. This was observed both in the field and in the laboratory. The sex ratio of the adults was approximately 1:1 based on the numbers of empty pupal cases in the samples. Moths were present from about the last week in July to the middle of August, 1974. The adults were relatively inactive during the day, but became active in the late afternoon or early evening, and this activity continued for several hours. Observations were not continued throughout the night. Moths were seen fluttering around the host trees, but not in active directional flight. The life span of an individual adult is approximately 14 days in the field. In laboratory experiments, the following sequence was noted: male moths emerged first; following the emergence of females, mating occurred shortly and oviposition began within 2 or 3 days after emergence, and egg laying was completed within 4 days from its start. Males lived for an average of only 7 days while longevity of females averaged 12 days.

Individual mating trials in 1973 were largely unsuccessful, because very few adults emerged from the pupae saved for this experiment. Therefore, little success was achieved with these mating trials and no results are available.

In 1974, greater success was obtained and the results are presented in Table 8. Females, collected as pupae from black spruce, had the largest number of egg masses per female ($\overline{X}$ = 6.3) and the largest number of eggs per mass ($\overline{X}$ = 21.8); females from white spruce had the smallest number of egg masses per female ($\overline{X}$ = 2.0) and the smallest

TABLE 8

RESULTS OF SINGLE-PAIR MATINGS OF SPRUCE BUDWORM ADULTS COLLECTED AS PUPAE FROM THE THREE HOST SPECIES, 1974

Host tree[1]	No. of females[2]	No. egg masses per female	Total No. of eggs	No. eggs per female	No. eggs per mass
		$\bar{X} \pm$ S.D.		$\bar{X} \pm$ S.D.	$\bar{X} \pm$ S.D.
Balsam Fir	12	4.8 ± 2.0	1,023	85.3 ± 54.7	17.2 ± 8.0
Black Spruce	11	6.3 ± 3.9	1,282	116.6 ± 50.3	21.8 ± 8.8
White Spruce	3	2.0 ± 1.0	98	32.7 ± 20.5	15.9 ± 8.0

[1]Specimens collected from a certain host tree (e.g. Balsam Fir) were given foliage from the same host species (i.e. Balsam fir).

[2]These represent the number of females that oviposited; actual number of pairs set up individually were: Balsam Fir = 18; Black Spruce = 16; White Spruce = 16.

number of eggs per mass ($\overline{X}$ = 15.9). It is important to note that only 3 of the 16 pairs set up from white spruce produced any eggs.

Table 9 presents the results of oviposition of spruce budworm adults under field conditions on small, caged balsam fir trees. Of particular note is the fact that the average number of eggs and the number of egg masses per female obtained in 1974 were twice the numbers obtained in 1973. It was not determined if all females laid their complete complement of eggs for either year.

In 1973 and 1974, laboratory experiments were conducted to determine if there was any host selection for oviposition sites by females. Pupae in both years were collected from balsam fir, the most common host tree species. In 1973, 20 pairs of adults were used, and in 1974, 30 pairs. The results of these experiments are presented in Table 10. Although only one experiment was conducted in both years and the results are not conclusive, the data nevertheless suggest some degree of host selection by females during oviposition. The smallest number of eggs, in both years, was laid on black spruce; white spruce and balsam fir had the largest number of eggs in 1973 and 1974, respectively.

Life History on Host Trees

Appendices A and B provide a comprehensive tabulation of the results of sampling conducted in 1973, and Appendix C presents the results of the sampling from the three host tree species performed in 1974. The numbers of living and dead larvae and pupae, and emerged adults (determined by the presence of empty pupal cases) are given for the basic sample unit of an 18-inch branch tip and for 10 square feet of

TABLE 9

OVIPOSITION OF SPRUCE BUDWORM MOTHS ON SMALL CAGED BALSAM FIR TREES UNDER FIELD CONDITIONS

Year	Tree No.		No. of females/ cage	No. of egg masses	Total No. eggs		No. egg masses per female ($\bar{X}$)	No. eggs per female ($\bar{X}$)	No. eggs per mass ($\bar{X}$ ± S.D.)
1973	1		10	29	453		2.9	45.3	15.6 ± 10.2
	2		10	28	420		2.8	42.0	15.0 ± 11.2
	4		10	58	981		5.8	98.1	16.0 ± 8.2
		Total	30	115	1,854	Overall mean	3.83	61.8	16.1
1974	1		5	61	810		12.2	162.0	13.3 ± 7.9
	3		5	18	295		3.6	59.0	16.4 ± 7.3
		Total	10	79	1,105	Overall mean	7.9	110.5	14.0

TABLE 10

HOST SELECTION BY FEMALE SPRUCE BUDWORM ADULTS UNDER LABORATORY CONDITIONS

Year	No. of females	Foliage type	No. of egg masses	Total No. eggs	No. eggs per mass $\bar{X} \pm$ S.D.	No. eggs per female	Eggs as percent of total laid
1973	20	Balsam fir	29	726	25.0 ± 11.1		31.7
		Black spruce	15	255	17.0 ± 13.9		11.1
		White spruce	87	1,308	15.0 ± 7.3		57.1
		Total	131	2,289		114.5	
1974	30	Balsam fir	102	1,527	15.0 ± 12.4		68.2
		Black spruce	5	65	13.0 ± 4.7		2.9
		White spruce	38	646	17.0 ± 10.9		28.9
		Total	145	2,238		74.6	

foliage calculated from the 18-inch unit in Appendices B and C. Larval numbers are also given per feeding site for 1974, again based on the 18-inch unit. The 18-inch unit was chosen for comparison because it had the least variance among the three units. Figure 8 shows the total live and total dead for the three host tree species sampled in 1974. These three graphs are quite distinct. Referring to Fig. 8, sampling started before all the spruce budworm larvae had emerged from their hibernacula, as indicated by the fact that the peak in the number of larvae occurred one to two sampling days after the first day. Comparing the three curves, black spruce had the least spruce budworm larvae initially, and the decline of larval numbers over the development period was gradual. Peak larval numbers on white spruce and balsam fir were approximately three and four times respectively, the number on black spruce. The decrease in larval numbers on balsam fir and white spruce was more pronounced than on black spruce.

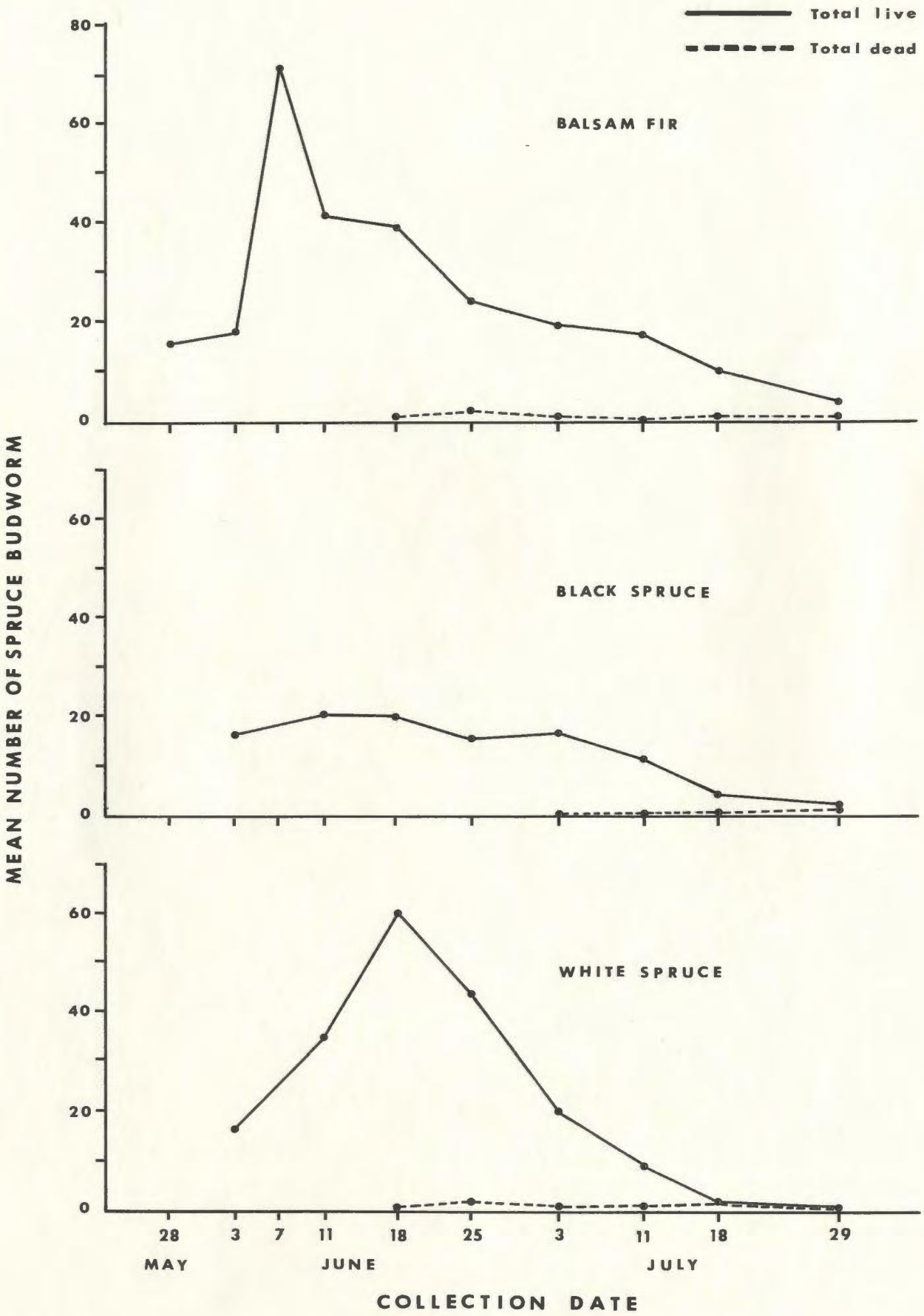
Natural Control

Weather

Only limited information was collected on the actual mortality caused directly by the weather. Heavy rain was observed to halt feeding for a time, but this had no adverse effect on survival. High humidity did, however, favor the development of fungi, particularly in 1973. Mortality of the overwintering larval population caused by low temperatures was not determined. An adverse effect of the storage of pupae at low temperatures was also noted during 1973. Pupae for the single pair matings were placed in a cooler at approximately 5°C for one week

FIGURE 8.

Mean number of spruce budworm per collection date based on 18-inch branch samples from the three host tree species, 1974.


Total live
Total dead
BALSAM FIR
BLACK SPRUCE
WHITE SPRUCE
MEAN NUMBER OF SPRUCE BUDWORM
80
60
40
20
0
28
3
7
11
18
25
3
11
18
29
MAY
JUNE
JULY
COLLECTION DATE

in order to synchronize the experiments. Very few of these pupae survived and no adults emerged.

Predators

Less than 5% of budworms showed any sign of predation. A particularly interesting observation was the presence of ants on budworm infested trees, crawling over the branches in search of food. The ants were identified as *Formica fusca* L. Some of these ants were either carrying budworm larvae down the tree trunks or attempting to do so. These budworm larvae were in the fourth or earlier instars. It is also possible that ants may manage to carry larger larvae which are injured or otherwise unhealthy.

Numerous spiders were observed on the collected branch samples of all three host species, and the spruce coneworm, *Dioryctria reniculloides* M. & M., was present on both spruce hosts. Neither of these were observed to feed on the spruce budworm, but several budworm pupae were found in the samples with a hole 'chewed' in the anterior part of the pupae and some of the contents missing.

Several bird species were seen feeding on insects on balsam fir (Appendix D). Apart from the smaller ants and spiders, spruce budworm larvae and pupae were the only possible prey available. On the spruce trees, coneworm moths appeared to provide an alternative source of food. In 1974, there appeared to be fewer birds at the study site than in 1973, attributed mainly to the late spring.

Parasitoids

A total of 4,136 spruce budworm larvae were reared during the

study and from these, 12 species of parasitoids were obtained. A breakdown of parasitoid species reared from budworm larvae collected from the different host tree species is given in Table 11. Table 12 presents data on the fate of all larvae reared in 1973 and 1974. The number of missing larvae was the remainder of larvae not accounted for from the original number.

Only two of the parasitoid species, *Apanteles fumiferanae* Vier. and *Glypta fumiferanae* (Vier.), were of any importance as control factors, accounting for 5.4% and 12.0% larval mortality, respectively. In 1973, the ratio of *Glypta* (Plate X) to *Apanteles* was 3.5:1 on balsam fir. In 1974, this ratio was 1.5:1 on balsam fir, 1.4:1 on black spruce, and approximately 1:1 on white spruce. The overall ratio for the two years was about 2:1. All the other parasitoid species combined accounted for less than 2% of the larval mortality.

Pupae were also collected and reared for parasitoids. Of the 295 pupae reared in 1974, only two specimens, both *Apechthis ontario* (Cress.), were obtained. No parasitoids were obtained from the 280 pupae reared in 1973. A small number of hyperparasitoids were also obtained (Appendix E). Based on the rearing of 4,711 spruce budworm larvae and pupae over a two year period, 13 primary parasitoid species, including one pupal parasitoid, were found at Pasadena.

Disease

In 1973 and 1974, most of the dead spruce budworm specimens found in the samples were diagnosed as diseased (Plate XI), caused mainly by fungal infection as determined by microscope examination (Plate XII). The fungal disease was caused by two species of

TABLE 11

PARASITISM OF SPRUCE BUDWORM LARVAE COLLECTED AND REARED BY HOST SPECIES, PASADENA, 1973 AND 1974*

Parasitoids	Year					
	1973	1974				1973 and 1974
	Host					
	Balsam fir	Balsam fir	Black spruce	White spruce	Total	Grand Total
	No. larvae reared					
	2843	499	160	634	1293	4136
HYMENOPTERA						
Braconidae						
Apanteles fumiferanae Vier.	3.48	8.82	10.00	9.94	9.51	5.37
Apanteles milleri Mason		0.40	0.63	0.95	0.77	0.24
Ascogaster argentifrons Prov.		0.80		0.95	0.77	0.24
Meteorus trachynotus Vier.				0.16	0.08	0.02
Ichneumonidae						
Campoplex sp.	0.04					0.02
Glypta fumiferanae (Vier.)	12.31	12.63	14.38	9.31	11.21	11.97
Sinophorus sp.	0.04					0.02
Chalcididae						
Copidosoma sp.		2.20		0.95	1.31	0.41
Mesopolobus (*Amblymerus*) *verditer* (Nort.)	0.11					0.07

TABLE 11 (CONTINUED)

Parasitoids	Year					
	1973	1974				1973 and 1974
	Host					
	Balsam fir	Balsam fir	Black spruce	White spruce	Total	Grand Total
	No. larvae reared					
	2843	499	160	634	1293	4136
DIPTERA						
Tachinidae						
Actia (*Gymnophthalma*) *iterrupta* Curr.	0.11					0.07
Eumea (*Aplomya*) *caesar* (Aldr.)		0.20			0.08	0.02
Nemorilla pyste (Wlk.)			0.63		0.08	0.02

*Parasitism was calculated as the percentage for each species, obtained as adults, (hyperparasites excluded) from the total number of budworm reared.

TABLE 12

RESULTS OF LABORATORY REARINGS OF FIELD COLLECTED SPRUCE BUDWORM LARVAE

Host sampled	Collection date	No. of larvae reared	Percent			
			Fungal infection	Killed by parasitoids	Missing	Adult emergence
1973						
Balsam fir	June 19	148	1.4	23.7	27.0	48.0
	June 21	617	10.2	11.7	29.5	48.6
	June 25	402	14.9	19.9	15.4	49.8
	July 2	1,150	20.8	14.4	29.8	35.0
	July 5	92	18.5	15.2	20.7	45.7
	July 9	349	31.2	24.4	23.5	20.9
	July 13	35	42.9	20.0	25.7	11.4
	July 17	50	22.0	26.0	22.0	30.0
Sub-total		2,843	18.2	16.6	26.3	39.0
1974						
Balsam fir	June 7	25	0.0	52.0	12.0	36.0
	June 11	60	1.7	28.3	30.0	40.0
	June 18	60	0.0	31.7	16.7	51.7
	June 25	115	12.2	17.4	7.8	62.6
	July 3	91	6.6	33.0	14.3	46.2
	July 10	123	25.2	21.1	1.6	52.0
	July 25	25	44.0	4.0*	24.0	28.0
Sub-total		499	12.6	25.3	12.2	49.9
Black spruce	June 25	30	13.3	30.0	10.0	46.7
	July 3	60	10.0	30.0	0.0	60.0
	July 10	55	20.0	20.0	3.6	56.4
	July 18	15	13.3	26.7	46.7	13.3
Sub-total		160	14.4	26.3	7.5	51.9

TABLE 12 (CONTINUED)

Host sampled	Collection date	No. of larvae reared	Percent			
			Fungal infection	Killed by parasitoids	Missing	Adult emergence
1974 (Continued)						
White spruce	June 18	240	6.3	30.4	9.2	54.2
	June 24	274	15.0	16.4	1.8	66.8
	July 3	95	21.1	22.1	0.0	56.8
	July 10	25	16.0	32.0	12.0	40.0
Sub-total		634	12.6	23.2	4.7	59.5
Total for 1974		1,293	13.2	24.9	8.2	53.8
Grand Total 1973 and 1974		4,136	16.5	19.0	20.6	43.9

*Most of the larval parasitoids already emerged in the field prior to collection.

PLATE X.

Glypta larva emerging from its spruce budworm host.

PLATE XI.

Cadaver of a spruce budworm larva infected with *Entomophthora* sp.

PLATE XII.

a) and b) Spruce budworm larvae showing different stages of sporulation of *Entomophthora* sp. (note the halo-like effect around the larvae made by ejected conidia).

c) Conidia of *E. egressa* in various stages of germination (note the pear shape conidia, characteristic of this species) (x 400).

a

b

c

Entomophthora, *E. sphaerosperma* Fres. and the new species identified as *E. egressa* MacLeod and Tyrrell. The two species could be separated with certainty only if the conidial spores (Plate XIIc) of the fungi were present. If only resting spores or mycelial growth were found in the dead insect, it was listed as being infected with *Entomophthora* spp. The percent diseased figures given here refer to the combined infection by the two species of *Entomophthora* because in most cases the distinction between the two was not possible. In 1973, 18.2% of the reared larvae and pupae collected from balsam fir were diseased, and in 1974, 12.6% from balsam fir, 14.4% from black spruce and 12.6% from white spruce were diseased (Table 12, p. 78). It is interesting to note that spruce budworm from balsam fir and white spruce had essentially similar mortality due to disease, but that larvae on black spruce had somewhat higher mortality.

DISCUSSION

Spruce budworm development in Newfoundland was 2 to 3 weeks behind development of this insect species in the eastern regions of mainland Canada. This is caused by the later spring and less favorable climatic conditions for insect growth on the Island.

In Newfoundland, the egg masses were almost invariably on the under side of balsam fir needles, while on the spruce species the masses occurred on either the 'upper' or 'lower' sides of the needles. This is similar to the results of Blais (1952), who found more eggs on the ventral surfaces of balsam fir needles. McGugan (1954), however, reported that egg clusters occurred on either side of the needles on balsam fir.

The average number of eggs per mass was 21 at the study area. However, this should not be taken as an indication of the number of eggs per mass for the whole island of Newfoundland, because there is a remarkable variation in the number of eggs per mass. Bakuzis and Hansen (1965) reported that the average number of eggs per mass for the spruce budworm was 20, but with a range from 10 to 100 eggs. McGugan (1954) also gave the average number of eggs per mass as 20, for northwestern Ontario, with a range from 1 to 60 eggs. Miller (1963d), working in New Brunswick, found an average of 20 eggs per mass with considerable variation. Many factors influence fecundity and these will be considered later.

The number of rows of eggs per mass in Newfoundland was similar

to that found by Leonard *et al.*,(1973) in Maine. In Newfoundland, 54% of the masses had two rows of eggs versus 49% in Maine, 20% had two rows plus a partial third versus 13%, and 26% had three rows versus 38%. The significance of the different numbers of rows of eggs among the egg masses is unknown.

The eggs in Newfoundland hatched in approximately two weeks. This is somewhat longer than that reported by McGugan (1954). He found that budworm eclosion varied from 8 to 12 days with an average of 10 days.

There are six larval instars in Newfoundland. The head capsule widths of the instars measured in this study are in agreement with those presented by McGugan (1954) as given in Table 3 (p. 39). The differences in the head capsule widths between the sexes for the fifth- and sixth-instar larvae found in Newfoundland agree with those reported by McGugan (1954) from northwestern Ontario. In addition, McGugan (1954) also reported significant differences in the head capsule width between male and female fourth-instar larvae. No such differences were detected in Newfoundland. However, no attempt was made to distinguish between parasitized and non-parasitized larvae during the present study and this may account for the different result from that of McGugan. In a later paper, McGugan (1955) reported that the sexing technique, based only on the external evidence of male gonads, was invalidated by parasitoids which inhibit gonadal as well as general development. McGugan (1954, 1955) found that the head capsule widths of parasitized larvae were smaller than average, and were near the lower end of the range, especially for fourth- and

fifth-instar larvae which have a greater head width range. This influence of parasitoids, as well as other factors such as disease and nutrition of the larvae, could explain some of the overlap of the ranges between the instars (Fig. 6, p. 34).

The first-instar larvae molt in the hibernacula and overwinter there as second-instar larvae (Atwood, 1944; McGugan, 1954).

The emergence of second-instar larvae at Pasadena in 1974 started on May 31, when the first larvae were seen, and the maximum daily temperature was 12°C. But it was not until June 3, three days later, that larvae were observed in large numbers hanging by silk threads, when the maximum daily temperature was 22°C. Maximum daily temperatures prior to June 3 were in the 4 to 7°C range. This seems to support the findings of Rose and Blais (1954) who reported that in northwestern Ontario, abundant larval emergence occurred after temperatures approached or exceeded 15.6°C. McGugan (1954) suggested that the beginning of larval emergence might vary as much as four weeks depending upon weather conditions. This would explain why Miller (1963d) found that in New Brunswick the emergence of larvae from the hibernacula often occurred in early May, or up to 4 weeks prior to that in Newfoundland.

It was observed that first- and second-instar larvae were initially positively phototropic. Wellington (1948) described all larval stages as positively phototropic and noted that the first- and second-instar larvae kept this orientation at room temperatures.

Larvae which emerged early from the hibernacula invariably mined needles. However, it was not determined during this study whether

or not all larvae engaged in needle mining before starting to feed on the vegetative buds. McGugan (1954) found that most budworm larvae mined only one needle on balsam fir, but 2 to 6 needles on the spruce trees before feeding on the buds. Some of the larvae did not mine needles at all, and a few mined more than one needle.

At Pasadena, branches with staminate flowers, particularly from balsam fir, had more larvae than non-flowering branches. This suggested that staminate flowers were an excellent source of food for the young larvae. This was confirmed because larvae found on the flowers were larger and in the next instar compared with larvae occurring elsewhere on the same branch or on non-flowering branches. Similar results were reported by Bess (1946) and Blais and Thorsteinson (1948). Jaynes and Speers (1949) observed, in laboratory experiments, that pollen-fed larvae matured three weeks earlier than foliage-fed larvae. Greenbank (1963b) showed that larvae, given a choice, settled on foliage containing staminate flowers more often than on non-flowering foliage, and that more larvae were found on branches with greater concentrations of flowers than on branches with only a few flowers. Greenbank (1963b) also found that in development, larvae which fed on staminate flowers in the field were three to seven days ahead of the non-flower feeders. Blais (1952) found that only fifth- and sixth-instar larvae could develop on old foliage, but with a reduction in the size of the pupae and the fecundity of the adults.

The increase in the number of specimens in the drop trays for the period from June 14 to July 2 in both years was believed to be a direct result of the progressive increase in larval size and exposure

(Fig. 7, p. 58). Larvae were larger and fed more in the open on each successive sample date, and consequently were more easily disturbed by wind, rain, and other larvae coming in contact with them. The larger number obtained on June 4, 1974 is thought to be due to the initial dispersal of emerging larvae. The number decreased on the next collection date as the larvae became established within the needles and were less likely to be dislodged. The loss of larvae, particularly in the last three instars, from the trees does not necessarily indicate mortality, since many larvae have been observed to crawl up the tree trunks.

The duration of the pupal stage at Pasadena was about 14 days against the 8 to 12 days reported by Miller (1963c) from New Brunswick. It is suggested that this difference is probably due to the less continental climate of Newfoundland.

Spruce budworm pupae were found on such non-host trees as larch during this study in Newfoundland. Miller (1963d) also reported finding budworm pupae on non-host trees in New Brunswick.

The first adults to emerge from the pupae were males; females emerged several days later. The sex ratio of the adults at Pasadena was approximately 1:1, similar to that reported from New Brunswick (Miller, 1963c). The flight activity of the moths lasted about three weeks at Pasadena, from the last week in July to the middle of August, in 1974. Swaine *et al.*, (1924) reported a similar duration of the flight activity of the moths. Dispersal of the adults is dependent upon wind, and large numbers of moths in flight have been reported. One such report was made by an Eastern Provincial Airways pilot who

flew through a large cloud of moths, believed to be spruce budworm, at 15,000 feet over central Newfoundland. To date no such report has been verified in Newfoundland. However, studies by Greenbank (1973) in New Brunswick showed that spruce budworm are commonly found at altitudes of 1,500 to 3,000 feet and might be carried higher by convective storm up-drafts.

The unsuccessful adult emergence from the pupae set aside for individual mating in 1973 may have resulted from the storage of these pupae at 5°C to permit the synchronization of the emergence. The storage of the pupae at this low temperature for about 1 week may have interfered with the transformation process within the pupae causing low adult emergence. Decreased adult emergence from pupae in the laboratory has also been noted by others (Miller, 1963c).

The average number of eggs laid by individual females, collected as pupae from the three host tree species, was as follows: 85 for balsam fir, 117 for black spruce and 33 for white spruce. These are considerably lower than the 200 eggs per female reported by Miller (1963c). The reason for the lower number of eggs laid by females at Pasadena is probably the amount and type of foliage consumed by the larvae and the effects of these on fecundity. Black spruce had the smallest number of larvae of the three host species and consequently sufficient new growth was present on the branches for the developing larvae in comparison with white spruce or balsam fir where larvae were often forced to feed on older needles. The difference between white spruce and balsam fir could possibly have resulted from the limited number of pupae from white spruce from which adults emerged that could be used

in the experiment. These results on fecundity are in agreement with those reported by Miller (1957, 1963b) and Blais (1952, 1953). Miller (1957, 1963b) showed that food quality was one of the important factors affecting fecundity, and Blais (1952, 1953) found that fecundity decreased when larvae were fed on old foliage. Greenbank (1963a), on the other hand, reported that fecundity was not affected by the type of host species.

The average number of eggs and the number of egg masses per female in 1974 were twice the numbers of those laid in 1973, on small, caged balsam fir trees in the field. In both years the pupae were collected from balsam fir at the study site, and the experiment was conducted the same way. Unfortunately, it was not determined in either year whether all the females laid their complete egg complement. However, there was a difference in female pupal weights between the two years. The average pupal weight was 0.05 gm in 1973 and 0.07 gm in 1974 suggesting that the greater number of eggs laid in 1974 was probably due to the higher fecundity of the heavier females.

The results of the study on host selection during egg laying by spruce budworm females agree with the findings of Swaine *et al.*, (1924) and Jaynes and Carolin (1952) who reported that balsam fir and white spruce were the preferred hosts for oviposition. Greenbank (1963a) and Miller (1963b) found no significant difference in oviposition on balsam fir and white spruce, and Greenbank (1963a) found that both were preferred to black spruce. The results reported above may explain the difference in preferred hosts at Pasadena in 1973 and 1974, when white spruce and balsam fir had the most eggs, respectively.

Jaynes and Speers (1949) and Wilson (1963) found that white spruce was preferred to balsam fir for oviposition, but this was not indicated in the present study at Pasadena.

Peak larval numbers on white spruce and balsam fir were approximately three and four times, respectively, the number on black spruce. The decrease in larval numbers on balsam fir and white spruce was more pronounced over the development period of the insect than on black spruce. This decrease might have been a result of the increased contact between larvae, the exhaustion of the food supply, a difference in the phenology of the host trees or a more intense predation on balsam fir and white spruce where larval density was greater. The peak in larval numbers on white spruce occurred between the second and third week in July, which is believed to be the result of larvae moving from severely defoliated balsam fir trees nearby to the white spruce trees. The peak in the number of larvae on balsam fir in early June was the result of larvae emerging from the hibernacula. The sharper decline of larval numbers on white spruce can be explained by the shorter developmental period of larvae on white spruce compared with those on balsam fir. Larval development on black spruce was slightly behind that on either white spruce or balsam fir, because black spruce is the slowest in development in the spring of the three species. Data in Table 5 (p.47) indicate that white spruce provides the maximum new growth for the larvae, followed closely by balsam fir and then black spruce. The development on black spruce was about one week behind that on the other two species. Blais (1957) found that development of larvae was slower and the mortality higher for budworm

larvae reared on black spruce than of those on white spruce or balsam fir.

One species of ant, *Formica fusca*, was observed to carry budworm larvae as 'booty'. These ants were described by Wheeler and Wheeler (1963) as scavengers, and predators of insects in particular.

Although *Dioryctria reniculloides* was not directly observed to prey on the budworm, they were present in large numbers on the spruce trees and are suspected of preying on the budworm, causing the 5% mortality attributed to invertebrate predators. Both Thomson (1957) and Warren (1954) suggested that *Dioryctria reniculella*, a species closely related to the one found in Newfoundland, may be important as a predator of the budworm. Thomson (1957) found that 5.8% of budworm pupae were preyed on by *D. reniculella*. This figure is comparable with the 5% predation found in the present study.

Unpublished data supplied by Dr. Otvos, Canadian Forestry Service, suggest that birds are important as control agents. Eight species of birds (Appendix D) were obtained throughout July, 1974 at Pasadena and their stomach contents examined. The following six species fed on the spruce budworm: *Dendroica coronata* (Linnaeus), *Dendrocopos villosus* (Linnaeus), *Zonotrichia albicollis* (Gmelin), *Seiurus noveboracensis* (Gmelin), *Catharus guttata* (Pallas), and *Pinicola enucleator* (Linnaeus). Spruce budworm larvae and/or pupae made up 100%, 100%, 49%, 38%, 17%, and 17% of the diet of these birds, respectively. Tothill (1923) estimated that 13% of spruce budworm mortality in New Brunswick in 1918 was due to avian predators. Kendeigh (1947) reported that birds consumed about 4% of all budworm

larvae in his study in Ontario. A similar figure, 3 to 7%, was obtained by George and Mitchell (1948) at Lake Clear, New York in 1946. Mitchell (1952) and Dowden *et al.*, (1953), both working in Maine, reported that budworm larvae comprised 20 to 40% of the diet of avian predators. In Newfoundland, spruce budworm comprised an average of 25% of the diet of birds examined. Gage (1968) reported that in New Brunswick, 58% of all birds collected in a low budworm density area, 78% in a medium density area, and 98% in a high budworm density area contained spruce budworm remains. The budworm population at Pasadena, Newfoundland was considered to be moderately high, and 56% of the birds collected contained budworm remains.

The parasitoid complex in Newfoundland is considerably smaller than that reported by McGugan and Blais (1959) who have listed some 75 parasitoid species, or Reeks and Forbes (1950) who listed 21 species attacking the budworm. Only 13 primary parasitoid species were reared at Pasadena during 1973 and 1974. The lack of alternate hosts is believed to be the most important reason for this relatively low number of species at Pasadena.

Apanteles and *Glypta* were the most important genera in Newfoundland during this study and this agrees with results from other regions of Canada (McGugan and Blais, 1959; Reeks and Forbes, 1950). Lewis (1960) reported that only one specimen of one of these species could survive in a single host larva if it is attacked by both parasitoids.

The higher incidence of disease in the spruce budworm population in 1973 compared with 1974 was probably a result of climatic conditions.

In 1973, there was greater rainfall than in 1974 (Table 4, p.41), which provided more favorable conditions for fungal development. It is also possible that wet weather would make the spruce budworm more susceptible to fungal infection. It was observed that the larvae did not readily feed when the feeding shelters were wet. If wet weather continues for some time, the reduced feeding would probably affect the resistance of the budworm to disease. The combined mortality of spruce budworm due to disease for both years was 16.5%. Neilson (1963) reported that disease in general accounted for from 10 to 35% of the larval mortality; the variance was believed to be due to food quality, weather, microclimate, stage of development, year, and plot. Harvey and Burke (1974) found that *Entomophthora sphaerosperma*, one of the two species found in Newfoundland, caused significantly higher mortality (30.6%) of spruce budworm on white spruce than on balsam fir (1.8%). They also reported finding little or no interference between the fungus and parasitoids.

Of the natural control factors affecting the spruce budworm population in Newfoundland, birds appear to offer the greatest potential for control, 56% of those examined fed on the budworm. Disease, mainly fungal infection, accounted for 17% mortality over the two years, and potentially could decrease the budworm population substantially, but requires optimum climatic conditions (warm, wet weather). Parasitoids accounted for 19% mortality over the two years and showed an increase in 1974, suggesting that this control could build up and contribute more towards budworm mortality. Essentially, none of the above control agents can effectively control the budworm alone, but the combined effect is significant.

SUMMARY

The spruce budworm is a univoltine species in Newfoundland with six larval instars. The seasonal occurrence is dependent upon climatic conditions for the commencement of larval activity in the spring and weather conditions during the various life stages.

Second-instar larvae become active in the spring from mid- to late May, depending on air temperatures. The first evidence of activity of the larvae in the spring is needle mining, which occurs on all three host tree species.

Later, larvae feed within and around the shelters they construct from new shoots and webbing. Larvae, which have consumed the existing foliage in and around their shelters, seek food nearby on other branches or other trees. When larval density is high and food is limited, back-feeding (the consumption of older needles) may occur.

Based on 18-inch branch samples, there were 3 times as many larvae on white spruce as on black spruce, and 4 times as many on balsam fir as on black spruce. Larval development was the shortest on white spruce and the longest on black spruce.

The average duration of the larval stages was estimated as 14 days for Instar I, 280 days for Instar II (overwintering stage), 8 days for Instar III, 9 days for Instar IV, 7 days for Instar V, and 16 days for Instar VI. Variation from these is dependent upon climatic conditions and host tree species.

The prepupal stage lasts about six days, and the pupal stage

about two weeks.

The adults are present from late July to mid-August. The first emerging adults are males, females emerging several days later. The sex ratio was found to be approximately 1:1. The life span of an adult is about 14 days in the field, females living longer than males. Females in the laboratory oviposited within 2 to 3 days after emerging, and egg laying lasted for 4 days.

Ovipositing females showed a preferenee for white spruce and balsam fir over black spruce in the laboratory.

Individual females laid an average of 96 eggs in 6 masses (16 eggs per mass) in laboratory experiments. Egg masses from the field had an average of 21 eggs.

The pale green egg masses are present in the field from late July to mid-August. The eggs in the field hatched in about two weeks from the time they were laid. Hatching success was high, about 99%.

Weather did not contribute greatly to mortality of the budworm during this study, but the influence of winter weather on the over-wintering larvae was not investigated. High humidity and above average rainfall favored the development of fungi.

Less than 5% of the budworm specimens collected showed any sign of invertebrate predation. Ants, *Formica fusca*, were seen to prey on smaller budworm larvae. Among the vertebrate predators, several species of birds were observed feeding in budworm infested trees in the study area.

Twelve species of parasitoids were reared from budworm larvae. The total larval mortality caused by all parasitoid species was about

16% in 1973 and 25% in 1974. Two species, *Apanteles fumiferanae* and *Glypta fumiferanae*, caused most of the mortality attributed to parasitoids, the other species accounted for less than 2% of the mortality. Only one species of pupal parasitoid, *Apechthis ontario*, was reared during the study, and it killed less than 1% of the total pupae reared.

Two species of fungi, *Entomophthora sphaerosperma* and *E. egressa*, caused 18% mortality among larvae and pupae in 1973 and only 13% during the drier year in 1974.

REFERENCES

Atwood, C. E. 1944. The feeding habits of the young spruce budworm larvae. Can. Entomol. 76: 64-66.

Baird, A. B. 1947. Biological control of the spruce budworm in eastern Canada by parasite introduction. Can. Dep. Agric. For. Insect Invest. Bi-Mon. Progr. Rep. 3(2): 1.

Bakuzis, E. V. and H. L. Hansen. 1965. Spruce budworm. In Balsam fir (*Abies balsamea* (L.) Mill.): A monographic review. University of Minnesota Press, Minneapolis. pp. 152-169.

Bean, J. L. 1961. Predicting emergence of second-instar spruce budworm larvae from hibernation under field conditions in Minnesota. Ann. Entomol. Soc. Am. 54: 175-177.

Bean, J. L. and W. E. Waters. 1961. Spruce budworm in the eastern United States. U.S. For. Serv. For. Pest Leafl. 58. 8pp.

Bess, H. A. 1946. Staminate flowers and spruce budworm abundance. Can. Dep. Agric. For. Insect Invest. Bi-Mon. 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: 1029.

Blais, J. R. 1953. Effects of the destruction of the current year's foliage of balsam fir on the fecundity and habits of flight of the spruce budworm. Can. Entomol. 85: 446-448.

Blais, J. R. 1957. Some relationships of the spruce budworm, *Choristoneura fumiferana* (Clem.), to black spruce, *Picea mariana* (Moench.) Voss. For. Chron. 33: 364-372.

Blais, J. R. 1960. Spruce budworm parasite investigations in the Lower St. Lawrence and Gaspe regions of Quebec. Can. Entomol. 92: 384-396.

Blais, J. R. 1965. Parasite studies in two residual spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks in Quebec. Can. Entomol. 97: 129-136.

Blais, J. R. and A. J. Thorsteinson. 1948. The spruce budworm in relation to flowering conditions of the host tree. Can. Dep. Agric. For. Insect Invest. Bi-Mon. Progr. Rep. 4(5): 1.

Campbell, I. M. 1953. Morphological differences between the pupae and egg clusters of *Choristoneura fumiferana* (Clem.) and *C. pinus* Free. (Lepidoptera: Tortricidae). Can. Entomol. 85: 134-135.

Clark, R. C. 1972. The spruce budworm in Newfoundland, 1972. A report presented at a meeting of the Nfld. Forest Research Committee, St. John's, Oct. 31, 1972. 18pp.

Clarke, L. J., E. C. Banfield, W. J. Sutton, D. M. Stone, D. S. O'Brien, K. E. Pardy, and G. C. Carew. 1974. Annual district report of the Forest Insect and Disease Survey in Newfoundland, 1973. Can. For. Serv. Nfld. For. Res. Cent. Infor. Rep. N-X-112. 39pp.

Coughlin, J. 1968. The spruce budworm in Maine, 1967. Maine For. Dep. Entomol. Div. 46pp.

Dowden, P. B., H. A. Jaynes, and V. M. Carolin. 1953. The role of birds in a spruce budworm outbreak in Maine. J. Econ. Entomol. 46: 307-312.

Dyar, H. G. 1890. The number of molts of lepidopterous larvae. Psyche 5: 420-422.

Freeman, T. N. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. I. Some new forms of *Choristoneura* allied to *C. fumiferana*. Can. Entomol. 99: 449-455.

Gage, S. H. 1968. Consumption by adult birds of the spruce budworm at different larval densities. Can. Dep. Fish. For. For. Res. Lab., Maritimes Region, Fredericton, N.B. Internal Rep. M-36. 5pp.

George, J. L. and R. T. Mitchell. 1948. Calculations on the extent of spruce budworm control by insectivorous birds. J. For. 46: 454-455.

Greenbank, D. O. 1963a. Host species and the spruce budworm. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 219-223.

Greenbank, D. O. 1963b. Staminate flowers and the spruce budworm. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 202-218.

Greenbank, D. O. 1963c. The development of the outbreak. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 19-23.

Greenbank, D. O. 1973. The dispersal process of spruce budworm moths. Can. For. Serv., Maritimes For. Res. Cent., Fredericton, N.B. Infor. Rep. M-X-39. 25pp.

Grisdale, D. G. 1970. An improved laboratory method for rearing large numbers of spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 102: 1111-1117.

Harvey, G. T. and J. M. Burke. 1974. Mortality of spruce budworm on white spruce caused by *Entomophthora sphaerosperma* Fresenius. Can. For. Serv. Bi-Mon. Res. Notes 30: 23-24.

Henson, W. R. 1951. Mass flights of the spruce budworm. Can. Entomol. 83: 240.

Heron, R. J. 1965. The role of chemotactic stimuli in the feeding behavior of the spruce budworm larvae on white spruce. Can. J. Zool. 43: 247-269.

Jaynes, H. A. and V. M. Carolin. 1952. Spruce budworm (*Choristoneura fumiferana*). In Important tree pests of the Northeast. Soc. Am. For. New Engl. Sect. pp. 51-54.

Jaynes, H. A. and A. T. Drooz. 1952. The importance of parasites in the spruce budworm infestations in New York and Maine. J. Econ. Entomol. 45: 1057-1061.

Jaynes, H. A. and C. F. Speers. 1949. Biological and ecological studies of the spruce budworm. J. Econ. Entomol. 42: 221-225.

Kendeigh, S. C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Ont. Dep. Lds. For. Biol. Bull. Div. Res. 1. 100pp.

Leonard, D. E., G. A. Simmons, and G. K. VanDerwerker. 1973. Spruce budworm: techniques to improve counting of eggs. J. Econ. Entomol. 66: 992.

Lewis, F. B. 1960. Factors affecting assessment of parasitization by *Apanteles fumiferanae* Vier. and *Glypta fumiferanae* (Vier.) on spruce budworm larvae. Can. Entomol. 92: 881-891.

Loughton, B. G., C. Derry, and A. S. West. 1963. Spiders and the spruce budworm. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 249-268.

McGugan, B. M. 1954. Needle mining habits and larval instars of the spruce budworm. Can. Entomol. 86: 439-454.

McGugan, B. M. 1955. Certain host-parasite relationships involving the spruce budworm. Can. Entomol. 87: 178-187.

McGugan, B. M. and J. R. Blais. 1959. Spruce budworm parasite studies in northwestern Ontario. Can. Entomol. 91: 758-783.

McKnight, M. E. 1968. A literature review of the spruce budworm, western, and two-year-cycle budworms, *Choristoneura fumiferana*, *C. occidentalis*, and *C. biennis*. U.S.D.A. For. Serv. Res. Pap. RM-44. 35pp.

Meyer, A. B. and F. H. Eyre (eds.). 1958. Forest Terminology Soc. Amer. For., Washington, D.C. 97pp.

Miller, C. A. 1953. Parasitism of spruce budworm eggs by *Trichogramma minutum* Riley. Can. Dept. Agric. Div. For. Biol. Bi-Mon. Progr. Rep. 9(4): 1.

Miller, C. A. 1957. A technique for estimating the fecundity of natural populations of the spruce budworm. Can. J. Zool. 35: 1-13.

Miller, C. A. 1958. The measurement of spruce budworm populations and mortality during the first and second larval instars. Can. J. Zool. 36: 409-422.

Miller, C. A. 1963a. Parasites and the spruce budworm. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 228-244.

Miller, C. A. 1963b. The analysis of the fecundity proportion in the unsprayed area. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 75-87.

Miller, C. A. 1963c. The analysis of pupal survival in the unsprayed area. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 63-70.

Miller, C. A. 1963d. The spruce budworm. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 12-19.

Mitchell, R. T. 1952. Consumption of spruce budworms by birds in Maine spruce-fir forests. J. For. 50: 387-389.

Mook, L. J. 1963. Birds and the spruce budworm. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31 pp. 268-271.

Morris, R. F. (ed.). 1963. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. 332pp.

Morris, R. F. and D. G. Mott. 1963. Dispersal and the spruce budworm. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 180-189.

Mott, D. B. 1963. The analysis of the survival of small larvae in the unsprayed area. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 42-52.

Neilson, M. M. 1963. Disease and the spruce budworm. In R. F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. pp. 272-287.

Otvos, I. S., D. M. MacLeod, and D. Tyrrell. 1973. Two species of *Entomophthora* pathogenic to the eastern hemlock looper (Lepidoptera: Geometridae) in Newfoundland. Can. Entomol. 105: 1435-1441.

Prebble, M. L. and V. M. Carolin. 1967. Spruce budworm, *Choristoneura fumiferana* (Clem.). In A. G. Davidson and R. M. Prentice, eds., Important forest insects and diseases of mutual concern to Canada, the United States, and Mexico. Dep. For. Rural Dev., Ottawa. pp. 75-80.

Reeks, W. A. and R. S. Forbes. 1950. Native parasites of the spruce budworm in the Maritime Provinces. Can. Dep. Agric. For. Insect Invest. Bi-Mon. Progr. Rep. 6(5): 1.

Renault, T. R. and C. A. Miller. 1972. Spiders in a fir-spruce biotype: abundance, diversity, and influence on spruce budworm densities. Can. J. Zool. 50: 1039-1046.

Rose, A. H. and J. R. Blais. 1954. A relation between April and May temperatures and spruce budworm larval emergence. Can. Entomol. 86: 174-177.

Sanders, C. J. 1967. Low fecundity of the spruce budworm attributed to unusually high temperatures during immature stages. Can. Dep. For. Bi-Mon. Res. Notes 23: 19.

Shaw, G. G. and C. H. A. Little. 1973. Dispersal of second-instar spruce budworm. Can. For. Serv. Bi-Mon. Res. Notes 29: 30-31.

Sippell, W. L. 1969. Report on monitoring low or incipient levels of spruce budworm populations in eastern Canada. Can. Fish For. For. Br., Ontario Region, Sault Ste. Marie, Ont. March, 1969. (Mimeographed report). 4pp.

Stairs, G. R. 1960. On the embryology of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Can. Entomol. 92: 147-154.

Swaine, J. M., F. C. Craighead, and J. W. Bailey. 1924. Studies on spruce budworm (*Cacoecia fumiferana* Clem.). Can. Dep. Agric. Bull. 37. 91pp.

Thomas, H. A. 1966. Parasitism by *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) in the spruce budworm outbreak in Maine. Ann. Entomol. Soc. Am. 59: 723-725.

Thomson, H. M. 1957. A note on the predation of spruce budworm pupae. Can. Dep. Agric. Div. For. Biol. Bi-Mon. Progr. Rep. 13(4): 2.

Thomson, H. M. 1958. The effect of a microsporidian parasite on the development, reproduction, and mortality of the spruce budworm, *Choristoneura fumiferana* (Clem.). Can. J. Zool. 36: 499-511.

Tothill, J. D. 1923. Notes on the outbreaks of spruce budworm, forest tent caterpillar, and larch sawfly in New Brunswick. Proc. Acadian Entomol. Soc. (1922) 8: 172-182.

Warren, G. L. 1954. The spruce needle worm, *Dioryctria reniculella* Grt., as a predator of spruce budworm. Can. Dep. Agric. Div. For. Biol. Bi-Mon. Progr. Rep. 10(3): 2-3.

Wellington, W. G. 1948. The light reactions of the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae). Can. Entomol. 80: 56-83.

Wheeler, G. C. and J. Wheeler. 1963. The Ants of North Dakota. University of North Dakota Press, Grand Forks. pp. 264-267.

Wilson, L. F. 1959. Branch 'tip' sampling for determining abundance of spruce budworm egg masses. J. Econ. Entomol. 52: 618-621.

Wilson, L. F. 1963. Host preference for oviposition by the spruce budworm in the Lake States. J. Econ. Entomol. 56: 285-288.

APPENDICES

APPENDIX A

AVERAGE NUMBER OF SPRUCE BUDWORM LARVAE COLLECTED BY TWO TYPES OF BEATING METHODS FROM BALSAM FIR, PASADENA, 1973.

3 ft x 3 ft x 3 ft beating method[a] [27 cu ft sampled (=0.75 m^3)]									
Sample date		Larvae		Pupae		Empty pupal cases	Live total	Dead total	Grand total
		Live	Dead	Live	Dead				
June 14	$\bar{X}$	37.85					37.85		37.85
	S.D.	22.50					22.50		22.50
June 19	$\bar{X}$	51.20					51.20		51.20
	S.D.	21.15					21.15		21.15
June 21	$\bar{X}$	79.65					79.65		79.65
	S.D.	21.43					21.43		21.43
June 30[b]	$\bar{X}$	104.25					104.25		104.25
	S.D.	77.71					77.71		77.71
July 2	$\bar{X}$	69.50					69.50		69.50
	S.D.	34.05					34.05		34.05
July 10	$\bar{X}$	15.10	6.00	10.70	0.25		25.80	6.25	32.05
	S.D.	6.54	2.73	5.71	0.55		7.72	2.63	8.98

APPENDIX A (continued)

7 ft x 9 ft beating method[c] [630 cu ft sampled (=17.8m^3)]									
Sample date		Larvae		Pupae		Empty pupal cases	Live total	Dead total	Grand total
		Live	Dead	Live	Dead				
June 14	$\bar{X}$	319.00					319.00		319.00
	S.D.	234.96					234.96		234.96
July 9	$\bar{X}$	116.33	13.67	35.33			151.67	13.67	165.33
	S.D.	30.37	7.51	17.79			46.00	7.51	38.50
July 13	$\bar{X}$	11.67	14.67	85.67	17.33	3.00	100.33	32.00	132.33
	S.D.	3.51	1.53	36.75	1.16	3.00	39.63	1.00	38.80
July 17	$\bar{X}$	2.00	9.33	37.33	7.00	6.33	45.67	16.33	62.00
	S.D.	2.00	5.13	17.16	2.00	4.93	22.03	3.21	19.00
July 21	$\bar{X}$	1.67	16.33	25.00	3.00	25.67	52.33	19.33	71.67
	S.D.	1.53	26.58	15.00	1.00	20.31	34.96	25.70	26.16
July 27	$\bar{X}$	0	15.00	1.33	0.33	15.00	16.33	15.33	31.67
	S.D.	0	10.00	1.15	0.58	9.54	10.12	10.50	20.11

[a]N = 10 trees, 2 sides sampled per sample date

[b] Only 2 trees sampled

[c]N = 3 trees, 1 side sampled

APPENDIX B

AVERAGE NUMBER OF SPRUCE BUDWORM (± S.D.) PER THE THREE TYPES OF SAMPLE UNITS BASED ON THE NUMBERS COLLECTED FROM 18-INCH (45.7 cm) BRANCH SAMPLES FROM BALSAM FIR BY COLLECTION DATES, PASADENA, 1973

Sample dates		Live larvae			Dead larvae		Live pupae		Dead pupae		Empty pupal cases		Live total		Dead total		Grand total	
		18" tip[a]	10 sq. ft.[b]	Feeding site[c]	18"	10 sq. ft.	18"	10 sq. ft.	18"	10 sq. ft.	18"	10 sq. ft.	18"	10 sq. ft.	18"	10 sq. ft.	18"	10 sq. ft.
May 31	$\bar{X}$	47.50	508.50	1.74	5.80	56.30							47.50	508.50	5.80	56.30	53.30	564.80
	S.D.	26.03	317.31	3.75	7.21	79.02							26.03	317.31	7.21	79.02	25.97	313.99
June 4	$\bar{X}$	28.60	432.40	0.40	0.80	11.20							28.60	432.40	0.80	11.20	29.40	443.60
	S.D.	16.96	306.20	0.57	1.23	15.88							16.96	306.20	1.23	15.88	17.46	309.58
June 7	$\bar{X}$	33.70	365.50	0.50	2.80	28.00							33.70	365.50	2.80	28.00	36.50	393.50
	S.D.	21.69	205.53	0.27	2.25	24.55							21.69	205.53	2.25	24.55	21.36	198.60
June 11	$\bar{X}$	36.10	628.10	0.54	8.80	141.00							36.10	628.10	8.80	141.00	44.90	769.10
	S.D.	13.98	553.22	0.27	3.88	109.27							13.98	553.22	3.88	109.27	15.99	656.24
June 25	$\bar{X}$	41.00	547.10	0.58	3.50	43.10							41.00	547.10	3.50	43.10	44.50	590.20
	S.D.	24.16	592.66	0.24	2.88	46.66							24.16	592.66	2.88	46.66	25.95	636.37
July 5	$\bar{X}$	11.00	134.80	0.13	3.10	38.10	1.20	14.40	0.30	3.90			12.20	149.20	3.40	42.00	15.60	191.20
	S.D.	10.21	126.60	0.10	2.60	39.97	1.40	19.77	0.48	6.35			10.15	127.60	3.03	45.57	11.53	152.36

[a]N = 10 tips. [b]Converted from actual foliage area of the ten, 18-inch branches. [c]Based on the actual number of feeding sites (buds + shoots + staminated flowers) found on the ten, 18-inch branches.

APPENDIX C

AVERAGE NUMBER OF SPRUCE BUDWORM PER THE THREE TYPES OF SAMPLE UNITS BASED ON THE NUMBERS COLLECTED FROM 18-INCH BRANCH SAMPLES FROM THE THREE HOST TREE SPECIES BY COLLECTION DATES, PASADENA, 1974

Collection date		Live larvae			Dead larvae			Live pupae		Dead pupae		Empty pupal cases		Total live		Total dead		Grand total	
		18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.
BALSAM FIR[a]																			
May 28	$\bar{X}$	15.67	154.67	0.230										15.67	154.67			15.67	154.67
	S.D.	2.89	31.90	0.020										2.89	31.90			2.89	31.90
June 3	$\bar{X}$	18.00	301.70	0.337										18.00	301.70			18.00	301.70
	S.D.	11.77	261.23	0.254										11.77	261.23			11.77	261.23
June 7	$\bar{X}$	72.00	777.60	1.217										72.00	777.60			72.00	777.60
	S.D.	46.46	551.78	1.638										46.46	551.78			46.46	551.78
June 11	$\bar{X}$	41.20	521.80	0.697										41.20	521.80			41.20	521.80
	S.D.	21.22	253.57	0.412										21.22	253.57			21.22	253.57
June 18	$\bar{X}$	39.50	497.00	0.687	1.00	16.50	0.012							39.50	497.00	1.00	16.50	40.50	513.50
	S.D.	16.52	303.63	0.403	0.81	21.11	0.010							16.52	303.63	0.81	21.11	16.68	322.30
June 25	$\bar{X}$	23.80	228.70	0.375	1.90	18.90	0.023							23.80	228.70	1.90	18.90	25.70	247.60
	S.D.	16.30	150.39	0.154	1.97	17.01	0.020							16.30	150.39	1.97	17.01	18.01	165.58
July 3	$\bar{X}$	19.30	326.30	0.327	0.90	19.50	0.012							19.30	326.30	0.90	19.50	20.20	345.80
	S.D.	14.13	305.28	0.175	0.88	25.17	0.010							14.13	305.28	0.88	25.17	14.17	329.34
July 11	$\bar{X}$	17.60	180.80	0.584	0.30	3.40	0.010	0.10	0.80					17.70	181.60	0.30	3.40	18.00	185.00
	S.D.	20.24	174.43	0.981	0.48	5.99	0.010	0.32	2.53					20.24	174.26	0.48	5.99	20.56	178.62
July 18	$\bar{X}$	2.40	24.70	0.041	0.50	4.30	0.010	7.60	84.70	0.10	0.90	0.10	0.80	10.10	110.20	0.60	5.20	10.70	115.40
	S.D.	1.90	17.56	0.031	0.71	5.77	0.020	10.61	126.83	0.32	2.85	0.32	2.53	12.06	139.07	0.84	7.13	12.19	141.57
July 29	$\bar{X}$				0.60	8.00	0.020	1.90	31.1	0.30	5.40	1.90	38.00	3.80	69.10	0.90	13.40	4.70	82.50
	S.D.				1.26	14.02	0.040	2.42	39.62	0.48	9.99	2.60	59.69	3.43	71.06	1.20	14.15	3.40	75.25

APPENDIX C (CONTINUED)

Collection date		Live larvae			Dead larvae			Live pupae		Dead pupae		Empty pupal cases		Total live		Total dead		Grand total	
		18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.
BLACK SPRUCE[b]																			
June 3	$\bar{X}$	16.40	212.30	0.140	0.10	0.80	0.001							16.40	212.30	0.10	0.80	16.50	213.10
	S.D.	9.64	300.08	0.084	0.32	2.53	0.003							9.64	300.08	0.32	2.53	9.85	300.27
June 11	$\bar{X}$	20.30	172.00	0.171										20.30	172.00			20.30	172.00
	S.D.	6.63	66.98	0.119										6.63	66.98			6.63	66.98
June 18	$\bar{X}$	20.20	232.60	0.304										20.20	232.60			20.20	232.60
	S.D.	9.07	125.90	0.077										9.07	125.90			9.07	125.90
June 25	$\bar{X}$	15.50	130.50	0.095										15.50	130.50			15.50	130.50
	S.D.	9.19	92.63	0.049										9.19	92.63			9.19	92.63
July 3	$\bar{X}$	17.00	156.29	0.150	0.43	3.57	0.003							17.00	156.29	0.43	3.57	17.43	159.86
	S.D.	15.56	132.27	0.107	0.53	4.54	0.005							15.56	132.27	0.53	4.54	15.54	132.29
July 11	$\bar{X}$	10.88	93.88	0.083	0.38	3.38	0.003	0.75	6.00					11.63	99.88	0.38	3.38	12.00	103.25
	S.D.	4.85	42.41	0.036	0.52	4.78	0.005	0.89	7.43					5.07	44.69	0.52	4.78	4.78	42.51
July 18	$\bar{X}$	1.30	13.00	0.025	0.20	1.60	0.001	2.80	27.60	0.10	1.30			4.10	40.60	0.30	2.90	4.40	43.50
	S.D.	1.64	20.58	0.062	0.42	3.41	0.003	1.62	17.08	0.32	4.11			2.81	33.42	0.48	4.89	2.99	36.58
July 29	$\bar{X}$	0.20	2.20	0.004	0.40	3.00	0.004	1.60	16.20	0.60	5.40	0.60	6.80	2.40	25.20	1.00	8.40	3.40	33.60
	S.D.	0.45	4.92	0.009	0.89	6.71	0.009	1.14	14.02	0.89	7.47	0.55	6.22	1.52	19.68	1.00	7.77	1.52	19.27

APPENDIX C (CONTINUED)

Collection date		Live larvae			Dead larvae			Live pupae		Dead pupae		Empty pupal cases		Total live		Total dead		Grand Total	
		18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	Feeding sites	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.	18" tip	10 sq. ft.
WHITE SPRUCE[c]																			
June 3	$\bar{X}$	16.50	156.60	0.102										16.50	156.60			16.50	156.60
	S.D.	13.37	94.66	0.067										13.37	94.66			13.37	94.66
June 11	$\bar{X}$	34.70	365.40	0.270										34.70	365.40			34.70	365.40
	S.D.	21.42	148.41	0.122										21.42	148.41			21.42	148.41
June 18	$\bar{X}$	60.60	579.00	0.502	0.60	5.70	0.004							60.60	579.00	0.60	5.70	61.20	584.70
	S.D.	34.37	372.80	0.103	1.07	11.53	0.007							34.37	372.80	1.07	11.53	34.81	376.90
June 25	$\bar{X}$	43.30	503.60	0.485	2.20	21.80	0.019							43.30	503.60	2.20	21.80	45.50	525.40
	S.D.	14.43	341.86	0.263	3.01	30.66	0.029							14.43	341.86	3.01	30.66	16.36	341.73
July 3	$\bar{X}$	19.70	238.10	0.294	0.60	7.00	0.006	0.30	2.20					20.00	240.30	0.60	7.00	20.60	247.30
	S.D.	12.61	220.18	0.191	0.70	9.31	0.007	0.67	4.73					12.94	219.94	0.70	9.31	13.38	226.02
July 11	$\bar{X}$	8.38	103.63	0.195	1.00	7.25	0.049	0.63	5.25					9.00	108.88	1.00	7.25	10.00	116.13
	S.D.	3.89	93.22	0.200	1.51	11.65	0.045	1.06	9.42					4.60	93.46	1.51	11.65	5.07	91.54
July 18	$\bar{X}$	0.20	2.00	0.004	0.90	11.20	0.012	1.20	16.30	0.90	12.20	0.30	3.40	1.70	21.70	1.80	23.40	3.50	45.10
	S.D.	0.42	4.24	0.008	0.99	12.15	0.012	1.32	17.96	0.74	10.10	0.95	10.75	2.26	26.58	1.14	15.03	2.73	34.57
July 29	$\bar{X}$				0.20	1.60	0.010	0.30	3.40	0.20	2.40	0.60	5.80	0.90	9.20	0.40	4.00	1.30	13.20
	S.D.				0.42	3.41	0.025	0.67	8.58	0.42	5.25	1.58	14.88	1.60	15.85	0.70	6.98	2.16	20.42

[a]N = 10 branch tips per sample dates. [b]N = 10 branch tips per sample dates, except on 18-6-74 (N = 5); 25-6-74 (N = 2); 3-7-74 (N = 7); 11-7-74 (N = 8); 29-7-74 (N =5); no samples were taken on 28-5-74 and on 7-6-74. [c]N = 10 branch tips per sample dates, except on 11-7-74 (N = 8); no samples were taken on 28-5-74 and 7-6-74.

APPENDIX D.

LIST OF BIRD SPECIES COLLECTED FOR STOMACH ANALYSIS AT PASADENA, 1974

Species	Common name	Number of specimens
PICIDAE		
Dendrocopos villosus (Linnaeus)	Hairy woodpecker	1
Dendrocopos pubescens (Linnaeus)	Downy woodpecker	2
TURDIDAE		
Turdus migratorius Linnaeus	American robin	1
Catharus guttata (Pallas)	Hermit thrush	1
PARULIDAE		
Dendroica coronata (Linnaeus)	Myrtle warbler	3
Seiurus noveboracensis (Gmelin)	Northern waterthrush	2
FRINGILLIDAE		
Pinicola enucleator (Linnaeus)	Pine grosbeak	3
Zonotrichia albicollis (Gmelin)	White-throated sparrow	3

APPENDIX E.

LIST OF HYPERPARASITOIDS RECOVERED DURING SPRUCE BUDWORM LARVAL REARINGS, PASADENA, 1973 AND 1974.

Species	Family	Number of specimens 1973	1974
Gelis apanteles (Cush.)	Ichneumonidae	5	
Mesochorus sp. (probably *M. discitergus* Say)	Ichneumonidae	1	
Mesochorus tachypus (Hlg.)	Ichneumonidae		1
Mesochorus vittator Zett.	Ichneumonidae	1	
Microchelonus ? recurvariae McComb.	Braconidae		1
Tetrastichus coerulescens Ashmead	Eulophidae	4	